

Estimation of survival and detection probabilities for multiple tagged salmon stocks with nested migration routes, using a large-scale telemetry array

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Abstract. Mark–recapture models for estimating survival and detection probabilities of tagged animals that migrate past successive receiver stations can incorporate multiple, linked stocks to improve detection probability estimates. When multiple release groups are analysed in a common framework, detection information can be shared to compensate for small sample sizes and provide generality beyond single-stock approaches. Methods for structuring complex detection history data and applying standard mark–recapture models are presented, allowing for information sharing among multiple stocks under nested migration route structures, where some portions of routes are shared with other stocks and other portions are unique. Possible biases from split-route migration patterns within a release group are described, along with a simple method of correcting these biases using stock-specific parameters that incorporate movement probabilities. Environmental covariates can be paired with stock-specific run timing data to model stock-specific detection probabilities that change seasonally. Finally, a method for assessing the redundancy of receivers on a multiple-receiver detection line is described, based on considerations of receiver line geometry. Examples are drawn from detection data of juvenile salmon on the Pacific Ocean Shelf Tracking Project (POST) array, but the methods presented here are transferable to other systems.

Additional keywords: capture–recapture, CJS, detection efficiency, fish mortality, Program MARK.

Introduction

Migration periods represent important life-history stages in many fishes because they are often associated with high mortality rates due to predation risk exposure, especially in juvenile stages (Pearcy 1992). Juvenile salmonids undergo challenging migrations that involve physiological transitions from freshwater to saltwater, long distances (Hartt and Dell 1986) and vulnerability to concentrations of predators that target salmon during the annual outmigrations (Greenstreet *et al.* 1993; Collis *et al.* 2001). Survival during this critical period can be estimated by tagging fish in freshwater and monitoring their die-off along migratory routes at a series of detection stations downstream and/or in the coastal ocean.

Mark–recapture methods such as Cormack–Jolly–Seber (CJS) models, originally derived for recapturing tagged animals at successive time periods, are commonly used for estimating survival in animal populations. Spatial forms of CJS models, where tagged animals are detected at fixed locations along a migration route (like PIT tag receivers in dam passages, radio receivers in rivers, or acoustic receivers in rivers and saltwater), have become increasingly common (Burnham *et al.* 1987; Skalski *et al.* 2001; Zabel and Achord 2004). Migration routes are separated into segments between detection stations, and survival can be estimated for each segment while simultaneously accounting for detection probabilities at receiver stations. Jointly estimating detection probabilities is often difficult due to small sample sizes and confounding with survival. If fish from more than one

population, release group or treatment are tagged and share at least part of a migration route, then there is an opportunity for ‘sharing’ detection information from other groups in the analysis of any one of these groups (e.g. Burnham *et al.* 1987; Lebreton *et al.* 1992). Survival or detection probability parameters can be considered fully independent among n groups (which is the same as n independent CJS models), fully pooled, or somewhere between these extremes.

In multi-stock studies where fish from geographically diverse locations are tagged and released, only part of a migration route may be shared among stocks. Fish from two stocks may share the same migratory route down a river, but then split after ocean entry. Alternatively, fish from two different river systems may enter the same body of saltwater and share a common early ocean migration route. Either of these migration route structures can be considered ‘nested’. It may be appropriate in these cases to share information among stocks for the segments and/or detection stations they share, but distinct parameter estimates for the segments and stations unique to each stock should be maintained.

Methods for structuring complex detection history data are presented, which allow standard CJS models to be applied to estimate survival and detection probabilities more precisely. They are intended for cases where multiple stocks are analysed in a common framework and definitions of detection history positions differ among stocks. These methods were developed to address limitations in standard models that arose while estimating survival rates of migrating juvenile salmon stocks in

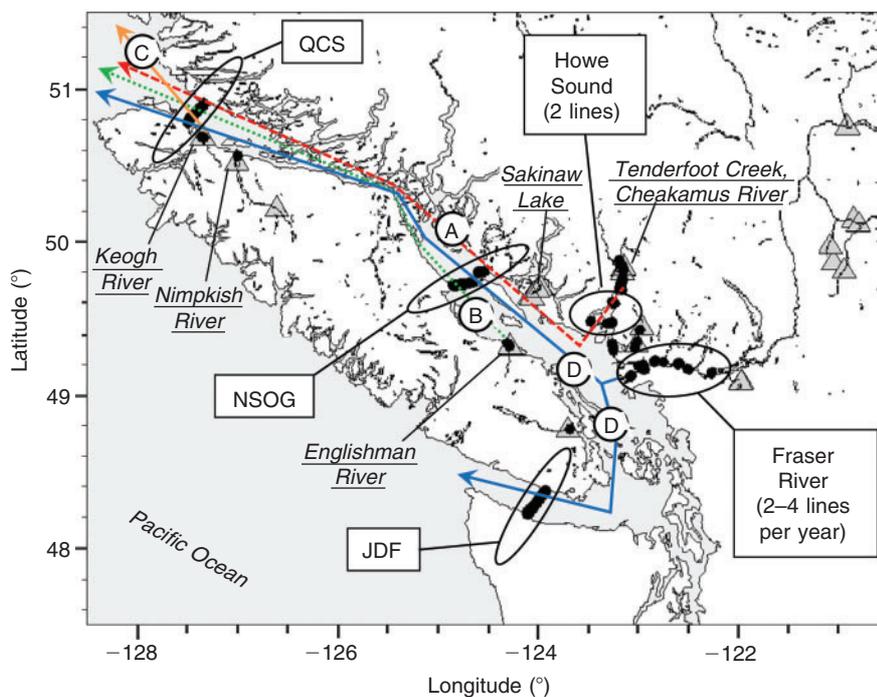


Fig. 1. Map of POST study area. Grey triangles show release locations of salmon smolts; labels of those that are referred to in the text are underlined. Black circles show locations of acoustic receiver stations in 2004–07. Not all release locations and stations were used in all years. Arrows A–D show example migration routes where D is a split route. Labels of major receiver stations are shown in boxes. The R package PBSmapping (Schnute *et al.* 2004) was used for the map.

southern British Columbia, Canada. Fish from these stocks were tagged with acoustic transmitters and their migrations were monitored at successive acoustic receiver stations deployed under the Pacific Ocean Shelf Tracking Project (POST, www.post-coml.org, accessed 1 December 2008). Examples are taken from these detection data, but the methods can be generalised to other systems. It is shown how the desired modifications can be achieved using Program MARK (White and Burnham 1999), but they can also be implemented in other commonly used capture–recapture software programs or by programming CJS models directly using platforms such as R or WinBugs.

First, the POST study (Welch *et al.* 2003) and general methods for applying CJS models to estimate survival and detection probabilities are described. Second, a simple method is illustrated for incorporating multiple groups by sharing model parameters among stocks at some detection stations (those in common) but not others (those from distinct migration routes). Third, possible biases from split-route migration patterns are reviewed along with a simple method for correcting these biases using stock-specific parameters that incorporate movement probabilities. Fourth, the importance of pairing stock-specific run timing data with environmental covariates is shown for detection probabilities that change seasonally in a river. Finally, a method for assessing the redundancy of receivers at a multi-receiver detection station is described, based on considerations of receiver detection range. This method is not necessarily specific to multi-stock studies, but shows that station-based

covariates can be useful in modelling detection probabilities and designing large-scale telemetry arrays.

Study system: nested migration routes of salmon smolt populations

Over 20 different populations of juvenile salmon in southern British Columbia (four species in total) were tagged with internal, individually coded acoustic transmitters during 2004–07 (V7 or V9 tags, VEMCO/AMIRIX Systems, Inc., Halifax, Canada). Their migrations downstream and through the Strait of Georgia ecosystem (49.4°N, 124°W) were monitored with the POST acoustic array (Welch *et al.* 2003; Fig. 1). The array consisted of a series of acoustic receivers (VR-2 or VR-3, VEMCO/AMIRIX Systems, Inc.) deployed in single units or pairs in rivers and arranged as lines (numbering between 4 and 30 receivers per line) across coastal inshore straits. Migration periods through the study system typically lasted several weeks or months from May–July. Four years of data and multiple stocks from different geographical areas were combined in the same dataset and models. Some detection stations were shared among all stocks and others were specific to only some stocks. The number and location of stations varied among years for some stocks.

The detection histories of individual fish at receiver stations were determined, where a station consists of either a single receiver or multiple receivers arranged in a line. To use Program

MARK, the detection history of each fish was represented as a string of ones and zeros. A ‘1’ represented release, then either a ‘1’ or a ‘0’ at all following digits represented whether the fish was detected or not at successive stations. Tagged smolts potentially passed between 2 and 12 detection stations during their migration out of the Strait of Georgia system (for a maximum of 13 digits in the detection history), with 0–8 of these in freshwater and 1–4 in the ocean. About two-thirds of stocks had fish that were detected only moving northward after ocean entry across the northern Strait of Georgia (NSOG) and Queen Charlotte Strait (QCS) lines (Fig. 1, arrows A–C), while the remaining one-third had some fish move north and others move south across the Strait of Juan de Fuca (JDF) line (Fig. 1, arrow D). To quantify the proportion of fish that survived their early ocean migration, regardless of the particular direction taken after ocean entry, detections at the outer lines (QCS and JDF) were pooled in the final digit of the detection history sequence to represent exit from the Strait of Georgia system. This pooling of outer lines complicates mark–recapture estimates of survival probability (ϕ) in the segment to NSOG and detection probability (p) at NSOG, as discussed below, and could be avoided by deploying two closely spaced lines of receivers at the last detection stations (Skalski 2006).

To illustrate the application of a CJS model to a single-stock dataset, consider a group of hatchery-reared steelhead (*Oncorhynchus mykiss*) smolts from the Keogh River in 2004. Fish ($n = 92$) were tagged and released in the river. Smolts generally migrated directly to sea then northwards, potentially crossing a receiver station at the river mouth and another at QCS (Fig. 1, arrow C). With two detection stations, four detection histories are possible: 25 fish were detected at both stations (111), two were detected at QCS but not at the river mouth (101), 38 were detected at the river mouth but not QCS (110) and 27 were never detected (100). Failure to detect a fish at a station could result from either mortality before arriving at it or non-detection at it given that the fish crossed it. To distinguish between these possibilities, we specify a likelihood function for the CJS model and find the maximum-likelihood estimates (MLEs) of parameters ϕ in each segment ($\hat{\phi}_{\text{Seg}}$) and p at each station (\hat{p}_S) given the detection data. The final $\phi_{\text{Keogh} \rightarrow \text{QCS}}$ and p_{QCS} parameters are confounded and not separately identifiable (call their product β_3), but $\phi_{\text{Release} \rightarrow \text{Keogh}}$ (ϕ_1) and p_{Keogh} (p_2) are estimable given the data. The observed numbers of each mutually exclusive detection history are multinomially distributed. The product of these probability terms gives the total likelihood, L :

$$L \propto [\phi_1 p_2 \beta_3]^{25} [\phi_1 (1 - p_2) \beta_3]^2 [\phi_1 p_2 (1 - \beta_3)]^{38} [\phi_1 (1 - p_2)(1 - \beta_3) + (1 - \phi_1)]^{27}. \quad (1)$$

The log-likelihood becomes a sum rather than a product over all detection histories, and typically the log-likelihood, $\ln(L)$, is maximised by using optimisation routines. Using MARK, the MLEs and estimated standard errors (\hat{SE}) of model parameters for the steelhead example were found to be $\hat{\phi}_1 = 0.740$ (0.055), $\hat{p}_2 = 0.926$ (0.050) and $\hat{\beta}_3 = 0.397$. This example is straightforward, because the number of fish detected at and after the first detection station was sufficient to estimate ϕ_1 and p_2 . This is not always the case, however, as in other populations original tagged sample sizes may be smaller, mortality during the migration may be higher, or at other stations p may be lower, resulting in sparse

detection data in other cases. Along with these hatchery-reared steelhead in the example, there were also wild steelhead and wild coho salmon smolts released in the Keogh River in 2004. Fish from all three release groups were implanted with the same tag type and all migrated around the same time; the following section will present ways to incorporate detection data from all these groups to increase pooled sample sizes for estimating p . Further descriptions, assumptions and more examples of fitting CJS models can be found in Pollock *et al.* (1990), Lebreton *et al.* (1992), Skalski *et al.* (2001) and the user guide accompanying White and Burnham (1999).

Additional assumptions specific to spatial forms of CJS models include: (1) animals migrate continuously past receiver stations and do not permanently reside between them or residualise (remain resident) in freshwater before arriving at the first station. This is unlikely to be an issue for species such as sockeye salmon (*Oncorhynchus nerka*) known to undergo long-distance migrations (Hartt and Dell 1986; Groot and Cooke 1987), but may confound estimated survival rates for species such as coho salmon (*Oncorhynchus kisutch*) that do not necessarily migrate continuously after ocean entry (Healey 1980; Pearcy and Fisher 1988). Downstream survival rates could also be underestimated if they failed to account for species such as steelhead that may not migrate downstream and instead residualise in freshwater (Viola and Schuck 1995). (2) Tag batteries last longer than the time required to cross all receiver stations during the migration. This is not likely to be a problem for most stocks as fish generally leave the study area before the expected date of tag death, but could bias estimates $\hat{\phi}$ and \hat{p} if transmissions stop prematurely (Townsend *et al.* 2006). (3) Detected tags are in live fish and not in predator stomachs or in dead fish floating past river receivers. Movement rates from tag detection data at different stations can be quantified to look for travel speeds that are faster than smolts can possibly travel, as evidence of a predator carrying a tag. Dead fish can be tagged and left to float downstream to estimate the probability of false positive detections (Skalski *et al.* 2001). Finally, (4) losses on recapture (Jolly 1965) can be ignored because tagged fish are not handled after release, and crossing a detection station should not affect survival.

For the remainder of this paper, we turn to situations involving analysis of multiple release groups. The number of fish detected at a given receiver station varied widely among release groups (i.e. combinations of a particular species, stock and release year). For groups with few detections on some lines, mark–recapture estimates of ϕ or p may not be reliable if separate CJS models were constructed for each stock in each year. Instead, groups were analysed jointly, linked in terms of a common p with the assumption that a particular tag type from one stock should have the same probability of being detected at a station as the same tag type from a different stock (unless environmental conditions differ markedly among the run timing periods of stocks; see below). At a given receiver station, p was modelled as year-specific and tag type-specific as tag types differed in acoustic power and hence detection range (V7 tags, 136 dB re 1 μPa at 1 m; V9 tags, 142 dB). The relative difference in p between tag types was constrained to be constant (in logit space) among years and among detection stations (i.e. an additive effect of tag type). This required combining years in the same dataset. Independence among groups was maintained in

terms of survival probabilities in each segment of their migration ($\phi_{\text{Seg:Group}}$). Unless one is interested in an overall effect of segment or group, main effects *per se* are not necessary to model (i.e. $\phi_{\text{Seg+Group+Seg:Group}}$, or equivalently, $\phi_{\text{Seg}\times\text{Group}}$), especially in a nested migration context since the n th segments of different groups may occur in different geographic locations. A full suite of interaction terms without main effects can still provide full independence among stations and groups. Essentially, CJS submodels were constructed for each species, stock and year combination in terms of segment-specific ϕ , but p for a given station, tag type and year was shared across species and stocks.

Variable detection stations along nested migration routes: multi-stock clusters

In a multi-stock analysis, stocks may be released at different geographic locations and may potentially pass different numbers of detection stations. Along the migration route of a stock, some stations may be shared with other stocks while others may be unique. We expect that stocks sharing the same tag type have the same p at a given station (assuming there are no stock-specific behaviour or swimming speed differences that cause variation in p), so p can be constrained to be shared among all stocks that cross that station (Burnham *et al.* 1987; Lebreton *et al.* 1992). To analyse multiple stocks and/or years together in the same model (e.g. to maintain a consistent relative difference in p between different tag types, or to share information among stocks to compensate for sparse data in some groups), it is necessary to appropriately pair the detection history digits for each population with those from other populations.

Drawing from the POST study to illustrate, one release group (Tenderfoot Creek coho in 2007) had a 13-digit detection history, the longest among all years and stocks in this analysis, with fish possibly crossing eight river stations and four ocean stations during the smolt migration (Fig. 1, arrow A). The final digit of this sequence represents detection at QCS or JDF. To combine stocks and years in the same model with Program MARK, all other release groups must also have QCS/JDF as their 13th digit since this station is common to all groups (Fig. 1, arrows B and C). For stocks 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 (Lebreton *et al.* 1992). For example, fish from stocks that potentially cross only one line prior to QCS/JDF would have a detection history consisting of 10 '0's, a '1' representing release, a digit for the next-to-last station, and a final digit for QCS/JDF.

In some cases, particular detection stations may not be common to all stocks. For example, the 11th digit (10th station) in the detection history of 2007 Tenderfoot Creek coho smolts represents the outer Howe Sound receiver line (Fig. 1, arrow A), but the 11th digit for other stocks represents other stations including the first Nimpkish River station in 2006, the second Englishman River station in 2005 (Fig. 1, arrow B), or else represents the '1' for release of Keogh River fish. This issue would not arise if stocks all shared the same general migration route and thus crossed the same detection stations, but since routes may be nested in a multi-stock context, it is necessary to keep stocks distinct when they do not share detection stations. An analogous case of a time-based CJS model with multiple

groups would be that different release groups occur in different 'sampling universes' (i.e. geographically distinct locations where at a particular location not all groups could be captured) at some recapture occasions (without movement to other sampling universes between occasions), but at later occasions they are mixed in the same sampling universe and share a common recapture rate.

To represent different receiver stations for different stocks at the same digit of a detection history sequence, extra parameters can be incorporated into the specification of p to represent the interaction of stations (S), years (Y), and general migration route clusters (C, which are geographically separate from other clusters). Some clusters may involve only a single release group while others may include several stocks or species that share the same general migration route across stations. Using the above examples for the 11th digit, extra parameters specify interactions such as 'S₁₁Y₂₀₀₇C_{Squamish watershed}', 'S₁₁Y₂₀₀₆C_{Nimpkish watershed}', or 'S₁₁Y₂₀₀₅C_{Englishman watershed}'. These interaction parameters can be either specified in the design matrix in Program MARK, or more easily incorporated as extra terms using the linear model formulation of RMark (which sources Program MARK; Laake and Rexstad 2009). They ensure that \hat{p} are common for stocks with the same tag type sharing the same general migration route across a station in some year but are independent from those of stocks with migration routes that bring them past different receiver stations at the same given digit of a detection history sequence.

The following two examples show that the inclusion of these extra interaction parameters into CJS models performs as intended. RMark code used for these examples and their accompanying data input files are available as an Accessory publication to this paper. Seven stocks from the 2004 study and six from 2005 shared QCS/JDF as their 13th digit of the detection history but differed in their 12th digit (as well as 10th and 11th digits, but p are given for the 12th digit in this example). The number of fish per stock tagged with V9 tags ranged from 8 to 107. In both years, three stocks (Tenderfoot coho, Englishman steelhead, and Sakinaw sockeye (2004) or Cheakamus steelhead (2005)) crossed NSOG at their second-to-last station (Fig. 1, arrows A and B). Two or three stocks (Keogh coho, Keogh hatchery steelhead, and in 2004, Keogh wild steelhead) crossed the Keogh River mouth station (Fig. 1, arrow C) at the 12th digit. In both years, Nimpkish coho crossed the lower Nimpkish River station at that digit. Survival probabilities were treated as fully independent among species, stocks, years and segments of the migration. Detection probabilities could also be treated as fully independent among groups and stations, essentially resulting in separate CJS models for each group constrained only by tag type (Tag) differences:

$$\text{logit}(p_i) = \beta_0 + \beta_1 \cdot \text{Tag} + \beta_x \cdot S_i Y_j \text{Spp}_k \text{Stk}_l \quad (2)$$

where release groups are represented by unique combinations of year (Y), species (Spp) and stock (Stk) at each station (S_i ; this represents a digit i in the detection history rather than a specific i th station in some particular location). Note the 'Y' and additive 'Tag' terms are not necessary in this simple example because all stocks considered had V9 tags in either 2004 or 2005 (years were analysed separately). The model coefficients correspond with an intercept (β_0), Boolean

Table 1. Estimated detection probabilities (and $\hat{SE}(\hat{p})$) under three model formulations
 Estimates are shown for stations at the 12th digit of the detection history of salmon stocks with V9 tags in 2004 and 2005

Stock	No. tagged	Station crossed	Stock-independent	Geographic cluster	Fully pooled
2004 stocks					
Tenderfoot Creek coho	100	NSOG	NA	0.82 (0.07)	0.95 (0.01)
Englishman River steelhead	67	NSOG	0.70 (0.14)	0.82 (0.07)	0.95 (0.01)
Sakinaw Lake sockeye	97	NSOG	0.89 (0.07)	0.82 (0.07)	0.95 (0.01)
Keogh River coho	107	Keogh	1.00 (0.00)	0.98 (0.02)	0.95 (0.01)
Keogh River steelhead (W)	78	Keogh	1.00 (0.00)	0.98 (0.02)	0.95 (0.01)
Keogh River steelhead (H)	92	Keogh	0.93 (0.05)	0.98 (0.02)	0.95 (0.01)
Nimpkish River coho	99	Nimpkish	0.97 (0.02)	0.97 (0.02)	0.95 (0.01)
2005 stocks					
Tenderfoot Creek coho	50	NSOG	NA	0.67 (0.11)	0.91 (0.03)
Cheakamus River steelhead	49	NSOG	0.69 (0.13)	0.67 (0.11)	0.91 (0.03)
Englishman River steelhead	43	NSOG	0.60 (0.22)	0.67 (0.11)	0.91 (0.03)
Keogh River coho	49	Keogh	1.00 (0.00)	1.00 (0.00)	0.91 (0.03)
Keogh River steelhead (H)	50	Keogh	1.00 (0.00)	1.00 (0.00)	0.91 (0.03)
Nimpkish River coho	8	Nimpkish	1.00 (0.00)	1.00 (0.00)	0.91 (0.03)

dummy variable for ‘Tag’ (β_1) and each existing combination of $S_i Y_j S_{ppk} Stk_l (\beta_2, \dots, \beta_x)$. It is these coefficients that are fitted to detection data, and from them the biological parameter estimates $\hat{\phi}$ and \hat{p} are re-constituted. In alternative notation (Lebreton *et al.* 1992), this is model ($\phi_{Seg:Y:Spp:Stk}, PS:Y:Spp:Stk+Tag$) or ($\phi_{Seg:Group}, PS:Group+Tag$) without main effects for segment, station, or group. The stock-independent CJS \hat{p} vary for stocks at the NSOG station in 2004 and 2005, ranging from 0.60 to 0.89 (Table 1). There were insufficient detection data of Tenderfoot coho downstream of NSOG to estimate p at NSOG in either year. At the Keogh station, stock-independent \hat{p} happen to be the same for two stocks in 2004 and both stocks in 2005 (Table 1). These four estimates of 1.00 with (asymptotic) $\hat{SE}(\hat{p})$ of 0 are estimated at a boundary but are not confounded with a survival parameter; the fish detected at the final QCS station from each of these stocks were also detected at the Keogh station so the MLE of \hat{p} is 1.00. The third Keogh stock in 2004 had a lower \hat{p} of 0.93. The \hat{p} for Nimpkish coho at the lower Nimpkish River station was 0.97 in 2004 and 1.00 in 2005 (again, estimated at a boundary but not confounded with a survival parameter; Table 1).

Detection probabilities could instead be (incorrectly) treated as fully pooled among stocks:

$$\text{logit}(p_i) = \beta_0 + \beta_1 \cdot \text{Tag} + \beta_x \cdot S_i Y_j, \quad (3)$$

or model ($\phi_{Seg:Y:Spp:Stk}, PS:Y+Tag$) under alternative notation. The fully pooled \hat{p} are all the same within each year (Table 1), which is not appropriate in a multi-stock context with different stocks crossing different stations at their second-to-last digit of their detection history (i.e. \hat{p} at Keogh, Nimpkish, and NSOG stations have been constrained to be equal in this model).

Between these two extremes, p could be pooled at a station for stocks that share that station but kept distinct from other

stations that are crossed by stocks from different clusters (i.e. a ‘geographic cluster’ model):

$$\text{logit}(p_i) = \beta_0 + \beta_1 \cdot \text{Tag} + \beta_x \cdot S_i Y_j C_m \quad (4)$$

or alternatively, model ($\phi_{Seg:Y:Spp:Stk}, PS:Y:C+Tag$). Looking at just the 12th digit (11th station) for the 2005 example, the interaction terms would be $S_{12} Y_{2005} C_{\text{Georgia}}, S_{12} Y_{2005} C_{\text{Keogh}}$ and $S_{12} Y_{2005} C_{\text{Nimpkish}}$. Here, Tenderfoot coho, Cheakamus steelhead and Englishman steelhead are all part of the Strait of Georgia cluster (Georgia) at the 12th digit (conversely, the Englishman stock has a distinct migration route from Tenderfoot and Cheakamus stocks across stations corresponding to the 10th and 11th digits of the detection history so it would be part of a separate cluster for those digits; see Accessory publication to this paper). Consequently, \hat{p} at NSOG are common across these stocks (Table 1). If a similar construction to Eqn 4 is modelled for the 2004 example, the three stocks also share a common \hat{p} at NSOG (Table 1). Although Tenderfoot coho contribute no data to \hat{p} at NSOG in either year, they borrow information from the other two stocks when pooled at this station. Note that in each year, \hat{p} at NSOG for the geographic cluster model is intermediate between the two stock-independent \hat{p} at NSOG; as data are pooled, the geographic cluster estimates are essentially a weighted average of the stock-independent estimates. Similarly, \hat{p} at the Keogh station in 2004 is intermediate between the three stock-independent estimates (Table 1). Since the two stock-independent \hat{p} at the Keogh station in 2005 were equal, the same estimate occurs under the geographic cluster model. In both years, \hat{p} at the Nimpkish station under the geographic cluster model was equal to that under the stock-independent model because only one stock contributed to this estimate.

Within each year, the three models can be compared in terms of Akaike’s information criterion (AIC, or QAICc when corrected for extra-binomial variation and small sample sizes). This

Table 2. Information-theoretic comparison of detection probability submodels used with two example datasets (2004 and 2005) of salmon stocks

Model comparison criteria include number of parameters, log-likelihood and AIC scores. Stocks included in each year are the same as shown in Table 1, all with V9 tags

p submodel ^A	np ^B	$2 \cdot \ln(L)$	QAICc ^C	Δ QAICc
2004 stocks				
Geographic cluster ^D	40	-1708.4	1471.5	0
Stock-independent ^D	48	-1701.9	1483.5	12.0
Fully pooled ^{D,E}	34	-1751.1	1493.6	22.1
2005 stocks				
Stock-independent ^D	56	-1009.6	963.0	0
Geographic cluster ^D	46	-1041.0	965.9	2.9
Fully pooled ^{D,E}	38	-1069.8	971.9	8.8

^ASurvival probability submodels were held fixed across all detection probability submodels, as $\phi_{\text{Seg:Spp:Stk:H/W}}$. The 'H/W' variable was only necessary in 2004 to distinguish hatchery and wild-reared Keogh River steelhead smolts.

^BThe parameter count is adjusted to include the number of potentially estimated parameters including those at boundaries of 0 or 1.

^CAIC values are adjusted for small sample sizes and extra-binomial variation with $\hat{c} = 1.23$ in 2004 and 1.20 in 2005 (Lebreton *et al.* 1992).

^DSubmodels of p were specified as: stock-independent, $ps_{\text{Spp:Stk:H/W}}$; fully pooled, ps ; geographic cluster, $ps + S_{11}C_{\text{Eng}} + S_{11}C_{\text{Nimp}} + S_{12}C_{\text{Nimp}} + S_{12}C_{\text{Keogh}}$ in 2004 and $ps + S_{10}C_{\text{Eng}} + S_{11}C_{\text{Eng}} + S_{11}C_{\text{Nimp}} + S_{12}C_{\text{Nimp}} + S_{12}C_{\text{Keogh}}$ in 2005. S_i indicates the $i - 1$ th station at the i th detection history digit. The Squamish geographic cluster, including both Tenderfoot and Cheakamus fish, is the reference cluster for all stations in both years so does not appear explicitly in these model formulae.

^EThe fully pooled model is not appropriate to use for multiple stocks with nested migration routes because some shared p parameters at a particular digit of the detection history sequence do not represent the same station for all stocks. It is included here only to show that it also performs poorly compared with the other two models in terms of AIC values.

information-theoretic approach allows several candidate models to be compared in their balance between accuracy and precision, or equivalently, their goodness-of-fit to the data and the number of parameters required to achieve that fit (Burnham and Anderson 2002). Comparing AIC among models is used to identify the most parsimonious model(s) in the model set; enough parameters should be contained in a parsimonious model(s) to explain important sources of variation in the data so as to reduce bias, but not so many that the precision of parameter estimates decreases below an undesirable level (Lebreton *et al.* 1992).

In 2004, the geographic cluster model greatly outperformed the other models by having a lower QAICc score (Δ QAICc = 12.0; Table 2). In 2005, the stock-independent model was the top-ranked model, but the geographic cluster model still had considerable support (Δ QAICc = 2.9). The log-likelihood was always greatest for the larger, stock-independent model (indicating a better goodness-of-fit), but it required several more parameters to be estimated than the geographic cluster model. The fully pooled model, in addition to being structurally inappropriate, had relatively little support in either year (Table 2). Across both years, the geographic cluster model was most parsimonious overall.

In some cases, there may not be unequivocal support for one particular model, as was the case in 2005. Model-averaging methods could be employed (Burnham and Anderson 2002), the decision to use a geographic cluster or stock-independent model could rest on biological realism (Lebreton *et al.* 1992), or parameter estimates and uncertainties could be investigated further. If stocks that cross the same station do so over a similar time period but still have differing \hat{p} under the stock-independent model (Table 1), differences could simply be related to sampling effects from sparse data (e.g. $\hat{p} = 0.60$ at NSOG for Englishman steelhead in 2005 is based on three of the five fish detected at QCS being previously detected at NSOG). In these cases, it may be preferable to pool fish at shared stations if they have the same tag type and migration timing, thereby reducing possibilities of either over-fitting due to small sample sizes (i.e. parameter estimates highly sensitive to sparse data) or confounding survival and detection parameters with one or the other estimated at a boundary. Standard errors were generally smaller for the geographic cluster model than for the stock-independent model (Table 1), again because this appropriate pooling increases sample sizes of the stock collective.

Additional interaction terms (i.e. other $S_i Y_j C_m$ terms in Eqn 4) could be used to differentiate migration route clusters at other digits of the detection histories as well (see Accessory publication). If multiple years are contained in a dataset, the interaction terms easily allow specifying which cluster(s) share which stations in which year.

Biases in detection and survival probabilities from split-route migration patterns

Spatial forms of CJS mark-recapture survival estimation (release and subsequent detection or recapture at successive fixed locations along a migration route) are unlike temporal forms (at successive fixed times) in that migration routes are not necessarily continual in a single path. Migration routes may split, with some individuals moving in one direction and other individuals in a different direction (e.g. around large islands, in forked rivers, along the outer coast continental shelf, through different dam passages). Detection stations can be deployed in each fork of the split route to estimate the proportion of animals that take each of the mutually exclusive directions. These forks may or may not re-join further along in the migration route.

Extensions of CJS models incorporate permanent split-route migration patterns where forks do not eventually re-join (Skalski 2006). At some point along a migratory route, a parameter, M , is built into the model to designate the probability of movement in one particular direction with $1 - M$ as the probability of movement in the other direction in a case with only two directions. After the split, the two forks become independent with detection and survival probabilities estimated within each fork.

In some cases, forks of a split-route migration may eventually physically re-join, with individuals sharing a common route after the reunion (Skalski *et al.* 2002). In other cases, different forks may conceptually re-join. For example, in the POST salmon study, there is interest in quantifying the overall survival of stocks during the early ocean migration regardless of the particular route taken to either of the final stations. About one-third of stocks showed split-route patterns after entry into the Strait of

Georgia south of NSOG with some individuals crossing the JDF line and other individuals crossing NSOG and QCS lines (Fig. 1, arrow D; the other two-thirds of stocks were detected moving only northward). Migration routes may or may not re-join after forks cross the outer QCS and JDF lines, but to estimate an overall survival rate out of the Strait of Georgia system regardless of the direction taken, detections on these outer lines were pooled in the final digit of the detection history (representing a ‘conceptual’ re-joining of forks). As there was only one segment along the southern route prior to JDF, however, there is not enough information in the detection data to untangle the confounded survival, detection and movement parameters within each fork. This precludes use of the temporary-fork methods of Skalski *et al.* (2002) to address this particular problem.

If we assume forks do not re-join, then in addition to there being only one or two segments within each fork, there were no detection stations after QCS or JDF. The permanent-fork methods of Skalski (2006) or multi-state models (Arnason 1973; Schwarz *et al.* 1993) with heavily constrained movement (ψ) parameters therefore cannot be used to untangle route-specific parameters p at QCS and JDF, ϕ to these outer lines and movement probability. If p at the outer lines were assumed as fixed values that would allow either the combined final segment survival or M (or ψ) to be estimated (conditioned on the fixed value of p), but not both. If there is no explicit interest in direction of movement, then to avoid having to estimate M , the forks of a split-route pattern can be ‘collapsed’ to carry out a CJS analysis.

The collapsing of forks of a split-route migration may lead to biases in estimated parameters under CJS models that do not explicitly account for such split routes (although there is a simple way of correcting biases in $\hat{\phi}$, shown below). This is particularly true if the number of detection stations or total survival probability differs among forks. Consider the POST example where two stations occur along the northern fork but only one occurs on the southern fork (Fig. 1, arrow D). If fish migrate directly south and are detected at the final JDF station, there is no opportunity to have been detected at the next-to-last station because an equivalent station to NSOG does not exist along the southern migration route. The detection history sequence of these fish, with a ‘0’ at the next-to-last digit before the final ‘1’, incorrectly implies they were present but not detected at NSOG.

Biases in CJS parameter estimates can be quantified by simulating detection histories under a split-route scenario and estimating ϕ and p with ‘naïve’ CJS models in which split routes are collapsed. Using a simplified POST example considering only ocean segments (i.e. using a 3-digit detection history where release is equivalent to leaving rivers), expected frequencies of the four possible detection histories (111; 101; 110; 100) from arbitrarily selected parameter values under split-route assumptions (call these ‘true’ parameters) can be easily calculated. Four example sets of true parameters are shown in Fig. 2. These include M , ϕ_{north1} and ϕ_{north2} for the two segments along the northern fork, ϕ_{south} for the southern segment, and p_{north2} , p_{north3} , and p_{south3} for the three stations. A classic CJS analysis would not account for these split-route patterns, but would instead collapse forks and pool detections at the final stations along northern and southern routes. The MLEs of $\hat{\phi}_{1,\text{CJS}}$, $\hat{p}_{2,\text{CJS}}$, and $\hat{p}_{2,\text{CJS}}$ are then compared with true parameter values to assess bias ($p_{3,\text{CJS}}$ can be fixed at the true value for this

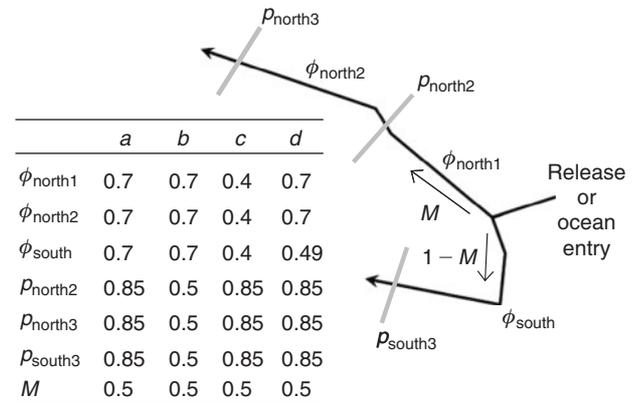


Fig. 2. Split-route migration pattern with two detection stations (grey lines) along one fork and one station along the other fork (similar to that of arrow D in Fig. 1). Parameters representing probabilities of survival, detection and directional movement are shown along with example sets (a–d) of these parameters.

optimisation so that it is not confounded with $\phi_{2,\text{CJS}}$). Bias is calculated as, e.g. $(\hat{\phi}_{1,\text{CJS}} - \hat{\phi}_{\text{north1}}) / \phi_{\text{north1}}$. A simple spreadsheet model to calculate expected frequencies of detection histories under split-route assumptions and subsequently use these for estimating CJS parameters is available from the author.

As expected, biases were observed when a true split-route pattern was collapsed into a classic CJS analysis (because of confounding with movement and because ϕ_{north1} and p_{north2} did not have equivalent parameters along the southern fork; Fig. 3). Biases were typically seen in $\hat{\phi}_{1,\text{CJS}}$ and $\hat{p}_{2,\text{CJS}}$, with zero bias in any parameters at $M = 1$ and bias worsening as M decreases. Estimates of $\phi_{2,\text{CJS}}$ were unbiased across all values of M in the cases considered. Consistent changes across detection stations in true p did not change the bias in either CJS parameter (Fig. 3, a v. b) although lower p would in general lead to reduced precision of estimates. Consistent changes across segments in true ϕ affected the bias in $\hat{\phi}_{1,\text{CJS}}$ (and, to a lesser degree in $\hat{p}_{2,\text{CJS}}$) with greater bias seen at lower ϕ across all values of M (Fig. 3, a v. c). Bias in $\hat{\phi}_{1,\text{CJS}}$ partly arises because true survival rates along the full northern and southern forks differ in examples a–c; two survival components occur in the northern fork while only one occurs in the southern fork with all three components equal. Instead, if ϕ_{south} is set equal to the product of ϕ_{north1} and ϕ_{north2} , the bias in $\hat{\phi}_{1,\text{CJS}}$ disappears (Fig. 3d; although bias in $\hat{p}_{2,\text{CJS}}$ still occurs). This situation of equal total survival among forks could occur if total distances and per-distance survival rates were similar among forks (unlike the POST situation where distances of the three components were similar so total distance of the northern fork was roughly double that of the southern fork).

If split-route migration patterns occur but classic CJS analyses are preferred that do not account for M explicitly, it is possible to correct the bias in $\hat{\phi}_{1,\text{CJS}}$, even if forks with unequal numbers of detection stations are collapsed for the analysis. Consider a situation in which p is modelled as common across stocks that share a particular station (Eqn 4). In a multi-stock context where split-route migration patterns exist (Fig. 2), some of the stocks that share p_{north1} may have $M = 1$ while others have $M < 1$. For each stock that shows evidence of split-route patterns with $\hat{M} < 1$, an

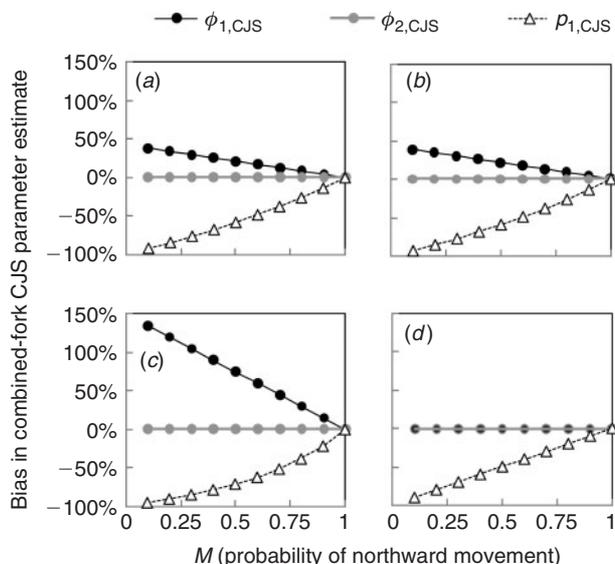


Fig. 3. Percentage biases in estimated survival and detection probabilities. Detection histories were simulated under a ‘true’ split-route scenario and were then analysed with CJS models that failed to account for split-route flexibility, pooling detections at the final stations along the two forks shown in Fig. 2. True parameter values in subplots *a–d* correspond to the example sets shown in Fig. 2, except *M* is shown ranging from 0.1 to 1.0.

extra parameter for *p* specific to that stock and station can be incorporated into the model. For example, Eqn 4 can be extended by the terms:

$$\dots + \beta_Y \cdot S_{12} Y_{2005} \text{Stk}_a + \beta_Z \cdot S_{12} Y_{2006} \text{Stk}_b + \dots \quad (5)$$

where S_{12} represents NSOG and stocks *a* and *b* displayed $\hat{M} < 1$ in years 2005 and 2006, respectively. These interaction terms result in stock-specific \hat{p}'_{NSOG} for stocks *a* and *b* whereas other stocks with $\hat{M} = 1$ share a common \hat{p}_{NSOG} . For stocks with $\hat{M} < 1$, these stock-specific \hat{p}'_{NSOG} are not true detection probabilities *per se*, but rather are joint probabilities of *M* and detection. The extra interaction parameters that result in these joint probabilities incorporate *M* implicitly rather than explicitly; they essentially ‘absorb’ the bias due to $M < 1$, leaving $\hat{\phi}_{1,\text{CJS}}$ unbiased under CJS models where forks are collapsed. Estimates of $\phi_{2,\text{CJS}}$ remain unbiased as well.

In situations where split-route migration patterns occur and there are sufficient detection stations in each fork, it is preferable to use models that explicitly account for movement. These include methods that incorporate *M* in permanent split-route patterns (Skalski 2006), in split-route patterns that physically re-join (Skalski *et al.* 2002), or multi-state models (Arnason 1973; Schwarz *et al.* 1993) in which individuals may move from a main migration route to a different fork’s sampling universe and then back again later in the migration. The bias correction method above (Eqn 5) for classic CJS models should only be used in a multi-stock context when: (1) there is not enough information to simultaneously estimate survival, detection, and movement parameters (which could be provided by using ‘double lines’ deployed at final stations if logistics and budgets allow) and (2) the interest is in estimating overall survival regardless of the direction taken by fish.

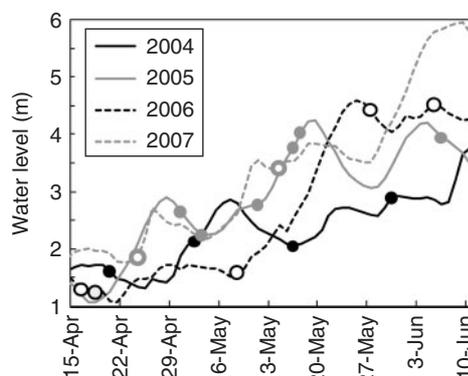


Fig. 4. Relative water level of the Fraser River during the salmon smolt migration in 2004–07. Circles indicate release dates and corresponding water levels of tagged Fraser stocks in each year. River levels were measured at the Mission gauge by Environment Canada (near the receiver station furthest upstream in the Fraser River, Fig. 1).

Environmental covariates of stock-specific detection probabilities

In some cases, it may be inappropriate to pool stocks that share a common detection station during their migration even if stocks are from the same geographic cluster. If stocks migrate at different times throughout the year, their staggered arrival at a station may result in different *p* among stocks if environmental conditions change over time. Background noise sources such as wind, boat traffic, soniferous invertebrates like snapping shrimp, or turbulence due to river flow could change over time, affecting the signal: noise ratio of acoustic or radio tags and therefore impacting *p* (Voegeli and Pincock 1996; Heupel *et al.* 2006; Simpfendorfer *et al.* 2008).

Within a population, attempts to account for heterogeneity in *p* among individuals can improve estimates if *p* does vary among individuals (Pledger *et al.* 2003). If *p* is determined more by tag and hydrophone characteristics than by the behaviour of tagged animals, then homogeneity can be reasonably assumed provided that individuals encounter similar environmental conditions as they migrate past receiver stations. In a multi-stock context, the within-stock distributions of run timing past receivers may be considerably narrower than the distribution of mean run timing among stocks. In such cases, variation among stocks in run timing could lead to variation in *p* that should be explicitly estimated.

In rivers, water level and discharge often increase during late spring to early summer due to snow melt (Fig. 4). Higher water levels result not only in greater background noise, but also in faster flow so that, on average, tags are within range of a receiver for a shorter period of time. Both factors should decrease *p* during high flow periods, which in the POST case tend to occur later in the migratory season. In that example, multiple Fraser River stocks were tagged and released at varying times throughout the migratory season each year (Fig. 4). Release times spanned nearly 2 months, and the corresponding relative water levels and flows at these times increased substantially.

The effect of different release times or flows on *p* can be observed by initially treating release groups independently to

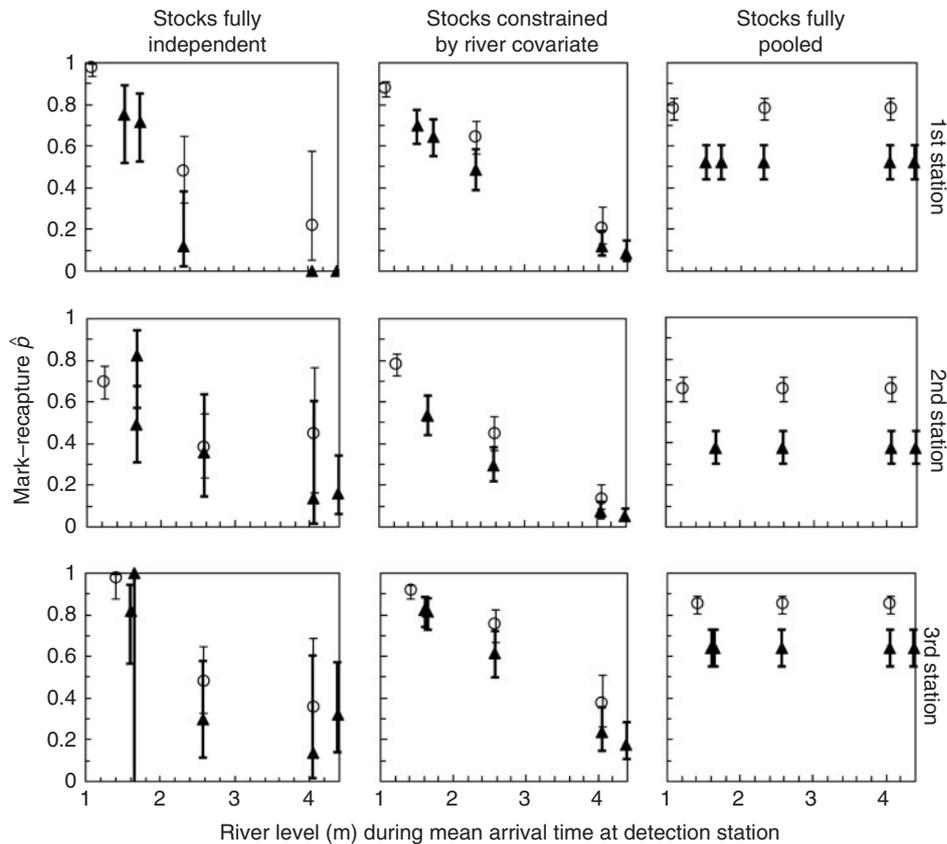


Fig. 5. Detection probability estimates (\hat{p}) at three successive Fraser River detection stations in 2006 v. river level at the mean arrival time of a stock at a detection station. Survival submodels are fully independent among release groups and segments ($\phi_{\text{Seg:Y:Spp:Stk}}$). Detection probability submodels are either fully independent among stocks and tag types ($p_{\text{S:Y:Spp:Stk:Tag}}$), constrained by river level ($p_{\text{S:Y+Tag+RiverLevel}}$), or fully pooled among stocks ($p_{\text{S:Y+Tag}}$). Error bars show 95% confidence intervals and are thick for V7 tags (\blacktriangle) and thin for V9 tags (\circ). River levels were measured at the Mission gauge by Environment Canada.

calculate CJS p estimates using a model such as ($\phi_{\text{Seg:Y:Spp:Stk}}, p_{\text{S:Y:Spp:Stk:Tag}}$). On average, and within each tag type, these stock-specific \hat{p} decreased as the river level increased during the migration season. The left panels of Fig. 5 show stock-independent \hat{p} for Fraser River stocks in 2006 at the first, second and third receiver stations encountered in the river, plotted against the water level measured at the mean arrival time of each stock at a particular station. Generally, the later-migrating stocks experienced greater flow during the downstream migration and their \hat{p} were lower. At a given water level, \hat{p} was generally higher for V9 tags than for V7 tags. Other years showed similar patterns when sufficient stocks were released over a wide range of dates and therefore river levels.

The overall negative relationship between \hat{p} and seasonal run timing (or river level) suggests that \hat{p} should be at least somewhat independent among groups. If, instead, stocks were pooled at a particular detection station, year and tag type combination to estimate a common p , this would fail to capture the general trend of decreasing p over the migration season (right panels of Fig. 5). In this case, p is underestimated at lower water levels earlier in the season and overestimated at higher water levels later in the season, which in turn biases stock-specific ϕ estimates.

Indeed, comparing models in terms of QAICc scores, the fully pooled model ($p_{\text{S:Y+Tag}}$) is poorly supported by the data compared with the fully independent model ($p_{\text{S:Y:Spp:Stk:Tag}}$) due to lack of fit, as seen in the smaller log-likelihood values (Table 3). However, keeping groups fully independent like the left panels of Fig. 5 requires many more parameters to be estimated (Table 3). Estimates of p in this fully independent model are also more variable and are prone to larger sampling errors as numbers of fish from a particular stock detected at and after a particular river station were often small. This resulted in \hat{p} for many groups being estimated at boundaries or having confidence intervals that spanned the full range of 0–1 (Table 3; Fig. 5), which is typical of having sparse data. Considering only the \hat{p} that were reasonably well estimated across all models, $\hat{S}E(\hat{p})$ tended to be larger for the stock-independent model (median $\hat{S}E(\hat{p}) = 0.09$) than for the fully pooled model (0.04; Table 3).

To maintain desirable properties of each of these extremes, candidate models can be considered that balance the trade-off between accuracy and precision. Models can incorporate run timing or environmental variables like river level as covariates of p (Pollock *et al.* 1984; Lebreton *et al.* 1992), with \hat{p} for each stock

Table 3. Information-theoretic comparison of detection probability submodels and other model-fitting criteria in the Fraser River salmon smolt dataset, 2004–07

Model comparison criteria include number of parameters (np), log-likelihood and AIC scores. Other model-fitting criteria include number of \hat{p} poorly estimated (either at boundaries of 0 or 1, or where 95% confidence limits (CL) span 0–1), and quantiles of the distribution of properly estimated $\hat{S}E(\hat{p})$ at all river stations, years, tag types and release groups

p submodel ^A	np ^B	$2 \cdot \ln(L)$	QAICc ^C	Δ QAICc	\hat{p} poorly estimated ^D		Percentile of distribution of $\hat{S}E(\hat{p})$ ^E		
					At boundary	95% CL span 0–1	5th	50th	95th
$PS:Y+Tag+RiverLevel$	121	–5760.3	4365.2	0.0	0	0	0.02	0.04	0.07
$PS:Y:Spp:Stk:Tag$	193	–5566.2	4384.5	19.3	13	6	0.03	0.09	0.22
$PS:Y+Tag+DOY$	121	–5794.4	4389.6	24.4	0	0	0.02	0.04	0.07
$PS:Y+Tag$	120	–5955.9	4502.8	137.6	0	0	0.02	0.04	0.07

^ASurvival probability submodels were held constant across all detection probability submodels, as $\phi_{Seg:Y:Spp:Stk}$, where ‘Group’ represents a unique combination of year, species and stock.

^BThe parameter count is adjusted to include the number of potentially estimated parameters including those at boundaries of 0 or 1.

^CAIC values are adjusted for small sample sizes and extra-binomial variation with $\hat{c} = 1.40$ (Lebreton *et al.* 1992).

^DOut of a total 61 across river stations, years, tag types, species and stocks.

^ETaken from the distribution of the remaining 45 $\hat{S}E(\hat{p})$ after excluding across all models the \hat{p} parameters that were estimated poorly.

constrained to be a linear function (in logit space) of one or more such covariates at the appropriate mean run timing of that stock. Using additive covariates as ‘forcing functions’ of p can result in estimates that capture the general trend in p over time among stocks (centre panels of Fig. 5), but require fewer parameters to be estimated. Two such covariates were used: the day-of-year (DOY) and the relative river level at the mean time of arrival of each stock at each station. These models require one additional parameter to be estimated compared with the fully pooled model. The river level covariate model ($PS:Y+Tag+RiverLevel$) was well supported by the data in the balance of goodness-of-fit and number of estimated parameters with a QAICc that was 19.3 less than that of the fully independent model (Table 3). The \hat{p} were well estimated and the decrease in precision from the fully pooled model was only minor (Table 3; Fig. 5).

In some cases, a model constrained by a covariate may be a poorer choice than a fully independent model, as was the case for the DOY model (Δ QAICc = 5.1), suggesting that this covariate did not properly capture the decreasing trend in p . Several environmental covariates can be considered in candidate models to evaluate the best predictor of p . In other cases, a fully pooled model may be appropriate. Smith *et al.* (2003) found that \hat{p} of PIT-tagged smolts at dams were similar across release locations and dates within a year so groups were pooled for estimating p . As environmental covariate models involve only one parameter more than fully pooled models, however, it is likely that some hypothesised covariates will contribute to explaining additional variation in the data. By incorporating multiple stocks and years into a common analysis framework, the relative effect of a covariate on p (i.e. the slope of $\text{logit}(p)$ v. the covariate) can be made consistent across detection stations, years, tag types and stocks while permitting the intercepts to differ. Estimates of p therefore differ among combinations of detection station, year, tag type and stock (as their run timing and thus covariate values differ), but are related through the covariate. The following section describes another potential covariate of p for large-scale telemetry arrays.

Assessing redundancy in detection capacity of stations with multiple receivers

In large-scale acoustic or radio telemetry studies where several fixed stations are used and each station consists of several receivers, there is generally a trade-off in the number of possible stations versus detection probability at each station. For a fixed total number of receivers, deploying them sparsely in lines or grids may allow more lines to be deployed, but at the expense of reduced p at any given line (Heupel *et al.* 2006). Conversely, spacing receivers close together on a line may reduce the chance of a tagged animal crossing the line undetected, but those receivers then cannot be used for an additional line in another area (or for ‘doubling up’ lines at final detection stations). Whether a single stock or multiple stocks are monitored during their migration, tracking studies can likely benefit from both careful planning (Welch *et al.* 2003) and data-based assessments of how p varies with the spacing between receivers on a line.

Consider a detection station that consists of eight receivers arranged in a line spanning a strait or channel through which tagged animals migrate (Fig. 6). We assume some common detection radius, r , around each receiver within which tags are reliably detected most of the time. If r is large, there is much overlap of radii and consequently p is expected to be relatively high. If r is small, a smaller proportion of the total transect line (grey dots in Fig. 6) is covered by detection radii so p is expected to be lower. Two other factors affect this proportion of one-dimensional coverage on a line: the spacing between two adjacent receivers, $d_{i \rightarrow i+1}$ (or between shore and either end receiver, $d_{shore \rightarrow 1}$) and the proportion of receivers successfully recovered and downloaded. After excluding receivers not recovered (Fig. 6), the proportion of the transect line covered by the detection radius of at least one receiver can be easily calculated under some assumed value of r . If receivers are not equidistant from one another, that simply means the overlap will be greater between some adjacent receiver pairs and less between other pairs, but the usual interest is in p for the entire line.

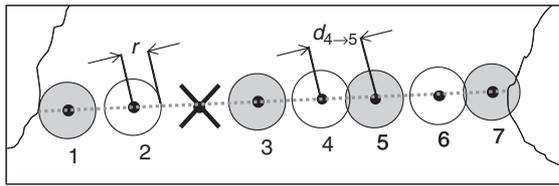


Fig. 6. Hypothetical detection station consisting of multiple receivers (black dots) arranged in a line between two land masses. x denotes a receiver not recovered. Circles of radius r are drawn around each recovered receiver, which are numbered. Odd numbered receivers are shaded.

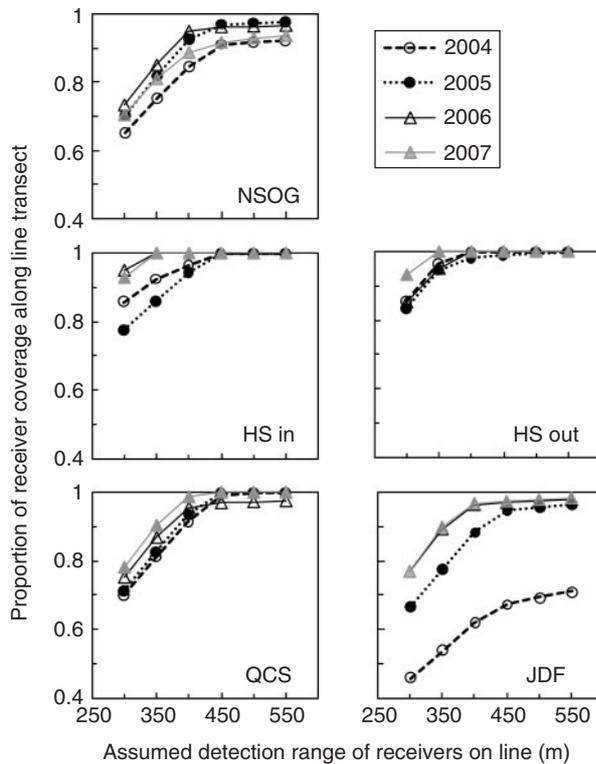


Fig. 7. Proportion of a receiver line covered by the detection radius, r , of at least one receiver for five stations operated by POST. Coverage is shown for a range of assumed values of r .

Using five POST detection lines as an example, recovery coordinates of each receiver were used to calculate values of d on each line. Assuming various values of r , the proportion of coverage was determined for each line in each year (Fig. 7). In most lines and years, assumed r of ≥ 400 m resulted in coverage > 0.9 as receivers were typically spaced approximately 800 m apart. At $r < 400$ m, coverage decreased as r decreased. Upper limits of coverage are mainly determined by the proportion of receivers recovered; one-third of receivers on the JDF line in 2004 were not recovered so coverage was comparatively low even at high assumed values of r . As this measure of coverage incorporates both spacing and recovery variables, it could reasonably be used as a predictor or covariate of p on a particular line. Receiver coverage could alternatively be quantified on a two- (Hedger *et al.* 2008) or three-dimensional basis rather than a one-dimensional basis as shown here, estimating the area or

volume in which receivers overlap at some assumed r and the area or volume not covered by the array.

Mark-recapture \hat{p} were determined for the POST lines at NSOG, inner Howe Sound and outer Howe Sound (p is not estimable for the final lines QCS and JDF). To estimate p on these three lines as accurately as possible, shortened detection history datasets were constructed representing digits for release, detection at the line of interest and detection anywhere after the line of interest. These shortened versions reduced the dependence of \hat{p} and $\hat{SE}(\hat{p})$ on parameters from other segments and detection stations, and eliminated the effect of confounding with any southward movements after entering the Strait of Georgia. Survival submodels were kept as flexible as possible ($\phi_{\text{Seg} \times (\text{Y}:\text{Spp}:\text{Stk}:\text{Tag})}$). Detection submodels involved pooling stocks but maintaining independence in p among years and an additive difference among V7 and V9 tag types ($p_{\text{S} \times \text{Y} + \text{Tag}}$). Among the values of coverage at assumed values of r ranging from 300 to 550 m, the best statistical predictor of \hat{p} (in terms of r^2 and AIC scores, data not shown) was the coverage covariate at $r = 400$ m ('coverage₄₀₀'). Estimates of p are plotted against coverage₄₀₀ for each line in each year (Fig. 8a). A large difference is observed among tag types with the higher energy output of V9 tags translating into higher \hat{p} . The effect of coverage₄₀₀ appears to be moderate, with \hat{p} decreasing from approximately 0.95 to 0.85 for V9 tags and approximately 0.8 to 0.6 for V7 tags as coverage₄₀₀ decreases from 1 to 0.85 (the best fit lines for V9 and V7 tags are parallel in logit-space). After accounting for coverage, there was little effect of region (NSOG v. Howe Sound) on \hat{p} .

The range of coverage₄₀₀ spans only from approximately 0.85–1 for these ocean receiver lines (Fig. 8a). This provides little opportunity aside from extrapolation to assess how p would change at much lower levels of coverage₄₀₀ like 0.5 (which would be important in deciding if a limited number of receivers should be deployed more sparsely to allow for additional lines elsewhere). To simulate the effect of wider receiver spacing, the level of coverage can be artificially reduced by using only data from subsets of receivers on a line, essentially a jackknife approach. For example, every second receiver along with its detection data could be excluded, after which p and coverage levels could be re-estimated. Excluding even numbered receivers (Fig. 6) would leave only the four shaded receivers, while excluding odd numbered receivers would leave the three receivers without shading. When this approach was used with the POST data, coverage₄₀₀ and \hat{p} both decreased (Fig. 8b). Coverage₄₀₀ of only-odd or only-even receiver subsets ranged from 0.45 to 0.65. Subsetted \hat{p} ranged from approximately 0.4–0.9, with best fit predicted values of approximately 0.77 for V9 tags and 0.57 for V7 tags at a coverage₄₀₀ of 0.55. This decline in \hat{p} with declining coverage₄₀₀ was less precipitous than expected based on the full-receiver dataset (compare slopes of the solid and dotted logistic best fit lines in Fig. 8b). Coverage₄₀₀ declined by 43% (from an average of 0.96 to 0.55) when odd or even receivers were eliminated, but \hat{p} declined by only 17% and 23% for V9 and V7 tags, respectively, as a result of the subsampling. This suggests that some redundancy existed among receivers on a line, i.e. many fish were detected on more than one receiver while crossing. In this particular study, cutting the number of receivers on a line in half would result in a corresponding decrease in \hat{p} of only approximately 20%.

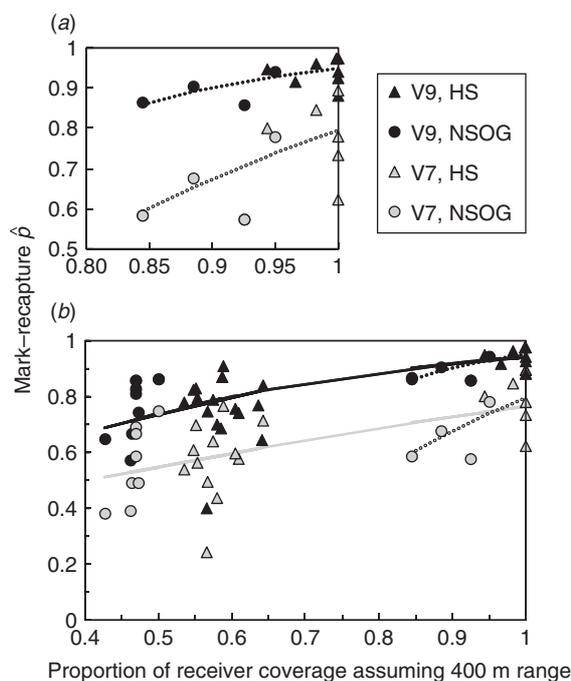


Fig. 8. Detection probability estimates (\hat{p}) at three multi-receiver detection stations plotted against calculated coverage_{400} values for the corresponding line and year. Tag types are shown separately. Both Howe Sound lines are shown as triangles. (a) \hat{p} and coverage_{400} values when all receivers on a line are considered; (b) the same estimates from (a) as well as \hat{p} and coverage_{400} values recalculated after eliminating data from either even- or odd-numbered receivers on each line. Dotted lines in (a) and solid lines in (b) show best logistic fits to \hat{p} estimates.

Subsampling receivers on a line increased the uncertainty in \hat{p} . When all receivers were included, \hat{p} were closer to the boundary of 1 than when odd- or even-numbered receivers were excluded, so comparing $\hat{SE}(\hat{p})$ is not appropriate. Average coefficients of variation (CV, i.e. $\hat{SE}(\hat{p})/\hat{p}$) when all receivers were included on a line were smaller (V9 tags, 0.04; V7 tags, 0.10) than when only half the receivers on a line were included (V9 tags, 0.09; V7 tags, 0.15). This greater uncertainty results in greater uncertainty in $\hat{\phi}$ as well.

Assessments of receiver redundancy at stations with several receivers can be carried out for either single- or multi-stock studies. Multiple receiver lines and/or years of data will generally be required to quantify the relationship between \hat{p} and coverage. The choice of eliminating every second receiver in the example presented here was arbitrary. Subsets could instead be random, either in the number or positions of receivers included. At one extreme, \hat{p} and coverage levels could be calculated for every single receiver on a line, which would further extend the range of the covariate and produce novel combinations of relatively low \hat{p} and low coverage. If the number of lines and/or years of study are limited, a large series of random subsets could be drawn from the receivers on some line, with \hat{p} and coverage calculated for each subset (similar to bootstrapping techniques). Aside from assessing receiver redundancy using a covariate such as coverage_{400} , covariates can be used directly

in specifications of candidate models (e.g. $PS:Y+Tag+coverage_{400}$) to evaluate whether they explain an important part of the total variation in p compared with models without the covariate.

Conclusions

Several gains can be achieved by analysing multiple stocks or release groups in the same framework. By linking stocks that share similar tags in terms of p , information can be shared for stations in common to improve estimates that might otherwise be based on small sample sizes for some stocks. Plausible constraints on model parameters can be incorporated (e.g. a consistent difference in p among different tag types), which results in fewer parameters to estimate overall than are required in purely single-stock models. Information-theoretic methods can be used to objectively assess to what extent models should be constrained. Additionally, some patterns cannot be quantified within single stocks or groups, but are only apparent when multiple groups are considered together (e.g. relationships between stock-specific \hat{p} and environmental covariates at a detection station). If multiple stocks have a nested migration route structure, it is relatively straightforward to specify which information should be shared among stocks (where migration routes are common) and which should be independent (where routes are unique).

The trade-off between p at a multi-receiver detection station versus number of receivers available for other stations is inherent in spatial mark-recapture studies along migration routes. It is often recommended to 'get p as high as possible' to improve the precision of ϕ estimates. This might be possible by reducing the spacing between receivers on a line, but it prevents those receivers from being used in a different location (further, detection ranges and probabilities vary temporally due to variation in environmental noise so that even at short spacing we should still expect $p < 1$ over the long term). Instead, an additional station might be more advantageous, thereby partitioning a segment of the migration into two separate segments and allowing ϕ to be estimated within each of them. The redundancy assessment method presented here can be further extended to show how much $CV(\hat{\phi})$ increases as subsets of receivers on a line are eliminated.

The data structuring methods presented here for applying CJS models to situations with complex detection histories were implemented with Program MARK in the examples used. Some of them, especially in a multi-stock context with large numbers of inter-related groups and nested migration structures, benefit from the efficiency provided by RMark in which models are specified with formulae rather than with design matrices. The methods presented here are transferable ideas; other mark-recapture software packages could also be 'tweaked' to incorporate these modifications or they could be programmed manually into models with platforms that permit more user control.

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References

- Arnason, A. N. (1973). The estimation of population size, migration rates, and survival in a stratified population. *Researches on Population Ecology* **15**, 1–8. doi:10.1007/BF02510705
- Burnham, K. P., and Anderson, D. R. (2002). 'Model Selection and Multi-Model Inference: A Practical Information-Theoretic Approach.' (Springer-Verlag: New York, NY.)
- Burnham, K. P., Anderson, D. R., White, G. C., Brownie, C., and Pollock, K. H. (1987). 'Design and Analysis Methods for Fish Survival Experiments Based on Release-Recapture.' (American Fisheries Society Monograph 5: Bethesda, MD.)
- Collis, K., Roby, D. D., Craig, D. P., Ryan, B. A., and Ledgerwood, R. D. (2001). Colonial waterbird predation on juvenile salmonids tagged with passive integrated transponders in the Columbia river estuary: Vulnerability of different salmonid species, stocks, and rearing types. *Transactions of the American Fisheries Society* **130**, 385–396. doi:10.1577/1548-8659(2001)130<0385:CWPOJS>2.0.CO;2
- Greenstreet, S. P. R., Morgan, R. I. G., Barnett, S., and Redhead, P. (1993). Variation in the numbers of shags *Phalacrocorax aristotelis* and common seals *Phoca vitulina* near the mouth of an Atlantic salmon *Salmo salar* river at the time of the smolt run. *Journal of Animal Ecology* **62**, 565–576. doi:10.2307/5205
- Groot, C., and Cooke, K. (1987) Are the migrations of juvenile and adult Fraser River sockeye salmon (*Oncorhynchus nerka*) in near-shore waters related? In 'Sockeye Salmon (*Oncorhynchus nerka*) Population Biology and Future Management'. Canadian Special Publication of Fisheries and Aquatic Sciences No. 96. (Eds H. D. Smith, L. Margolis and C. C. Wood.) pp. 53–60. (Department of Fisheries and Oceans: Ottawa.)
- Hartt, A. C., and Dell, M. B. (1986). Early oceanic migrations and growth of juvenile Pacific salmon and steelhead trout. International North Pacific Fisheries Commission Bulletin No. 46. Vancouver, Canada.
- Healey, M. C. (1980). The ecology of juvenile salmon in Georgia Strait, British Columbia. In 'Salmonid Ecosystems of the North Pacific'. (Eds W. J. McNeil and D. C. Himsworth.) pp. 203–230. (Oregon State University Press: Corvallis, OR.)
- Hedger, R. D., Martin, F., Dodson, J. J., Hatin, D., Caron, F., et al. (2008). The optimized interpolation of fish positions and speeds in an array of fixed acoustic receivers. *ICES Journal of Marine Science* **65**, 1248–1259. doi:10.1093/ICESJMS/FSN109
- Heupel, M. R., Semmens, J. M., and Hobday, A. J. (2006). Automated acoustic tracking of aquatic animals: Scales, design and deployment of listening station arrays. *Marine and Freshwater Research* **57**, 1–13. doi:10.1071/MF05091
- Jolly, G. M. (1965). Explicit estimates from capture-recapture data with both death and immigration-stochastic model. *Biometrika* **52**, 225–247.
- Laake, J., and Rexstad, E. (2009). RMark – an alternative approach to building linear models in MARK (Appendix C). In 'Program MARK: A Gentle Introduction'. 7th edn. (Eds E. Cooch and G. White.) pp. C1–C109. Version 1.8.8. Available at www.phidot.org/software/mark/rmark/ [accessed 27 March 2009].
- Lebreton, J. D., Burnham, K. P., Clobert, J., and Anderson, D. R. (1992). Modeling survival and testing biological hypotheses using marked animals: A unified approach with case studies. *Ecological Monographs* **62**, 67–118. doi:10.2307/2937171
- Pearcy, W. G., and Fisher, J. P. (1988). Migrations of coho salmon, *Oncorhynchus kisutch*, during their first summer in the ocean. *Fishery Bulletin* **86**, 173–195.
- Pearcy, W. G. (1992). 'Ocean Ecology of North Pacific Salmonids.' (Washington Sea Grant Program: Seattle, WA.)
- Pledger, S., Pollock, K. H., and Norris, J. L. (2003). Open capture-recapture models with heterogeneity: I. Cormack–Jolly–Seber model. *Biometrics* **59**, 786–794. doi:10.1111/J.0006-341X.2003.00092.X
- Pollock, K. H., Hines, J. E., and Nichols, J. D. (1984). The use of auxiliary variables in capture–recapture and removal experiments. *Biometrics* **40**, 329–340. doi:10.2307/2531386
- Pollock, K. H., Nichols, J. D., Brownie, C., and Hines, J. E. (1990). Statistical inference for capture–recapture experiments. *Wildlife Monographs* **107**, 1–97
- Schnute, J. T., Boers, N. M., and Haigh, R. (2004). PBS Mapping 2: user's guide. *Canadian Technical Report of Fisheries and Aquatic Sciences* **2549**, 1–126.
- Schwarz, C. J., Schweigert, J. F., and Arnason, A. N. (1993). Estimating migration rates using tag-recovery data. *Biometrics* **49**, 177–193. doi:10.2307/2532612
- Simpfendorfer, C. A., Heupel, M. R., and Collins, A. B. (2008). Variation in the performance of acoustic receivers and its implication for positioning algorithms in a riverine setting. *Canadian Journal of Fisheries and Aquatic Sciences* **65**, 482–492. doi:10.1139/F07-180
- Skalski, J. R. (2006). Evaluation and recommendations on alternative hydroacoustic array deployments for the mouth of the Columbia River to provide estimates of salmonid smolt survival and movements. The design and analysis of salmonid tagging studies in the Columbia Basin No. 20, U. Washington, Seattle. Report No. DOE/BP-00025091-1.
- Skalski, J. R., Lady, J., Townsend, R., Giorgi, A. E., Stevenson, J. R., et al. (2001). Estimating in-river survival of migrating salmonid smolts using radiotelemetry. *Canadian Journal of Fisheries and Aquatic Sciences* **58**, 1987–1997. doi:10.1139/CJFAS-58-10-1987
- Skalski, J. R., Townsend, R., Lady, J., Giorgi, A. E., Stevenson, J. R., et al. (2002). Estimating route-specific passage and survival probabilities at a hydroelectric project from smolt radiotelemetry studies. *Canadian Journal of Fisheries and Aquatic Sciences* **59**, 1385–1393. doi:10.1139/F02-094
- Smith, S. G., Muir, W. D., Hockersmith, E. E., Zabel, R. W., Graves, R. J., et al. (2003). Influence of river conditions on survival and travel time of Snake River subyearling fall chinook salmon. *North American Journal of Fisheries Management* **23**, 939–961. doi:10.1577/M02-039
- Townsend, R. L., Skalski, J. R., Dillingham, P., and Steig, T. W. (2006). Correcting bias in survival estimation resulting from tag failure in acoustic and radiotelemetry studies. *Journal of Agricultural Biological & Environmental Statistics* **11**, 183–196. doi:10.1198/108571106X111323
- Viola, A. E., and Schuck, M. L. (1995). A method to reduce the abundance of residual hatchery steelhead in rivers. *North American Journal of Fisheries Management* **15**, 488–493. doi:10.1577/1548-8675(1995)015<0488:AMTRTA>2.3.CO;2
- Voegeli, F. A., and Pincock, D. G. (1996). Overview of underwater acoustics as it applies to telemetry. In 'Underwater Biotelemetry: Proceedings of the First Conference and Workshop on Fish Telemetry in Europe'. (Eds E. Baras and J. C. Phillipart.) pp. 23–40. (University of Liège: Liège, Belgium.)
- Welch, D. W., Boehlert, G. W., and Ward, B. R. (2003). POST – the Pacific Ocean salmon tracking project. *Oceanologica Acta* **25**, 243–253. doi:10.1016/S0399-1784(02)01206-9
- White, G. C., and Burnham, K. P. (1999). Program MARK: Survival estimation from populations of marked animals. *Bird Study* **46**(Suppl.), 120–139. Version 5.1. Available at www.phidot.org/software/mark/ [accessed 27 March 2009].
- Zabel, R. W., and Achord, S. (2004). Relating size of juveniles to survival within and among populations of chinook salmon. *Ecology* **85**, 795–806. doi:10.1890/02-0719

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