

In situ measurement of coastal ocean movements and survival of juvenile Pacific salmon

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Many salmon populations in both the Pacific and Atlantic Oceans have experienced sharply decreasing returns and high ocean mortality in the past two decades, with some populations facing extirpation if current marine survival trends continue. Our inability to monitor the movements of marine fish or to directly measure their survival precludes experimental tests of theories concerning the factors regulating fish populations, and thus limits scientific advance in many aspects of fisheries management and conservation. Here we report a large-scale synthesis of survival and movement rates of free-ranging juvenile salmon across four species, 13 river watersheds, and 44 release groups of salmon smolts (>3,500 fish tagged in total) in rivers and coastal ocean waters, including an assessment of where mortality predominantly occurs during the juvenile migration. Of particular importance, our data indicate that, over the size range of smolts tagged, (i) smolt survival was not strongly related to size at release, (ii) tag burden did not appear to strongly reduce the survival of smaller animals, and (iii) for at least some populations, substantial mortality occurred much later in the migration and more distant from the river of origin than generally expected. Our findings thus have implications for determining where effort should be invested to improve the accuracy of salmon forecasting, to understand the mechanisms driving salmon declines, and to predict the impact of climate change on salmon stocks.

acoustic arrays | Pacific Ocean Shelf Tracking | mark-recapture

Existing knowledge about the marine movements of salmon is primarily based on analysis of fish marked with simple mechanical tags (1–7). Such tags are recovered at very low rates (typically <1%) and usually in fishing gear, so the species of interest must generally be the target of a substantial fishery, and many fish must be tagged to generate useful information. This dependence greatly limits the range and size of species studied and introduces bias as a result of the movements, techniques, gear, and reporting behavior of the fishermen. Further, only release and recovery locations are known, precluding detailed movement information of individuals. Electronic tags that transmit archived data to satellites or cell phones transcend some of these limitations but are limited to use on large animals (8–10). Of equal importance, survival cannot be measured on fine temporal or geographic scales by using archival tags.

Here we report direct in situ survival and movement estimates for greater than 3,500 juvenile Pacific salmon (“smolts”) that were tagged and released in British Columbia (BC), Canada, during their migration downriver and a substantial portion of their journey north along the continental shelf, for the years 2004 through 2007 (Table S1). These fish represent four of the six North American species of Pacific salmon: coho (*Oncorhynchus kisutch*), chinook (*Oncorhynchus tshawytscha*), sockeye (*Oncorhynchus nerka*), and steelhead (*Oncorhynchus mykiss*). Each fish was surgically implanted with an individually identifiable acoustic transmitter and the tags were detected with a large-scale acoustic telemetry system, the Pacific Ocean Shelf Tracking (POST) array

(Fig. 1), which currently extends more than 1,500 km along the North American continental shelf.

The overall POST array is formed from a series of regional subarrays, with each subarray consisting of several acoustic receivers (“nodes”) independently positioned above the sea (or river) bed in a 3D spatial geometry that provided a high probability of detecting tagged animals passing over each subarray. By successfully recovering the stored detection data on the majority of these receivers, it is possible to describe both the early marine movements of individuals and the survival of groups as they exit rivers and migrate out along the continental shelf.

The POST array is part of a new generation of acoustic technologies that are beginning to yield an understanding of fish movement and behavior on a very large scale (11, 12). Telemetry arrays sited on the continental shelf-slope are particularly well suited for the study of juvenile salmon, as this period of their life history is thought to be essentially shelf-limited (3, 5, 6, 13–15). Continental shelves are also of key ecological importance: although they cover less than 8% of the global ocean by area (16), they contribute 69% of the world fish catch [89% if upwelling zones are included (17)], and support high biodiversity and large populations of marine mammals (18) and seabirds (19).

Results

Migration Routes. The unprecedented detail stemming from extensive telemetry arrays can most effectively be demonstrated by animating the movements of the tagged animals (*SI Materials and Methods*); from this, a general picture of the direction and speed of movement for the salmon smolts immediately emerges. Our data demonstrate two distinct species-specific patterns of marine migration, with sockeye and steelhead undertaking sustained long-distance migration and coho and chinook apparently remaining resident in the Salish Sea for the duration of the tags’ batteries (>4 mo). Emigration from the Salish Sea occurred almost exclusively via the northern route through Queen Charlotte Strait [QCS; Fig. 1; sockeye, 91%; steelhead, 81%; calculated as a proportion of the total tags detected on either QCS or Juan de Fuca (JDF) subarrays], a finding consistent with earlier studies (2). However, some individual steelhead populations exited only or predominantly via the southern JDF route whereas other

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Conflict of interest statement: D.W.W. is architect of the Pacific Ocean Shelf Tracking (POST) acoustic array concept and President of Kintama Research Services, an environmental consultancy and the company that developed and operates substantial elements of the overall POST telemetry array.

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All data used in this paper have been deposited in the publicly accessible Pacific Ocean Shelf Tracking (POST) database, www.postcoml.org.

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showed consistently higher or lower survival across all populations, and a population's freshwater survival during the downriver migration did not appear to be related to its survival during the early coastal ocean migration (Fig. 4A). Further, the variation in survival within these environments appeared roughly similar.

Some differences between species were apparent. In general, survival during the marine coastal migration was roughly comparable for sockeye and steelhead (Figs. 3B and 4A). The extremely low early marine survival estimates of coho and chinook are confounded with patterns of residency, as noted earlier, preventing direct comparison. There were no consistent differences in survival among wild and hatchery-reared groups, although only two populations (Keogh and Sakinaw) had fish tagged from both rearing histories in the same year. In those two cases, survival was similar for hatchery and wild groups.

Comparison of marine and freshwater survival rates is complicated because survival may be measured relative to either the time over which fish were observed or the distance they traveled (22, 28). We estimated lower overall survival for sockeye and steelhead during their early marine migration than during their down-river migration (Fig. 4A; all but three estimates lie below the 1:1 line). However, when scaled by time, survival rates of Cultus Lake sockeye were consistently higher during the marine migration than during the down-river migration (above the 1:1 line), whereas steelhead survival rates were roughly equivalent (Fig. 4B). When scaled by distance traveled (Fig. 4C), survival rates of both species were higher during the marine migration.

Estimates of the uncertainty in the survival values shown in Fig. 3 are relatively small compared with other methods for estimating survival, despite the modest numbers of juveniles tagged (Table S1). This primarily results from relatively high detection probabilities, particularly of the larger V9 tags, achieved at the marine subarrays (Fig. S2). The variation in detection probability on subarrays that did occur was mainly accounted for by loss of receivers to commercial fishing activity and secondarily by year-to-year variation in the spacing between the receivers on a sub-

array. In freshwater, detection probability was more variable than at marine subarrays, and lower overall in the Fraser River but higher on average in other rivers. We also observed a seasonal degradation of detection probability on some freshwater subarrays (likely caused by faster migration speeds past the receivers sited in freshwater during high flow events) that was not seen on ocean subarrays (32) (*SI Materials and Methods*).

Smolt Size and Survival. The relatively simplistic architecture forming the pilot phase (POST) array was developed in 2001 to 2003 when only the larger V9 acoustic tag was commercially available. The smaller (and acoustically quieter) V7 tag only became available in 2005, after the pilot array was deployed; the prototype array design detected approximately 90% of V9 tagged smolts but only approximately 70% of V7 tagged smolts (Fig. S2). This is a large performance difference because the fraction of V9 tagged smolts detected on the subarrays needs to be increased by only approximately 10% (i.e., 0.9^{-1}) to account for detection inefficiencies in the coastal ocean, a relatively trivial correction. However, this correction is more important and error-prone for V7 tags because their lower acoustic power means that the correction factor is larger ($0.7^{-1} = 43\%$), and small estimation errors in detection efficiency cause larger errors in estimated survival.

The full size spectrum of wild Pacific salmon smolts other than steelhead cannot be surgically implanted by using the V7 or V9 tag, so the applicability of our current survival measurements to animals smaller than our minimum size limits is unclear. (These size limits were set at 130 and 140 mm fork length in 2006 to 2007, although some individuals smaller than these limits were tagged in 2004 and 2005.) As acoustic tags appropriate for implantation in smaller animals transmit signals that are more difficult to detect, a redesigned array that can effectively be used with smaller-sized animals will require some combination of increased numbers of receivers and tags to compensate for the reduced detection rates. Is there evidence that (i) smaller animals have lower survival because the relatively larger tag burden

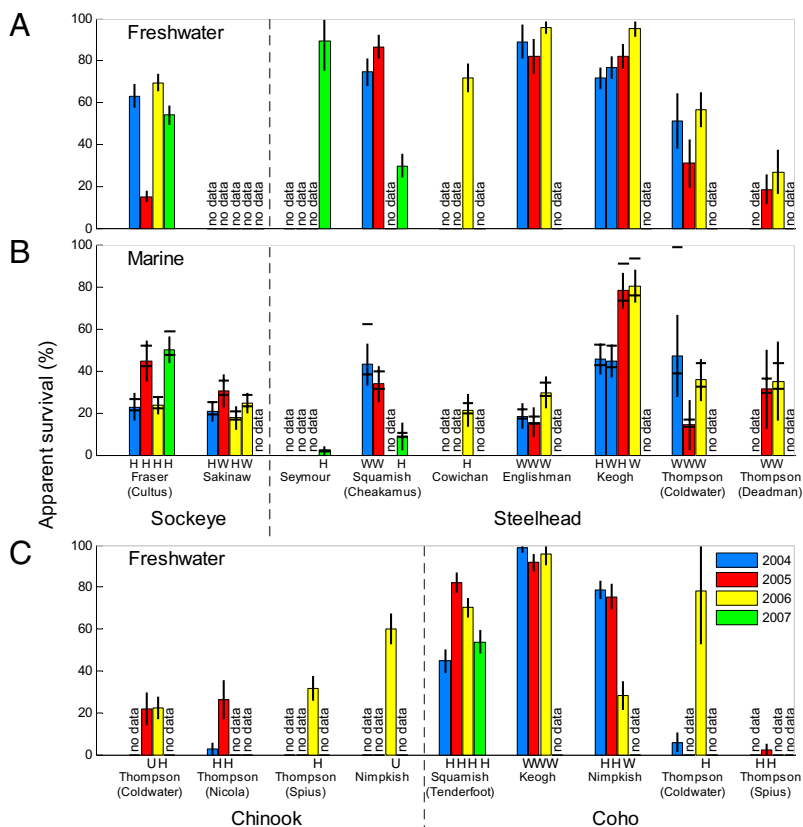


Fig. 3. Survival estimates for southern BC salmon populations. (A and B) Freshwater and early marine survival for sockeye and steelhead populations. (C) Freshwater estimates for Chinook and coho. Freshwater survival is from the release site to the river mouth subarray and early marine survival is from the river mouth to exit from the Salish Sea (operationally defined as the QCS and JDF marine lines). Error bars indicate ± 1 SE on survival estimates. Horizontal bands in B show bracketed estimates of early marine survival arising from uncertainty in the fixed value of p assumed for the QCS and JDF lines (*SI Materials and Methods*). Rearing origin (H, hatchery; W, wild; U, unknown) is indicated below the bar for each population. "No data" indicates tagging did not occur in that year.

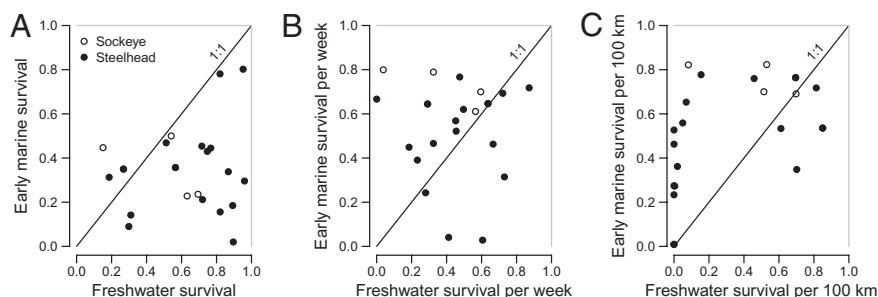


Fig. 4. Comparisons of survival of steelhead and sockeye during downriver migration and early marine migration: (A) survival, (B) survival scaled by time, and (C) survival scaled by distance. Freshwater travel times were estimated for each population as the median time between release and arrival on the river mouth line. Early marine travel time was estimated as the median time between departure from the river mouth line and arrival at the final (QCS/JDF) marine lines. The solid line shows the 1:1 line where early marine survival and downriver survival are equal.

reduces their fitness after release, or that (ii) within the size range of smolts tagged, larger smolts survive better because they are less vulnerable to predators? Both questions raise important issues concerning the applicability of baseline survival estimates to the full size spectrum of wild populations; they also have substantial cost implications if more sophisticated array designs are contemplated.

To evaluate the effect of smolt and tag size on survival, we compared the change in the frequency distribution of smolt sizes at the time of tagging with the size distribution of survivors detected at outer reaches of the array (Fig. 5). We defined sockeye and steelhead survivors as smolts detected at the JDF Strait or QCS subarrays, as these species consistently migrated out of the Salish Sea. We defined coho and chinook survivors as smolts detected at the mouth of the Fraser River, as these two species ceased migration in the Strait of Georgia but had long freshwater migrations down the Fraser River (Fig. 1) (22, 33); for Cheakamus coho, which enter Howe Sound, we defined survivors

as fish reaching the outer Howe Sound subarray, because out-migration occurred consistently to this point.

The overall shape of size–frequency distributions changed little between the released animals and the survivors detected after substantial freshwater and early marine mortality occurred (Fig. 5A), and their mean size was generally indistinguishable (Fig. 5B). The SD of the two normally distributed distributions (sockeye and steelhead) showed some evidence that the size of survivors was more tightly distributed around the mean than at release (Fig. 5C), but this could be a result of the small number of smolts in the largest and smallest size categories (Fig. 5A) rather than size-related mortality. The SD was unchanged for coho and chinook.

Quantile-quantile plots (34) are effective at detecting changes in distributional shape (i.e., skew or kurtosis), which would occur if mortality was preferentially acting to remove the smallest or largest tagged animals after release. The results (Fig. 5D) indicate that the shape of the size–frequency distribution remained similar between the release groups and survivors; there is some slight

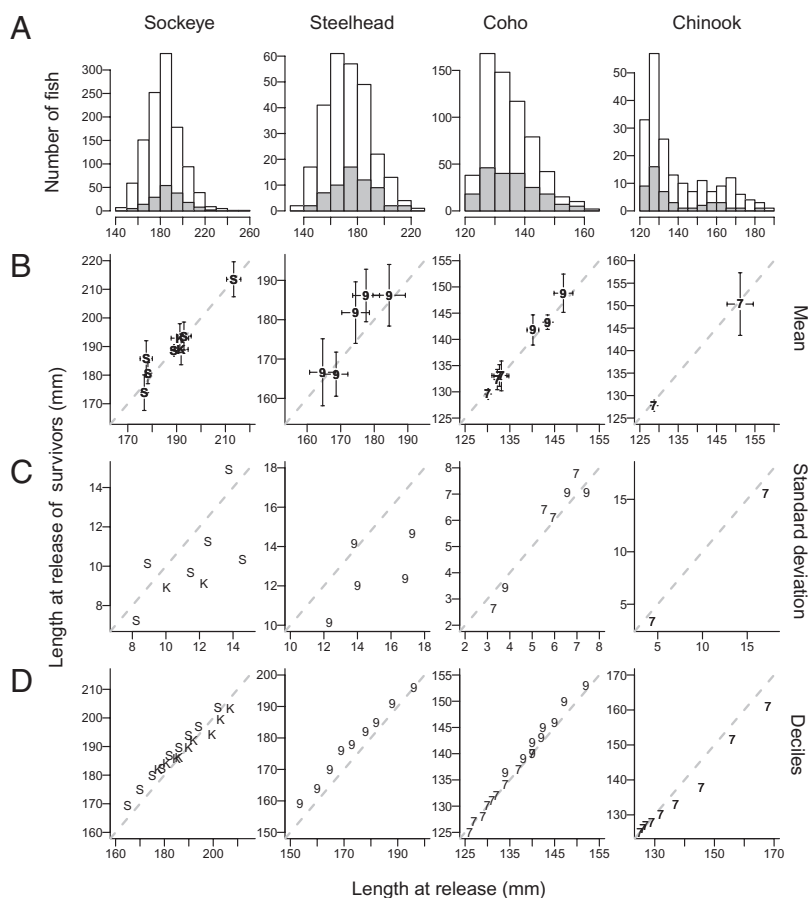


Fig. 5. Evaluation of possible size-dependent effects of downstream and early marine survival. Plots show summaries of length differences between the tagged smolts at release and the subset of animals surviving to reach distant parts of the array, separated by species. (A) Frequency distribution of fork length at time of tagging for released animals (white) and survivors (gray), with all release groups combined. (B) Mean fork length for individual release groups (± 2 SE). (C) SD for individual release groups. (D) Quantile-quantile (qq) plots of the deciles of the empirical length distributions of released fish and survivors (years and stocks are pooled within species and tag size categories). The 1:1 lines are indicated. Individual release groups are identified by an asterisk in [Table S1](#), and consist of all species, stock, hatchery/wild provenance, acoustic tag type, and release year combinations consisting of at least 25 individuals released and at least 10 individuals detected. The smaller V7 and larger V9 acoustic tag types implanted into smolts from these individual release groups are distinguished in the plots by 7 and 9; sockeye (S) and kokanee (K) were all tagged with V9 tags. Individual panels consisted almost entirely of hatchery or wild origin smolts, so these are not distinguished.

evidence that larger chinook smolts were slightly underrepresented among survivors, whereas smaller steelhead were slightly overrepresented. A very slight difference is also evident for Sakinaw Lake kokanee (a genetically distinct life history type of sockeye generally considered to remain exclusively in freshwater), with the largest animals possibly underrepresented among outmigrating animals. In each species, the effect is, at most, a few millimeters. Although morphologically indistinguishable from sockeye at the time of tagging, additional data show that some Sakinaw kokanee and sockeye remained resident in the Strait of Georgia after release off their river mouth, and 12% of Sakinaw kokanee (but no sockeye) then migrated back into their natal lake within a few weeks of release (35); size dependence in residency behavior may therefore confound these apparent size-survival relationships for kokanee. This pattern is not evident for Sakinaw or Cultus Lake sockeye, which showed an essentially identical size distribution between released animals and survivors.

Discussion

Many salmon populations in both the Pacific and Atlantic oceans have experienced sharply decreasing returns and high ocean mortality in the past two decades, with some populations facing extirpation if current marine survival trends continue (36, 37). The need for a better understanding of the spatial and temporal patterns of salmon mortality in the sea is frequently cited (37, 38), particularly in the period just after ocean entry when most mortality is thought to occur (15, 39). Our findings provide a new perspective on where and when this mortality occurs. Historically (40), fisheries biologists argued that mortality rates were highest early in the life history (when the fish were smallest), so this was the time period likely to determine the number of adult fish that survived.

The median survival of the steelhead and sockeye populations estimated in this study was 16.5% (i.e., one in six juveniles surviving to exit from the Salish Sea), with population-specific marine travel times as long as 28 d depending on the distance traveled. In contrast, survival over the entire juvenile-to-adult lifespan of many Salish Sea salmon populations has decreased to only 1% to 4% in the past two decades (28, 41–45), with concerns raised about the relative role of salmon aquaculture, hatcheries, climate change, and ecosystem changes in causing the decline (46–48). Our measurements of survival within the first weeks of the migration (i.e., one of six smolts surviving) can thus be compared with total survival over the period of approximately 2.5 y until adult return generated by other methods (approximately one in 25–100 of outmigrating juveniles); the implication is that the cumulative total mortality beyond the Salish Sea is approximately four to 17 times larger than what is experienced within the geographic limits of the Salish Sea array in roughly the first month of life in the sea, making it unlikely that year-class strength is primarily determined very early in the marine life history.

The 2007 outmigrating Cultus Lake (Fraser River) sockeye smolts, whose adults returned in 2009, provided a particularly clear example. A catastrophically low return of adult sockeye occurred in the summer of 2009, with nearly all Fraser River populations experiencing survival rates of only 1%, including the Cultus Lake hatchery population reported here (49, 50). The smolts were implanted with specially programmed tags that transmitted during both the outbound smolt and subsequent 2009 inbound adult migration phases, with an intervening 25-mo quiet period to conserve battery power (49). Although the 2007 smolts experienced 28% survival after migrating downriver and out of the Salish Sea (which was equal to or higher than the survival in the previous 3 y) (44), only 1% of the released smolts (two of 200) returned as adults, consistent with the smolt-to-adult survival of both the untagged Cultus Lake hatchery smolts (0.5%) and wild-origin smolts (1.4%) (49). Both adults were detected returning to BC within 1 d of each other via the JDF Strait in 2009, even though they had emigrated via QCS as smolts in 2007 1 wk apart (Movies S2 and S3).

Survival experienced in the freshwater and early marine period (28% in the first 6 wk until the smolts migrated out of the Salish Sea) relative to what must have occurred in the following approximately 2 y can be expressed as:

$$\frac{S_{\text{EarlyMarine}}}{S_{\text{Later}}} = \frac{28/100}{1/28} = \frac{28^2}{100} = 7.84 \quad [1]$$

Our survival measurements for Cultus Lake sockeye, which encompass the whole marine life history, therefore indicate that mortality within the Salish Sea is only approximately one eighth the mortality still to come, or that S_{Early} is approximately $8 \cdot S_{\text{Later}}$, consistent with the general calculation developed earlier. Thus, much mortality (and thus the chances for major changes in that value) likely occurs later in the life history of Pacific salmon, after the first month of life in the sea has passed.

Our results support the longstanding assumption that the rate of mortality is highest in the first month of the migration, but also show that much of the (cumulative) juvenile-to-adult mortality occurs after juvenile salmon leave the waters of the Salish Sea. The results further suggest that the conditions that caused the costly collapse in 2009 of Fraser River sockeye probably occurred outside the Salish Sea. A common concern in tagging studies is that the tagging process may reduce survival. If it were true that survival of untagged fish is greater than survival of tagged fish (and our size-survival results show little evidence for this), then there would necessarily be even greater mortality beyond the Salish Sea than what we have estimated for tagged fish.

The extent to which significant mortality occurs later in the oceanic life phase of other salmon populations is unknown, given that we are only now beginning to develop a baseline of early marine survival estimates. The size of available tags has until recently limited current studies on salmon survival to the use of larger smolts representing only part of the naturally occurring size spectrum, range of species, and diversity of life histories. Expanding the size range of juveniles tagged, as well as broadening the range of release dates, will be important steps toward increasing the utility and relevance of the survival measurements, although our analysis suggests that mortality seems to be rather uniform across the size range of salmon smolts tagged to date. Telemetry arrays may also be useful in combination with other methods for testing hypotheses concerning the relative fitness of hatchery and wild fish (51), the need for water releases from dams to support juvenile migrations to the ocean (52), the impact of transfer of sea lice and other pathogens from farmed to wild salmon (47, 53, 54), and determining the linkage between the physiological state and health of individual fish and their subsequent survival (55). Given the projected major changes in climate (56), more broadly based survival baselines should be developed and used to explicitly test the many theories that will be put forward to explain the large-scale changes likely in marine fish populations.

Materials and Methods

Analysis of movement speeds for individuals and population aggregates was obtained by calculating the elapsed time for individuals to travel between subarrays (calculated as the time difference between last and first detection on successive arrays) and dividing this value into the minimum straight-line distance in water between arrays. Survival was estimated using standard Cormack–Jolly–Seber (CJS) statistical models (SI Materials and Methods).

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Supporting Information

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SI Materials and Methods

Deploying and Detecting Acoustic Tags. Between 2004 and 2007, we tagged 3,692 juvenile salmon from four species and 20 populations in BC rivers with uniquely coded acoustic transmitters (Table S1). The tags were surgically implanted into the abdominal cavity by using established surgical procedures annually reviewed by institutional animal care committees and met or exceeded requirements specified by the Canadian Council on Animal Care. A number of studies have evaluated tag effects on survival using our methods, both of captive salmon held for 6 to 8 mo (longer than the approximate 3-mo operational lifespan of the tags used here) and of double-tagged fish released into the environment. Both types of studies showed low rates of mortality or tag loss relative to the apparent survival rates observed for free-ranging smolts (1–4).

The POST array logged detections of the ID codes transmitted by the tags; briefly, POST is a pilot or demonstration phase prototype network of receivers that is positioned in specific geometric configurations and maintained year-round for the purpose of tracking marine species. The telemetry array currently comprises approximately 400 acoustic receivers positioned in a series of subarrays that cover the distance between the shoreline and the continental shelf edge (200 m isobath) or across marine straits (Fig. 1). Receivers are also deployed in the Fraser and Columbia Rivers, and collaborators operate compatible receiver networks in Puget Sound, the Sacramento River, and various coastal estuaries, making it feasible to reconstruct migration routes of individual animals and to estimate survival rates of experimental groups of tagged animals in areas partitioned by these subarrays (5–8).

We estimated survival probabilities of tagged juvenile salmon during their migration using variants of the standard open-population, “recaptures”-only CJS mark-recapture model (9–11) to estimate survival probabilities (ϕ) in each segment of the migration and detection probabilities (p) at each subarray by using the MARK program (as detailed later) (12).

Detection Database Filtering. We identified a list of suspect detections likely to be false positives if the following criteria were all observed: (i) a tag ID was detected only once on a subarray within a 30-min period; (ii) there were one or more other tags heard on the same receiver around the time of the suspect detection; and (iii) the tag ID did not have supporting detections from other time periods or subarrays. Supporting detections are defined as a chronological sequence of detections from release date along typical migration paths for each population. Only the detections whose ID codes matched up with BC salmon smolts tagged under POST were screened. The total number of detections each year on all POST subarrays for the BC salmon smolt populations presented in this study varied from 83,741 to 365,148. The number of false detections identified ranged from 43 to 343, and the resulting proportion of false detections ranged from 0.02% to 0.22%. After eliminating suspect detections, we used these filtered data to estimate the reported survival and detection probabilities, travel times and rates, and migration routes of tagged smolts.

Mark-Recapture Model Construction. Spatial forms of CJS models, whereby tagged animals are detected at fixed locations along a migration route rather than recaptured at fixed sampling times, are widely used for modeling survival in migrating salmon smolts (e.g., refs. 12–14). Sampling at successive subarrays occurred

over several weeks or months during the smolt migration. Multiple years of data and multiple populations from different geographical areas were combined in the same dataset so that populations of tagged fish could be linked where appropriate to compensate for small sample sizes of fish from some populations at some subarrays (15). Some subarrays were shared among all populations whereas others were specific to only some. The number and location of subarrays varied among years for some populations. Survival probabilities (ϕ) were treated as separate among populations, whereas detection probabilities (p) were generally treated as shared among populations with similar acoustic tag types experiencing similar environmental conditions. These factors resulted in more complex models than typical CJS models, and development of these models required several steps described later. Some of these assumptions and modifications were presented previously (16), but are briefly outlined here to be comprehensive. All mark-recapture models were implemented with the MARK program, version 5.1 (17), through the R package RMark, version 1.8.8 (18).

Variations on the classic CJS model were based on several major assumptions that shaped model construction: (i) ϕ in each segment was estimated independently among populations, whereas p at a subarray was pooled across populations with the same tag type; (ii) at Fraser River subarrays, p was modeled as a function of the water level at the mean time of population crossing; (iii) some populations exhibited split-route migration patterns in the Salish Sea, so extra parameters were incorporated to allow for this flexibility and reduce the bias in ϕ estimates; and (iv) p on the outer subarrays (i.e., final subarrays at QCS and JDF) was predicted from p estimates on other ocean subarrays and was assumed as a fixed value to untangle the confounded ϕ and p parameters in the final segment/subarray.

First, we determined the detection history of individual fish at subarrays, wherein a subarray consists of either a single receiver or multiple receivers arranged in a line. Detection histories consist of a string of ones and zeros, with a 1 representing release, then either a 1 or a 0 for all following digits, depending on whether they were detected, respectively, at successive subarrays. Tagged smolts potentially passed between two and 12 subarrays during their migration (for a maximum of 13 digits in the detection history). The number of freshwater or estuary subarrays passed during the downstream migration varied from zero (for Sakinaw Lake sockeye) to eight (for Tenderfoot Creek coho and Cheakamus steelhead in 2007). The number of ocean subarrays potentially crossed was only one (at QCS) for Nimpkish and Keogh River populations leaving freshwater north of NSOG (these fish were detected only moving northward). The number of ocean subarrays potentially crossed for populations entering the Salish Sea south of NSOG was one (JDF) or two (NSOG and QCS), depending on the direction taken. Before entering the Salish Sea, some populations potentially crossed an additional one (across Burrard Inlet) or two (in Howe Sound) ocean subarrays.

We focus our analysis on estimating the proportion of fish that survived their early ocean migration, regardless of the particular direction that fish took after ocean entry. To represent exit from the Salish Sea system, detections at the outer subarrays (QCS and JDF) were pooled in the final digit of detection history sequences. Early ocean survival was estimated as the fraction of fish entering saltwater that left the system via either northern or southern routes. Pooling outer subarrays somewhat complicates ϕ and p estimates at NSOG, but this can be easily resolved (as detailed later). For fish entering the southern Salish Sea, the southern

route from the river mouth to JDF is generally shorter than to QCS, so this could confound per-distance estimates of survival (this was accounted for in estimating survival scaled by distance, by using weighted averages of the distances to each of these two subarrays, weighted by the number of fish detected at each subarray). Approximately one third of BC salmon smolt populations showed patterns of split migration routes after ocean entry (16). Fish from the other populations were detected only moving north.

Typical assumptions of open-population mark-recapture models are reviewed in detail elsewhere (12–15, 19). The most important of these include:

- Tagged animals are representative of the population of interest. Fates of individuals are independent of all other individuals with respect to ϕ and p .
- Probabilities of ϕ in each segment and p at each subarray are homogenous among individuals within the groups specified in the model structure.
- Sampling events (or locations) are short relative to intervals between sampling events.
- Tagged animals are not affected by tagging procedures or implanted tags.
- Tag loss or failure are negligible.
- Detected tags are in live smolts, not in predator stomachs or in dead fish floating downstream past receivers.
- All detections in a final (filtered) dataset are legitimate, not false positives.
- Smolts do not permanently reside between successive subarrays—they either die during the migration or continually migrate past subarrays. The possible state of residency is not treated explicitly for estimating survival, so actual survival is underestimated for any populations that have some fish residualizing in freshwater or residing between subarrays (like coho and chinook after ocean entry, as mentioned).

In general, survival estimators are fairly robust to the partial failure of assumptions (compared with population size, for example, refs. 15, 19).

Occasionally, tagged smolts exhibited “back-and-forth” movements among successive subarrays. This occurred in riverine, estuarine, and marine habitats. For mark-recapture analyses, this did not affect estimates of ϕ or p as only a single (legitimate) detection was required to infer survival from release to that receiver subarray. For travel time and swimming speed analyses, only the first detection of a particular tag at a particular subarray was considered, i.e., the arrival times of each fish at each successive subarray.

Survival and Detection Probability Submodels. Sample sizes of tagged fish and survival during the migration varied among populations, so the number of fish from each population detected at a receiver subarray varied widely. Many populations had few detections on some subarrays, and mark-recapture estimates of ϕ ($\hat{\phi}$) or p (\hat{p}) would not have been reliable for these populations if separate CJS models were constructed for each population in each year (16). Instead, we combined all data into two large models, but maintained independence among populations in terms of survival, so segment-specific ϕ varied freely between groups, i.e., $\phi_{\text{Segment:Group}}$, where “Group” is a unique combination of species, population, hatchery or wild-reared provenance, and year. Main effects of segment and group per se were not of interest, especially as the n th segments of different groups were often in different geographic locations.

Detection probabilities were modeled as station-specific, year-specific and, in some models considered, tag type-specific, as V9 tags (142 dB re 1 μ Pa at 1 m) are louder and can be detected from further away than V7 tags (136 dB). In these models, we assume that a particular tag type from one population should

have the same probability of being detected at the same subarray in the same year as the same tag type from a different population (unless environmental conditions differ markedly among the run timing periods of populations, as detailed later). We also constrained the relative difference in \hat{p} between tag types to be additive (i.e., constant in logit space) across years and subarrays. Two datasets were constructed, one for Fraser River watershed populations and the second for all other populations, each containing data from 2004 to 2007. (With the number of populations and detection occasions considered, numerical estimation using a single combined dataset proved to be computationally infeasible.) Separation of the two datasets meant the relative difference in \hat{p} between tag types could be inconsistent between datasets, although it turned out to be similar. Essentially, separate CJS models were constructed for each species, population, provenance, and year combination in terms of ϕ , but p for a given subarray, tag type, and year were shared across these groups.

Tagged salmon smolts originated from diverse locations in southern BC (Fig. 1). Along the migration route of a population, some subarrays were shared with other populations and some were unique. To analyze multiple populations and years together in the same model required appropriately pairing the detection history digit for each population with those from other populations. For example, Tenderfoot Creek coho smolts in 2007 had a 13-digit detection history. The final digit of this sequence represents detection at QCS or JDF; to combine populations in the same model, all other populations must also have QCS/JDF as their 13th digit, as this subarray is common to all populations. For populations with fewer than 13 digits in their detection history, this means the detection history must begin with an appropriate number of zeros before the first 1 representing release (15).

In some cases, particular subarrays at a given digit of the detection history were not common to all populations. This was not an issue for the Fraser River dataset, as, at least within each year, all populations shared the same subarrays along migratory routes. For the non-Fraser dataset, having different subarrays represented at a given digit was dealt with by incorporating extra parameters to represent the interaction of subarrays, years, and general migration route clusters (16). These parameters were additive components of all p submodels. They ensured that \hat{p} were common for populations with the same tag type at some subarray in some year, but were separate for populations with migration routes that brought them past different subarrays at the same given detection history digit. Eleven such parameters were required to specify these distinctions over all subarrays, years, and populations outside of the Fraser River.

We estimated a variance inflation factor (c) to compensate for overdispersion in estimated parameters (12). This factor was used to expand SEs of real parameter estimates and values in the variance-covariance matrix. Estimated c values were also used for model comparisons, with computed QAICc values corrected for both extrabinomial variation [“Q” (for quasi-) correction on Akaike’s Information Criterion (AIC); ref. 15] and small sample sizes (“c” correction on AIC; ref. 20). We estimated c assuming the general CJS model ($\phi_{\text{Segment} \times (\text{Group:TagType})}, p_{\text{Station} \times (\text{Group:TagType})}$). We used two bootstrapping methods in the MARK program. The deviance ratio method ($\hat{c} = 1.400$ for the Fraser River dataset and 1.177 for the non-Fraser dataset) proved to be more conservative on average than the \hat{c} ratio method ($\hat{c} = 1.387$ for the Fraser River dataset and 1.013 for the non-Fraser dataset), so the larger estimates were used. Separation of the two datasets allowed for separate \hat{c} to be applied to each dataset rather than a single common value (which would be approximately $\hat{c} = 1.245$ using the deviance ratio method).

The product of segment-specific $\hat{\phi}$ during either the downstream or early ocean migration of each population was calculated as an estimate of total downstream or early ocean survival,

respectively. The variances of these products were calculated using the Delta method.

Environmental Covariates on Fraser River Detection Probabilities. Detection probability of tags passing subarrays depends on background noise and therefore on environmental conditions. In rivers, water level often increases during late spring as a result of snow melt. Higher water levels result in (i) faster flow, so that, on average, tags are within range of a receiver for a shorter period, and (ii) greater noise. Both factors may act to decrease p during greater flow periods, which in southern BC tend to occur later in the migratory season. In the Fraser River, multiple populations were tagged and released at varying times throughout the migratory season (16), so this potential effect was taken into account for some candidate models of p .

The effect of different release times or flows on p can be observed by initially treating populations independently. Fig. S1 shows fully independent \hat{p} for all Fraser River populations, i.e., model $\phi_{\text{Segment}:\text{Group}} \cdot p_{\text{Station}:\text{Group}:\text{TagType}}$, where Group represents unique combinations of species, population, and year. The number and locations of subarrays in the Fraser River varied among years, so the first subarray encountered in one year is not necessarily the same as the first subarray in another year. Estimates of p for a particular population and tag type are plotted against the water level measured at the mean arrival time of that population at a particular subarray. On average, and within each tag type, these population-specific \hat{p} values decrease as river level increases during the migration season. This is especially apparent in 2005 and 2006 when there were many fish groups released over a wide range of dates and therefore water levels. Generally, the later-migrating populations experienced greater flow during the downstream migration and their \hat{p} estimates were lower. At a given water level, \hat{p} was generally higher for V9 tags than for V7 tags.

Modeling p as fully independent among populations resulted in small p sample sizes detected at and after river subarrays for several populations, so many of these \hat{p} were imprecise and susceptible to over-fitting. At the other extreme, fully pooling all populations at a given subarray in a given year would result in a single, average \hat{p} so would not capture any seasonal trend (16). To find a good balance in this tradeoff between bias and precision, models incorporating an environmental covariate were considered. These submodels accounted for seasonal variation in p by constraining p to be a linear function (in logit space) of one or more covariates at the appropriate mean run timing of each group. One model used the day of year (DOY) of mean arrival at a detection subarray. Daily water level data from two Environment Canada gauge subarrays in the lower Fraser River (at Mission and Port Mann) were matched to the DOY of mean arrival time at each receiver subarray; these provided two other models. A fourth model incorporated both water level covariates, with the measure for each subarray taken from a combination of both gauges. (The Mission gauge was closest to the first subarray in 2004 and 2007, but to avoid over-fitting to only two subarrays, the water level at Mission was used as a covariate for all subarrays and years. In addition to this, the water level at Port Mann was used as another additive covariate at all later river subarrays in all years.) This fourth model was hypothesized because p at Mission subarrays likely correlates best with the Mission water level, but increased inflow from tributaries and increased industrial activity downstream of this subarray are such that p at subarrays further downstream may correlate better with water level at the Port Mann gauge, further downstream. These covariate effects were additive: slopes of p versus DOY or water level were assumed to be constant across years, subarrays, and tag types, but the intercepts were permitted to vary for year/subarray combinations and for each tag type. Along with maintaining a consistent relative difference in p between V7 and V9

tags, this was a second reason for grouping together all 4 y in the Fraser River dataset.

Run timing and river flow may affect p in other rivers as well, but no other river studied had such a wide range of release dates among populations, so there was little opportunity to quantify a trend in p . In these other rivers, \hat{p} were allowed to vary among subarray and year combinations, but were constrained to be common for populations sharing the same tag type. Even if run timing or flow effects on p were as pronounced in these smaller rivers as they were in the Fraser, the difference in release dates among these populations was much smaller, so any difference in p would likely be minor, further justifying the pooling of populations.

Correction of Biases in Survival Probabilities from Split-Route Migration Patterns. Spatial forms of CJS models (release and subsequent detection at successive fixed locations along a migration route) are unlike temporal forms (at fixed times) in that migration routes may not be continual in a single path. Migration routes may split and fail to rejoin before the next detection subarray (13, 21). This occurred in approximately one third of populations that entered the Salish Sea south of NSOG, with some fish migrating south over JDF whereas others migrated north over NSOG and QCS. If fish migrated directly south and were detected at JDF, there was no opportunity to have been detected at the next-to-last subarray, as an equivalent subarray to NSOG did not exist along the southern route. If forks of this split-route pattern are pooled together (for estimating overall early ocean survival regardless of direction taken), this leads to biases in $\hat{\phi}_{\text{River mouth} \rightarrow \text{NSOG}}$ and \hat{p}_{NSOG} in CJS models, with the bias worsening as the proportion of fish migrating south increases (16). Methods have been developed to account for split-route migration patterns in similar situations (21), but in the present models with multiple interrelated release groups crossing variable numbers and locations of subarrays, specifying the likelihoods manually can be prohibitive as they become largely intractable.

To correct the bias in $\hat{\phi}_{\text{River mouth} \rightarrow \text{NSOG}}$, some candidate models incorporated extra terms for p at NSOG (16). Any group (i.e., combination of species, population, provenance, and year) that exhibited some degree of southward movement after entry into the Salish Sea (as evidenced by detection at JDF) was given a single, freely varying parameter that represented p at NSOG for that group in particular. (All other groups detected only moving northwards shared a common \hat{p}_{NSOG} .) The group-specific \hat{p}_{NSOG} values were not detection probabilities per se, but joint probabilities of northward migration and detection. Use of these extra parameters resulted in unbiased ϕ in ocean segments. There were seven such groups in the Fraser River dataset and nine groups in the non-Fraser dataset that exhibited some degree of southward movement and had extra parameters associated with them in the candidate models that incorporated this flexibility.

Assumptions of Detection Probability at Final Subarrays. There is no information after a final detection subarray with which to separate the confounded parameters of ϕ in the final segment and p at the final subarray, unless a value is assumed for one or the other. Because of the cost and resulting limited ocean detection subarrays and the importance of the final segment (in some cases, the only ocean segment) to our inferences of early ocean survival, we assumed a fixed value for p_{final} to estimate ϕ_{final} . This assumption carries the risk of misestimating ϕ_{final} if the fixed value of p_{final} is incorrect. Determining values of p_{final} to assume as fixed involved two main steps (i): accurately estimating p on other ocean subarrays and (ii) using these values to predict p for the outer ocean subarrays, adjusting for slight differences in line geometry. Because of the risk involved with this approach, we

evaluated the sensitivity of early ocean survival estimates to values assumed for p_{final} .

Isolated detection probability analysis on NSOG and HS subarrays. To estimate p on inner ocean subarrays (NSOG, HS_{in}, HS_{out}) as accurately as possible, we constructed a shortened detection history of tags with digits for release, the subarray(s) of interest, and detection anywhere downstream of the subarray of interest. To estimate p_{NSOG} , populations that originated south of NSOG and migrated north were included in a three-digit dataset (detections at JDF were not paired with QCS in this case, to avoid confounding p_{NSOG} with the probability of southward movement after entering the Salish Sea). To estimate p_{HSinner} and p_{HSouter} , populations that originated from the Squamish River watershed were included in a four-digit dataset. These shortened detection history versions reduced the dependence of \hat{p} and uncertainty in \hat{p} on parameters from other segments and subarrays. For each of these datasets, several candidate submodels for p were considered, whereas the ϕ submodel assumed full independence between segments and groups (including tag type) to be as flexible as possible ($\phi_{\text{Segment} \times (\text{Group} : \text{TagType})}$). All submodels for p assumed full independence between subarray and year. The best p submodel overall in terms of Akaike Information Criterion (AIC) scores assumed an additive difference between V7 and V9 tags with species and populations pooled together ($p_{\text{Station} \times \text{Year} + \text{TagType}}$; Table S2; Fig. S2). All models involving group-specific p required many extra parameters to be estimated but did not gain enough improvement in the goodness of fit to compensate, so had less support in the data. There was no evidence of a consistent seasonal trend in p at these three ocean subarrays (unlike the situation in the Fraser River) despite run timing periods being widespread among populations crossing NSOG, so pooling of species and populations was further justified. Only tags with a random delay of 30 to 90 s were included in the analysis, as the delay between transmissions should affect p in theory.

The sample size of V7 tags detected at and downstream of NSOG was insufficient to estimate $p_{\text{V7,NSOG}}$, even when all years were pooled (this is why the effect of tag type was less important at NSOG in Table S2). We assumed that the relative difference in p between V7 and V9 tags (i.e., the intercept difference between parallel slopes in logit space) assessed on HS subarrays from the other dataset also held for the NSOG subarray. A simple regression between $\hat{p}_{\text{V7,HS,year}}$ and $\hat{p}_{\text{V9,HS,year}}$ was performed in logit space. The regression slope and intercept parameters were used to infer reasonable values of $\text{logit}(\hat{p}_{\text{V7,HS,year}})$ from $\text{logit}(\hat{p}_{\text{V9,HS,year}})$, after which values were back-transformed to the probability scale. Isolated \hat{p} for these receiver subarrays, tag types, and years are shown in Fig. S24.

Predicting detection probability on QCS and JDF subarrays. We cannot estimate p at final subarrays QCS and JDF with mark-recapture methods, but we assume that they are similar to \hat{p}_{NSOG} . These three receiver subarrays experience similar oceanographic conditions and are deployed at similar depths, so we expect a similar probability of detecting a tag as it crosses the subarray. Nevertheless, these receiver subarrays do differ slightly in terms of geometry, or the average spacing between receivers and the proportion of receivers successfully recovered, so we accounted for these differences in making predictions of p_{QCS} and p_{JDF} .

Using \hat{p}_{NSOG} , \hat{p}_{HSinner} , and \hat{p}_{HSouter} for each of the two tag types derived from the isolated p analysis, we used multiple regression to model \hat{p} as a function of one or more subarray geometry covariates. These covariates included mean horizontal spacing between receivers on a subarray, mean deployment depth, the proportion of receivers recovered and successfully downloaded, and the proportion of coverage on a subarray under an assumed value of receiver detection range. (For example, if a detection range of 400 m is assumed for all receivers on a subarray, what fraction of the one-dimensional receiver subarray is covered by the radius of at least one receiver?) Detection

ranges of 300, 350, 400, 450, 500, and 550 m were considered for these “proportion of coverage” covariates, with larger assumed detection ranges (e.g., 450–550 m) implying greater coverage on the subarray, and smaller assumed detection ranges (e.g., 300–350 m) implying a smaller proportion of coverage across the entire subarray (16). These “coverage” covariates combined effects of average spacing between receivers and proportion of successfully recovered receivers. Tag type was incorporated as an additive covariate in all candidate models. In some models, we also considered a main effect for receiver subarray, hypothesizing that possible differences in local noise conditions among subarrays could result in overall differences in p .

For each tag type and year, \hat{p}_{NSOG} , \hat{p}_{HSinner} , and \hat{p}_{HSouter} were logit-transformed for the regression. The candidate regression models were ranked in terms of AIC and adjusted r^2 values (not shown). The best model overall involved a covariate of proportion of coverage assuming a detection range of 400 m, i.e., $\hat{p} \sim \text{TagType} + \text{cover}_{400}$ (adjusted r^2 values of 0.28 for V9 tags and 0.23 for V7 tags when regressed separately). A similar model containing an additive “line” effect had less support in the data ($\Delta\text{AIC} = 2.9$), but did admit more uncertainty in the predictions. To be more conservative, we assumed this model, $\hat{p} \sim \text{TagType} + \text{line} + \text{cover}_{400}$, for predicting p_{QCS} and p_{JDF} even though the line effect was weak. This simply suggests that after accounting for variation in \hat{p} due to cover_{400} , there was little further explanatory power in a geographical effect, which strengthens our assertion that p_{QCS} and p_{JDF} can be reasonably predicted from \hat{p} at subarrays in other geographic areas. The cover_{400} effect allowed for p_{QCS} and p_{JDF} predictions to be specific to those outer subarrays by using their specific cover_{400} covariate values in the regression relationship established for the other subarrays. The line effect value for NSOG was assumed for QCS and JDF, i.e., $\hat{p}_{\text{QCS}} \sim \text{TagType} + \text{line}_{\text{NSOG}} + \text{cover}_{400,\text{QCS}}$. Values of $\text{logit}(\hat{p}_{\text{QCS}})$ and $\text{logit}(\hat{p}_{\text{JDF}})$ were generated for each year and tag type because subarray geometry varied slightly from year to year, and then back-transformed to the probability scale.

Uncertainty for predicted p_{QCS} and p_{JDF} values was approximated, comprised of two sources that were assumed to be independent (i): the maximum of yearly $\text{SE}(\hat{p}_{\text{NSOG}})$ using the reduced-digit CJS model (i.e., uncertainty in \hat{p} caused by binomial probabilities at limited sample sizes and uncertainty in survival, assumed to be similar among NSOG, QCS, and JDF subarrays); and (ii) uncertainty in p_{QCS} and p_{JDF} predictions associated with the regression against cover_{400} (i.e., uncertainty in \hat{p} caused by differences in line geometry among lines and years). The 95% confidence limits for the first component were estimated with profile likelihoods in logit space by using MARK. The largest of the resulting variances over the 4 y (range, 0.153–0.194 in logit space) was used to be conservative. For the second (and usually smaller) component, $\text{SE}(\hat{p}_{\text{QCS}})$ and $\text{SE}(\hat{p}_{\text{JDF}})$ from the regression were computed in logit space. The resulting variance was added to that of the first component, assuming independence of variance components. The combined variance was used to calculate combined 95% confidence limits on the logit scale, which were back-transformed to the probability scale.

Detections on QCS and JDF were pooled in the final digit of the detection history to represent exit from the Salish Sea system, so a combined prediction of p , $\hat{p}_{\text{QCS/JDF}}$, is required for these outer subarrays. A weighted mean of \hat{p}_{QCS} and \hat{p}_{JDF} for each year and tag type was taken, weighted by the estimated number of tags crossing these two subarrays (the number of tags detected on a subarray divided by \hat{p} for that subarray, year, and tag type). The same approach was used for combined estimates of upper and lower 95% confidence limits of $\hat{p}_{\text{QCS/JDF}}$. Predictions of p for both outer subarrays as well as their combined estimate are shown in Fig. S2B.

To quantify the uncertainty in early ocean survival estimates associated with assuming a fixed value for $p_{\text{QCS/JDF}}$, the un-

certainly of this final \hat{p} was taken into account. Mark-recapture models were fit to detection data for both Fraser and non-Fraser datasets, but rather than assuming only $\hat{p}_{\text{OCS/JDF}}$, the approximate 95% confidence limits of $\hat{p}_{\text{OCS/JDF}}$ were also assumed as fixed values. Fixing \hat{p}_{final} to the upper 95% confidence limit results in a lower $\hat{\phi}_{\text{final}}$, and fixing \hat{p}_{final} to the lower 95% confidence limit results in a higher $\hat{\phi}_{\text{final}}$ of all groups. This bounded a range of uncertainty for $\hat{\phi}_{\text{final}}$ and thus for the total early ocean survival estimate. This error is additional to the mark-recapture error estimated with fixed values of $\hat{p}_{\text{OCS/JDF}}$ at the final subarrays; both types of error are presented in Fig. 3.

List of Candidate Models. The objective of this study was to quantify survival estimates of smolt populations as reliably as possible (i.e., balancing accuracy and precision; avoiding under-fitting or over-fitting). Attributing variation in survival to any factors in particular is beyond the scope of this paper. The same, general submodel for ϕ was therefore assumed across candidate models in both datasets, $\phi_{\text{Segment:Group}}$, where Group is a unique combination of species, population, provenance, and year. This allowed for separate ϕ in each segment of the migration for each group.

Submodels of p allowed for separate estimates for each particular detection subarray and year combination, $p_{\text{Station:Year}}$, and most submodels involved additional parameters that increased the flexibility of \hat{p} . In all models, tags of the same acoustic output crossing a particular receiver subarray around the same time were assumed to have a common p even if they were implanted into smolts from different populations (16); noting that the use of population-specific covariates for constraining \hat{p} at Fraser River subarrays is a partial exception to this). In some models, \hat{p}_{V7} and \hat{p}_{V9} were allowed to differ (consistently across subarrays and years), and in other more constrained models, a common \hat{p} was assumed with tag types pooled. Some models corrected the bias of \hat{p} and $\hat{\phi}$ as a result of split-route migration patterns by allowing for additional parameters in p submodels, which represented population-specific joint estimates of movement and detection at NSOG. Other models did not incorporate these parameters. In the Fraser River dataset, various run timing or river flow covariates were used to characterize seasonal changes in p . Finally, in all models, p_{final} was fixed at a value derived from the isolated analysis of p on ocean receiver subarrays, adjusting for geometrical properties of individual receiver subarrays. Fixing this parameter untangled the confounded $\hat{\phi}_{\text{final}}$, allowing it to be estimable but conditioned on the fixed value assumed for p_{final} .

The number of candidate models considered follows from these inclusions or exclusions of additional parameters for p . In the Fraser River dataset, there were two possibilities for tag type (pooled or distinct), two possibilities for split-route bias-correction parameters (included or not), and five possibilities for environmental covariates during mean arrival time at subarrays (DOY, Mission water level, Port Mann water level, water level from both gauges at specific subarrays, and none), whose product totaled 20 candidate models. In the non-Fraser dataset, there were two possibilities for tag type and two possibilities for split-route bias-correction parameters, giving four candidate models.

Mark-Recapture Model Selection Results. Several models for detection probability were considered to find the best in terms of the balance between accuracy (as measured by the goodness of fit to the data) and precision (from having to estimate fewer parameters) of p and ϕ estimates. Models that allowed fully independent \hat{p} among populations were not considered for two reasons: (i) detection probabilities were assumed to be based on characteristics of tags and subarrays, not on population-specific

behaviors; and (ii) as many populations had few tags detected at some subarrays, we wanted to avoid over-fitting to these sparse data. Estimates of p were independent among subarrays and years in all models, but the remaining components of the p submodels were incorporated as additive effects. Model selection methods were used to compare candidate models (20). Models with lower QAICc values (i.e., AIC values adjusted for small sample sizes and extrabinomial variation) are considered better in the balance of goodness of fit and the number of parameters required to achieve that fit.

Of the 20 p submodels evaluated for the Fraser River population dataset, the strongest support was found in the submodel that involved tag type, two river level covariates, and parameters allowing for split-route flexibility after ocean entry. This model, with the greatest number of parameters of all models considered, had an Akaike weight of 0.997, so was clearly the best model within the model set (Table S3). The second- and third-best models, with ΔQAICc values of 12.0 and 16.3, were similar to the first but did not involve a tag type effect or a second river level covariate, respectively. The remaining models had essentially no support within the model set. The top four models all involved the flexibility of population-specific \hat{p}_{NSOG} (which are actually joint estimates of detection and northward movement probabilities) in populations that exhibited split-route migration patterns after entering the Salish Sea. An extra 11 parameters were required to allow this flexibility, but the fit improved substantially, with a difference in ΔQAICc of approximately 24 to 27 between models with and without these split-route parameters. The second strongest effect on p appeared to be the incorporation of a second flow covariate corresponding with the mean arrival time of a population at a detection subarray. The top 16 submodels all involved at least one flow or DOY covariate (the bottom four did not), outlining the importance of incorporating seasonal decreases in p among populations as a result of increasing river flows over the salmon migration season (e.g., Fig. S1). This trend is only apparent by analyzing multiple populations with a wide range of release times or outmigration periods in the same river system. The top two models involved two covariates, giving greater flexibility for quantifying the relationship with flow. Tag type also had an important effect on p , with all 10 of the models that incorporated the extra parameter having lower QAICc values than their corresponding models that did not. The model coefficient (i.e., logit-link β parameter) for the tag type parameter in the top model was >0 (0.88; 95% confidence limits, 0.50–1.27), suggesting that V9 tags were more likely to be detected than V7 tags on average, as expected on the basis of their higher acoustic output. This constant difference among tag types on the logit scale becomes a variable difference on the probability scale, dependent on the magnitude of p (Fig. S2).

Of the four submodels of p evaluated for the non-Fraser River dataset, the strongest support was again seen in the largest model within this model set, incorporating effects of tag type and parameters allowing for split-route flexibility after entry into the Salish Sea (Table S4). Tag type appeared to have a very strong effect: the two models that incorporated the extra parameter had QAICc values approximately 21 to 24 smaller than the two models without tag type considered. The model coefficient was >0 (0.71; 95% confidence limit, 0.46–0.97), again with \hat{p} higher for V9 tags than for V7 tags. Incorporating the flexibility of population-specific \hat{p}_{NSOG} caused by split-route migration patterns required 10 parameters, and the associated reduction in the model's likelihood was sufficient to make this the better model ($\Delta\text{QAICc} = 2.8$) when tag type was also incorporated.

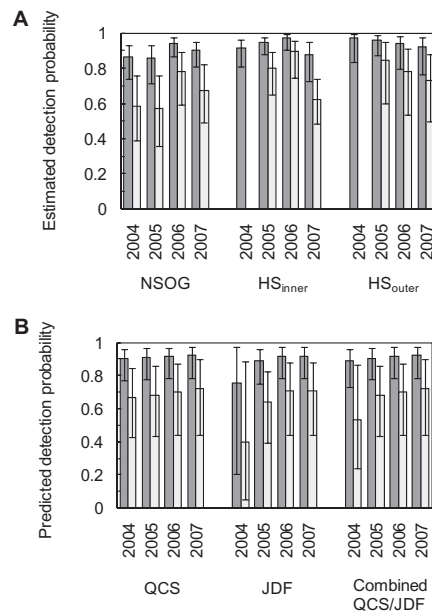


Fig. S2. Detection probability (*A*) estimates at intermediate ocean subarrays and (*B*) predictions at the most distant ocean lines for the two acoustic tag types used in this study (HS_{inner}, Howe Sound inner line; HS_{outer}, Howe Sound outer line). V9 tags are shown in light gray; V7 in dark gray; acoustic signal strengths of 142 and 136 dB re 1 μ P at 1 m, respectively. Detection probabilities in *A* were estimated with standard mark-recapture methods. Predicted detection probabilities in *B* were based on values in *A*, and adjusted for variation in receiver geometry among years and subarrays in a regression model. Approximate 95% confidence limits in *B* combine both mark-recapture uncertainty and regression uncertainty associated with the prediction (*SI Materials and Methods*).

Table S1. Provenance of the 3,692 tagged salmon juveniles used in this study

Map code	Species	Population	H/W	Tag type	Number released			
					2004	2005	2006	2007
A	Coho	Keogh river	W	V9	107	49	50	—
A	Steelhead	Keogh river	H	V9	92	50	—	—
A	Steelhead	Keogh river	W	V9	78	—	50	—
B	Chinook	Nimpkish river	U	V7	—	—	50	—
C	Coho	Nimpkish river	H	V9	99	8	—	—
C	Coho	Nimpkish river	H	V7	—	49	—	—
C	Coho	Nimpkish river	W	V9	—	—	50	—
D	Steelhead	Englishman river*	W	V9	67	43	50	—
E	Steelhead	Cowichan river*	H	V9	—	—	50	—
F	Kokanee	Sakinaw lake*	W	V9	—	47	49	—
F	Sockeye	Sakinaw lake*	H	V9	97	—	61	—
G	Coho	Tenderfoot creek*	H	V9	100	50	50	—
G	Coho	Tenderfoot creek*	H	V7	—	50	70	199
G	Steelhead	Cheakamus river*	H	V9	—	—	—	81
G	Steelhead	Cheakamus river*	W	V9	51	49	—	—
H	Steelhead	Seymour river*	H	V9	—	—	—	60
I	Sockeye	Cultus lake*	H	V9	100	376	200	200
J	Steelhead	Deadman river*	W	V9	—	57	38	—
J	Steelhead	Deadman river*	W	V7	—	—	26	—
K	Chinook	Nicola river*	H	V9	49	—	—	—
K	Chinook	Nicola river*	H	V7	—	50	—	—
L	Chinook	Coldwater river	U	V9	—	19	—	—
L	Chinook	Coldwater river*	U	V7	—	50	—	—
L	Steelhead	Coldwater river*	W	V9	31	50	50	—
L	Steelhead	Coldwater river*	W	V7	—	—	25	—
M	Chinook	Spius creek*	H	V7	—	—	99	—
N	Coho	Spius creek*	H	V7	—	50	—	—
O	Chinook	Coldwater river*	H	V7	—	—	100	—
O	Coho	Coldwater river	H	V9	28	—	—	—
O	Coho	Coldwater river*	H	V7	12	—	100	—

Map release locations are shown in Fig. 1. The average size of the juveniles tagged in a given release group and year was generally ≥ 125 mm for V7 tags (≥ 130 mm in 2006–2007) and ≥ 140 mm for V9 tags. Origin: H, hatchery-reared fish; W, wild-caught and lacking hatchery marks; U, unknown. Kokanee are a land-locked sockeye life history type; it was discovered from DNA analysis after tagging of wild Sakinaw Lake sockeye smolts captured in the lake and released directly into the ocean that they were kokanee and not the sea-run sockeye life history type; Sakinaw hatchery smolts were all sockeye life history type (1).

*Population used in the assessment of size-related mortality (Fig. 5); stocks with release points close to the final telemetry subarrays were excluded as relatively little mortality could occur.

1. Wood CC, Welch DW, Godbout L, Cameron J (2011) Marine migratory behaviour of hatchery-reared anadromous and wild non-anadromous sockeye salmon revealed by acoustic tags. *Advances in Fish Tagging and Marking Technology*, eds McKenzie J, Phelps Q, Kopf R, Mesa M, Parsons B, Seitz A (American Fisheries Society, Symposium 76, Bethesda, MD).

Table S2. Comparison of detection probability models for isolated estimation of p on Howe Sound and NSOG lines

Detection probability model*	k^{\dagger}	$-2 \cdot \ln(L)$	AICc	$\Delta AICc$
Howe Sound dataset				
$p_{\text{Station} \times \text{Year} + \text{TagType}}$	43	1,645.4	1,734.7	0
$p_{\text{Station} \times \text{Year}}$	42	1,657.1	1,744.3	9.6
$p_{\text{Station} \times (\text{Year} : \text{Species} : \text{Population}) + \text{TagType}}$	58	1,636.7	1,758.8	24.1
$p_{\text{Station} \times (\text{Group} : \text{TagType})}$	60	1,632.8	1,759.4	24.7
$p_{\text{Station} \times (\text{Year} : \text{Species} : \text{Population})}$	57	1,644.8	1,764.8	30.1
NSOG dataset				
$p_{\text{Station} \times \text{Year}}$	104	3,434.6	3,648.3	0
$p_{\text{Station} \times \text{Year} + \text{TagType}}$	105	3,434.4	3,650.2	1.9
$p_{\text{Station} \times (\text{Year} : \text{Species} : \text{Population}) + \text{TagType}}$	181	3,404.1	3,783.5	135.3
$p_{\text{Station} \times (\text{Year} : \text{Species} : \text{Population})}$	180	3,407.1	3,784.3	136.0
$p_{\text{Station} \times (\text{Group} : \text{TagType})}$	192	3,404.1	3,807.8	159.5

*The survival probability model assumed was $\phi_{\text{Segment} \times (\text{Group:TagType})}$.

[†]The parameter count (k) is adjusted to include the number of potentially estimated parameters including those at boundaries of 0 or 1. Detection probabilities at the final detection station were fixed at estimated values from isolated analyses (see text) so are not included in the parameter count.

Table S3. Model selection results for recaptures-only survival (ϕ) and detection probability (p) estimates for Fraser River populations in years 2004–2007

Detection probability model*	k^{\dagger}	$-2 \cdot \ln(L)$	QAICc	Δ QAICc	Akaike weight
$p_{\text{Station:Year}} + \text{TagType} + \text{Mission} + \text{partial_PM} + \text{Split_Route_Pars}^{\ddagger}$	118	5,734.7	4,340.5	0.0	1.00
$p_{\text{Station:Year}} + \text{Mission} + \text{partial_PM} + \text{Split_Route_Pars}$	117	5,754.5	4,352.5	12.0	0.00
$p_{\text{Station:Year}} + \text{TagType} + \text{Mission} + \text{Split_Route_Pars}$	117	5,760.6	4,356.8	16.3	0.00
$p_{\text{Station:Year}} + \text{Mission} + \text{Split_Route_Pars}$	116	5,772.6	4,363.3	22.8	0.00
$p_{\text{Station:Year}} + \text{TagType} + \text{Mission} + \text{partial_PM}$	107	5,802.1	4,365.1	24.6	0.00
$p_{\text{Station:Year}} + \text{TagType} + \text{PM} + \text{Split_Route_Pars}$	117	5,783.3	4,373.1	32.6	0.00
$p_{\text{Station:Year}} + \text{PM} + \text{Split_Route_Pars}$	116	5,789.8	4,375.6	35.1	0.00
$p_{\text{Station:Year}} + \text{Mission} + \text{partial_PM}$	106	5,824.4	4,379.0	38.5	0.00
$p_{\text{Station:Year}} + \text{TagType} + \text{DOY} + \text{Split_Route_Pars}$	117	5,794.7	4,381.2	40.7	0.00
$p_{\text{Station:Year}} + \text{TagType} + \text{Mission}$	106	5,828.9	4,382.2	41.7	0.00
$p_{\text{Station:Year}} + \text{Mission}$	105	5,842.7	4,389.9	49.4	0.00
$p_{\text{Station:Year}} + \text{DOY} + \text{Split_Route_Pars}$	116	5,814.7	4,393.4	52.9	0.00
$p_{\text{Station:Year}} + \text{TagType} + \text{PM}$	106	5,852.2	4,398.8	58.3	0.00
$p_{\text{Station:Year}} + \text{PM}$	105	5,860.0	4,402.2	61.7	0.00
$p_{\text{Station:Year}} + \text{TagType} + \text{DOY}$	106	5,862.5	4,406.2	65.7	0.00
$p_{\text{Station:Year}} + \text{DOY}$	105	5,884.8	4,420.0	79.5	0.00
$p_{\text{Station:Year}} + \text{TagType} + \text{Split_Route_Pars}$	116	5,956.1	4,494.4	153.9	0.00
$p_{\text{Station:Year}} + \text{TagType}$	105	6,022.4	4,518.3	177.8	0.00
$p_{\text{Station:Year}} + \text{Split_Route_Pars}$	115	6,008.5	4,529.6	189.1	0.00
$p_{\text{Station:Year}}$	104	6,077.9	4,555.8	215.3	0.00

QAICc values are adjusted for small sample sizes and extrabinomial variation with $\hat{c} \approx 1.40$.

*Models for p are compared whereas the fully segment and group-varying submodel for ϕ with interactions only is held constant, $\phi_{\text{Segment:Group}}$. Groups consist of unique combinations of species, population, provenance, and year.

† The parameter count (k) is adjusted to include the number of potentially estimated parameters including those at boundaries of 0 or 1. Detection probabilities at the final detection station were fixed at estimated values from isolated analyses (see text) so are not included in the parameter count.

‡ DOY, water level at Mission, and water level at Port Mann (PM) represent run timing or river level covariates used to constrain p estimates. In models where multiple covariates were used (..Mission + partial_PM..), water level at the Mission gauge applied to all river stations whereas water level at the Port Mann gauge applied to all stations downstream of Mission. Additional parameters for detection probability at NSOG ("Split_Route_Pars") were used for populations that exhibited split-route migration patterns after ocean entry.

Table S4. Model selection results for recaptures-only survival (ϕ) and detection probability (p) estimates for all populations outside the Fraser River in years 2004–2007

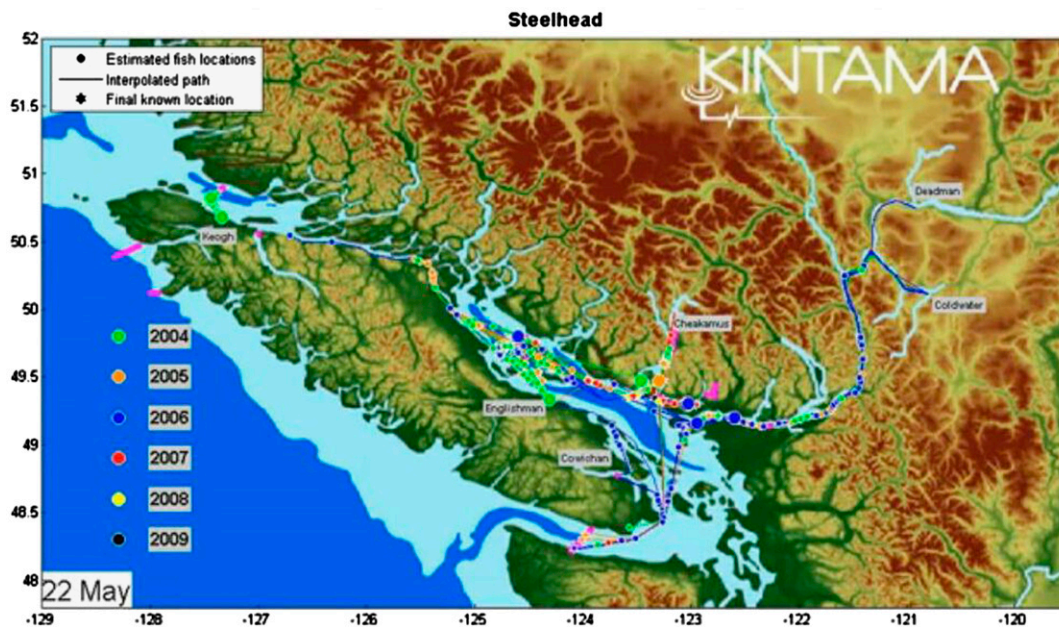
Detection probability model*	k^{\dagger}	$-2 \cdot \ln(L)$	QAICc	Δ QAICc	Akaike weight
$p_{\text{Station:Year}} + \text{TagType} + \text{Split_Route_Pars} + \text{Cluster_Pars}^{\ddagger}$	202	7,618.1	6,865.7	0.0	0.80
$p_{\text{Station:Year}} + \text{TagType} + \text{Cluster_Pars}$	192	7,589.4	6,868.5	2.8	0.20
$p_{\text{Station:Year}} + \text{Split_Route_Pars} + \text{Cluster_Pars}$	201	7,645.9	6,889.3	23.6	0.00
$p_{\text{Station:Year}} + \text{Cluster_Pars}$	191	7,619.8	6,889.9	24.3	0.00

QAICc values are adjusted for small sample sizes and extrabinomial variation with $\hat{c} \approx 1.177$.

*Models for p are compared whereas the fully segment and group-varying submodel for ϕ with interactions only is held constant, $\phi_{\text{Segment:Group}}$. Groups consist of unique combinations of species, population, provenance, and year.

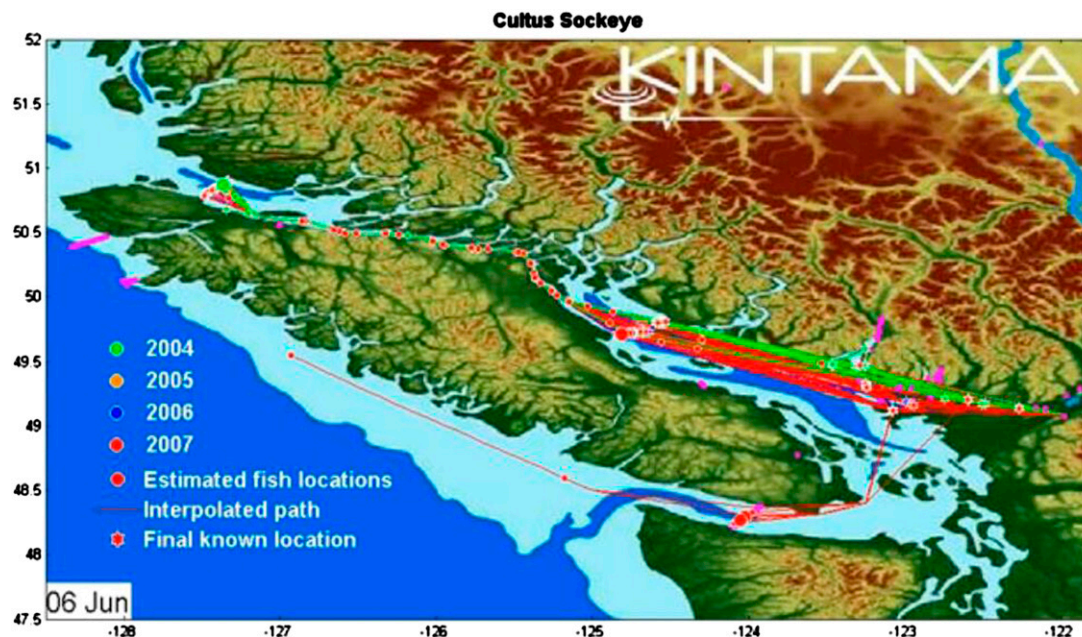
† The parameter count (k) is adjusted to include the number of potentially estimated parameters including those at boundaries of 0 or 1. Detection probabilities at the final detection station were fixed at estimated values from isolated analyses (see text) so are not included in the parameter count.

‡ Additional parameters for detection probability at NSOG ("Split_Route_Pars") were used for populations that exhibited split-route migration patterns after ocean entry. Additional parameters ("Cluster_Pars") were used in all models which ensured that populations sharing a detection station along migration routes were grouped at their n th detection history digit, and were separated from other populations that crossed a different station at their n th digit.



Movie S1. Movements of tagged steelhead smolt movements, 2004-2009. The locations of the POST array are shown in magenta and the day of year is shown in the lower left.

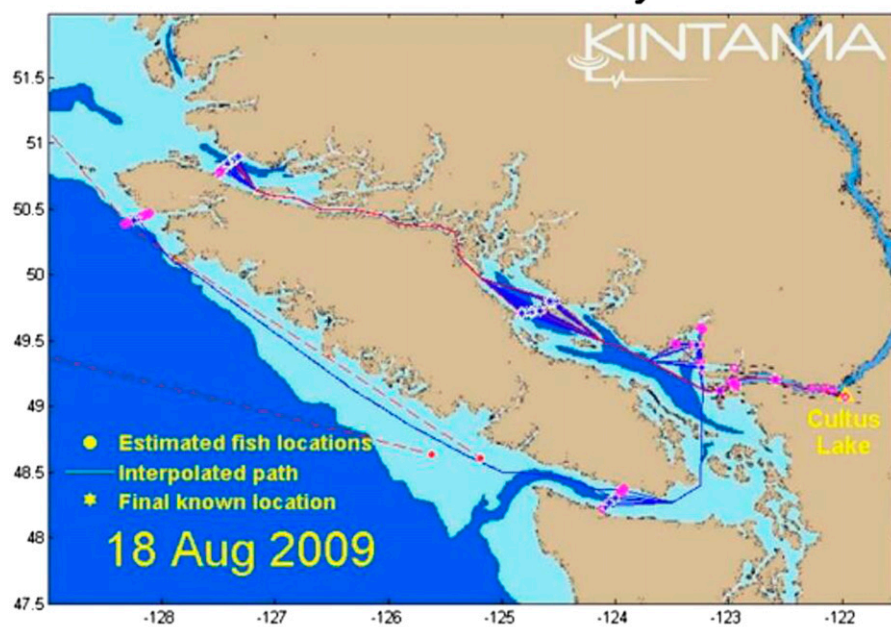
[Movie S1](#)



Movie S2. Movements of tagged Cultus Lake sockeye smolt movements, 2004-2007. The locations of the POST array are shown in magenta and the day of year is shown in the lower left.

[Movie S2](#)

2007-09 Cultus Sockeye



Movie S3. Animation of movements for the 2007 Cultus Lake sockeye smolt outmigrant and the return path of the two smolts surviving to return as adults in 2009 (red dots).

[Movie S3](#)