MORTALITY OF MIGRATING PACIFIC SALMON SMOLTS IN
SOUTHERN BRITISH COLUMBIA, CANADA

by

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Abstract

Determination of causes for recent declines in marine survival rates of many Pacific salmon populations has been hindered by lack of information on where and when mortality predominantly occurs. Acoustic telemetry was used to monitor movements of tagged outmigrating juvenile salmon, and mark-recapture models were used to estimate survival. Several methods were developed for estimating detection probabilities \( (p) \) of tagged fish: models for combining multiple populations with partially-overlapping migration routes allowed for sharing of information among populations to compensate for small sample sizes; models for estimating \( p \) using only local information at detection stations reliably predicted mark-recapture \( p \) at large sample sizes; estimated \( p \) during mobile transect surveys attenuated from transect lines and depended on boat speed; variation among tags in acoustic strength resulted in minor heterogeneity in \( p \); and \( p \) estimates derived from test tag passes were used to estimate freshwater residualization rates.

Migration patterns varied among species, with steelhead and sockeye salmon quickly leaving Georgia Strait, and coho and Chinook salmon instead likely residing in the inshore Strait during summer months, thereby confounding interpretation of early ocean mortality. High mortality often occurred before ocean entry. Variation in survival during the downstream and inshore coastal migration was largely attributed to size-selective mortality against smaller fish and variation in migration distance or travel time. Some components of mortality during the downstream and inshore migration were independent of distance travelled, suggesting high mortality periods soon after release in freshwater and soon after ocean entry. Compared to wild conspecifics, hatchery-reared steelhead suffered high mortality immediately after release, and this survival difference was maintained through the inshore migration. In an experiment to test the effect of solar ultraviolet radiation during freshwater rearing on smolt mortality, no survival differences were observed between UV-shaded and UV-exposed treatment groups of coho or sockeye salmon. Overall, instantaneous mortality rates (time-based or distance-based) were highest soon after release, declined during the inshore migration, and were lowest for the remainder of smolt-to-adult ocean life, supporting hypotheses of high mortality early in the migration but not ruling out hypotheses of high mortality during the first marine winter.
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List of Symbols (for Chapter 4)

Detection probabilities:

\( \hat{p}_{mr,j} \) Estimate of mark-recapture detection probability at a particular combination \( j \) of station, year, and tag type (requires non-local information)

\( p'_{loc,j} \) Estimator of detection probability at \( j \) using only local information

\( p_{ping} \) Probability of detecting a single tag transmission during a crossing event

Crossing sequences:

\( X \) Crossing sequence vector of ‘1’s and ‘0’s

\( n \) Number of detections in \( X \)

\( m \) Length of \( X \) including \( n \) ‘1’s and \( n - m \) ‘0’s

\( X_i \) Individual signal transmitted within \( X \); \( i \) ranges from (1-50) to (\( m+50 \))

\( M_{logit} p_{ping} \) model:

\( p_{max} \) Maximum \( p_{ping} \) during a crossing event

\( x_{min} \) Value of \( X_i \) (not necessarily an integer) at the first inflection point

\( \omega \) Distance in units of \( X \) between the inflection points

\( \sigma \) Steepness^{-1} around each inflection point

Calculations of \( p'_{loc} \):

\( \hat{p}_{seq} \) Probability of detecting at least one tag transmission during a hypothetical crossing event, given the parameter set describing its detected crossing event.

\( p^1_{max,j} \) Extrapolated \( p_{max} \) at \( j \) for \( X \) containing \( n = 1 \)

\( N_{n,j} \) Number of fish detected at combination \( j \) of station, year, and tag type, with \( X \) containing \( n \) detections

\( \bar{N}_{n,j} \) Estimated number of fish passing by undetected at \( j \), corresponding to fish detected with \( X \) containing \( n \) detections

\( F_j \) Correction factor to standardize differences among \( j \) in the time within detection range during a crossing event
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Co-authorship Statement

All analyses and writing presented in this thesis are my own. These were assisted by the ideas, guidance, editing, and field work of mentors and colleagues. In particular, Carl Walters and David Welch were heavily involved in the identification and early design of my research program. Carl Walters contributed largely to fitting attenuation models to crossing sequence data (Chapter 4), advised for survival analyses (Chapters 7-10), and assisted with experimental design (Chapter 10). Most of my thesis would not have been possible without access to POST data; David Welch was largely responsible for the POST study design and is a co-author for manuscripts describing those data for multiple populations (Chapters 7 and 9). He also contributed to the design and field work for smaller, population-specific studies (Chapters 8 and 10). Villy Christensen contributed largely to the study design and field work of all mobile tracking surveys, and is a co-author for all manuscripts involving these surveys (Chapters 5, 7, 10). Other co-authors for individual chapters are listed in the footnote on the first page of each chapter.

Chapter 9 will be separated into parts for publication. Estimates of survival under the general CJS model (Fig. 9.3) will be presented in an overview paper of the POST project, with authors listed as: “Welch, D.W, Melnychuk, M.C., et al.” David Welch is the chief scientist for POST so will take the lead on the paper, but I conducted all survival analyses so I include them in this thesis. The remainder of Chapter 9 is based on these survival estimates from the general CJS model for the same populations, but will be submitted as a different paper, for which I will be first author.
1 General introduction

Pacific salmon exhibit highly variable marine survival rates, and several populations have shown alarming declines in survival over the past two decades. This thesis utilizes acoustic tagging methods to better understand where and when high mortality rates may occur during the migration of several populations of juvenile salmon in southern British Columbia (B.C.), Canada. The thesis is organized as a collection of papers. An introduction to general ecology and survival trends is provided in this chapter, along with an outline of the chapters to follow.

1.1 Juvenile salmon life-history and migration ecology

Organisms face numerous mortality threats throughout their lives. Causes of mortality are diverse, involving both biological and abiotic mechanisms, and will often vary with the organism’s age or life-history stage. Mortality rates of juvenile stages in fish and other aquatic species are as a rule much higher than later-stage mortality rates (Lorenzen 1996). Predation is usually a major cause of mortality in juvenile fish, especially since foraging activity required for growth makes them vulnerable to predators (Walters and Juanes 1993).

Ontogenetic habitat shifts might also increase the exposure of fish to predation. Stream or lake-rearing anadromous Pacific salmon species such as coho salmon (*Oncorhynchus kisutch*), steelhead trout (*O. mykiss*, the anadromous form of rainbow trout), ‘stream-type’ (or ‘spring’) Chinook salmon (*O. tshawytscha*), and sockeye salmon (*O. nerka*) rear more than one year in freshwater and then migrate as smolts to marine habitats. Migration distances may involve up to hundreds of kilometres of downstream travel before arriving in the ocean, then hundreds or even thousands of kilometres from the river mouth to marine feeding grounds. Marine prey of salmon are generally higher in energy, fats, and protein than typical prey of salmonids in freshwater, hence they provide greater potential for growth (Higgs et al. 1995). Due to their small size and exposure to predation risk while moving (or while feeding during the migration), anadromous juvenile salmonids may be particularly susceptible to mortality.

Migration periods represent important life history stages in many fishes, as they often are associated with high mortality 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 annual outmigrations (Greenstreet et al.
1993, Collis et al. 2001). Although juvenile mortality rates (on a age- or stage-specific basis) may be higher than those of adults, we would expect them to be stable over time, fluctuating around some mean value, if causal factors influencing mortality remain relatively constant over time. If mortality causes change persistently over time, however, we would expect the mean age- or stage-specific mortality rates to also change over time.

1.2 Declines in abundance and survival of Pacific salmon populations

Widespread declines in the abundance of salmon populations from many Northeast Pacific regions sparked a major conservation concern in western North America during the last two decades. At least some populations from all species are now at critical levels or have been extirpated (Gustafson et al. 2007). These declines occurred primarily in the coastal upwelling domain, from central B.C. southward to California, where offshore oceanographic conditions are dominated by the California Current. In contrast, populations north of central B.C. in the coastal downwelling domain dominated by the Alaska Current show opposite production regimes to those in the upwelling domain (Hare et al. 1999, Mueter et al. 2002) and have been relatively stable over this period. Within each of these domains, some salmon species show covariation in abundance (Smith and Ward 2000), productivity (Peterman et al. 1998, Pyper et al. 2005) or marine survival (Coronado and Hilborn 1998, Welch et al. 2000, Hobday and Boehlert 2001) on a regional scale, suggesting that common factors affect populations within a region.

Salmon are faced with different kinds of mortality threats throughout their life cycle. Some of these are associated with the egg, larval, fry, or parr stages during the freshwater rearing phase. Others are associated with the smolt stage, during which juvenile salmon migrate from freshwater to the ocean. After maturing, adults return from the ocean to spawn in freshwater, usually in the same river from which they emerged. Considerable mortality occurs during both freshwater and marine phases (Bradford 1995, Quinn 2005). Mortality causes during freshwater life such as habitat alteration, as well as recruitment overfishing on adults, have certainly had some impact on many populations, but in general there is considerable evidence that declines in abundance were largely caused by marine factors (Coronado and Hilborn 1998, Beamish et al. 2000, Pyper et al. 2005). At the same time as the abundance declines, smolt-to-adult survival (commonly referred to as ‘marine’ survival) also declined (Smith and Ward 2000).

Smolt-to-adult survival has typically been estimated by implanting small coded-wire tags (CWT) into smolts prior to their migration and later recovering tags in adults either in fisheries
or at spawning grounds. Alternatively, weirs in some rivers allow outmigrating smolts and returning adults to be enumerated. These methods have been applied to smolts from many populations in B.C. since the mid-1970s. Smolt-to-adult survival has varied among years, species, and populations, but in general has declined for stream-rearing species (coho, steelhead, and stream-type Chinook) over the last 20–30 years (Fig. 1.1). Survival declines of most coho populations entering the Strait of Georgia typically began in the late 1970s and worsened in the 1990s. In contrast, survival of populations from the west coast of Vancouver Island showed no consistent trend within the time series (Fig. 1.1a). Survival of one Chinook population was variable but showed no decline, while that of two other populations was low to begin with in the early 1980s but declined further (Fig. 1.1b). Survival of wild Keogh River steelhead (monitored with a weir) declined beginning in the early 1980s, and has been variable since the 1990s but lower on average than pre-1984 levels (Fig. 1.1c). Survival declines for Puget Sound steelhead began in the early 1980s and remain low through the present. Similar patterns are seen at a broader regional level. For coho further south, survival declines began earlier, in the late 1970s, for the Oregon Production Index (OPI; comprised mostly of coastal Oregon populations), worsened in the early 1990s, then survival rose somewhat in the early 2000s but is still less than pre-1975 levels (Fig. 1.2). The overall pattern for Georgia Strait coho was a decline beginning in the late 1970s from about 15% to currently <1%. Survival of hatchery coho from Puget Sound showed a similar pattern, although in recent years has increased somewhat. Survival of wild coho from Puget Sound also declined since the mid-1980s, but is generally higher than that of hatchery fish. Finally, no consistent trends are observed for populations from the outer coast of Washington, although the time series are shorter and it is possible that survival was higher in the 1960s, similar to the OPI case.

These estimates are natural survival estimates, exclusive of fishing, so when fishing mortality rates on coho were drastically cut in the mid-1990s (Fig. 1.3) in response to reduced abundances, smolt-to-adult survival did not (nor was expected to) subsequently increase. Causes of the survival declines are not yet well understood.

1.3 Hypotheses for declines in total marine survival

There has been no shortage of hypotheses to explain the declines in natural smolt-to-adult survival and the continued persistence of low survival in most populations. These hypotheses involve various mechanisms relating to feeding ecology, shifts in the abundance and
distributions of predators, physiological tolerance limits due to changing environmental conditions (Welch et al. 1998, Friedland et al. 2003), disease (Arkoosh et al. 2004, Jacobson et al. 2008), nutrient deficits (Gresh et al. 2000) and anthropogenic factors such as pollution (Barry et al. 2000, Heintz et al. 2000, Coghlan and Ringler 2005, Johnson et al. 2007) or habitat alteration (Magnusson and Hilborn 2003).

Many of these possible factors changed at the same time as the abundance and survival declines, making it difficult to isolate causal mechanisms. Leading hypotheses for variation in smolt-to-adult survival have involved two main possibilities: decreased growth rate versus increased predation intensity. Growth rate hypotheses generally involve either unfavourable ocean conditions reducing food availability (Fisher and Pearcy 1988), or density-dependent competition causing food limitation (Peterman 1978, Walters et al. 1978). Both of these sub-hypotheses predict that slow growth increases the length of time that smolts are vulnerable to size-selective predation, leading to higher mortality. The strength of size-dependent predation may be mediated by environmental factors, as selection against small body sizes may be stronger in years of poor ocean conditions (Holtby et al. 1990). Suggestions of negative effects of hatchery releases on survival of wild smolts (Noakes et al. 2000, Levin et al. 2001, Naish et al. 2008) generally fall under the hypothesis of density-dependent competition leading to reduced growth. Predation intensity hypotheses involve either an increase in the number of predators (Holtby et al. 1990), a change in predator functional responses resulting from changes in the abundance of alternate prey (Fisher and Pearcy 1988), or a change in the distribution of salmon or their predators (Ware and McFarlane 1986).

These hypotheses are not mutually exclusive (Fisher and Pearcy 1988, Holtby et al. 1990). The critical size and critical period hypothesis (Beamish and Mahnken 2001) is a combination of them, where mortality may occur mainly in two phases: an early phase of high predation upon ocean entry, and a later phase of high mortality over the first ocean fall or winter for smolts that fail to reach some critical size by late summer (most growth occurs during summer months; Quinn 2005). Smaller fish may not have the necessary energy stores to survive the winter, as suggested by the low lipid content in tissues of pink and chum salmon in winter (Nomura et al. 2000).
1.4 Critical mortality periods in smolt-to-adult life

“After more than 100 years of study, there is no life table for any species of Pacific salmon and rarely are we able to distinguish freshwater and marine mortality”

(Pearcy and McKinnell 2007)

‘Critical periods’ in fish populations, i.e., periods of high and variable mortality that determine recruitment of a year class, are generally thought to occur in the early juvenile stage (Hjort 1914). Mortality rates per unit time then generally decrease as fish grow (Lorenzen 1996). In diadromous or migrating species, however, a shift in habitat or a long distance travelled (exposing the fish to predation risk en route) may represent a second critical period in a juvenile fish’s lifespan, where mortality rates are once again high and variable (Friedland 1998). For salmon, considerable mortality is thought to occur shortly after ocean entry (Parker 1968, Mathews and Buckley 1976, Ricker 1976, Hartt and Dell 1986, Pearcy 1992).

Much debate exists about whether mortality principally occurs in the first ocean summer shortly after leaving freshwater, or in the first ocean fall/winter. One line of evidence—the number of male coho ‘jacks’ from coastal populations that return to spawn one year early after only a few months in the ocean—suggests that much of this mortality occurs by the end of the first ocean summer. In contrast to the high interannual variability of smolt-to-adult survival, jack-to-adult survival is more constant (Pearcy and Fisher 1988). Positive correlations between returns of age-2 jacks and age-3+ adults from the same cohort suggest that the year class strength becomes established before jacks return (Pearcy and Fisher 1988). Further partitioning the first summer, positive correlations between coho post-smolt catches off the Oregon coast in June and the return of jacks a few months later suggest that the year class strength becomes established by June, during the first 1–2 months after ocean entry (Fisher and Pearcy 1988). Typically, mortality during the downstream migration in rivers is considered a part of ‘early ocean mortality’ even though it may occur before smolts reach saltwater.

Other lines of evidence suggest a large proportion of marine mortality occurs over the first ocean fall or winter for fish that fail to achieve some critical size. In Georgia Strait, surface trawl surveys suggested that at least 22–37% of hatchery coho smolts entering the Strait survived to late summer but only 2–3% of smolts survived to return as adults (Beamish and Mahnken 2001). Second, coho smolts held in marine net pens displayed stunted growth related to food supply, and experienced an abrupt mortality between September-October (Beamish and Mahnken 1999). Stunted growth was a result of low insulin-like growth factor-I levels, which
occurred primarily in smaller fish (Beamish and Mahnken 2001). Even aggressive feeding cannot always compensate for stunted growth, since stunting involves a reduction in intestinal nutrient uptake (Collie and Stevens 1985). Third, analyses of scale circuli spacing before and after the first marine fall/winter (Beamish et al. 2004) and otolith size before and after October (Beamish and Mahnken 2001) showed a disproportionate loss of small individuals over this period. Scale circuli spacing and otolith weights are both correlated with body length, and in both cases larger fish before fall/winter (or October) were better represented in post-winter (or October/November) samples than smaller fish.

None of these or other studies have been able to directly estimate early ocean survival of juvenile salmon cohorts to determine when and where within the first ocean year mortality predominantly occurs. Total smolt-to-adult mortality is routinely estimated for some populations, but it is largely unknown how this is partitioned into components of downstream and estuarine mortality, early ocean mortality, adult natural mortality, and unreported fishing mortality. Because the time period over which total mortality is measured is long and the area covered by migrating salmon is large, it is difficult to attribute temporally and spatially-specific causes to mortality that could occur anytime and anywhere during ocean life. A first step to addressing the causes is in better understanding basic patterns of mortality during the smolt migration. These patterns have traditionally been difficult to study in the ocean, especially in juveniles, but recent advances in acoustic telemetry have made it possible to track the movements of small tagged fish and estimate survival rates of populations.

1.5 Monitoring migrations of salmon smolts with acoustic telemetry

After ocean entry, salmon species typically show a wide range of migration patterns. Sockeye tend to leave inshore areas rapidly and migrate northward along the continental shelf (Hartt and Dell 1986, Welch et al. 2003). Steelhead tend to also leave inshore areas rapidly, but may move directly offshore rather than migrating along the shelf (Hartt and Dell 1986). Coho and Chinook, on the other hand, may in some cases move north along the continental shelf (Welch et al. 2003) but in other cases reside in inshore straits, on the continental shelf, or offshore in close proximity to their river of origin (Milne 1950, Godfrey et al. 1975, Healey 1980, Hartt and Dell 1986, Pearcy and Fisher 1988). After migrations or residence on the continental shelf during the first ocean summer (Welch et al. 2003, Fisher et al. 2007), salmon post-smolts tend to head offshore in the fall.
Movements of juvenile salmon have been tracked in the ocean for decades (Stasko 1975, Labar et al. 1978) using electronic tags that emit a sound signal, which is received by a hydrophone either lowered from a boat or integrated with a data-logging device. Relatively small acoustic tags (9 mm diameter) have been available for over 15 years (Voegeli et al. 1998). Until recently, however, few studies have tracked fish movements for long enough or at a combination of spatial scales necessary to quantify mortality patterns and estimate early ocean survival.

Survival during this critical period can be estimated by tagging fish in freshwater and monitoring their movements along migratory routes at a series of detection stations in rivers, estuaries, and the coastal ocean. The Pacific Ocean Shelf Tracking Project (POST) is a continental-scale acoustic array that was used to monitor the migrations of tagged salmon smolts from several different populations in southern B.C. (Fig. 1.4; for convenience, I define population as a group of fish of the same species and rearing history (wild or hatchery) from the same watershed near a release site). Smolts entered the ocean from several different rivers surrounding the Georgia Strait system (which includes Queen Charlotte Strait (QCS) and Johnstone Strait to the north, and Juan de Fuca Strait (JDF) to the south). Smolts from some species migrated rapidly through these inshore areas, while others moved more slowly and may have resided within Georgia Strait.

1.6 Mark-recapture methods applied to migrating species

Tagged salmon smolts were not always detected at receiver stations placed along migration routes. Failure to detect a tagged fish at a station could result from the fish not surviving to the station or passing by the station without being detected. Open-population mark-recapture methods have been used for decades to distinguish between survival and recapture probabilities of tagged animals. The most common open-population model is the Cormack-Jolly-Seber model (CJS; Cormack 1964, Jolly 1965, Seber 1965), traditionally used for tagged animals that are captured, marked, released and recaptured at fixed sampling occasions over time. More recently, these models have been applied in a spatial context, with animals captured, tagged, released and detected at fixed sampling locations along migration routes (Burnham et al. 1987, Skalski et al. 2001). By employing multiple detection stations and using individually-coded tags, there is information at later detection stations about the tags that were not detected at earlier stations along a migration route. This permits probabilities of survival in each segment of the migration and detection at each station to be teased apart.
To properly assess survival of migrating salmon smolts using telemetry approaches, considerable focus must be placed on estimating detection probabilities \( (p) \). Fortunately, this is simpler than traditional mark-recapture studies for two reasons: tagged fish do not have to be handled during ‘recapture’ events, and much of the behavioural element of recapture (e.g., ‘trap-happiness’) is removed since \( p \) is instead likely determined primarily by tag and receiver characteristics. Much of this thesis involves the development of methods to better estimate this simple nuisance parameter, \( p \), especially in the context of: multiple populations with small to moderate sample sizes analyzed in a common framework; multiple tag types or environmental variables that can affect \( p \); mobile sampling studies; and estimation of \( p \) at terminal receiver stations where there is no detection information later along migration routes.

In the last two decades, approaches to analyzing mark-recapture data have increasingly involved consideration of multiple candidate models, each representing a specific hypothesis about how variation in detection data may be represented by a particular model structure of survival and detection probability (Lebreton et al. 1992). This greatly increases the flexibility of mark-recapture models for purposes of both parameter estimation and assessment of important effects (explanatory variables) on survival or detection probability. Candidate models can be compared using formal model selection procedures (e.g., Burnham and Anderson 2002).

### 1.7 Thesis outline

This thesis is divided into two parts. The first mainly presents methods for estimating detection probabilities in telemetry studies with migrating fish. Chapter 2 describes different types of \( p \), factors that typically influence \( p \), and common ways of estimating \( p \). Chapter 3 presents methods for applying mark-recapture models to the analysis of multiple populations that share some portion of their migration routes. Chapter 4 describes a method for estimating \( p \) using only local information at a detection station rather than from stations further along a migration route. Chapter 5 presents methods for assessing \( p \) during mobile transect surveys for acoustic tags. Chapter 6 describes a test of the assumption of homogeneity in \( p \) among individual tags of the same type. General methods are presented in Appendix A.

In the second part, I apply mark-recapture models to detection data of tagged salmon smolts to estimate survival during the migration and identify factors explaining variation in survival. Chapter 7 describes basic migration patterns of salmon smolts from southern B.C. populations. Chapter 8 compares survival and freshwater residualization between wild and
hatchery-reared steelhead from the same watershed. Chapter 9 presents survival estimates of multiple salmon populations during the downstream and inshore migration, and attributes variation in survival to several different factors. Finally, Chapter 10 compares early ocean survival between smolts under sunlight-exposed and sunlight-shaded treatments during freshwater rearing to address the hypothesis that solar ultraviolet-B radiation negatively affects survival.

Throughout this thesis, I will use the following conventions. I use ‘survival rate’ or ‘mortality rate’ only to indicate a per-unit-distance or per-unit-time measure, and will use ‘survival probability’ or simply ‘survival’ to indicate the probability of surviving from one point in space or time to another, represented by ‘φ’. Estimates of φ and p are denoted by \( \hat{\phi} \) and \( \hat{p} \), respectively. Mark-recapture sub-models for survival or detection probability are denoted by [φ] and [p], respectively, and the combined full model is denoted by [φ, p]. Factors contained in the model are indicated either as subscripts or in parentheses. For example, [φ_{segment×group}, p_{station×group}] or [φ_{segment×group}, p_{station×group}] describes a model where separate \( \hat{\phi} \) are estimated for each release group in each segment of the migration and \( \hat{p} \) are estimated independently (i.e., separately, such that \( \hat{p} \) are distinct among release groups) for each release group at each detection station.
Figure 1.1. Smolt-to-adult survival of coho salmon (a), stream-type Chinook salmon (b), and steelhead trout (c) populations in southern B.C. for smolt years 1974–2007. Wild populations are shown with filled symbols and solid lines, while hatchery populations are shown with open symbols and dashed lines. Colours across (a)-(c) show: blue, Strait of Georgia (SOG) populations from the east coast of Vancouver Island (ECVI); dark green, SOG populations from the lower Fraser River (LFR); light green, SOG populations from the South Thompson River (STR); purple, SOG populations from the south mainland coast north of the Fraser River mouth (SC); red, populations from the west coast of Vancouver Island (WCVI); orange, Queen Charlotte Strait (QCS) populations from northeast Vancouver Island; and black, Puget Sound (PS) populations. Smolts are typically age 2 for coho and steelhead and age 1 for coastal stream-type Chinook. Survival estimates are calculated from coded wire tag recoveries and/or smolt and escapement enumeration. Data provided by S. Baillie and R. Cook (Fisheries and Oceans Canada), Washington Department of Fish & Wildlife, Ward (2000), and the B.C. Ministry of Environment.
Figure 1.1 cont.
Figure 1.2. Regional-scale smolt-to-adult survival indices of coho salmon from the Strait of Georgia, Washington, and Oregon for smolt years 1960–2006. Wild populations are shown with filled symbols and solid lines, while hatchery populations are shown with open symbols and dashed lines. Smolts are typically age 2 and return at age 3. Strait of Georgia and Puget Sound (triangles) estimates are from Beamish et al. (2000, 2008), and R. Beamish (Fisheries and Oceans Canada, pers. comm.). Wild and hatchery estimates for Washington State (circles) are from J. Haymes (Washington Department of Fish & Wildlife) through J. Beetz (U. Washington). They represent averages of populations: PS (W) – Big Beef Creek, Baker River, Deschutes River, and South fork Skykomish River; PS (H) – Skookum Creek, Kalama Creek, Minter Creek, Voights Cr., Soos Creek, Big Quilcene Creek, Wallace River, Kendall Creek, George Adams Hatchery, Berny Gobin Hatchery, and Marble Mount Hatchery; WC (W) – Bingham Creek; WC (H) – Sooes River, Solduc River, Salmon River, Quinault River, Stevens Creek, and Bingham Creek. Oregon Production Index estimates are from Beamish et al. (2000) and Peterson et al. (2006).
Figure 1.3. Exploitation rates of southern B.C. coho salmon populations in return years 1975–2008. Return year is generally 1 year after the smolt year of a cohort. Wild populations are shown with filled symbols and solid lines, while hatchery populations are shown with open symbols and dashed lines. Colours show: blue, Strait of Georgia (SOG) populations from the east coast of Vancouver Island (ECVI); dark green, SOG populations from the lower Fraser River (LFR); light green, SOG populations from the South Thompson River (STR); and red, populations from the west coast of Vancouver Island (WCVI). Exploitation estimates are calculated from coded wire tag recoveries. Data provided by S. Baillie (Fisheries and Oceans Canada).
Figure 1.4 (next page). Map of study area in southern British Columbia. Locations of acoustic receivers are shown with red circles. Multi-receiver ocean lines were in place for years 2004–2008 at Queen Charlotte Strait (QCS), the northern Strait of Georgia (NSOG), Juan de Fuca Strait (JDF), inner Howe Sound (HS\textsubscript{inner}), outer Howe Sound (HS\textsubscript{outer}), and Lippy Point (LIP). Not all receivers in rivers or at river mouths shown were in place every year. Not shown on this map are receiver lines off the west coast of Washington State, Oregon, or southeast Alaska, since B.C. smolts were rarely detected at these stations and analyses did not include them. Release locations of tagged salmon smolts are shown with triangles, in blue for populations included in multi-stock analyses of migration patterns and survival (Chapters 7 and 9), and in green for populations not included. Release locations are labelled with letters that correspond to those in Tables A.2 and A.3 (Appendix A):

Mid-Fraser River:
- A, Coldwater River hatchery release site
- B, Coldwater River rotary screw trap site
- C, Nicola River hatchery release site
- D, Spius Creek downstream hatchery release site
- E, Spius Creek upstream hatchery release site
- F, Deadman River rotary screw trap site

Lower Fraser River:
- G, Sweltzer Creek release site downstream from Cultus Lake
- H, Alouette River rotary screw trap site
- I, Coquitlam Reservoir

B.C. south coast:
- J, Seymour River hatchery release site
- K, Cheakamus River upstream hatchery release site
- L, Tenderfoot Creek hatchery release site
- M, Cheakamus River downstream hatchery release sites and wild side channel trap sites
- N, Sakinaw Lake

East coast Vancouver Island:
- O, Cowichan River hatchery release site
- P, Englishman River rotary screw trap site
- Q, Big Qualicum River hatchery release site
- R, Nimpkish River rotary screw trap site and Gwa’ni Hatchery
- S, Nimpkish River upstream release site (Woss Hatchery)
- T, Keogh River fish fence

West coast Vancouver Island:
- U, Stamp River release site (Robertson Creek Hatchery).
Figure 1.4 cont.
1.8 References


2 Detection probability in tracking studies: definitions and evaluation methods

2.1 Introduction

Acoustic and radio telemetry tags are valuable tools for studying the movements and dynamics of animal populations. Some studies combine tracking methods with mark-recapture or tag-recovery modelling to estimate abundance or demographic rates such as survival, individual growth, and transition among habitats (reviewed in Pine et al. 2003). Other studies use telemetry for assessing movement patterns as they relate to habitat use, foraging, or interactions with other species. Many kinds of biological questions can be posed, and answering them often involves estimating how many tagged animals are still alive and/or present in a study area at some time.

Some tagged animals may not be detected under a given sampling regime, so estimates of numbers alive and biological rates (survival, movement) depend on the probability of detecting a tag during sampling processes. This detection probability ($p$) nuisance parameter must be estimated to obtain unbiased estimates of the survival or movement parameters of interest. Despite the widespread and increasing use of telemetry, there has generally been a paucity of studies that evaluate different methods for estimating $p$ (Clements et al. 2005).

Biological hypotheses and study objectives should drive the design of telemetry arrays and sampling methods (Heupel et al. 2006). Similarly, the meaning of $p$ and methods to quantify it also differ depending on study objectives. This chapter is written to present the diverse usage of ‘detection probability’ or ‘detection efficiency’ in acoustic or radio telemetry studies and to describe evaluation methods under this variety of study objectives. Several environmental and technological factors that can affect $p$ are also outlined. The text generally refers to fish, but the ideas are transferable to telemetry studies involving other aquatic taxa and/or terrestrial animals.

2.2 Objectives for estimating detection probability

Life history strategies, behaviours, and movement patterns are diverse among aquatic taxa. Some species (or individuals, or stages within a species) are relatively sessile, with restricted home ranges and forays of only short distances or duration. Others are far-ranging, spending little time in a particular area during dispersal or migration events. As a result of this diversity, definitions of $p$ have varied among tracking studies depending on study objectives.
2.2.1 Probability of detecting a single tag transmission

A common measure of $p$ is the proportion of known tag transmissions that are detected by a receiver or an array of multiple receivers over some time period. This gives the average probability of detecting a single tag transmission, $p_{\text{ping}}$, typically specified at some distance from tag to receiver. Systematic range testing with test tags makes extensive use of this measure, often for designing tracking studies (Clements et al. 2005; Hobday and Pincock In review). A common objective is to determine an appropriate spacing between individual receivers deployed in a line (or equivalently, ‘gate’ or ‘curtain’) or grid pattern. At increasing distance from tag to receiver, the proportion of transmissions successfully decoded decreases, and the researcher can determine from this relationship what the necessary maximum spacing should be to maintain some minimum $p_{\text{ping}}$ (Lindholm et al. 2007) or to evaluate the distance beyond which tags are no longer detected (Topping et al. 2006). A similar metric is the number of detections recorded over a fixed time period (Simpfendorfer et al. 2002, Grothues et al. 2005, Heupel et al. 2006). This can be used to compare the effect of distance on tag reception, but can only be transformed to a proportion if the number of signals transmitted during this period is known.

The relationship between $p_{\text{ping}}$ and tag-to-receiver distance is also used in positioning algorithms (Simpfendorfer et al. 2002). To evaluate fine-scale movement patterns within a grid array of receivers, it is necessary to quantify the proportion of detections received on multiple receivers in proximity of a tag over some short time period (or, an alternative method is to use ≥3 synchronized receivers and measure differential arrival times of a tag signal to triangulate position). The differential proportion of transmissions detected among receivers provides information on the most likely position of the tag within the array. The temporal sequences of detections or centres of activity are used in turn to quantify movement patterns and speeds within the array (Simpfendorfer et al. 2002, Ohta and Kakuma 2005, Hedger et al. 2008).

There is little direct interest in $p_{\text{ping}}$. Compared to the definitions that follow, $p_{\text{ping}}$ rarely has any direct relevance to vital population rates or movement parameters. This measure is more of an indicator of how an array of receivers might perform in addressing biological hypotheses.

2.2.2 Probability of detecting a resident fish

Telemetry is often used for studying movement patterns of species within or away from some defined area. Some species show high degrees of site fidelity with small home ranges. Others may use some particular area repeatedly, but move to different areas intermittently for
spawning, foraging, or searching for new territories (Lindholm et al. 2007). Quantifying the time spent on such forays, time within the main area of residence, or the timing of removal from the study area due to fishing (Hightower et al. 2001) are often of interest. These can only be reliably estimated if there is a high probability of detecting the tagged fish within the study area over some period of time, given that it is present there, \( p_{\text{res}} \). If this probability of detecting the fish was instead low (e.g., Hedger et al. 2008), it would be confounded with the probability of its absence from the study area due to foray behaviours (Meyer et al. 2007) or removal.

The \( p_{\text{res}} \) measure differs from \( p_{\text{ping}} \) in that determining presence in an area may require only one or two detections within some time period. It can be estimated either on a per-receiver basis or over an entire grid; multiple receivers within the area of interest will usually provide a higher \( p_{\text{res}} \) for establishing presence. If receivers in stationary grid arrays are deployed densely enough that complete, continuous coverage is achieved for a tag in the study area, \( p_{\text{res}} \) can be assumed to be 100% (Heupel and Simpfendorfer 2002). As a result, biological quantities of interest like movement or mortality rates can be estimated more precisely than if \( p_{\text{res}} \) were also estimated. Incorrect assumptions of 100% \( p_{\text{res}} \), however, will cause underestimates of the proportion of time that tagged fish spend within the array of receivers.

### 2.2.3 Probability of detecting a migrating fish

Receiver stations can be deployed along migratory routes of populations to estimate migration and survival rates or passage across dams. Multiple receivers, arranged typically in lines but also in grid patterns, can be used to effectively ‘seal off’ possible migration routes of tagged fish. In constricted areas especially like rivers, estuaries, fjords, straits, and channels, a line of receivers can cover the full width of such passageways. However, migrating fish may travel rapidly, through gaps between adjacent receivers, or at different depths from the receivers, and may therefore be within detection range for only a short period of time. This can result in a relatively low probability of detecting a tag moving across a receiver station, \( p_{\text{mig}} \). This probability changes over time due to variation in background noise; typically, an average probability over the migratory period is quantified.

Remaining chapters make extensive use of \( p_{\text{mig}} \), which unless otherwise indicated will be simply referred to as ‘\( p \)’. The Cormack-Jolly-Seber (CJS) open-population mark-recapture model accounts for \( p_{\text{mig}} \) in estimating survival, where instead of the classic temporal form, a spatial form is considered for migrating fish. Survival estimates in each segment of the migration between successive stations depend on the probability of tagged fish being detected at stations as...
they cross. When $p_{\text{mig}}$ is assumed to be 1, the modelling approach becomes that of known-fate models (Kaplan and Meier 1958). When there are additional receiver stations after the one of interest, $p_{\text{mig}}$ is estimable either in CJS models, or independently as the ratio of fish detected at and after the line of interest to those detected after the line of interest (Manly and Parr 1968). The CJS framework is often used to study salmonids that migrate in rivers and coastal areas, either adults returning upstream to spawn (Eiler 1995) or juveniles migrating downriver to the ocean (Skalski et al. 2001, Rechisky et al. 2009, Welch et al. 2009). Comeau et al. (2002) used a typical mark-recapture calculation to estimate $p_{\text{mig}}$ on a line where, instead of later lines providing information on the proportion of fish not detected at the line of interest, it was the same line at different times of year. Cod moved offshore past the line in the fall, and then returned onshore past the same line in the spring.

Generally, $p_{\text{ping}}$ is a reasonable index of $p_{\text{mig}}$, but there may be exceptions. If $p_{\text{ping}}$ is low (e.g., <0.5, Simpfendorfer et al. 2008), that does not necessarily imply that $p_{\text{mig}}$ will be low. Only one detection (or two, to rule out the possibility that a single detection is a false positive) is required to substantiate the presence of a fish as it crosses a receiver line. If receivers are deployed with a short enough spacing between them to ensure that a minimum of several tag signals are transmitted during the time a tagged fish crosses the line (Welch et al. 2003), the probability that all transmissions will be missed will usually be small. Conversely, if $p_{\text{ping}}$ is relatively high, $p_{\text{mig}}$ could still be low. If the programmed pulse rate of tags is low enough relative to the maximum swimming speed of the fish (or travel speed assisted by river currents), the fish could cross the line with an expectation of <1 signal transmitted while within detection range. At typical tag pulse rates of <120 s$^{-1}$, this last possibility would be rare for acoustic tags except perhaps for fish moving downstream in very fast rivers (>1m·s$^{-1}$ water velocity). It is unlikely that intervals between pulses in a pulse train would affect $p_{\text{ping}}$ at these speeds.

### 2.2.4 Probability of detecting a tag during mobile surveys

The previous three definitions primarily relate to studies that use stationary receivers. Detections at these fixed stations depend on tagged fish moving close enough to a receiver to be detected. If a tagged fish dies early in its migration, ceases its migration, or has limited range of movement outside of a receiver grid array, the tag may never come within detection range of a receiver. In these cases, mobile tracking surveys can be used to sample in areas surrounding an array or between successive detection stations (Ng et al. 2007, Lowe et al. 2009, Chapter 5). Researchers can conduct continual transects with a hull-mounted or towed hydrophone (e.g.,...
Holland et al. 1985) or periodically stop a boat at sampling stations to monitor for tags. Similar to the case of migrating fish crossing over a stationary array, however, mobile sampling for relatively stationary tags can result in a relatively low probability of detecting a tag given that it is within an area sampled by mobile surveys, \( p_{\text{mobile}} \).

Mobile tracking studies have different objectives. Many studies involve continuously following tagged individuals to quantify movement patterns, habitat use, and environmental correlates with these patterns (Holland et al. 1985, Block et al. 1997, Topping et al. 2005). In these types of studies, there is little need for estimating \( p_{\text{mobile}} \). Other studies involve sampling for an unknown number of tags currently present in some area, where the location of each tag is initially unknown (Hightower et al. 2001, Chapter 5). Tags may or may not be easily detected. In transect surveys, it is crucial to estimate \( p_{\text{mobile}} \) if any inferences are to be made about either the number of tagged fish present in the study area during the sampling period or survival rates of tagged populations. The number of tags detected by periodic mobile searches is sometimes reported (e.g., Voegeli et al. 1998), but if \( p_{\text{mobile}} \) associated with this sampling process is not quantified, it is not possible to estimate how many tagged individuals were in the area but not detected during mobile surveys.

Similar to the preceding definitions, achieving a higher \( p_{\text{mobile}} \) results in less ambiguous inferences about biological movement patterns and population vital rates. As \( p_{\text{mobile}} \) (or relocation probability, where the same area is repeatedly sampled for the same group of tags over the course of a study) decreases, so does the precision of other model parameters like natural and fishing mortality rates (Pollock et al. 2004). As \( p_{\text{mobile}} \) increases, the failure to detect a particular tag increasingly implies that it is not present within the sampling area rather than the alternative of it being present but not detected.

### 2.2.5 Other definitions of detection efficiency

Comeau et al. (2002) presented two definitions of \( p \). One of these was a typical mark-recapture definition for tagged fish migrating across a fixed receiver line, but the other did not involve detection data. This second metric was simply calculated as a ratio of the average detection range based on test tag measurements to the average separation distance between adjacent receivers on the line. Although this estimate was close (72%) to the mark-recapture \( p_{\text{mig}} \) (80%), using it involves risk of relying too heavily on range tests. If oceanographic conditions or tag depth vary between the period of range testing and when fish actually cross the receiver line,
range testing results may not reflect actual detection processes at the time of fish crossing events. Using data from tagged fish to determine $p$ eliminates the need for detection range assumptions.

2.3 Factors affecting detection probability

Several factors have been shown to affect detection efficiencies. Many have been recently summarized (Heupel et al. 2006, Simpfendorfer et al. 2008), so this section is not exhaustive. These factors may be controlled by users through technology or study designs, can be affected by environmental conditions, and can be affected by the behaviour of tagged fish in the study area. They likely have similar influence for all definitions of $p$ identified above.

2.3.1 Tag-to-receiver distance

The distance between a transmitting tag and receiver is the most commonly assessed factor affecting $p$, forming the basis for range tests. Two types of losses of acoustic strength occur as a result of increased distance: geometrical spreading of the wavefront through water, and absorption of sound which is affected by salinity, air bubbles, turbulence, silt, and other matter suspended in the water (Voegeli and Pincock 1996). Over the long term (as environmental acoustic conditions vary), the decline of $p$ with increasing distance has been suggested to be linear (Simpfendorfer et al. 2002, Heupel et al. 2006), near-Gaussian (Hobday and Pincock In review), logistic (Szedlmayer and Schroepfer 2005), or exponential beyond some threshold distance (R. Hedger, pers. comm.). At any given moment (during a short period of constant acoustic conditions), the relationship between $p$ and distance has been suggested to be near-uniform (Hobday and Pincock In review) or logistic with variable rates of decrease (Chapter 4). For acoustic tags in rivers, turbulence is an especially severe problem; detection distance can drop from order 100 m to order 1 m quite abruptly, with a shift from smooth (laminar) to turbulent river flow.

2.3.2 User-controlled factors

Researchers have direct control over how receivers are deployed as well as the programming characteristics of tags. Some hydrophones are omni-directional, but others are most sensitive to signals in a particular plane. For a receiver oriented vertically, this plane is typically perpendicular and radial to the receiver, so sounds are detected at longer distances when they are within a broad horizontal plane of the hydrophone (Clements et al. 2005). In some
environments this plane of greatest sensitivity can be narrow, with $p$ decreasing when tags are more than a few metres above or below the hydrophone plane (Farmer et al. *In review*). Users cannot control the depth of tagged fish, but receivers can be deployed at a depth where tagged fish are most likely to occur. Receivers can also be deployed to maintain direct line-of-sight between tags and receiver by not having topographical or vegetative obstructions near the hydrophone (which will sometimes block the signal and prevent detection). Mounting equipment for the receiver such as submerged floats, lines, or even mounting parts of the receivers themselves (Clements et al. 2005) may also obstruct sound signals reaching the hydrophone.

The acoustic output and frequency of transmitters directly affect transmission distance and therefore $p_{\text{ping}}$ (Simpfendorfer et al. 2002). Many manufacturers provide a range of frequencies or power levels among tag models. Lower frequencies generally transmit further in water, but require a tag transducer with greater diameter to emit the sound, so are typically associated with larger-sized tags. Even within the same tag model, minor variation in strength among individual tags may translate into heterogeneity of $p$ among tags (Chapter 6). When several tags transmit within a study area, some signals may collide (i.e., overlap) and prevent detection if coding schemes involve long pulse trains (e.g., VEMCO tags). The frequency with which this occurs is a function of the number of tags present and how often tags transmit their signal (Voegeli et al. 1998, Hightower et al. 2001, Simpfendorfer et al. 2002), which are both controlled by users. To note, collisions are less likely in coding schemes that use short, single-pulse methods (e.g., HTI, JSATS, and Lotek tags).

In mobile transect surveys, boat speed is probably the most important user-controlled factor affecting $p_{\text{mobile}}$. At faster speeds, tags along a transect are within detection range for a shorter period of time, engine-related noise and flow-related noise of water moving past the hydrophone are greater (thereby reducing the signal:noise ratio) and, if the hydrophone is towed behind the boat, it travels at shallower depths where background noise levels are usually higher (Voegeli and Pincock 1996, Chapter 5). As surveys are generally conducted at the surface, the depth of tags also affects $p_{\text{mobile}}$. This is particularly a concern for deep-water fish or for tags laying on the bottom (Chapter 5) either inside dead fish or after defecation by a predator.

### 2.3.3 Environmental and behavioural factors

Any factor that increases background noise near the same frequency as a tag signal will decrease the signal:noise ratio and therefore $p$. Wind may be the dominant environmental factor that reduces detection ranges and efficiencies (Hobday and Pincock *In review*). Hydrologic
conditions that create noise include tidal currents, turbulent flow, and broken water surfaces due to waves or rain (Voegeli et al. 1998). Gradients within the water column like haloclines or thermoclines may decrease detection ranges due to refraction or reflection (Voegeli and Pincock 1996), or more rarely, might promote further ranges. Seasonal variation in river discharge and related noise levels may lead to a systematic change in $p$ over this same period for receivers placed in rivers (Simpfendorfer et al. 2008, Chapter 3). Soniferous invertebrates or fishes, whether on or near receivers, can increase background noise levels (Simpfendorfer et al. 2002, Heupel et al. 2006, Heupel et al. 2008). Finally, human sources like boat traffic, dams, and fish farms can all generate noise and introduce air bubbles or suspended matter into the water column, thereby reducing $p$ (Voegeli et al. 1998, Hightower et al. 2001, Simpfendorfer et al. 2002, Heupel et al. 2006, Simpfendorfer et al. 2008). Variation over time in any of the above noise sources can result in diurnal or seasonal variation in $p$.

Detection probabilities can be reduced by environmental obstructions between tag and receiver such as submerged aquatic vegetation (Hightower et al. 2001, Simpfendorfer et al. 2002), bottom topography like large rocks or coral reefs (Simpfendorfer et al. 2002, Farmer et al. In review), or aquatic life that grows on receivers (Heupel et al. 2008). Even without any direct sound barrier, the bottom type over which studies are conducted can affect $p$ through absorption of sound by various substrates like soft sediments (Heupel et al. 2006). Noise sources can be less problematic for signal detection when using narrow-band receivers than broad-band receivers due to the wider range of frequencies received on broad-band receivers.

Although it is usually assumed that $p$ should be homogeneous among individuals if they are tagged with the same type of transmitter, the behaviour of tagged fish can affect $p$. The depth of tagged fish may vary with respect to a deployed receiver. In some cases this has little effect on detecting tags and is even of biological interest (Block et al. 1997). In other cases, if tag depths are above or below the horizontal plane of greatest sensitivity for a receiver oriented vertically, detection ranges and $p$ may be reduced. Some tagged individuals may spend a greater proportion of time either outside the sampling area of a receiver array, in locations within it that are noisier (Hightower et al. 2001), or in locations near benthic structures that lead to obstructed transmissions (Simpfendorfer et al. 2008). Any of these possibilities could lead to reduced $p$ for this behavioural subset of the tagged population. Similarly, in migrating fish that cross a line of receivers, faster individuals will be within detection range for a shorter period of time, so on average may have reduced $p_{mig}$. 
2.4 Evaluation methods

Despite the above factors that can reduce detection probabilities, the design of tracking studies is also user-controlled and can compensate for these factors. When designing receiver grids for quantifying the presence of tagged fish within the array over time, receivers can be deployed densely to increase the overlap of detection ranges thereby reducing the probability of a tagged fish returning to the array but not being detected. Similarly, when designing a line array for detecting migrating fish, shorter distances between adjacent receivers will decrease the probability of a tagged fish crossing the line undetected. In mobile tracking studies, shorter distances between parallel transect lines and slower boat speeds will decrease the probability of not detecting a tag within the sampling area. There are trade-offs associated with these strategies for increasing $p$ within a particular area: for a fixed number of receivers (Chapter 3) or mobile transects (Chapter 5) available, deploying them densely implies the total sampling area will necessarily be smaller.

Whichever measure of $p$ is of interest for study objectives, this probability should be quantified over a range of variables and conditions that may occur during the biological study. Users can evaluate background noise at specific locations using broad-spectrum hydrophones (Heupel et al. 2006), or can evaluate detection ranges at specific locations under a range of environmental conditions. Both of these measurement types are useful for designing tracking studies and both can be important indicators of $p$, but neither are direct measures of $p$ that can be used to estimate a proportion of tagged fish that have died or are no longer in a study area.

2.4.1 Proportion of transmissions detected

Two factors that should always be taken into account when assessing $p_{\text{ping}}$ are tag power output and tag-to-receiver distance. The same type of test tag should be used as is used with fish. Researchers should assess $p_{\text{ping}}$ at several distances to determine the shape of the decay with increasing distance. A test tag can be deployed at fixed distances from a receiver, ensuring that a sufficient number of signals are transmitted at each distance (the more transmissions the better; 50 transmitted signals will allow $p_{\text{ping}}$ to be estimated at 2% increments). If multiple receivers are available, these can be simultaneously deployed at varying distances from a fixed-location test tag so this effect of distance is isolated from possible confounding of testing different distances at different times. An alternative approach is to deploy multiple tags at varying distances from a
fixed-location receiver; in this case, if tags use long pulse trains (e.g., VEMCO tags) then long, fixed signal intervals should be used, offset from one another to avoid signal collisions.

A test tag evaluation took place one day in March 2005 over a period of 2.2 hours in Howe Sound, a coastal fjord in B.C. Twelve VEMCO VR-2 receivers were deployed in a line, raised from the seabed at a depth of ~145 m each. From one end of the line (‘X’), they were spaced at 0, 100, and every 50 m thereafter to a maximum distance of 600 m at the other end of the line (‘Y’). In addition, three VR-3 receivers were deployed at 200, 300, and 400 m from ‘X’. A boat was positioned above ‘X’ and two test tags of differing acoustic power (VEMCO V7 and V9, 136 and 142 dB at 1 m, respectively) were lowered to a range of depths (2, 5, 10, 20, 40, 70, 100, and 130 m) for 15 min at each depth. This corresponded to 40 signals transmitted from each tag at each depth; tags were offset at a fixed repeat rate so their signals would not collide. The proportion of signals detected on each receiver was calculated for each tag at each depth. Raw data are not shown (D. Welch, unpubl. data), but a Lowess bivariate fit was used to interpolate \( p_{\text{ping}} \) as a function of tag-to-receiver horizontal spacing and tag depth (Fig. 2.1). The probability surfaces show that >90% of transmissions were detected at a wide range of distances and depths, but this declined sharply after a range of about 500 m for V9 tags and 400 m for V7 tags, and also declined sharply when test tags were in surface waters to a depth of 30 m (V9 tags) or 60 m (V7 tags). The probability surfaces for VR-3s suggested a shorter detection range than for VR-2s, but these were based on only three receivers and other tests have shown similar detection ranges for these receiver types. All four surfaces show irregular contour trends that are sensitive to \( p_{\text{ping}} \) at particular depths and distance combinations; these may simply result from chance, as relatively few transmissions were emitted at each tag placement.

When assessing \( p_{\text{ping}} \), it is crucial that environmental conditions during test tag evaluations reflect those that occur during the biological study. If favourable weather conditions occur during a test tag evaluation, detection ranges and \( p_{\text{ping}} \) could be considerably lower under less favourable conditions during the actual study. Three general approaches are possible:

1. If tags whose coding schemes involve single, short pulses are used (or else tags with long pulse trains that have long delay intervals between trains), it is possible to deploy a test tag in the area during the study with little interference to signal reception of fish tags. Decreases in \( p_{\text{ping}} \) may reveal increased background noise or obstructions around the hydrophone; near-continuous on-site monitoring would allow such problems to be dealt with immediately, or accounted for in data analyses after the study. Conversely, if tags with coding schemes involving long pulse trains...
are used, then the presence of test tags in the study area during the study runs the risk of test tag signals colliding with fish tag signals. The last two approaches deal with this issue.

(2) Test tag evaluations can be conducted under a range of specific, known environmental conditions at different times before and/or after the biological study. Then, specific, known environmental conditions observed during some portion of the biological study can be matched with appropriate \( p \) evaluations that occurred under similar conditions. This approach has the advantage of explicitly recognizing temporally-varying detection ranges and \( p \) so that biological inferences can make use of this detailed information. Disadvantages include having to measure specific conditions during both test tag evaluations and at all times during the biological study, and also that much effort is needed to characterize how \( p \) changes under a range of conditions.

(3) \( p \) can be ‘integrated’ across all possible environmental conditions. This involves deploying a test tag(s) for a long enough time to experience a range of different conditions, which is assumed to reflect the range of conditions during the biological study. If \( p \) evaluations are conducted nearby the study area at the same time as the biological study, then temporal variation during test tag assessments (due to weather, etc.) will likely be representative of that during the biological study.

In addition to temporal variation in environmental conditions, spatial variation in acoustic conditions can occur within a study area. Variation in \( p \) can occur among sub-areas as a result of variation in bottom topography, depth, sediment type, aquatic vegetation, and the influence of tides, river flow, or boat traffic at each sub-area. Detection efficiency assessments should be conducted across these spatially-varying conditions, either during the study if possible (so that test tag assessments are more reflective of current conditions during the study), or if test tags with long pulse trains are used, then before and after the biological study (to avoid interference from test tags). Test tag tows from a boat with recording GPS can be used to efficiently cover a large number of transmission locations in order to evaluate from which specific sub-areas tag signals are received less consistently (Hedger et al. 2008). This information can assist in strategies for re-deploying receivers to increase \( p \) in these sub-areas, as well as to recognize the possibility of lower \( p \) in these sub-areas during analyses.

If the effect of multiple factors on \( p \) can be evaluated, these should be analyzed in a common framework instead of one at a time. This permits an assessment of whether interactions between factors also affect \( p \) (Farmer et al. In review). For example, the effects of horizontal spacing and depth on \( p \) (Fig. 2.1) were evaluated together. At horizontal distances <100 m, the effect of depth on \( p \) was less than at distances >100 m (in this particular habitat at this
particular time). If such an evaluation were extended over a wider range of environmental conditions (Farmer et al. *In review*), effects of several interactions could be revealed.

### 2.4.2 Movement around stationary arrays

If continuous contact with a tag is desired for accurately monitoring tag positions over time, receivers should be densely deployed with overlapping detection radii (Heupel et al. 2006) to ensure that $p_{res} \approx 1$. If only occasional detections are required to address questions related to presence within a study area, then receivers can be deployed further apart (Heupel et al. 2006) and in these cases it becomes especially important to estimate $p_{res}$.

Test tag evaluations can be used to estimate $p_{res}$ over some time period. Test tags can be either deployed at fixed locations or towed by boat within a grid array. The depth and speed of towed tags should represent general movement patterns of the study species. Using GPS to record the position and speed of a towed test tag through the array, detection patterns on stationary receivers can be used to calibrate positional and speed estimates of tagged fish (Hedger et al. 2008). Similarly, mobile tracking within an array of stationary receivers can be used to follow a fish and evaluate how often it is detected on stationary receivers, based on known locations from manual tracks (Topping et al. 2006). This method eliminates biases from test tags that might be towed at depths or speeds not reflecting those of the study species.

Initially, a relatively long time interval can be considered to verify whether at least one test tag transmission is detected by at least one receiver. The test tag sequences can then be randomly subsampled, selecting a shorter time interval within the deployment or tow through the grid array and assessing whether tags are still detected at least once within this shorter interval. This can be repeated at shorter and shorter intervals, randomly sampling several sequences for each defined interval. At the extreme, evaluations at the shortest possible time interval become equivalent to assessing $p_{ping}$ over the entire grid array.

Once $p_{res}$ is evaluated over a specified time interval, this can be interpreted as the probability that non-detection implies the fish is not present within the study area (as opposed to present, but not detected over that interval). Longer time intervals will generally give higher $p_{res}$, but shorter intervals are of interest to study fine-scale movements within and away from the array. An optimal interval can be selected that is as short as possible but still at or near 100% $p_{res}$. This provides a high level of confidence in establishing presence, so that tags are consistently detected while they are within the study area, and absence of detection over some time period implies they have left the area. Such patterns of absence could be suggestive of feeding or
spawning forays outside of the study area (Topping et al. 2006, Lindholm et al. 2007, Afonso et al. 2008) or of natural or fishing mortality (Hightower et al. 2001, Heupel and Simpfendorfer 2002). A high relocation or detection efficiency is required to make reliable estimates of the timing of these movement or mortality rates (Hightower et al. 2001) and to ensure high precision of parameter estimates (Pollock et al. 2004). Conversely, if detections of a tag within an array are sporadic, possible forays outside of the study area would be confounded with low $p_{res}$. If many tagged fish are present, signal collisions can lower $p_{res}$, especially if tag repeat rates are frequent and pulse trains are relatively long. A longer sampling interval may be required in these cases to ensure that $p_{res}$ remains near 100%.

If users rely on a temporal sequence of detections to establish presence, sampling effort (the number or proportion of fully functioning receivers within the array) should be quantified over time (Dewar et al. 2008). Variation in the number or position of receivers in a grid array over time could explain temporal variation in $p_{res}$. Even if receivers are operational over some time period, the probability of detecting a given transmission may decrease over time due to biofouling (Heupel et al. 2008), so test tag evaluations should occur before, after, and (if possible) during a study period. Likewise, they should occur over a range of weather or tidal conditions to quantify how these factors affect $p_{res}$.

2.4.3 Migrations past stationary receiver stations

Several measures can be taken to increase $p_{mig}$. These include spacing receivers closer together on a line, staggering receivers in a zigzag pattern rather than in a straight line (Clements et al. 2005), using higher power tags, and decreasing the tag repeat rate. All of these have associated trade-offs, so $p_{mig}$ will rarely be 100%. Estimating this probability can rely on a combination of field-based methods and mark-recapture modelling.

On lines of ocean receivers, multiple tows of a test tag past a line of receivers can be used to assess the proportion of tows where the tag is detected, as well as patterns in detection ranges. Tows should be done at a depth and speed reflective of the migrating fish. When multiple receivers are arranged in a line, it is especially important to conduct tows across the gaps between adjacent receivers (Pecl et al. 2006). Knowing the position and speed of a test tag crossing a line, the temporal pattern in tag transmissions can be converted into a measure of approximate distance from tag to receiver line. Distances can be estimated as either perpendicular distance from tag to receiver line regardless of whether the tag crosses overtop a receiver or in a gap, or distance from tag to any particular receiver while crossing (accounting for
the position crossed along the line). Tows with a VEMCO V9 test tag were conducted across two lines of acoustic receivers deployed on the seabed in Howe Sound in 2005 (Fig. 2.2; unrelated to receiver lines for Fig. 2.1). VEMCO VR-2 and VR-3 receivers were paired at each position on a line to compare detection rates. The test tag had a fixed repeat rate, so the distance between successive transmissions was easily calculated from average boat speed. Most test tag tows across receiver lines resulted in several detections. One tow on line ‘B’ had no detections on VR-2 receivers, and another on line ‘B’ had no detections on either receiver type. There is some indication that tags were detected from further away while the boat approached the line than after it passed over (Fig. 2.2), which could suggest that engine-related noise was greater aft of the boat than ahead. Although the number of tows was limited, the number of detections in a crossing event was inversely correlated with boat speed \((r = -0.39;\) probably related to boat noise rather than tag speed) and inversely correlated with the distance to the nearest receiver when crossing the line \((r = -0.46),\) as might be expected. There were insufficient tows conducted to provide a good estimate of \(p_{\text{mig}}\) (and tow speeds were faster than juvenile salmon typically swim), but it is straightforward to conduct enough passes at a more representative speed to estimate this ratio. Tows should be conducted across a range of environmental conditions and at different positions along the line to evaluate these effects on \(p_{\text{mig}}\). Tows by boat may underestimate \(p_{\text{mig}}\) for a given speed and depth due to added background noise from the boat engine.

In rivers, \(p_{\text{mig}}\) can be estimated by snorkelers with test tags floating past receiver stations (Chapter 8). This has the advantage that \(p_{\text{mig}}\) can still be estimated during periods when few or no fish migrate past receiver stations. As \(p_{\text{mig}}\) often varies with river discharge, test tag passes should be conducted across a wide range of flow conditions, at least bracketing those occurring during fish migration periods.

Test tag passes provide an expectation of \(p_{\text{mig}}\) for tagged fish, but this index could be biased due to depth, speed, and movement pattern differences. Actual \(p_{\text{mig}}\) can be estimated from fish tag detection data using CJS models. If survival during a migration is low such that few tagged fish cross a particular receiver line, or if \(p_{\text{mig}}\) is relatively low at and after a detection line, large sample sizes may be required to achieve reasonable precision in estimates. If survival and \(p_{\text{mig}}\) are both relatively high, reasonable precision can be achieved with a tagged sample size of 50–100 fish. Estimating \(p_{\text{mig}}\) from actual fish detection data ensures that the depth and speed of tags during crossing events are representative of the study species.

Finally, \(p_{\text{mig}}\) could be predicted based on the results of fine-scale range testing. If the relationship between \(p_{\text{ping}}\) and distance is quantified at several distance intervals with stationary
test tag range testing or with test tag tows by boat, these probabilities can be used along with fish speed and tag interval time to predict $p_{\text{ping}}$ for each transmission during a crossing event. The complement of the product of $(1 - p_{\text{ping}})$ for all transmissions gives an overall $p_{\text{mig}}$.

### 2.4.4 Mobile tracking studies

When the number and location of tags in some area at some time are unknown, mobile tracking surveys can be used to search for tags. Surveys usually consist of linear transects, typically arranged in parallel lines spaced some distance apart. The probability of detecting a tag present in an area swept, $p_{\text{mobile}}$, can be estimated at least three ways. First, similar to how $p_{\text{ping}}$ may decline with increasing distance from tag to stationary receiver, we expect that tags further away from the centre line of a mobile transect are less likely to be detected (either at any given moment, or over the long term). When tags are detected during blind transects and their locations are triangulated, the perpendicular distance to the centre line can be estimated. When a sufficient number of tags are detected to produce a frequency distribution of estimated perpendicular distances ($\geq 20$ or 30 tags), attenuation functions can be fit to these estimates to determine how $p_{\text{mobile}}$ decreases with increasing distance from the centre line (Anderson et al. 1979, Chapter 5).

Another method for estimating $p_{\text{mobile}}$ involves simultaneous use of a second sampling method to detect tagged fish. If sampling methods are independent, the probability of detecting a tag with both methods equals the product of the probabilities of detecting a tag with each method. For example, in mobile tracking laps around oil platforms on two days, Lowe et al. (2009) found more tags with a VEMCO VR-100 mobile receiver than were detected by an array of stationary VR-2 receivers over that same time period (the VR-100 typically has greater detection range). Different tags were heard on different systems, so neither system was perfect: of 100 fish originally tagged, 17 were detected only with mobile tracking, six were detected only on the VR-2 array during mobile tracking periods, and 15 were detected with both methods. The unknown number of tagged fish currently present in the study area, $X$, can be estimated using the Lincoln-Petersen method (Seber 1982). We equate: $(15/X) = ((17+15)/X) \cdot ((6+15)/X)$, which requires that $X = 44.8$. Thus the best $\hat{p}$ on the mobile tracking system is $32/44.8 = 0.714$. The $\hat{p}$ is biased high if the two methods are not independent but share positive covariation. This can occur if some behavioural subset of fish are relatively easy to detect on both systems (e.g., pelagic-oriented fish) while another subset is difficult to detect on both systems (e.g., benthic-oriented fish). A similar calculation for two mobile tracking systems operating simultaneously on the same tracking vessel is presented in Chapter 5. Enders et al. (2007) used a combination of hand-
held radio telemetry, PIT tag telemetry, and underwater visual surveys to compare $p$ of sampling methods for studying the behaviour of juvenile salmonids in small streams. Even if $p$ cannot be estimated explicitly for the second sampling method, the method can still be used to calibrate $p_{mobile}$ estimates. If acoustic-tagged fish are also given external markings like spaghetti tags, SCUBA diving can be used to visually verify whether tagged fish are present in an area swept by mobile tracking transects. Overhead and surrounding benthic structures may interfere with acoustic signal detection even though the fish is easily seen (or vice versa). Alternatively, telemetry can provide the calibration for other sampling programs. Edwards et al. (2007) used telemetry and time-depth data loggers for estimating the detection probability of aerial surveys for manatees. Korman et al. (2002) used radio telemetry to calibrate estimates of visual observer efficiency during snorkel surveys for steelhead trout spawners.

A third method for estimating $p_{mobile}$ again involves test tag evaluations. A tag can be deployed at a depth representative of the study species (especially important if fish are typically near the bottom surrounded by interfering structures), and transect passes can be repeatedly conducted to quantify the proportion of passes where the tag is detected. Since $p_{mobile}$ is expected to vary with boat speed (Chapter 5), tag depth, tag-to-receiver distance, and environmental conditions, test tag passes should be conducted across a range of these variables. If tagged fish are confined to some area (e.g., a lake or reservoir) and the entire area is sampled, then the probability of relocating tags on successive surveys can be calculated from the number missed but known to have been there because they were detected in later surveys (Hightower et al. 2001). This proportion might vary among sampling trips or seasonally. If mobile tracking is conducted in an area where acoustic conditions show little variation over time, then prior calibrations of test tag acoustic strength at specific distances can be used to later estimate the approximate distance to a fish tag in the study area (Block et al. 1997).

Since boat-related noise may dominate the total background noise in mobile tracking studies, maximizing the distance between boat and hydrophone or taking other measures to reduce boat noise reaching the hydrophone will aid with increasing $p_{mobile}$. 
Figure 2.1. Detection probability of a single transmission at different tag depths and tag-to-receiver distances. Receivers (VEMCO VR-2 or VR-3) were deployed at 145 m depth at various distances from two test tags (VEMCO V9 or V7). Probability surfaces are interpolated from a Lowess fit (smoothing parameter $\alpha = 0.2$), with shading ranging from white (100%) to dark grey (0%). Probability contours are shown. Note the different scales of x and y-axes. Raw data provided by D. Welch.
Figure 2.2. Detection sequences of ten test tag tows past two stationary receiver lines. Distance intervals were calculated from average boat speed (ranging from 7.4–12.7 km·h⁻¹ while crossing) so are approximate. VEMCO VR-2 and VR-3 receivers were paired at the same location. Empty circles show transmissions not detected, and circles with X’s show transmissions detected. Test tags were generally deployed >500 m from the line while approaching and retrieved >500 m from it after passing; transmissions not detected either before the first detection or after the last detection are not shown.
2.5 References


3 Estimating detection probabilities for multiple tagged salmon stocks with nested migration routes

3.1 Introduction

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 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 opportunity for ‘sharing’ detection information from other groups in the analysis of any one (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 (‘stock’ and ‘population’ are generally interchangeable in this thesis with regard to juveniles). 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 maintain distinct parameter estimates for the segments and stations unique to each stock.

Methods for structuring complex detection history data are presented in this chapter, which allow standard CJS models to be applied to estimate survival and detection probabilities more precisely. These methods are intended for cases where multiple stocks are analyzed 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 that were tagged under POST. Examples are taken from these detection data, but the methods can be generalized 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 like R or WinBugs.

First, the POST study 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 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 arrays.

3.2 Study system: nested migration routes of 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 2004–2007 (V7 or V9 tags, VEMCO/AMIRIX Systems, Inc., Halifax, Canada). Their migrations downstream and through the Georgia Strait ecosystem were monitored with the POST acoustic array (Welch et al. 2003; Fig. 3.1). 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 4–30 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 here. Some detection stations were shared among all stocks and others were specific to only 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 2–12 detection stations during their migration out of Georgia Strait (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 only detected moving northward after ocean entry across the northern Strait of Georgia (NSOG) and Queen Charlotte Strait (QCS) lines (Fig. 3.1, arrows A-C), while the remaining third had some fish move north and others move south across the Juan de Fuca Strait (JDF) line (Fig. 3.1, arrow D). To quantify the proportion of fish that survived their inshore 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 Georgia Strait system. This pooling of outer lines complicates mark-recapture estimates of survival probability ($\phi$) 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 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. 3.1, 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, one specifies a likelihood function for the CJS model and finds the maximum-likelihood estimates (MLEs) of parameters $\phi$ in each segment ($\hat{\phi}_{Seg}$) and $p$ at each station ($\hat{p}_S$) given the detection data. The final $\phi_{Keogh\to QCS}$ and $p_{QCS}$ parameters are confounded and not separately identifiable (call their product $\beta_3$), but $\phi_{Release\to Keogh}$ ($\phi_1$) 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, $L$:

$$L \propto [\phi_1 p_2 \beta_3]^{25} [\phi_1 (1 - p_2) \beta_3]^2 [\phi_1 p_2 (1 - \beta_3)]^{38} [\phi_1 (1 - p_2)(1 - \beta_3) + (1 - \phi_1)]^{27}.$$
The log-likelihood becomes a sum rather than a product over all detection histories, and typically the log-likelihood, $\ln(L)$, is maximized by using optimisation routines. Using MARK, the MLEs and estimated standard errors ($SE$) 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, as the number of fish detected at and after the first detection station was sufficient to estimate $\phi_1$ 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—perhaps there are ways to incorporate detection data from all these groups to increase pooled sample sizes for estimating $p$ at the Keogh River receiver station? Such methods are developed in this chapter.

Further descriptions, assumptions, and more examples of fitting CJS models can be found in Lebreton et al. (1992), Pollock et al. (1990), 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 residualize (remain resident) in freshwater before arriving at the first station. This is unlikely to be an issue for species like sockeye salmon known to undergo long-distance migrations (Hartt and Dell 1986, Groot and Cooke 1987), but may confound estimated survival of species like coho salmon that do not necessarily migrate continuously after ocean entry (Healey 1980, Pearcy and Fisher 1988). Downstream survival could also be underestimated for species such as steelhead that may not migrate downstream and instead residualize 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).

(4) Losses on capture (Jolly 1965) can be ignored since tagged fish are not handled after release, and crossing a detection station should not affect survival.

For the remainder of this chapter, 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 \( \hat{\phi} \) or \( \hat{p} \) may not be reliable if separate CJS models were constructed for each stock in each year. Instead, groups were analyzed 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 since tag types differed in acoustic power and hence detection range (V7 tags, 136 dB re 1\( \mu \)Pa 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 \[ \phi_{\text{Seg};\text{Group}} \].

Unless one is interested in an overall effect of segment or group, main effects per se are not necessary to model (i.e., \[ \phi_{\text{Seg};\text{Group}} \], 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 sub-models were constructed for each species, stock, and year combination in terms of segment-specific \( \phi \), but \( p \) for a given station, tag type and year were shared across species and stocks.

### 3.3 Variable detection stations along 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. One might 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 analyze multiple stocks and/or years together in the same model (for example, 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 stock with those from other stocks.

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. 3.1, 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. 3.1, 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. 3.1, 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. 3.1, 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 capture 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 ‘S\textsubscript{11}Y\textsubscript{2007}C\textsubscript{Squamish watershed}’, ‘S\textsubscript{11}Y\textsubscript{2006}C\textsubscript{Nimpkish watershed}’, or ‘S\textsubscript{11}Y\textsubscript{2005}C\textsubscript{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. 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 \( \hat{p} \) are given for the 12th digit in this example). The number of fish per stock tagged with V9 tags ranged from 8–107. 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. 3.1, 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. 3.1, 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:

\[
\text{logit}(p_i) = \beta_0 + \beta_1 \cdot \text{Tag} + \beta_x \cdot S_i Y_j Spp_k Stk_l, 
\]

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 \( i-I \)th station in some particular location).\(^1\) Note the ‘Y’ and additive ‘Tag’ terms are not necessary in this simple example since all stocks considered had V9 tags in either 2004 or 2005 (years were analyzed separately). The model coefficients correspond with an intercept (\( \beta_0 \)), dummy variable for ‘Tag’ (\( \beta_1 \), where ‘Tag’ takes a value of 1 for one tag type and 0 for the other

\(^1\) The term \( \ldots + \beta_x \cdot S_i Y_j Spp_k Stk_l \) is represented in this form to show that \( x-1 \) coefficients are required to code for all unique combinations of \( S \), \( Y \), \( Spp \), and \( Stk \), i.e., values from 2...x. A more familiar form may be \( \ldots + \beta_{i,j,k,l} \), such that there is one single coefficient for each combination of \( (i, j, k, l) \).
tag type), and each existing combination of $S_l Y_j Spp_k Stk_t (β_2, ..., β_x)$. It is these coefficients that are fitted to detection data, and from them the biological parameter estimates $\hat{ϕ}$ and $\hat{p}$ are reconstituted. In alternative notation (Lebreton et al. 1992), this is model $[ϕ_{Seg;Y:Spp;Stk} P_{S;Y:Spp;Stk+Tag}]$ or $[ϕ_{Seg;Group} P_{S;Group+Tag}]$ without main effects for segment, station, or group. The $\hat{p}$ vary among stocks at the NSOG station in 2004 and 2005 under the CJS stock-independent model, ranging from 0.60–0.89 (Table 3.1). There were insufficient detection data of Tenderfoot coho beyond NSOG to estimate $\hat{p}$ 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 3.1). These four estimates of 1.00 with (asymptotic) $SE (\hat{p})$ 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 3.1).

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

\[
(3.2) \quad \logit(p_l) = \beta_0 + \beta_1 \cdot \text{Tag} + \beta_x \cdot S_l Y_j ,
\]

or model $[ϕ_{Seg;Y:Spp;Stk} P_{S;Y+Tag}]$ under alternative notation. The fully-pooled $\hat{p}$ are all the same within each year (Table 3.1) 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):

\[
(3.3) \quad \logit(p_l) = \beta_0 + \beta_1 \cdot \text{Tag} + \beta_x \cdot S_l Y_j C_m ,
\]

or alternatively, $[ϕ_{Seg;Y:Spp;Stk} P_{S;Y:C+Tag}]$. Looking at just the 12th digit (11th station) for the 2005 example, the interaction terms would be $S_{12} Y_{2005} C_{SoG}$, $S_{12} Y_{2005} C_{Keogh}$, and $S_{12} Y_{2005} C_{Nimpkish}$. Here, Tenderfoot coho, Cheakamus steelhead, and Englishman steelhead are all part of the Strait of Georgia cluster (SoG) 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. Consequently, \( \hat{p} \) at NSOG are common across these stocks (Table 3.1). If a similar construction to Eq. 3.3 is modelled for the 2004 example, the three stocks also share a common \( \hat{p} \) at NSOG (Table 3.1). 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; since 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 3.1). 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 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 (\( \Delta \text{QAICc} = 12.0 \); Table 3.2). In 2005, the stock-independent model was the top-ranked model, but the geographic cluster model still had considerable support (\( \Delta \text{QAICc} = 2.9 \)). 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 3.2). 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 3.1), differences could simply be related to sampling effects 
from sparse data (for example, \( \hat{p} = 0.60 \) at NSOG for Englishman steelhead in 2005 is based on 3 
of the 5 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 lower for the geographic 
cluster model than for the stock-independent model (Table 3.1), 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 Eq. 3.3) could be used to 
differentiate migration route clusters at other digits of the detection histories as well. If multiple 
years are contained in a dataset, the interaction terms easily allow specifying which cluster(s) 
share which stations in which year.\(^2\)

### 3.4 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.

---

\(^2\) The data structuring methods presented here for applying CJS models to situations with complex detection histories were implemented with Program MARK. 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 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.
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, $N$, is built into the model to designate the probability of movement in one particular direction, with $1 - N$ 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 overall survival of stocks during the inshore 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 Georgia Strait south of NSOG, with some individuals crossing the JDF line and other individuals crossing NSOG and/or QCS lines (Fig. 3.1 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 overall survival out of Georgia Strait 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). Since 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 ($\psi$) parameters therefore cannot be used to untangle route-specific parameters $p$ at QCS and JDF, $\phi$ 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 $N$ (or $\psi$) 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 $N$, 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. 3.1, 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 since 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 $\phi$ 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. 3.2. These include $N$, $\phi_{north1}$ and $\phi_{north2}$ for the two segments along the northern fork, $\phi_{south}$ for the southern segment, and $p_{north1}$, $p_{north2}$, and $p_{south2}$ 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 $\phi_{1,CJS}$, $p_{1,CJS}$, and $\phi_{2,CJS}$ are then compared to true parameter values to assess bias ($p_{2,CJS}$ can be fixed at the true value for this optimisation so that it is not confounded with $\phi_{2,CJS}$). Bias is calculated as, for example, $(\hat{\phi}_{1,CJS} - \phi_{north1}) / \phi_{north1}$.

As expected, biases were found using simulated data when a true split-route pattern was collapsed into a classic CJS analysis (because of confounding with movement, and because $\phi_{north1}$ and $p_{north1}$ did not have equivalent parameters along the southern fork; Fig. 3.3). Biases were typically seen in $\phi_{1,CJS}$ and $p_{1,CJS}$, with zero bias in any parameters at $N = 1$ and bias worsening as $N$ decreases. Estimates of $\phi_{2,CJS}$ were unbiased across all values of $N$ in the cases considered. Consistent changes across detection stations in true $p$ did not change the bias in either CJS parameter (Fig. 3.3, a vs. b) although lower $p$ would in general lead to reduced precision of estimates. Consistent changes across segments in true $\phi$ affected the bias in $\phi_{1,CJS}$ (and, to a lesser degree in $p_{1,CJS}$) with greater bias seen at lower $\phi$ across all values of $N$ (Fig. 3.3, a vs. c). Bias in $\phi_{1,CJS}$ partly arises because true survival 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 $\phi_{\text{south}}$ is set equal to the product of $\phi_{\text{north}1}$ and $\phi_{\text{north}2}$, the bias in $\hat{\phi}_{1,\text{CJS}}$ disappears (Fig. 3.3d; although bias in $\hat{p}_{1,\text{CJS}}$ 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 $N$ 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, Eq. 3.3. In a multi-stock context where split-route migration patterns exist (Fig. 3.2), some of the stocks that share $p_{\text{north}1}$ may have $N = 1$ while others have $N < 1$. For each stock that shows evidence of split-route patterns with $\hat{N} < 1$, an extra parameter for $p$ specific to that stock and station can be incorporated into the model. For example, Eq. 3.3 can be extended by the terms:

$$\begin{align*}
(3.4) \quad & \cdots + \beta_Y \cdot S_{12} Y_{2005} \text{Stk}_a + \beta_Z \cdot S_{12} Y_{2006} \text{Stk}_b + \cdots,
\end{align*}$$

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

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 $N$ 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 (Eq. 3.4) 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.

### 3.5 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 detection probabilities among stocks if environmental conditions change over time. Background noise sources such as wind, boat traffic, soniferous invertebrates, or turbulence due to river flow could change over time, affecting the signal:noise ratio of acoustic or radio tags and therefore impacting detection probabilities (Voegeli and Pincock 1996, Heupel et al. 2006, Simpfendorfer et al. 2008).

Within a population, attempts to account for heterogeneity in detection probabilities among individuals can improve estimates if detection probability does vary among individuals (Pledger et al. 2003). If detection probability 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 detection probability that should be explicitly estimated.

In rivers, water level and discharge often increase during late spring to early summer due to snow melt (Fig. 3.4). 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 detection probability during high flow periods, which in the B.C. 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. 3.4). Release times spanned nearly two months, and the corresponding relative water levels and flows at these times increased substantially.

The effect of different release times or flows on detection probability can be observed by initially treating release groups independently to calculate CJS estimates, using a model such as \( \hat{p} \). On average, and within each tag type, these stock-specific estimates \( \hat{p} \) decreased as river level increased during the migration season. The left panels of Fig. 3.5 show stock-independent estimates.
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 higher 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. 3.5). 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 $\hat{p}$. Indeed, comparing models in terms of QAICc scores, the fully-pooled model $[p_{S,Y+Tag}]$ is poorly supported by the data compared to the fully-independent model $[p_{S,Y:Sp:Stk:Tag}]$ due to lack of fit, as seen in the lower log-likelihood values (Table 3.3). However, keeping groups fully independent like the left panels of Fig. 3.5 requires many more parameters to be estimated (Table 3.3). 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 0–1 (Table 3.3; Fig. 3.5). Considering only the $\hat{p}$ that were reasonably well estimated across all models, $\overline{SE}(\hat{p})$ tended to be larger for the stock-independent model (median $\overline{SE}(\hat{p}) = 0.09$) than for the fully-pooled model (0.04; Table 3.3).

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 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. 3.5) 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
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 3.3). The $\hat{p}$ were well estimated and the decrease in precision from the fully-pooled model was only minor (Table 3.3; Fig. 3.5).

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 ($\Delta$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 which is 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 $p$. However, as environmental covariate models involve only one parameter more than fully-pooled models, it is likely that some hypothesized covariate 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 logit($p$) vs. 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 (since 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.

3.6 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 $p$ 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. 3.6). 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 lower proportion of the total transect line (grey dots in Fig. 3.6) 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, \( d_{\text{shore-}1} \)) and the proportion of receivers successfully recovered and downloaded. After excluding receivers not recovered (Fig. 3.6), 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.

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. 3.7). In most lines and years, assumed \( r \) of \( \geq 400 \text{ m} \) resulted in coverage >0.9 since receivers were typically spaced about 800 m apart. At \( r < 400 \text{ m} \), 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 \( r \). Since 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, HS\text{inner}, and HS\text{outer} (\( p \) 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 downstream of the line of interest. These shortened versions reduced the dependence of \( \hat{p} \) and \( \overline{SE}(\hat{p}) \) on parameters from other segments and detection stations, and eliminated the effect of confounding with any southward movements after entering Georgia Strait (i.e., only fish moving northward were considered for estimating \( p \) at NSOG). Survival models were kept as flexible as possible, \([\phi_{\text{Seg}(Y:Spp:Stk:Tag)}] \). Detection
models involved pooling stocks but maintaining independence in \( p \) among years and an additive difference among V7 and V9 tag types, \([p_{S \times Y + \text{Tag}}]\). Among the values of coverage at assumed values of \( r \) ranging from 300–550 m, the best statistical predictor of \( \hat{p} \) (in terms of \( r^2 \) and AIC scores, not shown) was the coverage covariate at \( r = 400 \) m (‘coverage\(_{400}\)’). Estimates of \( p \) are plotted against coverage\(_{400}\) for each line in each year (Fig. 3.8a). A large difference is observed among tag types with the higher energy output of V9 tags translating into higher \( \hat{p} \). The effect of coverage\(_{400}\) appears to be moderate, with \( \hat{p} \) decreasing from about 0.95 to 0.85 for V9 tags and about 0.8 to 0.6 for V7 tags as coverage\(_{400}\) 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 vs. Howe Sound) on \( \hat{p} \).

The range of coverage\(_{400}\) spans only from about 0.85–1 for these ocean receiver lines (Fig. 3.8a). This provides little opportunity aside from extrapolation to assess how \( p \) would change at much lower levels of coverage\(_{400}\) 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. For example, every second receiver along with its detection data could be excluded, after which \( p \) and coverage could be re-estimated. Excluding even numbered receivers (Fig. 3.6) 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, coverage\(_{400}\) and \( \hat{p} \) both decreased (Fig. 3.8b). Coverage\(_{400}\) of only-odd or only-even receiver subsets ranged from 0.45–0.65. Subsetted \( \hat{p} \) ranged from about 0.4–0.9, with best fit predicted values of about 0.77 for V9 tags and 0.57 for V7 tags at a coverage\(_{400}\) of 0.55. This decline in \( \hat{p} \) with declining coverage\(_{400}\) was less precipitous than expected based on the full-receiver dataset (compare slopes of the solid and dotted logistic best fit lines in Fig. 3.8b). Coverage\(_{400}\) 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, 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 about 20%.

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 $\bar{SE} (\hat{p})$ is not appropriate. Average coefficients of variation (CV, i.e., $\bar{SE} (\hat{p}) / \hat{p}$) when all receivers were included on a line were lower (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 higher uncertainty results in higher uncertainty in $\hat{\phi}$ as well.

Assessments of receiver redundancy at stations with several receivers can be done 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. Aside from assessing receiver redundancy using a covariate such as coverage_{400}, covariates can be used directly in specifications of candidate models, e.g., $[p_{Y + \text{Tag} + \text{coverage}_{400}}]$, to evaluate whether they explain an important part of the total variation in $p$ compared to models without the covariate.

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 $\hat{\phi}$. This might be possible by reducing the spacing between receivers on a line but 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 one should still expect $p < 1$ over the long term). An additional station instead might be more advantageous, thereby partitioning some segment of the migration into two separate segments and allowing $\phi$ 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.
Table 3.1 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.

<table>
<thead>
<tr>
<th>Stock</th>
<th>No. tagged</th>
<th>Station crossed</th>
<th>Stock-independent</th>
<th>Geographic cluster</th>
<th>Fully-pooled</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>2004 stocks</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Tenderfoot Creek coho</td>
<td>100</td>
<td>NSOG</td>
<td>NA</td>
<td>0.82 (0.07)</td>
<td>0.95 (0.01)</td>
</tr>
<tr>
<td>Englishman River steelhead</td>
<td>67</td>
<td>NSOG</td>
<td>0.70 (0.14)</td>
<td>0.82 (0.07)</td>
<td>0.95 (0.01)</td>
</tr>
<tr>
<td>Sakinaw Lake sockeye</td>
<td>97</td>
<td>NSOG</td>
<td>0.89 (0.07)</td>
<td>0.82 (0.07)</td>
<td>0.95 (0.01)</td>
</tr>
<tr>
<td>Keogh River coho</td>
<td>107</td>
<td>Keogh</td>
<td>1.00 (0.00)</td>
<td>0.98 (0.02)</td>
<td>0.95 (0.01)</td>
</tr>
<tr>
<td>Keogh River steelhead (W)</td>
<td>78</td>
<td>Keogh</td>
<td>1.00 (0.00)</td>
<td>0.98 (0.02)</td>
<td>0.95 (0.01)</td>
</tr>
<tr>
<td>Keogh River steelhead (H)</td>
<td>92</td>
<td>Keogh</td>
<td>0.93 (0.05)</td>
<td>0.98 (0.02)</td>
<td>0.95 (0.01)</td>
</tr>
<tr>
<td>Nimpkish River coho</td>
<td>99</td>
<td>Nimpkish</td>
<td>0.97 (0.02)</td>
<td>0.97 (0.02)</td>
<td>0.95 (0.01)</td>
</tr>
<tr>
<td><strong>2005 stocks</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Tenderfoot Creek coho</td>
<td>50</td>
<td>NSOG</td>
<td>NA</td>
<td>0.67 (0.11)</td>
<td>0.91 (0.03)</td>
</tr>
<tr>
<td>Cheakamus River steelhead</td>
<td>49</td>
<td>NSOG</td>
<td>0.69 (0.13)</td>
<td>0.67 (0.11)</td>
<td>0.91 (0.03)</td>
</tr>
<tr>
<td>Englishman River steelhead</td>
<td>43</td>
<td>NSOG</td>
<td>0.60 (0.22)</td>
<td>0.67 (0.11)</td>
<td>0.91 (0.03)</td>
</tr>
<tr>
<td>Keogh River coho</td>
<td>49</td>
<td>Keogh</td>
<td>1.00 (0.00)</td>
<td>1.00 (0.00)</td>
<td>0.91 (0.03)</td>
</tr>
<tr>
<td>Keogh River steelhead (H)</td>
<td>50</td>
<td>Keogh</td>
<td>1.00 (0.00)</td>
<td>1.00 (0.00)</td>
<td>0.91 (0.03)</td>
</tr>
<tr>
<td>Nimpkish River coho</td>
<td>8</td>
<td>Nimpkish</td>
<td>1.00 (0.00)</td>
<td>1.00 (0.00)</td>
<td>0.91 (0.03)</td>
</tr>
</tbody>
</table>
Table 3.2 Information-theoretic comparison of detection probability sub-models used with two example datasets (2004 and 2005) of salmon stocks. Stocks included in each year are the same as shown in Table 3.1, all with V9 tags.

<table>
<thead>
<tr>
<th>p sub-model</th>
<th>(k^b)</th>
<th>2·ln((L))</th>
<th>QAICc (^c)</th>
<th>(\Delta)QAICc</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>2004 stocks</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Geographic cluster(^d)</td>
<td>40</td>
<td>-1708.4</td>
<td>1471.5</td>
<td>0</td>
</tr>
<tr>
<td>Stock-independent(^d)</td>
<td>48</td>
<td>-1701.9</td>
<td>1483.5</td>
<td>12.0</td>
</tr>
<tr>
<td>Fully-pooled (^d, e)</td>
<td>34</td>
<td>-1751.1</td>
<td>1493.6</td>
<td>22.1</td>
</tr>
<tr>
<td><strong>2005 stocks</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Stock-independent(^d)</td>
<td>56</td>
<td>-1009.6</td>
<td>963.0</td>
<td>0</td>
</tr>
<tr>
<td>Geographic cluster(^d)</td>
<td>46</td>
<td>-1041.0</td>
<td>965.9</td>
<td>2.9</td>
</tr>
<tr>
<td>Fully-pooled (^d, e)</td>
<td>38</td>
<td>-1069.8</td>
<td>971.9</td>
<td>8.8</td>
</tr>
</tbody>
</table>

\(^a\) Survival probability sub-models were held constant across all detection probability sub-models, as \(\phi_{\text{Seg:Spp:Stk:HW}}\). The ‘HW’ variable was only necessary in 2004 to distinguish hatchery and wild-reared Keogh River steelhead smolts.

\(^b\) The parameter count is adjusted to include the number of potentially estimated parameters including those at boundaries of 0 or 1.

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

\(^d\) Sub-models of \(p\) were specified as: stock-independent, \([p_{\text{S:Spp:Stk:HW}}]\); fully-pooled, \([p_{\text{S}}]\); geographic cluster, \([p_s + s_{11}\text{CEng} + s_{12}\text{C4Nimp} + s_{13}\text{CKeogh}]\) in 2004 and \([p_s + s_{10}\text{CEng} + s_{11}\text{CEng} + s_{12}\text{C4Nimp} + s_{13}\text{C4Nimp} + s_{14}\text{C4Keogh}]\) 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.

\(^e\) The 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.
Table 3.3  Information-theoretic comparison of detection probability sub-models and other model-fitting criteria in the Fraser River salmon smolt dataset, 2004–2007. Model comparison criteria include number of parameters \((k)\), 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 span 0–1), and quantiles of the distribution of properly-estimated \(\hat{SE}(\hat{p})\) at all river stations, years, tag types, and release groups.

<table>
<thead>
<tr>
<th>(p) sub-model(^a)</th>
<th>(k)(^b)</th>
<th>(2\cdot\text{ln}(L))</th>
<th>QAICc (^c)</th>
<th>(\Delta\text{QAICc})</th>
<th>(\hat{p}) poorly estimated (^d) at boundary</th>
<th>95% c.l. span 0–1</th>
<th>Percentile of distribution of (\hat{SE}(\hat{p})) (^e)</th>
</tr>
</thead>
<tbody>
<tr>
<td>(p_{S:Y+Tag+RiverLevel})</td>
<td>121</td>
<td>−5760.3</td>
<td>4365.2</td>
<td>0.0</td>
<td>0</td>
<td>0</td>
<td>0.02 0.04 0.07</td>
</tr>
<tr>
<td>(p_{S:Y:Spp:Stk:Tag})</td>
<td>193</td>
<td>−5566.2</td>
<td>4384.5</td>
<td>19.3</td>
<td>13</td>
<td>6</td>
<td>0.03 0.09 0.22</td>
</tr>
<tr>
<td>(p_{S:Y+Tag+DOY})</td>
<td>121</td>
<td>−5794.4</td>
<td>4389.6</td>
<td>24.4</td>
<td>0</td>
<td>0</td>
<td>0.02 0.04 0.07</td>
</tr>
<tr>
<td>(p_{S:Y+Tag})</td>
<td>120</td>
<td>−5955.9</td>
<td>4502.8</td>
<td>137.6</td>
<td>0</td>
<td>0</td>
<td>0.02 0.04 0.07</td>
</tr>
</tbody>
</table>

\(^a\) Survival probability sub-models were held constant across all detection probability sub-models, as \([\phi_{S:Seg;Y:Spp;Stk}]\), where ‘Group’ represents a unique combination of year, species, and stock.

\(^b\) The parameter count is adjusted to include the number of potentially estimated parameters including those at boundaries of 0 or 1.

\(^c\) AIC values are adjusted for small sample sizes and extra-binomial variation with \(c = 1.40\) (Lebreton et al. 1992).

\(^d\) Out of a total 61 \(\hat{p}\) across river stations, years, tag types, species, and stocks.

\(^e\) Taken from the distribution of the remaining 45 \(\hat{SE}(\hat{p})\) after excluding across all models the \(\hat{p}\) parameters which were estimated poorly.
Figure 3.1 Map of POST study area showing migration routes of stocks used as examples. Grey triangles show release locations; labels of those which are referred to in this chapter are underlined. Black circles show locations of acoustic receiver stations in 2004–2007. Not all release locations and stations were used in all years. Arrows A-D show example migration routes, with D being 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.
Figure 3.2 Split-route migration pattern with variable number of stations in each fork. Two detection stations (grey lines) are situated along one fork and one station is along the other fork (similar to that of arrow D in Fig. 3.1). Parameters representing probabilities of survival, detection, and directional movement are shown along with example sets (a-d) of these parameters.
Figure 3.3 Percent biases in estimated survival and detection probabilities. Detection histories were simulated under a ‘true’ split-route scenario and were then analyzed with CJS models that failed to account for split-route flexibility, pooling detections at the final stations along the two forks shown in Fig. 3.2. True parameter values in subplots a-d correspond to the example sets shown in Fig. 3.2, except \( N \) is shown ranging from 0.1–1.0.

Figure 3.4 Relative water level of the Fraser River during the salmon smolt migration in 2004–2007. 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. 3.1).
Figure 3.5 Detection probability estimates at three successive Fraser River detection stations in 2006 vs. river level at the mean arrival time of a stock at a detection station. Survival sub-models are fully independent among release groups and segments, $\phi_{\text{seg,Y:Spp:Stk}}$. Detection probability sub-models 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 (▲) and thin for V9 tags (○). River levels were measured at the Mission gauge by Environment Canada.
Figure 3.6 Hypothetical multi-receiver detection station. Receivers (black dots) are arranged in a line between two land masses. The X denotes a receiver not recovered. Circles of radius $r$ are drawn around each recovered receiver, which are numbered. Odd numbered receivers are shaded.

Figure 3.7 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 $r$. 

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Figure 3.8  Detection probability estimates 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 re-calculated 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 \( \hat{p} \).
3.7 References


4 Estimating detection probabilities of tagged fish migrating past fixed receiver stations using only local information

4.1 Introduction

Spatial approaches to CJS models (Cormack 1964, Jolly 1965, Seber 1965) are often used for migrating animals, where fish tagged with individually-coded transmitters may be detected at successive detection stations (lines or grids of receivers) along migration routes (Burnham et al. 1987). Routes are partitioned into segments between stations, with survival in each segment and detection probability at each station estimated jointly. In some of these spatial approaches, detection data may be limited to whether or not a tag was detected at a particular station, such as passive integrated transponder (PIT) tags detected in dam bypass channels. In other spatial approaches, if fish are tagged with radio (Skalski et al. 2001) or acoustic (Welch et al. 2009) tags and pass detection stations, additional information may be available other than simply a binary outcome. Radio and acoustic tag transmissions are often detected multiple times as a tagged fish passes a stationary receiver during its migration, or on multiple receivers at a station. Sequential patterns of detections during a crossing event may provide additional information about the probability of detection at a station.

Estimating a mark-recapture detection probability for fish migrating past a station of interest (\(p_{mr}\), the probability of detecting a tagged fish as it crosses a detection station) requires detection data at station(s) further along a migration route. The parameter is estimated as the ratio of number of fish detected at the line of interest to the estimated number alive and available to detection at the line, the latter derived from detection information after the line of interest. Detection probability at the final detection station along a migration route, and survival to that final station, are confounded in classic CJS models. This presents a problem for many radio or acoustic tracking studies where survival to the final detection station is often of biological interest, but budgetary or logistical factors limit the number of detection stations that can be deployed. A fixed value can be assumed for the final \(p_{mr}\) (Welch et al. 2009), but this could result in substantial bias in the resulting estimate of the final survival probability. Incorporating a covariate as a predictor of \(p_{mr}\) (Pollock et al. 1984), however, allows the final station’s \(p_{mr}\) to be estimated through its relationship with \(p_{mr}\) at other stations. Covariates that explain variation in
Among detection stations can therefore be of great use in survival estimation. While classic CJS models assume instantaneous sampling occasions with a single opportunity to detect or capture an animal that is alive, telemetry data generally provide several opportunities to detect a tagged animal crossing a station, with a variable probability of detecting transmissions during a crossing event.

In this chapter, we present a method to estimate $p_{\text{mr}}$ based on the sequence of detections and known missed tag signals of individual fish that swim past a station. Essentially, we estimate the proportion of fish not detected while crossing a station from the detection patterns of fish that were detected. Detection probabilities of individual tag transmissions may ‘attenuate’ with increasing tag-to-receiver distance. We fit attenuation models to crossing sequences of individual fish, and used estimated model parameters to calculate a local detection probability estimate, $p'_{\text{loc}}$. This estimate uses only information at the detection station of interest, not at stations further along a migration route. Specifically, we considered detection data from migrating juvenile salmon with acoustic tags passing one or more POST acoustic receiver stations, but the method could be used for other telemetry systems that log the time when individually-coded tags are detected on stationary receivers. The predictive ability of two other types of local-information detection probability estimates is also considered: fitting probability distributions to frequency distributions of the length of crossing sequences, and subsetting data from a multi-receiver line. We analyze crossing sequences at stations and estimate $p'_{\text{loc}}$ for a range of environments: a large river, small rivers, estuaries, and the coastal ocean. We compare $p'_{\text{loc}}$ against CJS detection probability estimates ($\hat{p}_{\text{mr}}$) at the same detection stations to evaluate the predictive ability of $p'_{\text{loc}}$.

4.2 Methods

4.2.1 Tag and tracking technology

POST detection data from juvenile coho, steelhead, sockeye, and Chinook salmon released in 2004–2006 (9–16 populations each year) were used for this chapter. Stationary VR-2 receivers detected implanted V7 or V9 acoustic tags that passed the stations. About half the tagged populations each year migrated out of the Fraser River, while the other half originated from smaller rivers in B.C. In rivers and estuaries, receivers were deployed as single or paired units, and on the ocean seabed, were arranged in transect lines perpendicular to typical migration
routes, spaced about 700–900 m apart. These tags can typically be detected up to 500 m from a fixed station in relatively calm conditions with low levels of background noise; this range can be substantially less in sub-optimal conditions, especially in rivers (Voegeli et al. 1998, Simpfendorfer et al. 2008). The two tags used differ in acoustic power output (V7 tags, 136 dB re 1µPa at 1 m; V9 tags, 142 dB), which affects detection range and hence the probability of being detected. On average, tags transmitted a signal every 62 sec. As tagged smolts were usually <200 mm long and swim at up to a few body lengths per second (Chapter 7), a tag generally transmits several signals as the fish crosses a receiver station. The number of signals transmitted within the detection range of a receiver while crossing a station depends on several factors: (1) noise levels, bubbles, and suspended matter in the water during the time of crossing, since these affect detection range (as well as the probability of detection within this range); (2) speed of the fish, including assistance by river or tidal currents; (3) location of passing along a multi-receiver line, since the distance while within detection range ranges from twice the detection radius, if passing directly over a receiver, to the chord length of overlapping detection radii, if passing in the gap between two receivers (Welch et al. 2003); and (4) random variation in the intervals between signals during the crossing event. Tags are often programmed with a random interval between signals to minimize the chance of repeated collisions with other tags. By chance, more or fewer signals than average can be transmitted during a crossing event.

4.2.2 Constructing sequences of detections and missed transmissions

Most tags used by POST for juvenile salmon had random uniform intervals of 30–90 s between coded signals. Each signal is a train of 7–8 pulses that takes approximately 2 s to transmit (the intervals between pulses contain the information for unique codes). The time between the start of successive signals therefore ranged from 32–92 sec, with an average of 62 sec. All the detections of a given fish at a given station were arranged in chronological order. In cases where a tag was heard more than once at a station, successive detections were often 32–92 s apart, but sometimes several minutes apart, indicating that an unknown number of transmissions was not detected between these times. If >60 min elapsed between successive detections, we parsed the sequence and considered only the first part as a crossing event. For stations with multiple receivers, if a tag was detected simultaneously on two or more receivers, we removed all but one of the simultaneous detections from the list since the interest was in detection sequences for the line as a whole, not for each individual receiver. A sequence of n detections remained.
From the temporal detection sequence, we created a crossing sequence of detected signals (‘1’s) and missed signals (‘0’s). Since tags were programmed with random intervals it was not possible to determine the exact number of missed signals between recorded detections. The distribution of intervals between signals is uniform, however, so we estimated the number of misses simply by comparing the actual time between successive detections with multiples of the average signal interval (62 s). Beginning with the time of actual first detection ($t_1$), we constructed a hypothetical sequence of signal times that incremented by the average interval. Whichever hypothetical time was closest to the next actual detection time ($t_2$), we assigned that time a ‘1’ in the corresponding crossing sequence. We assigned all hypothetical times between the two detections a ‘0’ in the crossing sequence, to represent signals not detected. We repeated this algorithm beginning with the next actual detection time ($t_2$) until the last actual detection time ($t_n$) was reached. Sequences of ‘1’s and ‘0’s were of length $m$, containing $n$ detections and $m - n$ misses. Sequence length ranged from 1 (a single detection of a tag crossing a station) to >2000 (where a fish likely stopped in proximity of a station). For estimation purposes, we added a sequence of 50 ‘0’s before and after the main sequence, to represent the signals that were not detected as a fish approached and left the station, before and after its first and last detection. This choice of 50 ‘0’s was arbitrary, but was generally robust to different numbers of ‘0’s considered (e.g., 10 or 100) in terms of parameter and detection probability estimates. Pseudocode for constructing crossing sequences is shown in Appendix B.

Several filtering steps were taken to ensure the local detection probability estimates derived from crossing event data were representative of migrating fish so they would be comparable to mark-recapture detection probabilities, and also to reduce variability in the estimates due to variation in tag technology. We only considered V7 or V9 low-power tags with a random interval of 30–90 s between transmitted signals. We only included tag codes for smolts tagged under POST. Some sequences from remaining tags were excluded for the following reasons. (1) Detections thought to be false positives were identified in an independent data screening based on: the number of detections of a tag at a station, the presence of other tags on the detecting receiver around the time of the detection, and the plausibility of the detection with respect to migration routes and legitimate detection times at other stations. False detections were rare and were likely the result of tag collisions (overlap in pulse trains of two or more tags) when they did occur; all were excluded before constructing detection sequences. (2) Some tags were detected sporadically or continuously from some point in time until the end of the study when receivers were retrieved. These were likely from fish that died close enough to a receiver to be
detected. All sequences of the tag at the station were excluded. (3) Only the first crossing event of a particular tag at a particular station was considered novel. Another series of detections a few hours later potentially represented milling behaviour around the station rather than continual migration across and beyond it. These later sequences were excluded, with two exceptions: (a) if a fish moved from station \( i \) to station \( ii \) and then back to station \( i \), the first crossing sequence after returning from the other station was also considered novel. (In this case, we would consider three crossing events to be novel, at \( i \), \( ii \), and again at \( i \).); and (b) if >24 h elapsed between detections at a station, we considered the crossing event after this period to also be novel, as the fish had likely travelled somewhere else over that period instead of milling near the station. (4) If a crossing event lasted >4 h, this was also considered likely to be milling instead of migratory behaviour. Less than 2% of all remaining crossing events lasted >4 h, and these were excluded from analyses. After applying these filters, 4918 sequences of crossing events remained.

4.2.3 Fitting detection probability attenuation models to crossing sequences

Each constructed sequence of detections and missed transmissions as a fish approached, passed over, and left a station is temporal. Assuming steady speed of travel past a station, the sequence can also be considered quasi-spatial. The sequence represents a continuum of movement across the station, although the specific point in the sequence of passing by the closest receiver at the station is unknown. We modelled this quasi-spatial detection process, albeit without knowing the true distances from tag to station at which transmissions were detected or missed.

During a crossing event, the probability of detecting a single tag transmission may vary \((0 \leq p_{\text{ping}} \leq 1)\). Rather than a near-uniform probability out to a maximum detection range (Hobday and Pincock in review), \( p_{\text{ping}} \) may decrease with increasing tag-to-station distance. We might expect \( p_{\text{ping}} \) to increase as a fish approaches a station, be at its maximum as it passes over the station (somewhere near the middle of the crossing sequence), and decrease as the fish moves away. That is, one might expect a greater proportion of signals missed near the beginning and end of a crossing sequence than in the middle. Such data on signals detected and signals missed can be described by attenuation models in a probabilistic framework.

We fit five different detection probability attenuation models (details in Appendix C) to each of the 4153 crossing sequences that contained \( \geq 2 \) detections (the 765 remaining sequences with \( n = 1 \) do not contain enough information to properly fit attenuation models). We define X
as the vector of ‘1’s and ‘0’s for a given crossing sequence, comprised of \( n \) detections and \( m - n \) misses, and \( X_i \) as an individual transmission. Excluding the 50 ‘0’s before and after the main sequence, \( X_i \) ranges from \( X_1 \) to \( X_m \). All models involved an increase in \( p_{\text{ping}} \) from \( X_1 \) towards approximately the middle of \( X \), followed by a decrease in \( p_{\text{ping}} \) from this approximate middle towards \( X_m \). All models contained either a centering parameter \( (x_c) \) or two centre-bounding parameters, where the centre point \( x_c \) represented the hypothesized point along \( X \) of minimum distance to the station during the crossing event. This centre point was somewhere near but not necessarily equal to the middle of \( X \), \( X_{m/2} \). Likewise, the increase in \( p_{\text{ping}} \) in the initial part of \( X \) and decrease in \( p_{\text{ping}} \) in the later part were symmetric about \( x_c \), but not necessarily about \( X_{m/2} \).

All five models had a single parameter in common, \( p_{\text{max}} \), which represented the maximum \( p_{\text{ping}} \) during the crossing event (\( p_{\text{max}} \) occurred at \( x_c \) or its equivalent in all models). In two models, \( p_{\text{max}} \) also extended from \( x_c \) some distance in both directions to represent a threshold effect of \( p_{\text{ping}} \) with distance. The values of \( p_{\text{max}} \) or other parameters were not constrained to be equal among models. Symbols for variables and parameters used in this chapter are listed on page xiv.

The first model \( [M_{\text{lin}} \ p_{\text{ping}}] \) was a simple linear decrease in \( p_{\text{ping}} \) with increasing tag-to-station distance (Simpfendorfer et al. 2002, Topping et al. 2006), from \( p_{\text{max}} \) at the centre point, \( x_c \), towards either end of \( X \) (Fig. 4.1). The second \( [M_{\text{norm}} \ p_{\text{ping}}] \) was a normal-shaped decrease in \( p_{\text{ping}} \) from \( p_{\text{max}} \) at \( x_c \) towards either end of \( X \). Two other models were mechanistic, predicting a decrease in \( p_{\text{ping}} \) with increasing tag-to-station distance according to physical properties of underwater attenuation of acoustic energy. One of these \( [M_{\text{ai}} \ p_{\text{ping}}] \) assumed that \( p_{\text{ping}} \) was proportional to acoustic intensity, so decayed with distance from \( x_c \) due to geometrical spreading and absorption (Richards et al. 1996, Leighton 1998). The other \( [M_{\text{ai-thr}} \ p_{\text{ping}}] \) involved similar assumptions, but had greater flexibility by incorporating a threshold of constant \( p_{\text{ping}} \) (at \( p_{\text{max}} \)) over some distance bracketing \( x_c \), beyond which \( p_{\text{ping}} \) decreased. The fifth model \( [M_{\text{logit}} \ p_{\text{ping}}] \) also incorporated a threshold effect of \( p_{\text{ping}} \) with distance. It allowed constant \( p_{\text{ping}} \) (\( \approx p_{\text{max}} \)) to a certain distance, and beyond this point \( p_{\text{ping}} \) followed a logistic decrease towards either end of \( X \) (Szedlmayer and Schroepfer 2005; Figure 4.1).

A likelihood equation was constructed for each model, and a non-linear search routine was used to find the parameter values that maximized this likelihood. Model selection procedures (Burnham and Anderson 2002) were used to compare the five attenuation models in their balance between goodness-of-fit to the data (since likelihood values differed among
models) and the number of parameters required to achieve that fit (which also differed). Model \([M_{\text{logit } p_{\text{ping}}}]\) had the most support in the data among these models (Appendix C). This model alone is used for estimating \(p'_{\text{loc}}\) in the remainder of this paper, but the other four \(p_{\text{ping}}\) models are described and compared in Appendix C.

Model \([M_{\text{logit } p_{\text{ping}}}]\) is a four-parameter model \((p_{\text{max}}, x_{\text{min}}, \omega, \sigma)\) that predicts a logistic-shaped increase in \(p_{\text{ping}}\) during the early portion of the crossing sequence \(X\) towards \(p_{\text{max}}\) and a symmetrical decrease in \(p_{\text{ping}}\) in the later portion of \(X\):

\[
(4.1) \quad p_{\text{ping},i} = p_{\text{max}} \left(1 - \frac{1}{1 + e^{-\left(X_i - x_{\text{min}}\right)/\sigma}}\right) \left(1 - \frac{1}{1 + e^{-\left(X_i - \omega - x_{\text{min}}\right)/\sigma}}\right).
\]

The first term in brackets controls the increasing phase of \(p_{\text{ping}}\) during the approach to the station, while the second term controls the decreasing phase during departure. Between these regions of increase and decrease is a flat portion of variable width, with \(p_{\text{ping}} \approx p_{\text{max}}\) (Fig. 4.1). The value of \(X_i\) (not necessarily an integer value) at the first logistic inflection point is represented by \(x_{\text{min}}\). The width of the curve between the two inflection points (in units of \(X\)) is represented by \(\omega\) (alternative parameterizations to \(\omega\) could include a second inflection point, \(x_{\text{max}}\), where \(x_{\text{max}} = x_{\text{min}} + \omega\), or a centering parameter, \(x_c\), where \(x_c = x_{\text{min}} + \omega/2\)). The slope around each inflection point is determined by the standard deviation, \(\sigma\). Lower values of \(\sigma\) result in a greater change in \(p_{\text{ping}}\) with change in \(X_i\). The portion of the curve where \(p_{\text{ping}}\) is flat (and \(\approx p_{\text{max}}\)) is wider when \(\omega\) is larger and/or \(\sigma\) is lower. Flexibility in the width of this flat portion of the curve (Fig. 4.2) implies a variable threshold effect, ranging from a \(p_{\text{max}}\) with no distance threshold (i.e., shaped like a normal density function) to a near-constant \(p_{\text{max}}\) with a knife-edged distance threshold (i.e., a near-uniform density function). Note that the total curve (Fig. 4.1) does not need to be symmetrical. Separate \(\sigma\) parameters could be modelled for the approach and departure phases if there was reason to suspect that fish speed or detection processes would vary between approach and departure phases. The following constraints were placed on the parameters for numerical estimation purposes: \(0.001 < p_{\text{max}} < 1\); \(0 \leq \omega\); \(0.1 < \sigma\). In addition, the two terms in brackets were each constrained to be \(\in (1.0 x 10^{-9}, 0.999999999)\).

Predicted \(p_{\text{ping}}\) models were fit to the observed binary detection sequence data by maximizing the following binomial log-likelihood for each crossing sequence with \(n \geq 2\):
\[
\ln(L) = \sum_{i=(1-50)}^{(m+50)} \{X_i \cdot \ln(p_{\text{ping},i}) + (1 - X_i) \cdot \ln(1 - p_{\text{ping},i})\}.
\]

The summed terms of Eq. 4.2 represent the likelihood of each observed value, \(X_i\), including the \(m\) observations in \(X\) as well as the 50 ‘0’s before and after \(X\) (hence the indexing starting at –49 and ending at \(m + 50\)). Individual terms and thus \(\ln(L)\) are negative quantities. Lower values of \(\ln(L)\) are expected for longer sequences and poorer fits to the detection data. Sequences of \(n = m = 1\) were excluded from model selection comparisons since these events do not contain enough information to discriminate among models.

### 4.2.4 Estimating local-information detection probability from attenuation model

The proportion of tagged fish crossing a station undetected (\(1 - p_{\text{mr}}\)) is unknown. Using only local information from a station, we estimated a detection probability from detection data of tags that were detected while crossing the station. For every detected crossing sequence, there is a set of maximum likelihood estimates (MLEs) of the four parameters that characterize the best fit \([M_{\text{logit}} p_{\text{ping}}]\) model to the data for that crossing sequence. These model parameters, specific to detected crossing events at a particular station, contain sufficient information to predict an overall probability of crossing a station undetected. In this analysis, we identify crossing sequences as belonging to a particular combination \(j\) of station, year, and tag type.

For each crossing sequence where a fish was detected, there is a corresponding non-zero probability that the fish, hypothetically, would not have been detected while passing the station. We define \(\hat{p}_{\text{seq}}\) as the probability that a fish would again be detected during a hypothetical crossing of the station, given the parameter set and sequence length describing its detected crossing event. This is calculated differently depending on whether 1 or \(\geq 2\) tag transmissions were detected during the crossing event:

\[
\hat{p}_{\text{seq}}^* = \begin{cases} 
p_{\text{max},j} & \text{if } X \text{ has } n = 1 \\
1 - \prod_{i=(1-50)}^{(m+50)} (1 - p_{\text{ping},i}) & \text{if } X \text{ has } n \geq 2.
\end{cases}
\]

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For $X$ with $n \geq 2$, $\hat{p}_{\text{seq}}^*$ can be estimated directly from the best fit logistic curve. Since $p_{\text{ping},i}$ describes the probability of detecting a single transmission at position $X_i$ of the sequence, there is a chance $1 - p_{\text{ping},i}$ that the transmission would not again be detected (again, the 50 $p_{\text{ping},i}$ corresponding to the ‘0’s before and after $X$ are included in the sum). If we consider the $p_{\text{ping},i}$ independent during a crossing event, the product of the probabilities of not detecting each of the $m$ transmissions in $X$ results in $1 - \hat{p}_{\text{seq}}^*$ (Eq. 4.3). Generally, sequences that are long or have $p_{\text{max}} \approx 1$ will have a near-zero probability of passing the station undetected in a corresponding hypothetical crossing event. For $X$ with $n = 1$, attenuation models cannot be properly fit, but $\hat{p}_{\text{seq}}^*$ can instead be estimated by using information from other crossing events at $j$. Since $p_{\text{max}}$ is simply $p_{\text{ping}}$ at the shortest tag-to-station distance during a crossing event, for a crossing event with $n = 1$, $\hat{p}_{\text{seq}}^*$ is simply $p_{\text{max}}$. Although $p_{\text{max}}$ is not estimable for single-detection crossings, we extrapolated $p_{\text{max}}$ from those of sequences with $n = 2$–20 using a simple least-squares regression (Fig. 4.3; lines were fit separately for each $j$). For these relatively short sequences, $p_{\text{max}}$ generally decreased as $n$ decreased, likely because near the edges of station detection ranges, crossing times are expected to be shorter while $p_{\text{max}}$ is concurrently expected to be less.

Extrapolated values of $p_{\text{max},j}$, $\hat{p}_{\text{seq},j}$, were constrained at $0.01 \leq p_{\text{max},j} \leq 1$ in case predicted values were outside the probability scale. Values of $\hat{p}_{\text{seq}}^*$ with $n = 1$ in $X$ tended to be lower than those with $n \geq 2$. Across all combinations $j$, $p_{\text{max},j}^\dagger$ ranged from 0.29–1.

The number of fish passing a station undetected ($\hat{N}_j^-$) is estimated from the number of fish detected at $j$ ($N_j$) for a given crossing sequence $n$ and $\hat{p}_{\text{seq},j}^*$ at that same $n$. This method explicitly accounts for non-linear variation in $N_j$ and $\hat{p}_{\text{seq},j}^*$ with $n$, which is expected from variation in detection ranges and crossing positions of fish past the receivers at a station (since $[M_{\text{logit} p_{\text{ping}}}]$ parameters vary with $n$, see Results). At a given $n$, the mean $\hat{p}_{\text{seq},j}^*$, $\bar{p}_{\text{seq},n,j}^\dagger$, is calculated from all crossing events at $j$, and by rearranging $\bar{p}_{\text{seq},n,j}^\dagger = \frac{N_{n,j}}{N_{n,j} + \hat{N}_j^-}$, it follows that:

$$
\hat{N}_n^x_j = \left( \frac{N_{n,j} (1 - \bar{p}_{\text{seq},n,j}^\dagger)}{\hat{p}_{\text{seq},n,j}^\dagger} \right).
$$

In the case of $X$ with $n = 1$, $\bar{p}_{\text{seq},n,j}^\dagger$ is simply $p_{\text{max},j}^\dagger$. A correction factor, $F_j$, is applied because habitat differences involving river currents (and to a lesser extent, tag type differences)
lead to expected differences in the time within detection range during a crossing event. In this example, the right hand side of Eq. 4.4 is divided by $F_j$ to obtain $\hat{N}_{n,j}^-$. Crossing sequence length, $m$, and duration, $\omega$, are both measures of this time. The estimate of undetected fish, $\hat{N}_{n,j}^-$, is considered proportional to the known $N_{n,j}$, but under swift flow conditions the ratio of $\hat{N}_{n,j}^-: N_{n,j}$ is expected to be higher than under low flow conditions (the same is true for weaker tags compared to stronger tags). That is, $\hat{N}_{n,j}^-$ is conditioned on $N_{n,j}$, but this relationship is sensitive to time-within-range differences among $j$. Weaker tags or tags in swift rivers are generally associated with lower $m$ and $\omega$, so $F_j$ helps to standardize $\hat{N}_{n,j}^-: N_{n,j}$ in terms of time within detection range. We chose to standardize predictions to crossing events involving V9 tags at an inner coastal station in relatively calm conditions, the outer Howe Sound line (HS$_{outer}$). The choice of a standardizing term is arbitrary—it could be an average of ocean stations or a different station in calm conditions. Four measures of $F_j$ were considered, in addition to an uncorrected model with $F_j = 1$: (i) $\bar{m}_j / \bar{m}_{HS_{outer}}$ (means), (ii) $\bar{m}_j / m_{HS_{outer}}$ (medians), (iii) $\bar{\omega}_j / \bar{\omega}_{HS_{outer}}$, and (iv) $\bar{\omega}_j / \omega_{HS_{outer}}$. The mean (and median) of crossing events at HS$_{outer}$ was 44.5 (26.0) for $m$ and 37.0 (17.4) for $\omega$. Those at other stations tended to be shorter, especially in rivers, but were occasionally longer.

The estimated number of fish crossing undetected for each given $n$, $\hat{N}_{n,j}^-$, is used to calculate the detection probability estimate across all $n$:

\[
(4.5) \quad p'_{loc,j} = \frac{\sum_{n=1}^{\infty} N_{n,j}}{\sum_{n=1}^{\infty} (N_{n,j} + \hat{N}_{n,j}^-)}.
\]

The estimator $p'_{loc,j}$ was calculated for each unique combination $j$ of station, year, and tag type (at Fraser River stations, $j$ was stock-specific as well).

### 4.2.5 Other local-information estimates of detection probability

Two alternative types of detection probability estimates that use only local information at a detection station were also considered and compared with $p'_{loc,j}$. First, the same crossing sequences $X$ were used, but instead of fitting $p_{ping}$ models to $X$, a $0 \to \infty$ probability distribution was fit directly to the frequency distributions of $m$ at each particular station, year, and tag type.
combination \( j \). These frequency distributions contain values of \( m \) from \( 1 \rightarrow \infty \) (actually to 240 after filtering, but this makes little difference). The missing frequency at \( m = 0 \), i.e., the number of fish at \( j \) that crossed the line undetected, is the value required for estimating detection probability. Five probability distributions were modelled, attempting to find the best overall fit to \( m \) rather than strictly adhering to whether the probability distribution properly describes the processes behind \( m \). The Poisson distribution (discrete, with a single parameter, \( \lambda \)), which describes the number of detectable transmissions \( m \) during a crossing event \([M_{\text{Poisson}}]\), would apply if the expected \( m \) were the same across all fish. Since this is unlikely due to variable detection ranges and locations of crossing a station relative to receiver(s), the variance:mean ratio is likely higher than provided by the Poisson distribution, so the negative binomial distribution (discrete, with two parameters, \( p \) and \( r \); \([M_{\text{neg-binom}}]\)), used in cases of over-dispersion, may more reasonably describe this process. We also considered the geometric distribution (discrete, with a single parameter, \( p \); \([M_{\text{geom}}]\)) and two continuous distributions that could reasonably fit the pattern of frequency distributions of \( m \) at \( j \): the log-normal distribution (with two parameters, \( \mu \) and \( \sigma \); \([M_{\text{log-norm}}]\)), and the gamma distribution (with two parameters, \( \kappa \) and \( \theta \); \([M_{\text{gamma}}]\)). The probability mass at \( m = 0 \) for the discrete distributions, or the area under the probability density functions from \( m = 0 \rightarrow 1 \) for the continuous distributions, represents the probability of a fish passing by undetected. For each probability distribution, the maximum-likelihood fit was obtained, and the cumulative probability at \( m = 1 \) was calculated to give the estimated zero proportion. The parameters of these distributions are not as easily interpretable as those of \( p_{\text{ping}} \) models for describing crossing events, but this method is simpler compared with fitting \( p_{\text{ping}} \) models to crossing sequences and estimating \( p'_{\text{loc},j} \) using Eqs. 4.3–4.5.

The second alternative local detection probability estimate was possible for stations that contained multiple receivers arranged in a line. Detection data from independent subsets of receivers on a line can be used to calculate \( p'_{\text{loc},j} \) if at least some fish tend to be detected on more than one receiver while crossing a line. For example, subsets of odd-numbered and even-numbered receivers can be taken, splitting the detection data at the station among these subsets accordingly. A probability \( p'_{\text{loc},j(\text{odd})} \) is calculated as the proportion of individual fish detected on even-numbered receivers that were also detected on odd-numbered receivers (i.e., \((\text{even} \cap \text{odd})/\text{even}\); and vice-versa). Treating these components as independent, we estimate an overall \( p'_{\text{loc},j} \) for this model \([M_{\text{odd-even subset}}]\) as:
This is the probability of detecting a fish on only odd, only even, or both odd and even-numbered receivers. A similar approach was used in Chapter 3 to assess the redundancy of receivers on a multi-receiver line when detection data at receiver stations further along migration routes are included as well. This method could also be applied to situations where two single-receiver detection stations are close enough that 100% survival between stations can be reasonably assumed. The probability of a fish crossing both stations undetected is equal to the product of the probabilities of crossing each station undetected.

### 4.2.6 Mark-recapture detection probabilities

Mark-recapture \( \hat{p}_{mr,j} \) were estimated independently of the local estimators, \( p'_{loc,j} \), for the same combinations of \( j \). Populations and species sharing the same tag type were similarly pooled for estimating \( \hat{p}_{mr} \) at a particular station in a particular year (Eq. 3.3). This pooling was not done in the Fraser River, since \( p_{mr} \) decreased over the migration season as a result of increasing water flow. Instead, stock-specific \( \hat{p}_{mr,j} \) were estimated using a river level covariate paired with stock-specific run timing values, as in Chapter 3. Note that \( \hat{p}_{mr,j} \) estimates were not possible for the final inner coast stations in the POST study area or for outer coast stations, where no or insufficient detection data were available beyond station \( j \). This limits the comparison of \( \hat{p}_{mr,j} \) and \( p'_{loc,j} \) in coastal areas to three stations prior to the final stations. Only \( p'_{loc,j} \) with \( N_j \geq 10 \) were compared with \( \hat{p}_{mr,j} \) to reduce bias from small sample size in either measure of \( p \). In total, the number of combinations \( j \) at which both \( \hat{p}_{mr,j} \) and \( p'_{loc,j} \) were estimated was, by habitat: Fraser River (25), smaller rivers (33), estuaries (3), and inner coast (15), except for the multi-receiver \( [M_{odd-even~subset}] \) estimator, where only the inner coast comparisons were possible.

### 4.3 Results

#### 4.3.1 Crossing sequences

After filtering out detections that were likely false, 16% of all crossing sequences had a single detection (Table 4.1). The proportion of single-detection crossing events was higher at river than at coastal detection stations. Related measures, the mean number of detections in a crossing sequence (\( n \)) and the mean length of crossing sequences including missed transmissions...
Crossing events consisted primarily of short sequences, with 73% of sequences containing $n \leq 15$ (Fig. 4.4a) and 57% containing $m \leq 15$ (Fig. 4.4b). As the time between $X_i$ and $X_{i+1}$ was about 1 min on average, $m \leq 60$ denotes a crossing event shorter than 1 h, which was true for 87% of all sequences. When separated by habitat type (shown later), histograms for crossing sequences at stations in small and large rivers were skewed more towards smaller $n$ and $m$ relative to the trend shown in Fig. 4.4, whereas those at stations in estuaries and coastal areas were skewed towards larger $n$ and $m$. This is reflected in the lower mean $n$ and mean $m$ as well as the higher proportion of sequences with single detections in the two river categories compared with estuary or coastal stations (Table 4.1).

### 4.3.2 $[M_{\logit} \ p_{\text{ping}}]$ parameter estimates

For each of the 4,153 crossing sequences (excluding the 765 sequences with $n = m = 1$), a set of four parameters was estimated for $[M_{\logit} \ p_{\text{ping}}]$. Histograms and co-plots of the MLEs of these parameters are shown in Fig. 4.5 ($n$ is not a parameter, but is also included to show co-variation with model parameters). Apart from $\omega$ which was roughly log-normally distributed, the three other parameters showed bimodal ($\sigma$ and $p_{\text{max}}$) or strongly skewed distributions, with parameter estimates often at or near boundaries. Since $X$ were preceded by 50 ‘0’s, $x_{\min}$ was typically near 50 (but was sometimes greater for long sequences when $\sigma$ was also high). The width of the curve, $\omega$, was typically proportional to $n$. The steepness$^{-1}$ around the inflection points, $\sigma$, was estimated at the lower boundary of 0.1 in 46% of sequences, especially short ones, which resulted in a logistic curve that approximated a uniform density function. Higher $\sigma$ were generally estimated for longer sequences. Nearly 45% of crossing sequences had $p_{\text{max}}$ estimated at $>0.99$, especially for sequences that had $n = m$. This parameter showed little consistent variation with $n$, $x_{\text{min}}$, or $\sigma$, but was negatively correlated with $\omega$ (Fig. 4.5).

The general patterns of co-variation between parameter estimates (Fig. 4.5) hold if sequences are separated by tag type and/or by the five habitat categories, although there are some differences in parameter distributions. Sequence length ($m$) and duration ($\omega$) tended to be longer...
for V9 tags than for V7 tags except in the Fraser River, where they were similar (Table 4.2).

There was no consistent difference among tag types in \( x_{\text{min}} \) (as expected) or in \( p_{\text{max}} \), although \( \sigma \) tended to be slightly higher for V9 tags. Comparing habitats, \( m \), \( \omega \), and \( \sigma \) were all lower in rivers than in estuaries or coastal areas. In rivers, \( p_{\text{max}} \) was slightly higher on average than in coastal areas, and there was little consistent difference among habitats in \( x_{\text{min}} \) (Table 4.2).

Using Eqs. 4.3–4.5, frequency distributions of \( n \) and \( m \) (Fig. 4.4) can be extrapolated to the unknown \( n = m = 0 \) category. The estimated number of crossing events at a combination \( j \) of station, year, and tag type during which no transmissions were detected is represented by the \( \sum_{n=1}^{\infty} \hat{N}_{n,j}^- \) term in Eq. 4.5. Summing these estimates across \( j \) within each habitat gives \( \hat{N}_{\text{hab}}^- \), i.e., \( \hat{N}_{\text{hab}} \) with \( n = m = 0 \) (Fig. 4.6). Frequency counts at \( n = 1\)–20 are the same as those shown in Fig. 4.4, separated by habitat. Predicted \( \hat{N}_{\text{hab}}^- \) values seemed to follow the general trends of the frequency distributions from \( n = 1\)–20. The \( n = 0 \) category was the most frequent in all habitats. The increase from \( \hat{N}_{\text{hab}} \) at \( n = 1 \) to \( \hat{N}_{\text{hab}}^- \) was least for estuary and outer coast stations and greatest for Fraser River stations (Fig. 4.6).

### 4.3.3 Comparison of \( p'_{\text{loc}} \) estimators with \( p_{\text{mr}} \) estimates

Paired estimates of the \( p'_{\text{loc},j} \) estimators with \( \hat{p}_{\text{mr},j} \) had correlation coefficients ranging from 0.28–0.54 at Fraser River stations, 0.53–0.76 at smaller river stations, and 0.38–0.81 at inner coast stations (Table 4.3). Among the \( [M_{\text{logit}} p_{\text{ping}}] \) models, the four corrected models tended to have higher \( r \) than the model with \( F_j = 1 \). The two models that had the highest overall correlations across habitats were those with \( F_j = \bar{m}_j / \bar{m}_{\text{HSouter}} \) \( (r = 0.54, 0.75, 0.81 \) for Fraser River, smaller rivers, inner coast; Fig. 4.7) and \( F_j = \bar{m}_j / \bar{m}_{\text{HSouter}} \) \( (r = 0.47, 0.72, 0.78) \). Local-information estimators based on direct fits of probability distributions to frequency distributions of crossing sequence \( m \) tended to have poorer overall correlations with \( \hat{p}_{\text{mr},j} \) than estimators based on the corrected \( [M_{\text{logit}} p_{\text{ping}}] \) models (Table 4.3). The Poisson distribution was the poorest of these and the negative binomial distribution, better able to deal with over-dispersion, was somewhat more correlated with \( \hat{p}_{\text{mr},j} \). Of these five models, the geometric distribution fit the pattern best on average across habitats \( (r = 0.48, 0.57, 0.64) \). Applying a correction factor \( F_j = \bar{m}_j / \bar{m}_{\text{HSouter}} \) or \( F_j = \bar{m}_j / \bar{m}_{\text{HSouter}} \) to these direct-fit distribution models improved the overall correlation across habitats slightly (not shown), but the corrected direct-fit distribution models were still less correlated with \( \hat{p}_{\text{mr},j} \) than the corrected \( [M_{\text{logit}} p_{\text{ping}}] \) models. At multi-
receiver inner coast stations, the correlation for [M_{odd-even subset}] was intermediate between the corrected [M_{logit p_{ping}}] models and the direct-fit distribution models (Table 4.3). Since there were only three paired estimates of p'_{loc,j} and \( \hat{p}_{mr,j} \) in estuaries, correlation or regression results are not presented for these stations. Similarly, no comparisons were possible for outer coast stations since \( \hat{p}_{mr,j} \) is not estimable. Both tag types are included in this paired analysis, since V7 tags generally had a lower p than V9 tags for both p'_{loc,j} and \( \hat{p}_{mr,j} \).

Local detection probability estimates were generally high compared to \( \hat{p}_{mr,j} \) (i.e., were likely biased upward) as regressions between p'_{loc,j} and \( \hat{p}_{mr,j} \) all had intercepts >0 (a, ranging from 0.18–1) and slopes <1 (b, ranging from 0–0.72; Table 4.3). This was especially true for the uncorrected [M_{logit p_{ping}}] model and the five direct-fit distribution models. The corrected [M_{logit p_{ping}}] models tended to have a closer to 1 and b closer to 0, i.e., p'_{loc,j} : \( \hat{p}_{mr,j} \) ratios closer to 1:1 (Fig. 4.7). Again, at multi-receiver inner coast stations, [M_{odd-even subset}] was intermediate between the corrected [M_{logit p_{ping}}] models and the direct-fit distribution models in terms of a and b (Table 4.3). Comparing the best overall p'_{loc,j} (the [M_{logit p_{ping}}] model with \( F_j = \bar{m}_j / \bar{m}_{HS_{outer}} \)) and \( \hat{p}_{mr,j} \) in different habitats, correlation between estimators was lower but the relationship was closer to 1:1 for Fraser River stations (Fig. 4.7a). Conversely, correlation was higher but the relationship was furthest from 1:1 at inner coast stations (Fig. 4.7c; the range of both measures of p was much less compared with river habitats, which may have contributed to the higher correlation). Smaller river stations had correlation intermediate between these as well as intermediate a and b (Table 4.3), although the fit was degraded by two estimates that had high leverage, with \( \hat{p}_{mr,j} \approx 0.27-0.30 \) and p'_{loc,j} ≈ 1 (Fig. 4.7b).

Paired comparisons (Table 4.3, Fig. 4.7) were limited to p'_{loc,j} based on \( N_j \geq 10 \). However, 10 ≤ \( N_j \) ≤ 20 or 30 may still be a low number of crossing events on which to base an estimate of detection probability. Small sample sizes can lead to biases in both p'_{loc,j} and \( \hat{p}_{mr,j} \), so p'_{loc,j} is likely a less reliable predictor of \( \hat{p}_{mr,j} \) when \( N_j \leq 20 \) or 30 compared with \( N_j \geq 30 \). Using p'_{loc,j} / \( \hat{p}_{mr,j} \) as an indicator of bias in the predictive relationship, this ratio deviates from 1 at smaller numbers of \( N_j \) (Fig. 4.8). A doubling or halving of the ratio is not uncommon at \( N_j \leq 20 \), but this ratio stabilizes near 1 as \( N_j \) increases.
4.4 Discussion

4.4.1 Utility of $p_{loc}'$ as a predictor of $p_{mr}$

The detection probability estimator presented here is based on patterns of detected and missed signal transmissions from fish tags that were detected while migrating past a station. From this local information, inferences are made about the proportion of fish not detected. It is assumed that these fish not detected at a station could have been, otherwise mark-recapture estimates of $\hat{p}_{mr,j}$ would be biased and the local estimator would be less reliable. For example, consider two situations: (i) a dense line of multiple receivers stretches only halfway across an inshore strait, but migration routes of fish are uniformly distributed across this strait; (ii) a dense multi-receiver line is deployed on an outer coast, but only half the fish from a tagged group cross over the line while the other half goes around it, further offshore. In both cases, assume there are sufficient detection stations further along the migration route to estimate $\hat{p}_{mr}$ at this station. Even if all fish that crossed over the receivers were detected, $\hat{p}_{mr}$ would only be 0.5 because half the fish did not cross over the receivers. Conversely, $p_{loc}'$ would be based on the fish that were detected at the station, so might be closer to 1. Using $p_{loc,j}'$ as a predictor of $\hat{p}_{mr,j}$ therefore assumes that receivers are deployed close enough to one another and cover the full range of possible migration routes across some point so that every fish migrating past that point has a non-zero probability of being detected. I.e., $p_{loc,j}'$ conditions on any tagged fish crossing the station transmitting at least once while within range of a receiver.

The best local estimator considered here, $[M_{logit} p_{Ping}]$ with $F_j = \bar{m}_j / \bar{m}_{HSouter}$, predicted mark-recapture detection probabilities reasonably well (Fig. 4.7; Table 4.3) considering that it uses only local information. The primary purpose of using a local estimator would be to address situations where $\hat{p}_{mr,j}$ is not known or precisely estimable, however, so correlations of $p_{loc,j}'$ and $\hat{p}_{mr,j}$ would not necessarily be routinely quantified. Instead, the local estimator could be used as either a covariate of $p_{mr,j}$ in mark-recapture models or an absolute predictor of $p_{mr,j}$; which of these is most appropriate may depend on the sample size of the study and magnitude of $p_{mr}$. If $N_j \leq 50$ to 100 at stations along migration routes as a result of moderate tag sample sizes, moderate $p_{mr,j}$, or mortality during the migration before arriving at later stations, the estimator could be used as a covariate where $\hat{p}_{mr,j}$ is constrained to be a function of $p_{loc,j}'$. (Similarly, $p_{loc,j}'$ could be used as a prior estimate of $p_{mr,j}$ in Bayesian formulations.) This could result in more
parsimonious mark-recapture models for estimating $p_{mr,j}$ and survival probabilities, in contrast to using more general CJS models with $p_{mr,j}$ estimated independently for each $j$. At modest $N_j$, however, the ratio of $p'_{loc,j}/\hat{p}_{mr,j}$ may have a large enough bias in either direction (Fig. 4.8) that absolute predictions of $p_{mr,j}$ are not reliable. Further, estimating $p'_{loc,j}$ for use as either a covariate or prior parameter from the same detection dataset as that used for mark-recapture analyses can be susceptible to over-fitting, and the precision of constrained $\hat{p}_{mr,j}$ can be overestimated, so caution should be used if using $p'_{loc,j}$ as a covariate. Conversely, if sample sizes are large, $p_{mr,j}$ is high, and levels of mortality during the migration are low to moderate such that $N_j \geq 100$ even at stations later in the migration, the local estimator could be used as an absolute predictor of $p_{mr,j}$ at the final detection station, where $p_j$ cannot be estimated with mark-recapture methods. For large $N_j$, if the ratio $p'_{loc,j}/\hat{p}_{mr,j}$ does actually stabilize near 1 as Fig. 4.8 would suggest, the possible bias in this absolute prediction could be acceptable. In making an absolute prediction for the final station, however, either a covariate $p'_{loc,j}$ should be used across all stations or correlations between $p'_{loc,j}$ and $\hat{p}_{mr,j}$ should be assessed to ensure that the prediction for the final station is likely reasonable. Whether $p'_{loc,j}$ is used as a covariate of $\hat{p}_{mr,j}$ or as an absolute predictor of $\hat{p}_{mr,j}$ at the final detection station, in both cases this allows the survival probability in the final segment to be estimable, conditioned on the final $\hat{p}_{mr,j}$.

Establishing a minimum $N_j$ for making comparisons between $p'_{loc,j}$ and $\hat{p}_{mr,j}$ can reduce biases in either estimate of $p$ from small sample sizes. Although $N_j \geq 10$ was used as a threshold in the comparisons, we found that $N_j \geq 30$ would have resulted in a ratio of $p'_{loc,j}/\hat{p}_{mr,j}$ closer to 1 (Fig. 4.8). The trade-off with increasing the $N_j$ threshold is that, in studies with small or moderate sample sizes, fewer paired estimates will be available for assessing the correlation within a given habitat, or fewer $p'_{loc,j}$ will be available for use as a covariate. If we had used $N_j \geq 30$ (or 20), the number of paired estimates of $p$ would have decreased from 25 to 7 (or 10) in the Fraser River, from 33 to 22 (or 26) in smaller rivers, and from 15 to 13 (or 14) at inner coast stations. If $N_j$ is generally large even at later stations in the migration route, or if enough stations or years of study are used, then a higher threshold of $N_j$ may be used while still leaving enough paired estimates to establish a relationship between $p'_{loc,j}$ and $\hat{p}_{mr,j}$. Conversely, if few crossing events occur above some $N_j$ threshold, there will be missing covariate values of the estimator at some stations.
Among the three habitats where $p'_{loc,j}$ was compared with $\hat{p}_{mr,j}$, the relationship was most variable at Fraser River stations (Fig. 4.7). This is likely at least partly the result of a strong relationship between $p_{mr,j}$ and river flow (Fig. 3.5). These $\hat{p}_{mr,j}$ are estimates for an entire release group (combination of station, year, tag type, and population), but individual fish within a group may cross the station at different times and may therefore have a variable probability of being detected (the crossing time of fish not detected is not known, but can be treated as a random variable in Bayesian formulations of CJS models; Muthukumarana et al. 2008). In contrast, the $p'_{loc,j}$ estimators are assessed from detection data of crossing events of individual fish, so these by definition reflect the river flow levels at the time of crossing. If heterogeneity in $p_{mr,j}$ exists, methods to account for it can improve mark-recapture estimates (Pledger et al. 2003). The local estimator accounts for heterogeneity among detected individuals; the researcher could assess whether $\hat{p}^*_{seq,j}$ changes under varying environmental conditions like increasing river flow during a migration season. Similarly, the estimator could be used to evaluate other assumptions of mark-recapture models like the partial-sampling scenarios from incomplete detection stations described above. If $p'_{loc,j}$ at some $j$ is unusually high relative to $\hat{p}_{mr,j}$, that might suggest that some proportion of the tagged population is not available to be detected at $j$, thereby biasing $\hat{p}_{mr,j}$.

### 4.4.2 Assumptions of $p'_{loc}$ attenuation models

In considering the temporal sequence of detections and missed transmissions as quasi-spatial in order to fit attenuation models, continuous travel at constant speed of tagged fish migrating past stations was assumed. If fish speed changes during a crossing event, or if direction changes to lateral or diagonal movement along a multi-receiver station rather than perpendicular movement across it, the quasi-spatial units of sequence length will not be proportional to actual distances from tag to receiver. The method is therefore best suited for species that consistently migrate with little chance of residing near detection stations where residency could be misinterpreted as long crossing events. Long detection sequences or repeated sequences at the same station can be easily identified; we excluded all non-novel and long (>4 h) crossing events before calculating $p'_{loc,j}$.

Travel speed across stations was also assumed to be constant among individual fish. Slower fish, either as a result of shorter body length or a higher proportion of time not continually swimming, are expected to have longer crossing sequence lengths than faster fish.
The probability of a fish crossing a line undetected is higher for faster fish; since slower fish contribute disproportionately more crossing sequences at $j$, $p'_{\text{loc},j}$ may underestimate $p_{\text{mr},j}$ (although we found that $p'_{\text{loc},j} \geq \hat{p}_{\text{mr},j}$ rather than $p'_{\text{loc},j} \leq \hat{p}_{\text{mr},j}$ most of the time).

The five $p_{\text{ping}}$ attenuation models all involved decrease in $p_{\text{ping}}$ with increasing tag-to-station distance (although two had a threshold effect of constant $p_{\text{ping}}$ to some distance). This assumption differs from other suggestions that at any given moment (i.e., a crossing event), the density function of $p_{\text{ping}}$ with increasing distance is nearly uniform, with $p_{\text{ping}} \approx 1$ to some threshold distance, beyond which $p_{\text{ping}}$ declines sharply to zero (Hobday and Pincock In review).

We found some support for the assumption of a simple uniform density function in sequences with $n \geq 2$: (i) 23% of sequences were uniform with $n = m$ (Table 4.1), (ii) 46% of sequences had $[M_{\text{logit}} p_{\text{ping}}]$ parameter $\sigma$ estimated at the lower boundary of 0.1, and (iii) 45% of sequences had $p_{\text{max}}$ estimated at $>0.99$ (21% of sequences met all three criteria). Remaining sequences, however, involved more of a gradual increase in $p_{\text{ping}}$ with decreasing tag-to-receiver distance (e.g., Fig. 4.1). The two threshold $p_{\text{ping}}$ models, including the logistic model used, are flexible in that the shape of their probability curves can be near-uniform if warranted by the detection data (Fig. 4.2).

Crossing sequences were treated independently when fitting $p_{\text{ping}}$ attenuation models, which resulted in a set of 3–5 parameters estimated for each crossing event (e.g., four parameters in the case of model $[M_{\text{logit}} p_{\text{ping}}]$), and thus a large number of total estimated parameters over all crossing events at $j$. Alternative approaches could involve modelling parameter values at $j$ as random effects, or moving to a Bayesian hierarchical model with $[M_{\text{logit}} p_{\text{ping}}]$ parameters described by hyper-parameters. This could allow information sharing between parameters at $j$ while still maintaining a local information-only approach to estimation of $p'_{\text{loc},j}$.

The predictive ability of $p'_{\text{loc},j}$ from $[M_{\text{logit}} p_{\text{ping}}]$ as an index of $\hat{p}_{\text{mr},j}$ is sensitive to the choice of the correction factor, $F_j$. The uncorrected model with $F_j = 1$ was not as good a predictor as models with $F_j$ standardized to a station with calm, relatively low net current conditions. Logistic models based on mean or median $m$ ($F_j = \bar{m}_j/\bar{m}_{\text{HSouter}}$ or $F_j = \bar{m}_j/m_{\text{HSouter}}$) gave similar and, overall, the best predictions of $\hat{p}_{\text{mr},j}$ among the set of 10 models considered (Table 4.3). Inclusion of $F_j$ (which standardizes for variation in average crossing times) in the calculation of $p'_{\text{loc},j}$ is reasonably justified since $\hat{N}_{\text{n},j}$ is based on the number of fish detected at $j$, the ratio $\hat{N}_{\text{n},j}/N_{\text{n},j}$ varies not only due to $[M_{\text{logit}} p_{\text{ping}}]$ fits to $X$ of
fish that were detected, but to time-within-range factors that result in variation in $N_{n,j}$ as well. Studies that are conducted only in rivers may not have a comparable low-current station that can be used in the denominator of $F_j$. Alternative approaches are to use either the station with lowest flow or the combination of station, year, and tag type (and possibly population) that have the highest $\bar{m}_j$ as the denominator. We do not consider use of $F_j$ to be a violation of this ‘only local information’ approach. The denominator is constant across all $j$ and could instead be replaced by a constant.

### 4.4.3 Crossing sequences and $[M_{\text{logit}} p_{\text{ping}}]$ parameters

There was considerable variation among crossing sequences in MLEs of $[M_{\text{logit}} p_{\text{ping}}]$ model parameters and in covariation among parameters (Fig. 4.5). This is expected due to variation in environmental conditions during fish crossing events and the specific position of crossing the station (i.e., closest distance from tag to receiver during the crossing event). The sequence length, $m$, or duration of the $[M_{\text{logit}} p_{\text{ping}}]$ curve, $\omega$, are expected to be shorter if fish cross the station near the edge of the detection range or in the gap between two receivers, or if travel speed is faster. High values of $p_{\text{max}}$ are expected when fish pass close to a station, or if acoustic conditions are favourable so that most or all transmissions are detected. A low $\sigma$ resulting in a near-uniform $p_{\text{ping}}$ probability curve could arise when acoustic conditions are such that $p_{\text{ping}}$ near $p_{\text{max}}$ is expected until some short detection range away, after which $p_{\text{ping}}$ drops sharply toward 0 (low $\sigma$ was typically associated with low $n$; Fig. 4.5). Crossing positions cannot easily be estimated from the data, but expected variation in these positions leads to the variation in parameter estimates and covariation among them.

Variation in detection processes among habitats was evident in both the length of crossing sequences (Fig. 4.6; Table 4.1) and MLEs of $[M_{\text{logit}} p_{\text{ping}}]$ parameters (Table 4.2). Crossing sequences at river stations had a higher proportion of single detections and a higher proportion of uniform probability curves at $n = m \geq 2$ than those from inner or outer coastal areas. This corresponds with the lower $\sigma$ and higher $p_{\text{max}}$ estimated for river stations. Crossing sequences at river stations also had shorter mean $n$, $m$, and $\omega$ than those from coastal stations. Since the minimum distance from tag to station should be shorter in rivers than at coastal stations (where fish can cross in the gaps between two receivers), this might explain why rivers showed a higher proportion of sequences without a missed detection, even if those sequences were shorter on average. Similar differences in sequence length and model parameters were seen between tag
types, with crossing sequences of the weaker V7 tags having shorter \( m \), lower \( \omega \), and lower \( \sigma \) than V9 tags. This relates to time-within-detection range differences among habitats and tag types, which were standardized by using \( F_j \) in the calculation of \( \hat{N}_{n,j}^- \). A greater contribution of \( \hat{N}_{n,j}^- \) comes from \( p_{\text{max},j}^1 \) extrapolations at \( n = 1 \) than from hypothetical \( \hat{p}_{\text{seq}}^* \) at \( n \geq 2 \). Summing over all crossing sequence \( n \) and combinations \( j \) in each habitat, \( \hat{N}_{\text{hab}}^- \) at least appears to follow the general trend from known crossing sequences at \( n = 1 \) to 20 (Fig. 4.6).

The choice of the number of ‘0’s added before and after \( X \) (50) was arbitrary, but did not have a large effect on estimates of \( p_{\text{max}} \) for sequences with \( n = 1 \) to 20 or on \( \hat{p}_{\text{seq}}^* \) for sequences with \( n \geq 2 \); estimates when \([M_{\text{logit}} \ p_{\text{ping}}]\) was fit to sequences with 50 ‘0’s before and after \( X \) were similar to those involving 10 or 100 ‘0’s. The largest deviations were observed for long sequences with 10 ‘0’s before and after \( X \), as the tails of \([M_{\text{logit}} \ p_{\text{ping}}]\) were not as ‘rooted’ to zero before and after \( X \). Deviations in these long sequences, however, had little effect on \( \hat{p}_{\text{seq}}^* \) since \( \hat{p}_{\text{seq}} \) is already near zero for long sequences, and had little effect on the \( p_{\text{max}} \) extrapolation since they were relatively few.

The possibility of false detections due to tag collisions and other factors leads to the common suggestion for acoustic or radio telemetry studies that single detections of a tag at a station be excluded from analyses. That may be appropriate for fish that spend considerable time near a station, but migrating fish may be within detection range of a station for enough time to transmit only a few signals, especially in rivers where travel speeds are assisted by currents. These results show that such exclusions would likely lead to biases of \( \hat{p}_{\text{mr},j} \) for migrating fish: 16% of all crossing events that were considered legitimate in this POST dataset involved only a single detection. If these detections were excluded from mark-recapture analyses, \( \hat{p}_{\text{mr},j} \) would be underestimated because legitimate detections would be treated as non-detection at \( j \). If fish are not detected after \( j \), survival probabilities to \( j \) could be either overestimated (since \( \hat{p}_{\text{mr},j} \) is underestimated) or underestimated (since evidence of survival to \( j \) would be excluded), depending on the degree of bias in \( \hat{p}_{\text{mr},j} \). The trade-off between willingness to accept a possible false single detection and exclusion of a legitimate single detection occurs along a continuum. If telemetry studies have direct relevance to estimating parameters important to fisheries management issues, risk assessments could be used to identify appropriate locations along this continuum in terms of optimal policy recommendations.
Table 4.1. Summary of number of detections, $n$, in crossing sequences ($X$) and sequence length including missed signals, $m$, separated by habitat type.

<table>
<thead>
<tr>
<th>Habitat</th>
<th>Total $X$</th>
<th>Mean $n$</th>
<th>Mean $m$</th>
<th>Number of $X$ with $n = m = 1$</th>
<th>% of $X$ with $n = m = 1$</th>
<th>Number of $X$ with $n = m \geq 2$</th>
<th>% of $X$ with $n = m \geq 2$</th>
</tr>
</thead>
<tbody>
<tr>
<td>Fraser River</td>
<td>945</td>
<td>9.8</td>
<td>18.2</td>
<td>199</td>
<td>21.1%</td>
<td>188</td>
<td>25.2%</td>
</tr>
<tr>
<td>Smaller rivers</td>
<td>1277</td>
<td>10.2</td>
<td>15.5</td>
<td>265</td>
<td>20.8%</td>
<td>530</td>
<td>52.4%</td>
</tr>
<tr>
<td>Estuaries</td>
<td>565</td>
<td>14.9</td>
<td>36.4</td>
<td>100</td>
<td>17.7%</td>
<td>47</td>
<td>10.1%</td>
</tr>
<tr>
<td>Inner coast</td>
<td>1751</td>
<td>19.3</td>
<td>31.7</td>
<td>170</td>
<td>9.7%</td>
<td>166</td>
<td>10.5%</td>
</tr>
<tr>
<td>Outer coast</td>
<td>380</td>
<td>17.1</td>
<td>32.0</td>
<td>31</td>
<td>8.2%</td>
<td>42</td>
<td>12.0%</td>
</tr>
<tr>
<td>All</td>
<td>4918</td>
<td>13.8</td>
<td>25.5</td>
<td>765</td>
<td>15.6%</td>
<td>973</td>
<td>23.4%</td>
</tr>
</tbody>
</table>
Table 4.2. Means (and medians) of crossing sequence lengths, $m$, and [$M_{\logit} p_{\text{ping}}$] model parameters fit to 4 153 sequences (765 sequences of $n = m = 1$ are excluded), separated by habitat and tag type.

<table>
<thead>
<tr>
<th>Habitat</th>
<th>Tag type</th>
<th>Total $X_\Sigma$</th>
<th>$m$</th>
<th>$\omega$</th>
<th>$\sigma$</th>
<th>$p_{\text{max}}$</th>
<th>$x_{\text{min}}$</th>
</tr>
</thead>
<tbody>
<tr>
<td>Fraser River</td>
<td>V7</td>
<td>152</td>
<td>24.0</td>
<td>20.5</td>
<td>0.86</td>
<td>0.73</td>
<td>52.1 (50.5)</td>
</tr>
<tr>
<td></td>
<td>V9</td>
<td>594</td>
<td>22.4</td>
<td>18.1</td>
<td>0.98</td>
<td>0.80</td>
<td>52.4 (50.5)</td>
</tr>
<tr>
<td>Smaller rivers</td>
<td>V7</td>
<td>313</td>
<td>16.1</td>
<td>14.7</td>
<td>0.50</td>
<td>0.88</td>
<td>51.2 (50.5)</td>
</tr>
<tr>
<td></td>
<td>V9</td>
<td>699</td>
<td>20.7</td>
<td>18.6</td>
<td>0.56</td>
<td>0.86</td>
<td>51.4 (50.5)</td>
</tr>
<tr>
<td>Estuaries</td>
<td>V7</td>
<td>32</td>
<td>25.9</td>
<td>20.1</td>
<td>1.44</td>
<td>0.71</td>
<td>52.4 (50.5)</td>
</tr>
<tr>
<td></td>
<td>V9</td>
<td>433</td>
<td>45.4</td>
<td>38.5</td>
<td>1.48</td>
<td>0.62</td>
<td>53.9 (50.5)</td>
</tr>
<tr>
<td>Inner coast</td>
<td>V7</td>
<td>224</td>
<td>28.4</td>
<td>22.4</td>
<td>1.30</td>
<td>0.66</td>
<td>53.6 (50.5)</td>
</tr>
<tr>
<td></td>
<td>V9</td>
<td>1 357</td>
<td>36.5</td>
<td>29.6</td>
<td>1.57</td>
<td>0.75</td>
<td>53.9 (50.5)</td>
</tr>
<tr>
<td>Outer coast</td>
<td>V7</td>
<td>0</td>
<td>34.4</td>
<td>27.1</td>
<td>1.69</td>
<td>0.81</td>
<td>54.1 (50.5)</td>
</tr>
<tr>
<td></td>
<td>V9</td>
<td>349</td>
<td>34.4</td>
<td>27.1</td>
<td>1.69</td>
<td>0.81</td>
<td>54.1 (50.5)</td>
</tr>
</tbody>
</table>
Table 4.3. Comparison of $\hat{p}_{mr,j}$ and estimators of $p'_{loc,j}$: five $[M_{\text{logit}} P_{\text{ping}}]$ models (four with a correction factor, $F_j$), five probability distribution fits to crossing sequence $m$ histograms, and one receiver subsetting method.

<table>
<thead>
<tr>
<th></th>
<th>Fraser River</th>
<th>Smaller rivers</th>
<th>Inner coast</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>$r^*$</td>
<td>$b^*$</td>
<td>$a^*$</td>
</tr>
<tr>
<td><strong>$M_{\text{logit}} p_{\text{ping}}$ model</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Uncorrected ($F_j = 1$)</td>
<td>0.31</td>
<td>0.14</td>
<td>0.80</td>
</tr>
<tr>
<td>$F_j = \bar{m}<em>j/\bar{m}</em>{HS_{outer}}$</td>
<td>0.54</td>
<td>0.71</td>
<td>0.20</td>
</tr>
<tr>
<td>$F_j = \bar{m}<em>j/\bar{m}</em>{HS_{outer}}$</td>
<td>0.47</td>
<td>0.68</td>
<td>0.18</td>
</tr>
<tr>
<td>$F_j = \bar{\omega}<em>j/\bar{\omega}</em>{HS_{outer}}$</td>
<td>0.52</td>
<td>0.66</td>
<td>0.23</td>
</tr>
<tr>
<td>$F_j = \bar{\omega}<em>j/\bar{\omega}</em>{HS_{outer}}$</td>
<td>0.45</td>
<td>0.59</td>
<td>0.29</td>
</tr>
<tr>
<td><strong>Direct fits to crossing sequence $m$</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>$M_{\text{Poisson}}$</td>
<td>0.32</td>
<td>0.10</td>
<td>0.90</td>
</tr>
<tr>
<td>$M_{\text{neg-binom}}$</td>
<td>0.34</td>
<td>0.19</td>
<td>0.67</td>
</tr>
<tr>
<td>$M_{\text{geom}}$</td>
<td>0.48</td>
<td>0.35</td>
<td>0.56</td>
</tr>
<tr>
<td>$M_{\text{log-norm}}$</td>
<td>0.34</td>
<td>0.15</td>
<td>0.80</td>
</tr>
<tr>
<td>$M_{\text{gamma}}$</td>
<td>0.28</td>
<td>0.11</td>
<td>0.79</td>
</tr>
<tr>
<td><strong>Multi-receiver subsetting method</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>$M_{\text{odd-even subset}}$</td>
<td>-</td>
<td>-</td>
<td></td>
</tr>
</tbody>
</table>

* Criteria for comparison include correlation coefficients ($r$), slopes ($b$) and intercepts ($a$) of a linear regression of $p'_{loc,j}$ against $\hat{p}_{mr,j}$. 
Figure 4.1. Five $p_{\text{ping}}$ attenuation models fit to a crossing sequence of detections and missed transmissions. The main sequence, $X$, of ‘1’s and ‘0’s ranges from $X_1$ to $X_m$, with 50 ‘0’s added to either end of $X$ (some ‘0’s not shown). Parameters for model $[M_{\text{logit}} p_{\text{ping}}]$, $p_{\text{max}}$, $x_{\text{min}}$, $\omega$, and $\sigma$, are indicated.
Figure 4.2. Four examples of \([M_{\text{logit}} p_{\text{ping}}]\) model maximum-likelihood fits to crossing sequence data. In each plot, the top row of points represents detections \((p_{\text{ping}} = 1)\) and the bottom row represents missed transmissions \((p_{\text{ping}} = 0)\), with the logistic curve ranging between these rows, as in Fig. 4.1. Crossing sequence data involve: (a) \(n = m = 6\); (b) \(n = 2, m = 4\); (c) \(n = 35, m = 59\); (d) \(n = 35, m = 141\). Note that 20 zeros on either side of \(X\) in (d) are not shown.
Figure 4.3. Two examples of $p_{\text{max}}$ extrapolation to crossing sequences with $n = m = 1$. Small points represent $p_{\text{max}}$ estimates for crossing sequences with $n = 2$ to 20 at the same station, year, and tag type combination: (a) inner Howe Sound line (inner coast), 2006, V9 tags; (b) lower Squamish River, 2006, V9 tags. Large points represent extrapolated $p_{\text{max}}$ values for $n = 1$.

Figure 4.4. Histograms and cumulative probability distributions of 4,918 crossing sequences: (a) number of detections in a sequence, $n$; (b) sequence length, $m$, including missed transmissions. Cumulative distributions are shown in both plots for comparison: solid grey line with circles corresponds with $n$ and black dashed line corresponds with $m$. 
Figure 4.5. Histograms (on the diagonal) and co-plots of MLEs of $M_{logit}$ parameters fit to crossing sequences. The number of detections in the crossing sequence, $n$, is also shown for $n \geq 2$. Three parameters and $n$ are log-transformed. A Lowess fit line with smoothing parameter 0.2 is shown in each co-plot. Correlation coefficients between parameters or $n$ are shown above the diagonal.
Figure 4.6. Frequency distributions of the number of detections per crossing sequence, \( n \), separated by habitat. Only sequences with \( n \leq 20 \) are shown. Symbols from \( n = 1 \) to 20 are from sequence data, whereas large symbols at \( n = 0 \) are estimates of the number of fish crossing stations undetected, \( \hat{N}_{\text{hab}} \), under model \([M_{\logit} p_{\text{ping}}]\) with \( F_j = \frac{\bar{m}_j}{\bar{m}_{\text{HSouter}}} \).
Figure 4.7. Comparison of local-information detection probability estimator ($p_{loc,j}'$) from $[M_{logit} p_{ping}]$ model and mark-recapture detection probability estimates ($\hat{p}_{mr,j}$) at the same station, year, and tag type (in the Fraser River, estimates are stock-specific as well). Paired estimates are separated by habitat: (a) Fraser River, (b) smaller rivers, and (c) inner coast. Open circles show uncorrected $p_{loc,j}'$ and grey circles show $p_{loc,j}'$ with $F_j = \bar{m}_j / m_{Souter}$. Regression lines are shown for grey circles. Dotted lines show 1:1 relationship.
Figure 4.8. Ratio of $p'_{\text{loc},j}$ (model $M_{\log p_{\text{ping}}}$ with $F_j = \frac{m_j}{m_{\text{HS, tot}}}$) to $\hat{p}_{\text{mr},j}$ at the same station, year, and tag type (and, in the Fraser River, population as well). Points are plotted against the number of detected crossing events, $N_j$ (only paired estimates with $N_j \geq 10$ are shown), and separated by habitat type: Fraser River ($\Delta$), smaller rivers ($\circ$), and inner coast ($\blacktriangle$). Note log scale. The horizontal line at 1 shows where $p'_{\text{loc},j} = \hat{p}_{\text{mr},j}$. 

\[ \frac{\hat{p}_{\text{loc},j}}{\hat{p}_{\text{mr},j}} \]

Number of crossing events with $\geq 1$ transmissions detected
4.5 References


5 Methods for estimating detection efficiency and tracking acoustic tags with mobile transect surveys

5.1 Introduction

Mobile tracking of animals with acoustic or radio tags has been used by researchers for decades to study animal movements. Studies have usually focused on fine-scale behaviour by following tagged fish, documenting habitat or territory usage, site fidelity, and diurnal or seasonal patterns in foraging or spawning behaviour (e.g., Holland et al. 1985, Matthews et al. 1990, Block et al. 1997, Zeller 1998, Ng et al. 2007). A few studies have used active tracking to quantify rates or patterns of mortality with mark-recapture models (Hightower et al. 2001, Keeler et al. 2007). Many studies use mobile tracking methods by themselves or in conjunction with a stationary array of receivers to make inferences about the number of tagged animals present in a particular area at a particular time and/or their survival rates. Estimating such metrics requires assumptions about the likelihood of tags being successfully detected.

Whatever biological or fisheries questions are posed, few studies have documented detection efficiencies during transect surveys for acoustic-tagged animals (but see Hightower et al. 2001, Edwards et al. 2007) in contrast, for example, to mobile tracking surveys of passive integrated transponder (PIT) tags (Roussel et al. 2000, Keeler et al. 2007, Linnansaari et al. 2007). Sometimes the acoustic power of tags used is sufficiently high and sampling methods conservative enough that virtually all animals within a sampling area are detected. In other cases detection ranges with a test tag are quantified, but it is not always clear whether these observed ranges can be assumed for tagged animals due to possible depth, substrate, and speed differences. Several factors might affect detection ranges. From one study to another, variables such as engine noise, different hydrophone or receiver units, tag strength, or local oceanographic conditions can imply that detection ranges should not be assumed from values quantified in other studies. Within a study, variables such as weather conditions, background noise, boat speed, depth of tag or receiver, and substrate type (if tags are on or near the bottom) can affect detection ranges from one day or hour to another. Even if detection ranges were static within or across studies, it is not certain how these translate into detection probabilities during tag surveys.
In the Howe Sound study system, the movements of salmon smolts that migrated through a deep coastal fjord were tracked by boat and stationary receivers to estimate mortality. The early ocean period is thought to be critical for determining recruitment of many salmon populations, but until recently was not intensively studied. It is technically challenging to study such mortality and movement: salmon smolts are small so tag size (and related acoustic strength) is often limiting; fish may spend little time in nearshore areas; mortality rates may be high during this brief period; and tags from dead fish on the seabed can be difficult to detect. The depth of coastal fjord waters is often close to detection ranges of tags, leaving little distance in the horizontal plane within which to detect tags when conducting surveys from the water surface.

In this chapter, methods are described for estimating detection probabilities and transect widths in mobile surveys where a large proportion of tags is unlikely to be detected. Survey results are presented showing variation in detection ranges and efficiencies due to boat speed, tag depth, tag strength, and receiver system. Strategies are outlined for balancing the trade-off between area swept and detection efficiency per unit area, and for improving detection and decoding efficiencies in mobile tracking studies.

### 5.2 Methods

Transect surveys were conducted by boat over 2003–2007 in Howe Sound, a coastal fjord near Vancouver, Canada. Individually-coded VEMCO V9-6L and V7-2L tags (142 and 136 dB signal strength at 1 m, respectively) were surgically implanted into Squamish River watershed salmon smolts under POST. In May of each year these smolts migrated out of freshwater and through Howe Sound (Fig. 5.1) towards Georgia Strait. POST operated an array of VEMCO VR-2 or VR-3 stationary acoustic receivers in and beyond Howe Sound, and mobile surveys were designed to supplement the detection data by quantifying mortality patterns on a finer spatial scale during and after the smolt migration.

#### 5.2.1 Towed hydrophone set-up

For mobile tracking surveys, VEMCO VR-28 receivers with VH-40 directional hydrophones were used. Receivers were borrowed from different researchers in different years. The VH-40 hydrophone consists of four elements whose differential reception of the signal allows the direction to a tag to be estimated in real-time. The hydrophone is most sensitive to sound on a broad horizontal plane, but can also detect sound coming from above or below. The
frequency of tag pulses and resonance of the hydrophone both occurred at 69.0 kHz. To reduce noise, the VR-28 receiver and a connected laptop computer were powered with 12 V batteries that were isolated from the boat electrical system.

In a 2003 pilot study, the directional hydrophone was mounted at the end of a pole fixed to the research vessel. In 2004–2007 the hydrophone was mounted on a V-Fin paravane and towed behind the boat (Fig. 5.2a). The V-Fin is designed to dive when under tow to keep the hydrophone below the water surface. A deck cable and, when possible, a Kevlar-lined haired fairing cable were used to connect the hydrophone to the receiver. As much cable as possible was let out to increase the distance from the hydrophone to the boat engine, ranging from about 20–50 m depending on cable availability. Most surveys were conducted from a 40 ft cabin cruiser using only one of two diesel engines and propellers to reduce noise.

The VR-28 system includes one stereo audio system and a separate mono audio system. Users select through which of the hydrophone elements to listen. Incoming signal amplification is controlled either automatically or manually: gain ranges from 0–60 dB for the stereo system (and electronic detection system), and 0–30 dB for the mono system. The electronic system also receives signals from all four directional elements, but in theory (Voegeli and Pincock 1996) and in experience human ears generally detect tag signals long before the software program can successfully register and decode a tag signal. A stereo headset was used by one crew member to listen to port and starboard and a mono headset was used by another person to listen aft.

5.2.2 Sampling methodology

The goals and hence strategies of these surveys evolved over the five years of study. In 2003–2004, survey focus was placed equally on finding approximate locations of fish mortalities (assuming tags settle to the bottom near the location of mortality; this is a concern because marine mammal or fish predators may carry the tags substantial distances before defecating them) and quantifying fine-scale movements and habitat usage of fish that were alive, so in those years sampling occurred during the peak of the migration. In 2005–2007, survey focus was almost entirely on identifying locations of fish mortality, so sampling occurred during the tail end of the migration and several weeks later to verify whether tags stopped moving and were still at previously-determined locations (Table 5.1).

Parallel transects were spaced 200–300 m from shore and 500–600 m from adjacent transect lines (Fig. 5.1). Boat speeds were typically between 5–8 km·h\(^{-1}\) in 2003, 9–12 km·h\(^{-1}\) in 2004, and 7–10 km·h\(^{-1}\) in 2005–2007 (Fig. 5.3). Variation in transect spacing and speed
depended on the acoustic strength of tags tracked, desired coverage of sampling area, and performance of the receiver system which was continually verified with each triangulated tag location and/or with range testing using a test tag. Speed data in Fig. 5.3 were smoothed using an asymmetrical running average of the present and previous four GPS location updates (40 s total) to reduce noise from GPS position inaccuracy.

Total sampling effort for each survey is shown in Table 5.1. Distances and durations include the portion of surveys spent circling around a tag to triangulate its location and decode its ID (ranging from about 6–9% of the total time in 2003–2004 and 10–13% in 2005–2007), but the majority of the effort represents active transect surveys searching for tags. This differs from many mobile tracking studies where locating individuals is straightforward, and time is instead spent closely following individuals to quantify movement patterns. Approximately 600 km of transects were required to sample 90–95% of the area of Howe Sound assuming a detection range of 300 m to each side of the boat. Sampling effort was typically 80–100 km·d\(^{-1}\) and 9–11 h·d\(^{-1}\) (Table 5.1), which included time to triangulate locations and decode tag IDs. As sampling days were long and distances to ports often far, volunteer crew members remained and slept on board for 2–3 d each while both authors remained on board throughout the trips.

5.2.3 Identifying tags and triangulating locations

Whenever a tag was heard, the hydrophone position, direction of signal, and relative (qualitative) signal strength were marked on a laptop computer using Memory Map\textsuperscript{TM} chart plotting software. Boat tracks were continuously overlaid on the plotter via GPS input signals. The boat was usually slowed after hearing a tag, the transect direction was maintained until the signal became faint, and then the boat was turned in the probable direction of the tag. Tags typically emitted a coded pulse every 60 s on average (30–90 s range, random uniform interval between pulses). After several audible detections, an area where the tag was likely located could be identified with reasonable confidence. Slow, short transects were conducted around this area until the tag was decoded by the VR-28 software (or by a towed VR-2, see below). When time allowed, two or more identifications of the tag were made, especially if more than one tag was heard in the area. The transect survey was then resumed.

After a tag was out of hearing range, all plotted positions from which it was heard were inspected (along with directions and signal strengths), and its most likely position was triangulated. Since many tags took 30–60 min to decode, there was often a large number of audible detections on which to base triangulations. Tag directions or signal strengths of audible
detections sometimes gave conflicting information about where the tag was likely located, possibly due to fish movement (Schmutz and White 1990), sound echoes, current effects from different directions, or uncertain alignment of the paravane. Accuracy for each triangulated position was therefore estimated. Usually a position was estimated to within a horizontal radius of 200 m, but in some cases estimated accuracy was less, occasionally up to 500 m error when triangulation was absent or unreliable. This positional accuracy is much less than what is typically achieved in shallower-water systems (± 10-20 m in water 15-20 m deep around coral reefs, Zeller 1998, and ± 6 m with radio telemetry in water < 8 m deep, Kobler et al. 2008).

Some analyses involved separating the data by the fate of the tagged fish at the time of detection. After stationary receiver data from the POST array were downloaded, an assessment was made whether each tag detected during mobile surveys was in a live smolt or not, primarily based on whether the tag subsequently crossed a stationary receiver line. It was assumed that when a tag remained in the same location over several days or weeks and was not detected thereafter on stationary lines, the fish had died during its migration, with the tag probably laying on the seabed (Hightower et al. 2001, Miller and Sadro 2003). Alternative explanations of tag stationarity are unlikely: tag shedding rates are low for similar sizes of fish and tags for several weeks after implantation (Chittenden et al. 2009), and juvenile salmon probably do not take up long-term residency in a narrowly-constricted area. Possible transport of tags in predator stomachs was not considered in the analysis.

5.2.4 Measures of detection and decoding efficiencies

Several distance and time indices of signal range and decoding efficiency were recorded for tags detected during blind transects (blind in the sense they were on regular sampling transects and not targeting locations where a tag had been previously detected). The shortest (i.e., perpendicular) distance from the triangulated tag location to the transect line (or to a hypothetical extension of the transect line if the boat veered off early in the direction of a detected tag) was estimated (Fig. 5.2b). This provides information on how far to either side of the transect line tags were regularly detected. Beginning in 2005, the distance from where a tag was first heard to its eventual triangulated location was also measured (Fig. 5.2b), as well as the maximum distance from where a tag was heard while circling it to its triangulated location. These latter two distance measures provide estimates of detection range for comparative purposes. The time from when a tag was first heard until it was successfully decoded with its location triangulated was recorded to provide an estimate of how efficiently tags were decoded after being audibly detected.
5.2.5 Comparison with omni-directional hydrophone

In 2007, an additional system was used to increase the efficiency of hearing tags: a Sonotronics USR-96 receiver with a custom-built towed SH-1 omni-directional hydrophone. As the focus was on locating tags that were likely on the seabed, and also to get the hydrophone below noisier surface waters, a reinforced section of the hydrophone cable was attached to a steel downrigger line 2 m from the hydrophone tip. A similar reinforced section of the cable was attached to the boat about 4 m from the receiver end so that no strain was placed on the cable/receiver connection. The full length of cable was let out (25 m in May sampling trip, 130 m in July) and as much downrigger line as possible was let out without allowing the hydrophone cable to bear the cannonball weight (about 21 m in May, 110 m in July). The hydrophone cable was only 2.6 mm in diameter so experienced relatively little drag at typical towing speeds. The SH-1 hydrophone cable and downrigger line trailed behind the boat at an angle of 10–15° beneath the horizon, but the length of cable was sufficient to keep the hydrophone several metres (May trip) or tens of metres (July trip) underwater. The Sonotronics hydrophone was towed off the side of the boat opposite to the VEMCO hydrophone to avoid crossing lines when turning.

The SH-1 hydrophone is near omni-directional, but as designed was most sensitive to tag signals aft of the boat while under tow. One crew member listened through headphones with this system. To increase the combined sampling coverage, in 2007 the mono headset of the VEMCO system was set to listen ahead of the hydrophone rather than aft as in previous years. Effective sampling required four crew members when both systems were operational: three people with headphones including the boat driver, and a fourth to deploy a dinghy when necessary and rotate listening duties with the others.

5.2.6 Attempts to improve decoding success of located tags

In many radio and acoustic tracking studies with stronger tag signals, tag IDs are determined relatively quickly and more time is spent moving around to obtain directional information for increasing the accuracy of triangulated locations. In this study, a tag location was often triangulated with reasonable accuracy (<100–200 m horizontal distance) long before the VR-28 receiver decoded the tag ID, if at all. Gain or boat position adjustments rarely helped with decoding tag IDs. Many of these difficult tags were likely on the seabed, either in smolts that died during their migration or after having passed through the gut of predators. In this fjord with typical depths of 200–250 m, much of a tag’s transmission range would be taken up by vertical
distance, leaving little range in the horizontal plane for hydrophones at the surface to detect it. This was especially true for the weaker V7 tags. Although some of our sampling occurred during windy or rainy periods (which reduce detection range), the majority of sampling occurred during relatively calm periods, with wave height rarely above 0.5 m and wind speed typically <10 knots.

Several means were used to decode tag signals when the VR-28 did not:

1. The boat was positioned on or upcurrent of the triangulated tag location and the engine was shut off to reduce noise. The hydrophone receiver mounted on the V-Fin paravane then fell directly beneath the boat. A VEMCO VR-2 receiver was also lowered from a line weighted by a lead cannonball over the side of the boat anywhere from 20–100 m deep. The boat slowly drifted over the likely tag location. The VR-2 receiver was left in the water for 10–20 min, after which it was retrieved and downloaded. If the tag was decoded, transects were resumed; if it was not, the boat was re-positioned in a slightly different location and another drift transect was attempted.

2. Deploying and retrieving the VR-2 from the boat was time consuming (although it usually gave better decoding success than the VR-28). In other attempts, a VR-2 was attached to a downrigger cable and lowered 20–30 m deep. A steel tether wire attached the VR-2 to the boat in case the VR-2 detached from the downrigger cable. Transects were conducted as usual. At typical speeds, the VR-2 and downrigger cannonball trailed behind the boat at a shallow angle. When the boat slowed upon hearing a tag, they sank deeper in the water. The boat stopped or slowly trolled around the area for several minutes before resuming transects. The VR-2 was not immediately retrieved, so it was unknown whether the tag was decoded until later, when the downrigger cable was raised to download the VR-2.

3. When a reasonably precise location of a tag was determined, a VR-2 was deployed, hanging from a buoy by a line 100 m long. The position of the buoy was marked on the chart plotter, and the boat continued circling around the area to refine estimates of the triangulated tag location and attempt to decode the tag with the VR-28. In some cases sampling transects were continued away from the area for about 30 min (keeping a watch on the buoy through binoculars) until returning to retrieve the VR-2. This had the added benefit of reducing boat noise in the area to improve signal strength:noise ratios and thus the decoding ability of the VR-2.

4. After hearing a tag, many attempts to decode it took 30–60 min or longer. When extra personnel were available for listening through headphones, sampling effort was separated in order to resume transects more quickly. After hearing a tag and triangulating a reasonably precise location, this location was plotted on a hand-held GPS receiver. One member of the team left the boat by dinghy and proceeded to that location while the main boat resumed transects. The
driver positioned the dinghy 100–150 m upcurrent of the likely tag location and lowered a VR-2 in the water 100–200 m deep with a lead weight attached (to lower the VR-2 faster and keep it deeper while drifting). The dinghy drifted over and beyond the likely tag location for a short transect of 200–300 m. Holding the line with VR-2 still deployed, the driver slowly re-positioned the dinghy to commence another drift transect. In total, three parallel drift transects were generally conducted, spaced 100–150 m apart and each 200–300 m long, with this sampling area centered over the most likely tag location.

5.3 Results

5.3.1 Assessment of transect width and detection efficiency

The horizontal component of the perpendicular distance from a blind transect line to a triangulated tag location can assist in providing a relative estimate of detection efficiency. If there was equal chance of detecting a tag out to some assumed detection width during transect surveys, e.g., 300 m to port or starboard, the expected frequency distribution of tag detections over that distance would be uniform. Most distributions quantified were clearly not uniform to 300 m, especially for V7 tags (Fig. 5.4). The distribution for V7 tags in 2005–2007 seemed to be fairly flat out to only about 150 m to either side of the boat, after which it dropped off precipitously. For V9 tags over these same years, the distribution seemed to approximate more of a linear decline with distance from the transect line to about 350 m, with about twice as many tags detected between 0–100 m from the transect line as those detected between 200–300 m away. There appeared to be a minor linear decline with distance for V9 tags in 2004, although the distribution was much closer to uniform out to ≥300 m than in later years. The 2003 distribution of V9 tags was based on only a few detections, so the shape of this distribution is less certain. The difference in shape of these distributions partly reflects the study objectives and proportion of live fish tracked. In 2003 and 2004 a higher proportion of the detections were of live fish (which are closer to the surface so can be detected at longer distances), whereas in 2005–2007, a higher proportion of detections were of tags in or from dead fish, presumably laying on the seabed (Table 5.2). Figure 5.4 (and subsequent Figs. 5.6, 5.9–5.11) shows only those detections where triangulated locations were estimated with <200 m error.

One way to quantify the drop-off in detection efficiency with increasing distance is to order the perpendicular distances of tag detections during blind transects and plot this cumulative proportion against distance. Figure 5.5 shows this relationship using the same data as for the
histograms in Fig. 5.4. The perpendicular distance at some high cumulative proportion of tag detections (e.g., 80 or 90%, shown by dotted grey lines) can be obtained by determining the intersection of cumulative distribution curves with this threshold value. For example, values corresponding to 80% cumulative proportions are estimated at 197, 263, 212 and 108 m for 2003 V9, 2004 V9, 2005–2007 V9, and 2005–2007 V7 groups, respectively. A threshold of interest could be determined a priori to meet some level of acceptance depending on study objectives. An appropriate threshold could also be determined conservatively from the data, the idea being to find as high a threshold as possible where the increase in cumulative proportion of detections with increasing perpendicular distance is fairly constant. In Fig. 5.5, the curves for V9 tags in 2004 and 2005–2007 bend sharply between the 80 and 90% threshold levels, so the distances at 90% cumulative proportions for these groups would be poor, or at least not very conservative, choices. Threshold distances could be determined as those immediately before such sharp bends. Note that even for the 2003 data (with relatively few total detections), this method of cumulative proportions generated a reasonable prediction of a distance threshold. The threshold estimates are closely comparable to those of V9 tags from other years (and appropriately slightly less, since the receiver was pole-mounted and fixed to the boat rather than towed behind it).

5.3.2 Balancing trade-offs of detection efficiency and area swept

Boat speed may affect the detection efficiency of tags along a sampling transect, since it affects the time within detection range of a tag. Faster boat speeds may therefore decrease detection efficiency per unit distance of transect surveys. On the other hand, faster speeds allow more distance to be covered in a fixed amount of time, which will generally result in a larger area swept. For a given sampling time or budget, it may be worthwhile increasing boat speed during transects to cover more area, even if that comes at the expense of reduced detection efficiencies. An optimum boat speed exists in theory and can be determined empirically through rigorous transect surveys of test tags or stationary tags with known locations.

Total area swept is a product of transect distance and (perpendicular) width to each side of the boat, \( A_t = D \cdot W \cdot 2 \) (although the actual relationship of \( A_t \) and \( D \) is not truly linear if boat tracks overlap). Transect distance is directly proportional to speed (Fig. 5.6a), while \( W \) decreases with speed due to effects of boat noise, noise of water rushing past the hydrophone, and paravane depth, as discussed later. This relationship between \( W \) and speed may take the form of an inverse logistic curve, with a relatively constant and high \( W \) at low speeds, after which it decreases as speed increases then levels out to remain non-negative at all possible boat speeds (Fig. 5.6b).
inflection point of the curve represents a threshold speed where \( W \) is half of the maximum \( W \), and the slope around this point can vary. The resulting \( A_1 \) is a skewed dome-shaped function with speed (Fig. 5.6c). Maximum \( A_1 \) occurs at the speed where the decrease in \( W \) with increasing speed is no longer compensated by the increase in \( D \), slightly less than the speed at the inflection point of the \( W \) curve. The spread of \( A_1 \) results from the steepness around this inflection point.

The total area swept overestimates the true area sampled because as speed increases the time spent within the detection range of a tag along a transect decreases, so the probability, \( E \), of hearing a tag at least once given that it is on the transect decreases. This detection efficiency, \( E \), is affected by boat speed, average pulse rate of tags, detection range, and average probability of hearing a single transmission within this range while sampling, \( P_{\text{ping}} \). It is obtained by calculating the expected number of transmissions emitted, \( N \), while the boat, at some speed, is within an assumed detection range of the tag. Since only one (or more) heard transmissions are required to detect the tag, the probability of hearing no transmissions is subtracted from 1: \( E = 1 - (1 - P_{\text{ping}})^N \). The function \( E \) takes the general form of a gradual, inverse logistic decline with increasing speed (Fig. 5.6d), but is sensitive to assumptions about \( P_{\text{ping}} \), average tag pulse rate, and detection range. Depending on the value of \( P_{\text{ping}} \), the shape of the function within the speed range considered may resemble either an exponential decay or a shallow, accelerating decline with increasing speed.

Multiplying the \( E(\text{speed}) \) and \( A_1(\text{speed}) \) functions results in the effective area swept function, \( A_e(\text{speed}) \) (Fig. 5.6e). This represents the proportion of the total area swept in which at least one transmission of a tag should be heard given that it is within the sampling transect. The relationship of \( A_e \) with speed is similar to that of \( A_1 \) at low speeds, and becomes disproportionately reduced at higher speeds. It passes through the origin, increases in a decelerating form to a maximum \( A_e \), then decreases before levelling out to remain non-negative. The speed that maximizes \( A_e \) depends principally on the speed at the inflection point of the logistic function \( W \). It also depends on other parameters, with a higher optimum speed realized when \( P_{\text{ping}} \) is higher, average tag pulse rate is faster, detection range is greater, and the standard deviation around the inflection point of \( W \) is lower (generating a steeper slope; Fig. 5.6e). It may be that maximum boat speed is less than the predicted optimum, in which case maximum \( A_e \) occurs at the maximum boat speed.
5.3.3 Effect of boat speed on detection efficiency

The prediction from the previous section, that detection efficiency for a given transect distance may be reduced at higher boat speed (Fig. 5.6d), can be assessed by comparing the distribution of boat speed used during blind transect surveys (‘transect speed’, $s_t$; Fig. 5.3) against the distribution of boat speeds at the moment when a tag was first heard during transects (‘detection speed’, $s_d$; Fig. 5.7). If these distributions have similar shapes, one can conclude that transect speeds were not limiting detection capabilities. Visually, this appears to be the case for detecting V9 tags during transects in 2004 and 2005–2007 studies (Fig. 5.7). In contrast, fast transect speed may have limited the detection capacity of V9 tags in 2003 and V7 tags in 2005–2007, as $s_d$ appears to be slightly lower than $s_t$. Means of the distributions of $s_d$ and $s_t$ were compared using a non-parametric, one-tailed Mann-Whitney $U$ test, separately for each study. To compare $s_d$ against only the portion of $s_t$ consisting of active blind transects, values of $s_t < 7$ km·h$^{-1}$ in 2004 and 2005–2007 studies were excluded (which represented the portion of transects while circling a tag). Note that some tags were first heard while boat speeds were < 7 km·h$^{-1}$; these values of $s_d$, in contrast, were not excluded. These tags were first heard while the boat had already slowed to circle around a different tag. They were not heard before this, when boat speed was > 7 km·h$^{-1}$ during active transects, so their inclusion is justified to test the hypothesis that transect speed limited detection capacity.

As suspected, differences were not detected between mean $s_d$ ($\bar{s}_d$) and mean $s_t$ ($\bar{s}_t$) for V9 tags during transects in 2004 ($\bar{s}_d = 9.79$, $\bar{s}_t = 10.11$ km·h$^{-1}$; $n(s_d) = 40$, $n(s_t) = 36,302$, $p = 0.188$) and 2005–2007 ($\bar{s}_d = 8.44$, $\bar{s}_t = 8.96$ km·h$^{-1}$; $n(s_d) = 36$, $n(s_t) = 146,026$, $p = 0.142$) studies. For V7 tags in the 2005–2007 study, however, $\bar{s}_d < \bar{s}_t$ when values of $s_d < 7$ km·h$^{-1}$ were included ($\bar{s}_d = 8.47$, $\bar{s}_t = 8.96$ km·h$^{-1}$; $n(s_d) = 28$, $n(s_t) = 146,026$, $p = 0.022$; although note that if the two values of $s_d < 7$ km·h$^{-1}$ were also excluded, this would result in $p > 0.05$). The width of the $s_d$ distribution was narrower for V7 tags than for V9 tags in 2005–2007 (Fig. 5.7), partly accounting for why a difference was observed only for V7 tags. Despite the visual suggestion that $\bar{s}_d < \bar{s}_t$ in the 2003 study (Fig. 5.7), the difference was not statistically significant at this small sample size of $s_d$ ($\bar{s}_d = 4.55$, $\bar{s}_t = 5.31$ km·h$^{-1}$; $n(s_d) = 8$, $n(s_t) = 23,136$, $p = 0.152$).
5.3.4 Effects of depth and fish fate on detection range

When perpendicular distance data from Fig. 5.4 are separated by the fate of fish (alive or dead) at the time of detection, sample sizes of each fate are often small within each study period and tag size; there were relatively few dead fish tracked in 2003–2004 and few live fish tracked in 2005–2007. Overall effects of fish fate on perpendicular distance are shown in Fig. 5.8 when study periods and tag sizes are pooled together. These data clearly show that the distribution of fish which were alive is much closer to uniform out to 300 m than the distribution of fish that were dead at the time of detection. The sharp decline in the proportion of tag detections from dead fish after 150 m is largely due to the decline of V7 tags shown in Fig. 5.4, although a similar (but weaker) pattern occurred in 2005–2007 for V9 tags as well. This suggests that, as expected, the horizontal component of detection range was shorter for tags from dead fish (at the bottom) than for live fish (closer to the surface).

The relationship between horizontal perpendicular distance from transect line to tag location and bottom depth at the tag location is expected to differ for tags in live and dead fish. No such relationship is expected for fish that are alive since salmon smolts probably use the upper 25–40 m of the water column (Orsi and Wertheimer 1995, Beamish et al. 2000). The data confirm this, whether tag type and study period are considered separately (Fig. 5.9) or together (Pearson’s correlation, $r = 0.03$). For tags laying on the bottom, a more or less uniform distribution of horizontal perpendicular distance would be expected at shallow depths, with the upper range of distance decreasing as depth increases since more tag-to-receiver distance is taken up in the vertical plane. Surprisingly, a slight trend in the opposite direction is seen ($r = 0.28$ with tag sizes and study periods grouped). Three data points >200 m depth and >300 m perpendicular distance have high leverage (Fig. 5.9; without these a weak trend in the expected direction would be seen), but there is no reason to exclude these detections.

5.3.5 Comparison of different receiver systems

There was evidence of variability in detection ranges and efficiencies between different VR-28 hydrophone/receiver units. The unit used in 2003 was pole-mounted and adjacent to the boat so distance or time metrics are not directly comparable to other years. In the 2004 study, average perpendicular distances from transect line to tag location were further than in 2005–2007 for V9 tags (Figs. 5.5–5.6). Similarly, the average time it took to decode a V9 tag from when it
was first heard (Table 5.3) was less in 2004 than in the 2005–2007 studies (2-sample t-test with unequal sample sizes and variances, d.f. = 34, p < 0.05).

There were also differences in detection ranges and efficiencies between the VEMCO VR-28 directional hydrophone/receiver system and the Sonotronics USR-96/SH-1 omni-directional system. After hearing a tag on one or both systems, the tag location was triangulated and short transects were conducted around this location to decode the tag ID on the VR-28 or on a VR-2 receiver. During this period of circling, tags were heard from a longer distance on average (paired t-test, d.f. = 18, p < 0.05; Fig. 5.10) with the omni-directional system than with the directional system. More importantly, detection efficiencies differed between systems (binomial sign test for two dependent samples with tag sizes grouped, n = 26, p < 0.05; Table 5.4). Under blind transects, more tags were heard with the omni-directional system (24 of 26 detections) than with the directional system (16 of 26).

5.4 Discussion

Quantifying detection efficiency in mobile tracking studies—the ratio of tags detected to tags present in a swept area at some time—is important for most if not all types of studies. It is crucial if any inferences are to be made regarding survival or current abundance of the tagged population in an area (Hightower et al. 2001, Edwards et al. 2007). It is also important in behavioural studies if the fish not detected exhibit different behaviours on average than the fish detected (e.g., swim deeper), thereby biasing results. Indeed, reasons for not detecting tagged fish might in some cases result from specific behaviours or habitats used (Matthews et al. 1990, Hightower et al. 2001, Keeler et al. 2007). While detection ranges are often assessed from tag to receiver, efficiencies are often overlooked for mobile surveys.

5.4.1 Transect width and detection efficiency

The distribution of perpendicular distances from blind transect line to triangulated tag location was generally not uniform out to some threshold distance (Fig. 5.4), suggesting that detection efficiency is a declining function of distance from a transect line. If sufficient data are collected to characterize the shape and spread of the perpendicular distance distribution, relative estimates of detection efficiency can be obtained by fitting an attenuation function to these data. Several functions are possible (linear decline, logistic, Gaussian, mechanistic declines involving geometrical spreading and sound absorption); these can all be fit to data and compared using
information-theoretic approaches. At least for stationary receivers, a logistic function with a variable plateau width generally outperforms other models in characterizing the relationship between detection success and distance from tag to receiver (Chapter 4). Assuming a detection efficiency of 100% exactly along the transect line (which is commonly assumed in line transect sampling, Anderson et al. 1979), the fitted function will decline from 1 towards 0 with increasing horizontal perpendicular distance. For a specified transect width, detection efficiency can be calculated as the ratio of the area under this curve to the area of a uniform probability distribution (of 100% detection efficiency). This estimate will be biased high if the actual detection efficiency of tags exactly along the transect line is <100%, which is of greatest concern for tags on the bottom in deep waters, buried in sand, or among complex benthic structure.

An absolute estimate of detection efficiency can be obtained by repeatedly running transects past a known tag location and quantifying the proportion of passes where the tag is detected (or proportion of surveys, in areas that are repeatedly sampled to relocate tags, Robichaud and Rose 2001). This tag can either be a deployed test tag or a stationary tag from a fish that died during its migration. With a test tag, particular attention must be paid to ensuring it is at a comparable depth or among benthic structure similar to that used by the study organism. Efficiencies can be assessed by varying boat speed and perpendicular distance from transect line to tag location. This should be repeated in several different locations within the study area and during different weather conditions to establish generality in quantified efficiencies. Several such test tag passes were conducted at various times, and when a tag was near the surface and passed within 50–100 m, it was generally detected at least once at near 100% efficiency. At longer perpendicular distances or when tags were in deep waters, detection efficiency was often much less, especially for V7 tags. In some cases tags were heard in less than half the transect passes.

The shape of the distribution of perpendicular distances from transect line to tag also varied among years, depending on whether a higher proportion of live fish (2003, 2004) or dead fish (2005–2007) were sampled along transects (Fig. 5.8). Salmon smolts likely travel in surface waters (Orsi and Wertheimer 1995, Beamish et al. 2000) or at least far above the bottom where tags from dead fish would lay. From a receiver at the surface, the horizontal component of detection distance is expected to be longer for tags near the surface than for those at depth. For example, Bunt et al. (2003) found that acoustic power of radio tags at some horizontal distance was greatly reduced when the range also included a vertical component of tag to hydrophone distance. This is particularly relevant for the VR-28 system, which is more sensitive to tag signals on the same horizontal plane.
These methods of assessing detection widths and efficiencies for transect surveys can be applied not only to acoustic or radio tracking studies, but to mobile PIT tag surveys as well. Detection ranges for PIT tags are typically only about 1 m. Estimated detection efficiencies of PIT tags in surveys have often been >80% (e.g., Roussel et al. 2000, Keeler et al. 2007), but these studies have generally occurred in narrow, shallow streams where the entire habitat area can be swept. In habitats of greater width or area where sampling may only occur along a transect line, detection efficiencies are likely to be much less, and this ratio can be quantified.

5.4.2 Boat speed, detection efficiency, and area swept

The effect of boat speed on detection efficiency involves at least three mechanisms. First, a tag is within range for less time at faster speeds, so on average there are fewer transmissions within range and the chance of missing all transmissions is therefore higher (Fig. 5.6d). Tag programming of pulse rate and boat speed will both determine how many transmissions occur within some range along a sampling transect. Second, noises from a boat engine, propeller, and water flow past the hydrophone are usually greater at faster speeds. This relationship is not necessarily linear, and at relatively high speeds a further small gain in speed may only be realized by a disproportionately large increase in noise (Voegeli and Pincock 1996; Fig. 5.6b). This can be easily quantified by measuring the noise level (e.g., with a VEMCO VR-100 or high-frequency oscilloscope) at different boat speeds. Third, at faster speeds a towed paravane will usually be situated closer to the water surface, where background noise is generally greater. The paravane depth at different boat speeds can be measured by attaching a data-logging depth gauge (e.g., a diver’s computer). The latter two mechanisms primarily affect transect width (Fig. 5.6b). The combined effect of these three factors on detection efficiency and ranges can be evaluated using a deployed test tag, keeping perpendicular distance from transect line to tag fixed while varying boat speeds among transects. Researchers using similar tags and tracking systems have found that optimum speeds for tracking occur below those used in this study (e.g., 3.7–5.6 km·h⁻¹ depending on environmental conditions; F. Goetz, pers. comm.). Others tracked at up to 13 km·h⁻¹ (Holland et al. 1985, Block et al. 1997) but used higher powered tags and followed fish in open water rather than conducting sampling transects near shore. Use of non-motorized watercraft for tracking can provide higher detection efficiency relative to motorized craft (F. Goetz, pers. comm.), although speeds would typically be lower.

The spacing between parallel transects affects the trade-off between area swept and detection efficiency per area. Transects spaced close together reduce the probability of missing a
tag located between them, but increase the potential redundancy in sampling effort thereby limiting the overall area swept. Rigorous range testing, fitting attenuation models to perpendicular distance data from blind transects, or quantifying sharp declines in perpendicular distances (Fig. 5.5) can all help to identify appropriate transect widths. Finding an appropriate balance in this trade-off as transect spacing and/or boat speed vary will depend on study objectives. If a total budget or time allotted for sampling is sufficient to thoroughly sample a study area, or if a high overall detection efficiency is desired for some particular portion of the study area, then transects can be spaced closely and speeds can be relatively slow. Alternatively, if only a portion of the study area can be sampled in an allotted time, then a less conservative approach of wide transect spacing and relatively fast speeds may be warranted, increasing the total area swept even if that is at the expense of some reduction in detection efficiency per unit transect length.

5.4.3 Depth, substrate, and detection efficiency

The overall positive relationship between perpendicular distance from transect line to triangulated tag location and depth was surprising. It may result from a confounding of bottom substrate and depth. Shallower depths tended to be associated with sandy, rocky, or occasionally gravel bottoms in Howe Sound, whereas deeper depths were associated with hard mud or occasionally rocky bottoms. Tags might become partially covered by sand or obscured by rocks at shallower depths, limiting their transmission range. Alternatively, shallower depths usually occurred closer to shore, so the potential for detections at long perpendicular distances would be half that of tags in deeper waters since transect lines closest to shore were generally only 200–300 m from shore. Shorter transmission range closer to shore was also observed in other studies, with a test tag lowered or towed by a boat through a dense array of stationary receivers (Dewar et al. 2008, Hedger et al. 2008). Others found effects of bottom substrate or complexity on detection ranges and frequency of detection (e.g., Matthews et al. 1990, Roussel et al. 2000, Keeler et al. 2007), but this source of variation is difficult to quantify in deep lake or marine systems.

5.4.4 Variation among receiver systems and dual-system tracking

For the same tag type, perpendicular distances from transect line to tag location were longer (Fig. 5.5) and the amount of time required to decode a tag was shorter (Table 5.3) in 2004 than in 2005–2007. This was partly related to the higher proportion of live fish tracked in 2004,
but could not fully explain the difference since similar patterns were observed for both measures when data were separated by alive/dead categories. The same research vessel and paravane method of hydrophone deployment were used in all years. Great care was taken to minimize electrical interference impacting the receiver signal strength:noise ratio, and it is unlikely that the inter-annual difference is caused by boat noise. Rather, the difference may be a result of different receiver units used (Table 5.1). Variation in hydrophone sensitivity or signal interpretation among these custom-made units may have translated into differences in detection range, detection efficiency, and temporal decoding efficiency.

During blind transects in 2007, tags were more likely to be detected by an omni-directional receiver system than by the directional system used in previous years. Other researchers have found similar results with these systems (F. Goetz, pers. comm.). This is not the result of a bias in early detection: if a tag was heard on only one system, the transect direction and speed were maintained until the boat was well out of range to verify whether or not the tag would have been heard by the second system in the absence of the first. This is likely the result of directional weaknesses, as the VR-28 system is designed mainly for detecting tags in a horizontal plane (D. Webber, pers. comm.). Due to the orientation of its four hydrophones, sensitivity to signals from directly below is less than out to the sides, front, or aft while under tow. As most tags tracked in 2007 were of fish that died during their migration, these were more difficult to detect with the VR-28 system than with the omni-directional system. Two of the 26 tags detected were in fish likely alive at the time; these were detected on both systems. A VEMCO VR-100 or VR-60 omni-directional hydrophone/receiver system were not available for concurrent comparison with the VR-28 or Sonotronics systems, but either of these would make good comparisons in future studies.

Simultaneous use of two separate receiver systems can not only improve the overall probability of detecting a tag along transects, but can also provide a means of estimating the maximum detection efficiency of each system. Failure to detect tags during transects can be seen as having two components: (1) a process component, where the average probability of missing a tag will depend on several factors including tag to transect distance, tag pulse rate, depth, substrate, weather conditions, and tag strength, and (2) a random sampling component, where for a given combination of these factors, tags will be missed some proportion of the time. If two receiver systems are used, it is assumed they are independent with respect to the random sampling component, but not the process component. Maximum detection efficiency for each system can be estimated, assuming random sampling, based on numbers of tags detected on each
or both systems. The total number of tags within the area swept is an unknown number, $X$.

Assuming independence between receiver systems, the ratio of the numbers of tags detected on both systems ($S_1$ and $S_2$) to $X$ should equal the product of the ratios of the tags detected on each system to $X$ (similar to the Lincoln-Peterson method; Seber 1982). Using numbers of detected V7 tags from Table 5.4, $11/X = (13/X) \cdot (20/X)$, which requires that $X = 23.6$. Thus, the maximum estimate of detection efficiency of V7 tags on the directional receiver system is $13/23.6 = 0.55$. This maximum overestimates the actual detection efficiency to some unknown degree due to the process component of not detecting tags, as detection efficiencies are rarely expected to be independent between systems. Given the data, the higher the positive covariation between systems in detecting tags, the lower will be the actual detection efficiency with respect to the estimated maximum. The ‘$S_1$ and $S_2$’ and ‘neither $S_1$ nor $S_2$’ categories become inflated relative to the ‘only $S_1$’ and ‘only $S_2$’ categories as this covariation increases, so $X$ becomes increasingly underestimated. If two receiver systems are available in a mobile tracking survey, calculating this maximum estimate of detection efficiency can be used to verify estimates calculated from fitting attenuation functions to horizontal perpendicular distances and/or test tag assessments.

### 5.4.5 Recommendations for future studies

Several methods for improving detection and decoding efficiencies were presented earlier; this section offers additional recommendations. Reducing noise as much as possible is crucial for increasing signal strength:noise ratios and thus improving the ability to hear tags. Towing a hydrophone by paravane as far behind the boat as possible will reduce the effect of engine noise. A thorough assessment of possible boat noises should be done while conducting range tests, so as to reduce noise when later conducting transect surveys. Possible noises include propeller cavitation, depth sounders, water pumps, boat DC systems, AC inverters (even if no equipment is connected), DC refrigerators, electromagnetic fields near the receiver or connected laptop, and GFCI AC outlets. Noise reducing headphones greatly assist in muffling in-air engine noise, allowing signals to be heard more clearly through headphones. Custom-built hydrodynamic hydrophone shields can be used to decrease noise of water rushing past the shield (Block et al. 1997; M. Shane, *pers. comm.*). Variation in detection ranges due to boat speed (hence boat noise) can be assessed with range tests, and an optimum boat speed can be determined for maximizing overall detection efficiency.
An important trade-off to consider when planning sampling studies is the proportion of time to spend range testing. For a fixed budget, time spent conducting range tests will be at the expense of total area swept. When beginning a study, initial information gained through range testing is required to determine initial transect spacing and expected detection efficiencies. After this initial learning curve, range testing can be used for brief periods to verify consistent equipment performance, preferably varying these tests over different habitats and weather conditions. When possible, located tags from tagged fish can be used for testing detection ranges. This has the drawback of not knowing the precise location of the tag, but has several benefits: it saves time from having to deploy a test tag; the depth and speed of the tag is appropriate for the study species; a tag in a live fish can be followed to quantify movement rates as well; and a stationary tag on the seabed can be revisited under different weather conditions to evaluate differences in detection ranges.

An additional factor calling for regular range testing on all surveys is the risk of equipment failure or reductions in detection range due to unknown factors. Even if the background noise on headphones sounds normal to the trained ear, or if test tags are easily heard in air or from short distances in the water, situations of considerably reduced maximum detection ranges were encountered. Sometimes this was rectified after adjustment of the equipment and connector cables. Other times the problem could not be identified, and reduced detection ranges were observed for several hours or several days within a sampling trip. Without regular range testing, assumed detection widths may be overestimated during some portion of transect surveys.

Detection data from mobile tracking can often be combined with those from a stationary receiver array, identifying locations of tagged animals either outside the detection range of the stationary array (Ng et al. 2007) or which cannot be detected by the stationary array due to obstructions (Lowe et al. 2009). This permits a retrospective determination of whether detected tags were likely in live fish or not at the time of detection, which has also proved to be an important factor in explaining variation in detection ranges and efficiencies in this study system due to depth and bottom substrate differences.
Table 5.1 Mobile tracking effort during Howe Sound trips. Distances and times include the portion of tracks spent circling around a tag to decode and triangulate its location.

<table>
<thead>
<tr>
<th>Survey trip</th>
<th>Number of sampling days</th>
<th>Total distance (km)</th>
<th>Total time (h)</th>
<th>Receiver system(s) a</th>
</tr>
</thead>
<tbody>
<tr>
<td>May 2003</td>
<td>8.25</td>
<td>500</td>
<td>94.2</td>
<td>VR-28 (A), pole-mounted</td>
</tr>
<tr>
<td>May 2004</td>
<td>17</td>
<td>1800</td>
<td>184.6</td>
<td>VR-28 (B), towed</td>
</tr>
<tr>
<td>May 2005</td>
<td>11.75</td>
<td>1273</td>
<td>136.1</td>
<td>VR-28 (C), towed</td>
</tr>
<tr>
<td>July 2005</td>
<td>2.25</td>
<td>190</td>
<td>21.0</td>
<td>VR-28 (C), towed</td>
</tr>
<tr>
<td>May 2006</td>
<td>6</td>
<td>470</td>
<td>65.3</td>
<td>VR-28 (C), towed</td>
</tr>
<tr>
<td>August 2006</td>
<td>6.75</td>
<td>593</td>
<td>72.0</td>
<td>VR-28 (C), towed</td>
</tr>
<tr>
<td>May-June 2007</td>
<td>8.75</td>
<td>687</td>
<td>89.5</td>
<td>VR-28 (C), towed; omni-directional USR-96</td>
</tr>
<tr>
<td>July-Aug. 2007</td>
<td>8.25</td>
<td>654</td>
<td>74.6</td>
<td>VR-28 (C), towed; omni-directional USR-96</td>
</tr>
</tbody>
</table>

a Different VR-28 systems were used in different years and are designated by different letters (A, B, C).

Table 5.2 Number of tag detections during blind transect surveys where triangulated locations were estimated with <200 m error. Fate of fish (alive/dead) was not known at the time but determined later with repeat mobile sampling and constructing detection sequences of each tag from stationary array data.

<table>
<thead>
<tr>
<th>Year</th>
<th>Tag type</th>
<th>Fish status</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>Alive</td>
</tr>
<tr>
<td>2003</td>
<td>V9</td>
<td>6</td>
</tr>
<tr>
<td>2004</td>
<td>V9</td>
<td>30</td>
</tr>
<tr>
<td>2005–2007</td>
<td>V7</td>
<td>3</td>
</tr>
<tr>
<td></td>
<td>V9</td>
<td>9</td>
</tr>
</tbody>
</table>

Note: In addition to these detections, other tags were heard in each study but either had a triangulated location with >200 m estimated error (2003 V9, 1; 2004 V9, 3; 2005–2007 V7, 5; 2005–2007 V9, 7) or were never decoded (2005–2007, 13 tags).
Table 5.3  Average time in minutes from when a tag was first heard during blind transects until it was successfully decoded with its location triangulated. Standard errors and sample sizes are shown in parentheses.

<table>
<thead>
<tr>
<th>Year</th>
<th>Tag type</th>
<th>Time from first heard to ID (min)</th>
</tr>
</thead>
<tbody>
<tr>
<td>2003</td>
<td>V9</td>
<td>10.3 (±3.6, 9)</td>
</tr>
<tr>
<td>2004</td>
<td>V9</td>
<td>8.1 (±2.2, 38)</td>
</tr>
<tr>
<td>2005–2007</td>
<td>V7</td>
<td>33.9 (±5.7, 19)</td>
</tr>
<tr>
<td></td>
<td>V9</td>
<td>22.8 (±6.2, 28)</td>
</tr>
</tbody>
</table>

Table 5.4  Number of times a tag was detected on directional (VEMCO VR-28) and/or omni-directional (Sonotronics USR-96) hydrophone/receiver systems during blind transects in 2007.

<table>
<thead>
<tr>
<th></th>
<th>V7 tags</th>
<th>V9 tags</th>
</tr>
</thead>
<tbody>
<tr>
<td>Detected on both systems</td>
<td>11</td>
<td>3</td>
</tr>
<tr>
<td>Detected only on omni-directional system</td>
<td>9</td>
<td>1</td>
</tr>
<tr>
<td>Detected only on directional system</td>
<td>2</td>
<td>0</td>
</tr>
<tr>
<td>Detected on neither system *</td>
<td>3</td>
<td></td>
</tr>
</tbody>
</table>

*The last row is not a total estimate of the fish that were missed. These are known missed detections while passing the location of a previously detected tag. On those targeted (i.e., not blind) passes the tags were not heard on either system the first pass, but after doubling back to check the previous location, were heard after. Not included in this category is the unknown number of tags that were missed with both receivers during blind transects.
Figure 5.1. Map of Howe Sound with parallel transect surveys (black lines) performed during the July-August 2007 sampling trip. Tagged fish enter Howe Sound at the northern end from the Squamish River and migrate south towards Georgia Strait. Map was created with the R package PBSmapping (Schnute et al. 2004).
Figure 5.2. Schematics of sampling equipment (a) and detection range definitions (b). For (a): the towed hydrophone is connected to the on-board receiver by the deck cable. When available, a hairfairing cable was inserted between the towing line/deck cable and the V-Fin/hydrophone to increase the distance from the boat. Diagram is not to scale. For (b): perpendicular (i.e., shortest) distances from transect line to the triangulated tag location were used for estimating detection efficiency. In some cases the tag was aft of the boat when it was first heard.
Figure 5.3. Frequency distributions of boat speeds used during transect surveys, calculated from ‘over ground’ GPS data. Left tails of the distributions (below about 3 km·h$^{-1}$ in 2003, 8 km·h$^{-1}$ in 2004, and 7 km·h$^{-1}$ in 2005–2007) represent speeds after hearing a tag where the boat slowly circled to decode the tag.
Figure 5.4. Frequency distributions of perpendicular distance from blind transect line to triangulated tag location. Only locations which were estimated with <200 m error are considered. Data are separated by tag type and year.

Figure 5.5. Cumulative probability distributions of perpendicular distance from blind transect line to triangulated tag location. Cumulative probability curves are shown for V9 tags in 2003 (■), V9 in 2004 (●), V9 in 2005–2007 (▲), and V7 in 2005–2007 (Δ). Grey horizontal dotted lines show 80% or 90% probability thresholds.
Figure 5.6. Hypothetical relationships between boat speed and (a) transect distance covered, $D$; (b) transect width, $W$; (c) total area swept, $A_t$ (the product of $D$ and $W$); (d) probability of hearing at least one transmission of a tag along a transect, $E$; and (e) the effective area swept, $A_e$ (the product of $A_t$ and $E$). Distance in (a) is over a 10 hour period. Parameters assumed in (b), (c), and (e) are: $W_{\text{max}}$ is 300 for solid and dashed lines, 150 for dotted lines; speed at inflection point is 10 for solid and dotted lines, 15 for dashed lines; S.D. around inflection point is 1 for grey lines, 3 for black lines. Parameters assumed in (d) are: average tag pulse rate is 60 s$^{-1}$; detection range is 300 for solid lines, 150 for dotted lines; probability of hearing a single transmission of a tag along a transect, $P_{\text{ping}}$, is 0.2 for black lines, 0.5 for dark grey lines, 0.8 for light grey lines. A $P_{\text{ping}}$ of 0.5 was assumed for the curves in (e).
Figure 5.7. Frequency distributions of boat speeds at which a tag was first heard during blind transects (black outlines). Distributions of boat speeds used during transects over an entire study from Fig. 5.3 are overlaid as grey bars. Speeds are calculated from ‘over ground’ GPS data.

Figure 5.8. Stacked frequency distribution of perpendicular distance from blind transect line to triangulated tag location. Data are separated by fish fate at the time of detection: alive (□), dead (■), or unknown (□), with study periods and tag sizes pooled.
Figure 5.9. Perpendicular distance from blind transect line to triangulated tag location vs. chart depth at that location. Data are separated by tag type, year, and whether tagged fish were likely alive (○), dead (●), or unknown (□) at the time of detection.

Figure 5.10. Maximum distance from where a tag was heard while circling to its eventual triangulated location. Distances are compared between tags heard on a VEMCO VR-28 directional hydrophone/receiver system and a Sonotronics USR-96 omni-directional system. Data are shown for both V7 (▲) and V9 (△) tags. Dotted line shows the 1:1 line of equal maximum distance between the two systems.
5.5 References


6 Effects of heterogeneity in acoustic tag strength on detection probabilities of migrating fish

6.1 Introduction

Mark-recapture or tag-recovery models often make the simplifying assumption that in a given capture period or at a detection location, tagged animals have the same probability of being captured or detected (i.e., homogeneity in capture or detection probability, $p$). In capture-mark-recapture studies that take place over time periods, animal behaviour often plays a role in capture probabilities. The likelihood of being captured may vary among individual animals. Further, the probability of capture may change for a particular individual animal contingent upon previous captures. Biases caused by such heterogeneity or behavioural change in capture probabilities on survival or abundance estimates have long been recognized and methods have been developed to deal with them (e.g., Pollock 1982, Pledger et al. 2003).

In capture-tag-detection studies for migrating animals that take place over detection locations, which are similar from a statistical point of view (e.g., Burnham et al. 1987), animals are not re-captured following the initial tagging period. Instead, they are detected as they pass acoustic or radio receiver stations deployed along migration routes. It is commonly assumed that heterogeneity in $p$ at each station can be ignored in these cases as long as tag types, swimming speeds and specific travel routes are similar among tagged animals. Also, since previous detection is not expected to affect the likelihood of detection at a particular station, ‘trap-dependent’ behaviour can be ignored.

Contrary to these commonly held assumptions, the acoustic intensity of tags might vary among tagged animals of a population. A tag with a stronger output will transmit its signal further through water than one with a weaker output. For example, the maximum variation among VEMCO acoustic tags is about ±3 dB around the average power output for a particular tag type, which could lead to about a 15–20% gain or reduction in expected detection range under normal ocean conditions (D. Pincock, pers. comm.). If such variation exists and does affect range, stronger tags might be more likely to be detected by acoustic receivers. If this variation is consistent over time, with stronger tags consistently transmitting signals of greater intensity throughout their lifespan, they should consistently be detected with higher chance at detection.
stations along a migratory route. Variation in tag strength could be due to variation in battery strength or electronic components of tags.

Here, I test the assumption of homogeneity in $p$ among tagged fish that migrated past several receiver stations. Prior to tagging fish from two populations, I measured a relative index of tag strength. After fish migrated through the study area and detection data were downloaded, I used mark-recapture models to estimate survival. In some models I used the tag strength index as a covariate of $p$ to evaluate the relative support for models with and without this covariate.

6.2 Methods

Acoustic tags sold by VEMCO often come with a small magnet attached which acts on a reed switch inside the tag. When the magnet is removed the tag begins to transmit pulse signals (in this case, 16 pulse trains in rapid succession after which pulse train intervals fell into the programmed delay period of 30–90 s between pulses). Tags are generally left deactivated until immediately before tagging fish in order to prolong battery life. As tags are activated, researchers will often verify that tag IDs are properly decoded using either a receiver with display panel (e.g., VEMCO VR-100) or a data-logging receiver (e.g., VEMCO VR-2).

6.2.1 Measuring indices of tag strength

In 2007, prior to tagging salmon smolts from two different populations, I quantified two simple indices of in-air tag strength (one for each population) while tags were being activated. In both cases, a small cradle was built from electrical tape to ensure that orientation was consistent among tags. One tag at a time was placed in the cradle with the transducer end of the tag always facing the same way. A hydrophone was placed on a folded towel on the same level and at a consistent distance from the tag, perpendicular to the long axis of the tag. These two indices were quantified as follows:

1. Tag strength index – A VEMCO VR-2 was placed flat on the towel with the hydrophone tip 80 cm away from the cradle and aligned so it was tilted towards the cradle about $15^\circ$ away from parallel with the tag. A V7-2L tag (136 dB re 1$\mu$Pa at 1 m) was placed adjacent to the hydrophone tip to ensure proper decoding, and the magnet was removed. Immediately after the first pulse train was transmitted and received by the VR-2, the tag was placed in the cradle for the remaining 15 rapid-succession pulse trains. After these 16 pulse trains were transmitted the tag was moved out of range of the receiver. The number of decoded transmissions out of the
last 15 for each tag was counted after downloading the VR-2. This index ranged from 1–15, with higher values representing more frequent detection.

(2) Inverse tag strength index – A VEMCO VR-100 omni-directional hydrophone tip was placed flat on the towel 115 cm away from the cradle and pointing directly towards it. A V9-6L tag (142 dB re 1µPa at 1 m) was placed in the cradle and the magnet was removed. With the gain of the VR-100 set to 6, I recorded the number of tag transmissions before the ID was decoded. If the tag was not decoded after 10 transmissions, the gain was increased to 12 and the number of transmissions before successful decoding was recorded. While gain was 12, a penalty of twice the number of transmissions before decoding was applied (for example, if a tag was not detected in 10 transmissions at gain-6 and was detected on the first or second transmission at gain-12, its index value would be 12 or 14, respectively). This index ranged from 1–14 (although it could be higher), with lower values representing fewer required transmissions until successful decoding.

It is important that measurements are consistent among tags, but the particular distances or angles between hydrophone tip and tag used in this study are not meaningful in themselves. Ambient noise wherever tag activation occurs will affect signal:noise ratios of tag transmissions and thus decoding success. In the present study, some tags were activated at a hatchery immediately prior to tagging fish rather than the day before in a quieter environment using the separation distances described above. At the hatchery, separation distances were reduced. Distances from tag to hydrophone in all cases were set to achieve a reasonable level of contrast in the indices. If separation distances are too short or too far, decoding success will be too high or too low, respectively, so contrast would be poor. For the tag strength index, 97 of the 199 tags tested were not decoded (Fig. 6.1a). The remaining 102 tags were spread across the index values, with fairly frequent occurrence at high index values. For the inverse tag strength index, 80 of the 118 tags tested were detected in the first 10 transmissions with receiver gain set to 6, and 38 tags were detected only after gain was increased to 12 (Fig. 6.1b). For values at gain-6, the shape of the distribution resembles a geometric decline, with more frequent occurrence at lower values of the inverse index.

One important caveat is that in-air measurements of tag strength are not necessarily correlated with in-water measurements due to the medium affecting electromechanical aspects of the transducer and its mounting; it is even possible that they are completely uncorrelated (D. Pincock, pers. comm.). In-water measurements were not feasible in this study, so the in-air indices were measured in hopes of revealing at least some correlation with what the tag strength would be in water as evidenced by detection patterns in the field.
6.2.2 Detection of tagged fish

Tagged fish from group 1 (Tenderfoot Creek coho), for which the strength index was measured on V7 tags, were released at a hatchery and migrated past seven receiver stations in rivers, one outside the river mouth, and past two POST lines of multiple receivers after ocean entry (HS<sub>inner</sub> and HS<sub>outer</sub>). Detection on up to two more ocean lines was possible (NSOG and QCS, or JDF), but this coho salmon population exhibited consistent migration behaviour only past the Howe Sound lines. Tagged fish from group 2 (Cultus Lake sockeye), for which the inverse strength index was measured on V9 tags, were released at a different hatchery and migrated past four receiver stations in rivers and two receiver lines in the ocean.

6.2.3 Mark-recapture models

Variants of the Cormack-Jolly-Seber open population, ‘recaptures’-only model (CJS) were used to estimate survival ($\phi$) and detection ($p$) probabilities. The two populations were analyzed separately. In all models, the survival sub-model had $\phi$ estimated independently for each segment of the migration [$\phi_{Seg}$]. Detection sub-models varied, one of which had $p$ estimated independently for each station [$p_{Station}$]. Three other models were fit that involved the (inverse) tag strength index as an additive individual covariate, i.e., $p$ was constrained to be a linear function (in logit space) of the strength index. The index was used as an additive covariate (rather than multiplicative) based on the assumption that relative tag strength measured during activation would remain consistent at all stations throughout the migration. The first model involved station-specific $p$ and a common covariate across all stations, [$p_{Station+tag strength}$]. A second model involved station-specific $p$, where the slope of the covariate was permitted to vary among river and ocean habitats, [$p_{Station+habitat\times tag\, strength}$]. The third model was more constrained. It replaced station-specific variation in $p$ with habitat-specific variation in $p$, where a common $p$ was assumed for all stations within a habitat, [$p_{habitat+tag\, strength}$]. The station outside the river mouth was considered to be part of the ocean habitat group.

Models were fit to detection data using Program MARK (White and Burnham 1999) implemented through RMark (Laake and Rexstad, 2009). Information-theoretic methods (QAICc) were used to compare candidate models (Burnham and Anderson 2002). First, a variance inflation factor (c) was estimated to compensate for extra-binomial variation in estimated probabilities (Burnham et al., 1987). I estimated $c$ assuming the general CJS model, [$\phi_{Seg}, p_{Station}$], using the deviance ratio bootstrapping method in Program MARK ($c = 1.239$ for
group 1 and 1.143 for group 2). This \( \hat{c} \) estimate was used for model comparison, with computed QAICc values corrected for both extra-binomial variation and small sample sizes.

After comparing candidate models, \([p]\) with reasonable support and involving the strength index covariate were compared with the model not involving the index as a covariate. First, the estimate and confidence limits of the coefficient for the strength index (\( \beta_s \)) was extracted for each group to assess whether slopes of logit(\( p \)) versus the strength index differed from zero. This \( \beta_s \) parameter affects \( p \) at station \( i \) by way of:

\[
\text{logit}(p_i) = \beta_0 + \beta_i \cdot \text{station}_i + \beta_s \cdot \text{strength}.
\]

Second, predicted fits of \( p \) across the range of the index covariate were calculated for each receiver station. Third, estimates and SEs of \( \phi \) and \( p \) were compared to assess how inclusion of the strength index covariate affected the precision of model parameters.

### 6.3 Results

#### 6.3.1 Model selection results

Maintaining a common \([ \phi ]\) across candidate models allowed the effect of each \([ p ]\) to be isolated. Models with lower QAICc values (i.e., AIC values adjusted for small sample sizes and extra-binomial variation) are considered better models in the balance of goodness-of-fit and the number of parameters required to achieve that fit. In both populations, the best overall \([ p ]\) was the simple detection station-varying model that did not involve the (inverse) tag strength individual covariate (Table 6.1). However, in both groups \([ p ]\) that involved the additive covariate with station-dependence also had a reasonable level of support. In both cases the \( \Delta \text{QAICc} \) was <2, indicating that including the station-dependence parameter did improve the goodness-of-fit to some extent. (Since \([ p ]\) with the additive covariate has one extra parameter compared to \([ p ]\) without, if the covariate had no explanatory effect a \( \Delta \text{QAICc} \) of 2 would be expected.) The other two \([ p ]\) had little support within the model set (Table 6.1).

The ratio of Akaike weights (i.e., the evidence ratio) between the top two models in Table 6.1 provides a measure of the strength of evidence for one \([ p ]\) over the other. This was 1.35 for group 1 and 2.29 for group 2, so the model not involving the strength index was only 35\% more likely (group 1) or 2.3 times more likely (group 2) to be the best model from an information-theoretic perspective than was the model involving the index as an additive covariate (Burnham
and Anderson 2002). Owing to the difference of a single parameter between the two models, these evidence ratios may underestimate the ‘true’ evidence of the simpler model being the better one, but there at least appears to be reasonable evidence that the tag strength index and possibly the inverse index should not be ignored as a factor affecting $p$ in these studies.

A discrete index of tag strength was also evaluated for each population. The continuous tag strength index was reduced to whether the tag was heard 0 or 1+ times out of 15 transmissions. The continuous inverse tag strength index was reduced to whether the tag was first heard in the first 10 transmissions with receiver gain-6, or not until after the gain was increased to 12. These discrete indices were used as group covariates of $p$ similar to the $p$ involving continuous individual covariates. In general they did not perform as well as the continuous covariates and are not shown in Table 6.1.

6.3.2 Effect of tag strength index on detection probability

Optimization routines of mark-recapture models are often run in a ‘link-space’ for numerical estimation purposes. Models in this study were fit to data in logit-space. In the second $[p]$ listed in each section of Table 6.1, involving station-dependence and the (inverse) strength index as an additive covariate without habitat dependence, $p$ was specified as in Eq. 6.1. If there was no effect of the tag strength index on $p$, the value of $\beta_S$ would be zero. Estimated $\beta_S$ values and 95% confidence limits were 0.020 (−0.009 to 0.050) for the tag strength index in population 1 and −0.018 (−0.065 to 0.029) for the inverse tag strength index in population 2. Confidence intervals from both indices included zero, although about 5/6 of the interval was positive for the strength index and about 2/3 of the interval was negative for the inverse index.

After models are fit to data, $p$ and its standard error can be estimated for a specified value of a covariate. These predicted values of $p$ over the range of covariate values (again, for the second model listed in each section of Table 6.1) are shown in Fig. 6.2 for the tag strength index and in Fig. 6.3 for the inverse tag strength index. There was considerable variation in $p$ among successive receiver stations on migration routes, attributable to site-specific depth, receiver array geometry, and environmental noise conditions. At each station, there is some effect of the tag strength index on predicted $\hat{p}$. Since the modelled covariate was additive, the same effect was assumed for all stations within each figure. The slopes of these fits are equal in logit-space, but were back-transformed to a probability scale so appear to vary among stations. There appears to be at least a small effect of the (inverse) tag strength index on $p$, with $\hat{p}$ differing by about 0.05–0.08 between low and high values of the index. In some cases when overall $p$ was low (e.g.,
station 4 in Fig. 6.2), this difference in percentage points amounts to a ~25% increase in $p$ from low to high values of the strength index.

For the two candidate models with reasonable levels of support, estimates $\hat{p}$ and $\hat{\phi}$ were compared. These models differed by only one parameter, the (inverse) tag strength index as an individual covariate, so its effect on estimates and their precision can be assessed. Estimates of $p$ and $\phi$ at each receiver station or in each segment were very similar between models, with <1% difference in all estimates for both groups (Fig. 6.4). The small differences that did occur were not consistent in direction, so it appears that the relative bias of incorporating (or perhaps not incorporating) the tag strength index (or the inverse index) is negligible. Similarly, the precision of $p$ and $\phi$ estimates was similar between the two models. Differences between models in coefficients of variation were <0.003 for all estimates in both groups. With two exceptions of lower precision in $\phi$ estimates for the CJS+tag strength model (station 8 for group 1 and station 3 for group 2; Fig. 6.4), differences between models in 95% confidence limit widths were <0.006 for all estimates in both groups.

6.4 Discussion

6.4.1 Effect of tag strength variation on detection probability

When conducting tagging studies researchers usually assume that tags of the same type will have the same transmission range and probability of being detected. This assumption of homogeneity in $p$ is crucial for mark-recapture models where inferences are made about abundance or survival. While heterogeneity in $p$ is unlikely to cause bias in $\hat{\phi}$ when survival is homogeneous (Pollock and Raveling, 1982), it could affect the precision. The model selection results from this study suggest some degree of variation in $p$ as a result of variation in acoustic strength among tags of the same type. The effect was not large in either index, as the model that did not include the tag strength covariate was the best overall, and the 95% confidence limits of the $\beta_S$ parameter did not exclude zero. The covariate did, however, have some explanatory power and improved the goodness-of-fit to the data, just not enough to compensate for having to include an extra parameter. The effect was perhaps large enough that the assumption of homogeneity in $p$ should not be taken for granted in tagging studies. That is not to say that such a strength index should replace station-dependence in $p$, but that it could be used in addition to station-dependent model specifications.
The effect of tag strength variation on \( p \) is likely minor compared with effects of spacing of receivers in an array, tag type, and river or oceanographic conditions that affect background noise and therefore signal:noise ratios. Tag types are generally identical within a study population, and station-dependence (which incorporates receiver spacing) is generally accounted for in mark-recapture models, so these factors are already often used to explain much of the total variation in observed detection data. A minor effect of tag strength was observed in two separate batches of acoustic tags in this study; it is unknown how often such variation occurs and how large it may be. Simple measurements of relative tag strength prior to tagging fish may help to explain some additional portion of the variation in \( \hat{p} \) within a population.

The tag strength index appeared to have slightly more explanatory power for \( p \) than the inverse index, as suggested by two lines of evidence: 95% confidence intervals of the estimated \( \beta_S \) parameter were closer to excluding zero; and the \( \Delta QAIC_c \) value was lower relative to the model not involving a strength covariate. Unfortunately only one index was measured for each population while activating tags, so this difference between indices could have been confounded by differences between groups in tag size, sample size, or the number of receiver stations past which fish from each group migrated. In future studies both indices could be measured for the same group of tags in a randomized order (measuring one index, replacing the tag magnet, then measuring the other), which would make for a better comparison between strength indices.

The tag strength index was modelled as an additive covariate assuming that its effect on \( p \) (i.e., the slope of the relationship between \( p \) and the covariate in logit space) was consistent at subsequent receiver stations along the migratory routes of these salmon smolt populations. As with any time-invariant individual covariate in a mark-recapture model, it was also assumed that the covariate value when measured has a lasting relative effect throughout the study, i.e., that the stronger tags when activated and remained stronger throughout the study. Either of these assumptions could be invalid if minor variation in tag pulses is random over time or if the ranking among tags of measured strength at activation changes at some time after activation. If this were the case, however, one would expect \( \Delta QAIC_c \) to be 2 for this model (Table 6.1), estimates of \( \beta_S \) would be closer to zero, and predicted fits of \( p \) over the covariate range would show no trend (Figs. 6.2, 6.3). There does appear to be a small effect of the strength index on \( p \) with all receiver stations considered together, suggesting that the relative measure of tag strength is maintained over the migratory period.

A trade-off in bias and precision is often inherent in mark-recapture models. Incorporating additional parameters into models often improves the accuracy of parameter
estimates, but also often reduces the precision of parameter estimates because an additional source(s) of uncertainty (i.e., way of explaining variation in the data) is admitted. In this study incorporating the tag strength index as an individual covariate of $p$ slightly improved the goodness-of-fit of model to data ($\Delta$QAICc <2, Table 6.1), but this was not associated with much of a reduction in precision in estimates of either $p$ or $\phi$ (Fig. 6.4). There was very little and no consistent difference between models in $\hat{p}$ or $\hat{\phi}$ suggesting that negligible relative bias exists from incorporating (or perhaps failing to incorporate) the strength index as a covariate.

The small effect of both indices on $p$ was in the expected direction. In the tag strength index, tags that were detected more frequently out of 15 transmissions after activation (high covariate values) tended to be the ones more likely to be detected by acoustic receivers. In the inverse tag strength index, tags that were detected soonest after removal of the tag magnet (low covariate values) were more likely to be detected by receivers. The variation in both indices was likely attributable to variation in acoustic output of the tag, with some tags transmitting signals slightly louder than others, possibly as a result of subtle differences in battery strength, electrical components, or mounting of the transducer.

### 6.4.2 Recommended set-up for measuring tag strength

The experimental set-up used for measuring relative tag strength indices was rudimentary. Within a group, some tags were activated at a hatchery and others were activated in a quieter room the evening before tagging fish. Only one index was measured for each group of fish. The distance between the tag cradle and hydrophone was decided after only a few tags were measured; spending more time assessing an appropriate distance in each group would have likely provided better contrast in the indices, with relatively more large values of the tag strength index and more small values of the inverse index (Fig. 6.1). Most importantly, the measurements were performed in air. Since these are not necessarily correlated with in-water measurements of tag strength, there could be no discernable effect of an in-air index on $p$ even if there were variation in tag strength in water. A ‘cleaner’ set-up and a relative strength index measured in water could potentially have more explanatory power for $p$. In the following paragraph several suggestions for improving an experimental set-up are listed, many of which were suggested by Dale Webber (VEMCO/Amirix, pers. comm.).

Maintaining a consistent level of background noise among activated tags is crucial, and reducing the level of background noise is better still. Fluorescent lights and electromagnetic interference can both create noise at the frequencies at which acoustic tags operate (in this case,
69 kHz). The tag should be consistently aligned and located in the same position on the cradle. A cradle designed to keep the tag vertical with the transducer end as free as possible from any physical objects can be used. Neither the cradle nor the hydrophone should be moved. The same hydrophone should be used for all tags in a batch. The hydrophone can be suspended from the ceiling to minimize physical transmission of tag signals or noise through a solid tabletop. Ideally, measurements should be taken in water in a controlled environment with sound-absorbing walls to ensure that an appropriate pressure will act on the tag so it transmits at the proper resonance.

Tag strength indices need not be relative measures. Instead of (or in addition to) measures of proportions of transmissions detected or number of transmissions until first detection, an index could be based on direct measurements of acoustic intensity. At some fixed distance from tag to hydrophone, the decibel level of a tag could be quantified with either a VEMCO-VR-100 receiver or a high-frequency oscilloscope. This has the advantage that the measurements could be made in water, unlike the relative measures used in this study that rely on tag decoding success (which would require a water tank several hundreds of metres long to provide enough contrast in detection success due to the differential sound transmission distance in water and air).

Whatever index of tag strength is used, it is important that it involves as much contrast as possible across its range. A 50:50 split of tags falling into the lowest and highest tag strength values would be statistically optimal in terms of precision, while a distribution closer to uniform would allow the form of the relationship between \( p \) and the index to be investigated. A larger number of programmed rapid-pulse intervals when tags are first activated could be requested by the user so that proportions of transmissions detected are based on a larger sample, thereby improving accuracy. All tags within a group should be activated in the same location with the same set-up over as short a time period as possible so as to maximize consistency. Several indices can be assessed for each tag to find a statistically preferable covariate, and the same index can be measured more than once on each tag to quantify random variation in the index value of each tag to ensure relative consistency.

The time cost of quantifying a relative tag strength index prior to tagging is not overly prohibitive. Depending on the index used, measurements may take about two or three minutes per tag. Indices measured in water would be highly preferable, and would create little further time cost. Considering that such an index may help to explain some of the variation in estimated detection probabilities in tagging studies, it may be worthwhile to spend the time assessing this potential source of variation before tagging fish.
Table 6.1. Model selection results for detection probability ($p$) sub-models.

<table>
<thead>
<tr>
<th>Model</th>
<th>$k^a$</th>
<th>QAICc $^b$</th>
<th>ΔQAICc</th>
<th>Akaike weight</th>
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<td>Group 1, tag strength index, $n = 199$ V7 tags, up to 12 detection stations</td>
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<td>$\phi_{Seg}P_{Station}$</td>
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<td>0.40</td>
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<tr>
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<td>0.00</td>
</tr>
<tr>
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<td></td>
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<td>0.00</td>
</tr>
</tbody>
</table>

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

$^b$ QAICc values are adjusted for small sample sizes and extra-binomial variation with $\hat{c}$ of 1.239 for group 1 and 1.143 for group 2.

Figure 6.1. Frequency distributions of tag strength indices, each measured for one group of tagged fish: (a) tag strength index defined as the number of detections out of 15 transmissions; (b) inverse tag strength index defined as the number of transmissions required until a tag was first detected (receiver gain was set to 6 for first 10 transmission and thereafter increased to 12). Tag indices were assessed prior to tagging fish. Tag types and sample sizes of tagged fish are indicated.
Figure 6.2. Predicted fits of mark-recapture detection probabilities at each receiver station over the range of tag strength index as an additive covariate. The model assumed is the second one listed in Table 6.1 in the upper section. Dashed lines show 95% confidence bands around the estimated means.
Figure 6.3. Predicted fits of mark-recapture detection probabilities at each receiver station over the range of inverse tag strength index as an additive covariate. The model assumed is the second one listed in Table 6.1 in the lower section. Dashed lines show 95% confidence bands around the estimated means.
Figure 6.4. Estimated detection probabilities at each receiver station and survival probabilities in each segment of the migration for two groups of fish. White bars represent estimates for the Cormack-Jolly-Seber model, and grey bars show estimates for the CJS model with (inverse) strength index as an additive covariate. Error bars represent 95% confidence intervals around the estimate.
6.5 References


7 Spatial and temporal migration behaviour of salmon smolts

7.1 Introduction

Migration is an important life history strategy in many animals, where individuals move among habitats at specific times of year or at specific ontogenetic stages to gain access to food resources, reduce predation risk, or find mates. Juveniles of most salmon species rear in freshwater and migrate to marine habitats to take advantage of better opportunities for growth; adults later migrate back to freshwater to spawn. Several costs are involved with migrations of salmon smolts: physiological changes for saltwater tolerance are metabolically costly, time spent migrating may in the short term take away from other possible uses of time such as feeding, and most importantly, smolts may be vulnerable to predators along migration routes.

Direction of travel after arrival in the ocean may be important to smolts: some migration routes may be shorter than others (e.g., different routes around islands), and a shorter route may reduce time spent migrating and hence exposure to predators in inshore waters. Other factors may differ among possible directions as well, such as predator density and distribution, food availability, or strength of ocean currents. Outmigrating salmon populations from different entry points into Georgia Strait tend to differ in the proportion of fish that move northwards through Queen Charlotte Strait versus southward through Juan de Fuca Strait. Recovery patterns of coded wire tags indicate that populations from mid- to northeastern Vancouver Island or from the B.C. mainland north of the Fraser River tend to move northward, while those from southeastern Vancouver Island and south of the Fraser River tend to move southward (Weitkamp and Neely 2002; C. Walters, pers. comm.). Variation within populations may also exist, with some individuals moving in one direction and others moving in another. Understanding direction of movement in juveniles may be particularly important in terms of fisheries management strategies if there is any correlation with direction taken during the return migration of adults.

Travel speed may also be important, as faster speeds allow smolts to arrive at foraging grounds sooner. They may also allow smolts to sooner escape from predation risk along riverine or inshore migration routes (Wood et al. 1993), where compared with open pelagic habitats, predator densities may be higher or smolts may be more vulnerable to a given predator due to the shallower and more constricted waterways. If predation risk is proportional to distance travelled (which may occur for sit-and-wait predators; Anderson et al. 2005), then a smolt is subject to the same risk whether it travels slowly or rapidly. If predation risk is instead proportional to the time...
spent within rivers or inshore areas (which may occur if predators are highly mobile and repeated encounters with predators are expected; Anderson et al. 2005), or is somewhere between these extremes, then travelling faster through inshore waters is expected to reduce exposure to predators. Different migration strategies with respect to diurnal patterns may also be employed by salmon smolts if migrating at particular times of day or night affects predation risk.

Between lines of stationary ocean receivers, where smolts do not have the possibility of detection, it is not known where smolts go. It is possible that they delay their migration temporarily, and move in either continuous or punctuated patterns; it is also not known how individual differences in such behaviours may affect survival. This is especially true for Georgia Strait, where large areas without any sampling lines create large uncertainties about migration behaviour. Even in Howe Sound, where the densest configuration of ocean stations was deployed under POST (Fig. 1.4), there are still large gaps within which the behaviour and fate of smolts is unknown. Finer scale movement patterns may hint at underlying processes that lead to mortality during the smolt migration.

In this chapter, we describe several migration patterns of smolts including migration direction after ocean entry, travel speed during downstream and inshore components of the migration, diurnal patterns of migration, and fine-scale movement and mortality patterns during the estuarine and early ocean migration. For most of these aspects, we consider migration patterns of all salmon smolts from southern British Columbia tagged under the Pacific Ocean Shelf Tracking Project (POST) that were released over five years (2004–2008) across a wide range of watersheds in southern B.C. (Fig. 1.4). We consider possible differences in migration behaviour among species, wild or hatchery-rearing histories, watersheds, and body size.

### 7.2 Methods

Salmon smolt populations considered for migration pattern analyses (Sections 7.2.1 and 7.2.2) are listed in Table A.2. (In addition, the five release groups of 2008 Cheakamus River steelhead listed in Table A.3 were also included in these analyses.) These release groups from Table A.2 are the same ones that will be considered in Chapter 9 for analysis of survival.

#### 7.2.1 Migration direction after ocean entry

The inshore Georgia Strait system framed by Vancouver Island and the B.C. mainland offers entry or exit points to the north (Queen Charlotte Strait) and to the south (Juan de Fuca
Strait). Smolts entered Georgia Strait or Queen Charlotte Strait from several different locations—some to the north of Johnstone Strait, some from southern Vancouver Island, some from the Fraser River, and some from the south mainland coast, north of the Fraser River mouth (Fig. 1.4). We estimated the proportion of fish from each release group listed in Table A.2 that migrated northwards after ocean entry. Evidence of northward versus southward movement for fish from Keogh and Nimpkish Rivers, entering the ocean north of Johnstone Strait, was based on estimated numbers of fish crossing the QCS station (north) and the NSOG station (south). For all remaining populations that entered Georgia Strait south of NSOG, northward movement was based on the estimated number of fish crossing NSOG and southward movement was based on the estimated number of fish crossing the JDF station. These estimated numbers of fish were calculated simply as the number of fish detected at a station divided by the estimated detection probability for the station in the appropriate year and for the appropriate tag type (\( \hat{p}_{\text{station}} \) was year-specific and tag type-specific; Appendix A). Within each release group, the proportion of fish migrating northward, \( P(N) \), was calculated as the estimated number crossing the northern line divided by the sum of the estimated numbers crossing northern and southern lines. Fish that migrated neither northward or southward (e.g., mortalities, residents) were not considered in the calculation, so \( P(N) + P(S) = 1 \).

For Fraser River and Cowichan River populations, distances from ocean entry to the northern station (NSOG) and southern station (JDF) were roughly equidistant (Fig. 1.4). For other populations, the distance to the northern station was shorter than to the southern station. This was especially true for Sakinaw Lake and Englishman River populations, which had only a short distance to NSOG, and for Keogh River and Nimpkish River populations, which had only a short distance to QCS. If a fish was first detected at NSOG and later detected at JDF, only the last detection was considered in order to establish direction of migration (this rarely occurred).

### 7.2.2 Travel speed analysis

Mean travel times of release groups were calculated for downstream (from release to detection near the river mouth) and inshore (from river mouth to ocean stations at NSOG, QCS or JDF) portions of the migration. These were plotted against minimum possible migration distance (determined using Memory Map™ chart plotting software) for the appropriate portion of the migration to evaluate variation in average travel speed among groups. Early ocean travel times were calculated as the difference between cumulative travel time from release to ocean ...
lines and cumulative travel time from release to river mouth (rather than from only the subset of fish detected at both river mouths and ocean lines).

Variation within release groups in travel speeds also exists, so most analyses focused on the level of individual fish. Travel speeds of salmon smolts were calculated for downstream and inshore portions of the migration, where inshore portions were from the river mouth to the terminal stations at QCS or JDF (so did not involve detections at NSOG). Two measures of travel speed were considered, which are commonly reported for fish speed: absolute rates in km·d$^{-1}$, and length-specific rates in body lengths per second (BL·s$^{-1}$; which were fork lengths measured at time of tagging). It is expected that large fish travel faster than small fish and that a conversion from average speed in km·d$^{-1}$ to average speed in BL·s$^{-1}$ corrects for this expected difference among individuals. Absolute travel speeds were calculated as the minimum migration distance from release point to river mouth or from river mouth to terminal ocean station at QCS or JDF divided by the time elapsed between release and detection or subsequent detections. For the inshore portion, this required that a fish was detected at both the river mouth and at QCS or JDF. In total, travel speeds were assessed for 1910 smolts spread among 42 release groups during the downstream migration, and for 487 smolts spread among 35 release groups for the inshore migration. Travel speed distributions were quantified, and were split among species and among wild or hatchery-rearing histories to assess possible differences among these grouping factors (sockeye and kokanee were grouped together for the inshore portion, as only 24 kokanee smolts were detected at QCS or JDF).

Hierarchical linear mixed effects models were used to assess the effect on travel speeds of several possible explanatory factors, modelled as fixed effects: species (spp), wild or hatchery-rearing history (HW), fork length (FL), and whether fish were from a Fraser River or non-Fraser watershed (FnF). Sampling units were individual fish, but travel speeds are expected to be correlated within watersheds, especially during the downstream migration. A mixed-effects approach was therefore used, where individuals are related through their watershed of origin. Watershed (nested within FnF) and year were considered as random effects, since travel speeds in particular years or of fish from particular watersheds were not of interest per se. These represented samples (although not strictly random samples) of a larger population of watersheds and years. Two datasets were analyzed independently, one for river travel speeds and the other

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3 Note that kokanee are typically regarded to be the non-anadromous form of sockeye, although here these fish confirmed by genetic samples to be kokanee (C. Wood, pers. comm.) were detected leaving Georgia Strait.
for inshore travel speeds. For each dataset, response variables of travel speed in km·d\(^{-1}\) and BL·s\(^{-1}\) were both considered.

Several candidate models for travel speed were considered and compared using model selection methods. Since Akaike’s Information Criterion (AIC) tends to select overly-parameterized models in many situations (Kass and Raftery 1995, Link and Barker 2006), the Bayesian Information Criterion (BIC; Schwarz 1978) was used to compare models.\(^4\) A global model was constructed assuming additive effects of the above fixed effects. For the river dataset, we also considered an interaction between FL and FnF as a fixed effect, which permitted different slopes of the relationship between travel speed and FL for these watershed categories. The reasoning behind this hypothesis is that river currents are stronger in the Fraser River, so travel speeds are likely largely dominated by river flow. In other rivers with weaker flow, directed swimming is likely more important so body size may reasonably have a greater effect on travel speeds in the absence of strong currents. This interaction was not considered for the ocean dataset since fish from different watersheds all experience relatively low net flow conditions after ocean entry. The global model for travel speed, \(u\), was specified as:

\[
(7.1) \quad u_{ijk} = \alpha_{0jk} + \beta_{1ijk} \cdot \text{spp} + \beta_{2ijk} \cdot \text{HW} + \beta_{3ijk} \cdot \text{FnF} + \beta_{4ijk} \cdot \text{FL} + \beta_{5ijk} \cdot (\text{FnF}:\text{FL}) + \varepsilon_{0ijk}
\]

\[
\alpha_{0jk} = \alpha_0 + \omega_{0j} + \gamma_{0k}.
\]

The term \(\alpha_{0jk}\) implies random intercepts for various levels of the random effects of watershed (\(\omega_{0j}\); nested within FnF) and year (\(\gamma_{0k}\), where these random effects are normally distributed around zero, i.e., \(\omega_{0j} \sim N(0, \sigma^{2}_{\omega_{0j}})\) and \(\gamma_{0k} \sim N(0, \sigma^{2}_{\gamma_{0k}})\). The residual error term is also assumed to be normally distributed after log-transformation of \(u\), i.e., \(\varepsilon_{0ijk} \sim N(0, \sigma^{2}_{\varepsilon_{0ijk}})\). Model coefficients pair with dummy variables for spp, HW, and FnF, and represent slopes for FL and FnF:FL. In more abbreviated notation, we will represent this same model as:

\[
(7.2) \quad u \sim \alpha_0 + \text{spp} + \text{HW} + \text{FnF} + \text{FL} + \text{FnF:FL}, \quad \text{rand}(\omega_{0j}, \gamma_{0k}).
\]

Two datasets and two measures of travel speed were considered. For each of these four combinations, several candidate models were compared. Given all the variables of interest, to

\(^4\) To note, an exception of AIC not selecting overly-parameterized models is when a variance inflation factor can be estimated and quasi-likelihood (Q) methods can be used to compare QAIC rather than AIC; this approach is described in Appendix A and will be used for comparing mark-recapture models with a multinomial likelihood formulation in following chapters.
avoid a very large number of candidate models, a two-step process was used. First, the full set of fixed effects from the global model was assumed for comparing random effects. Watershed nested within Fraser/non-Fraser, year, or both random effects were considered:

1. \( u \sim (\text{fixed}), \text{rand}(\omega_{0j}, \gamma_{0k}) \) Random intercepts for watersheds nested within Fraser/non-Fraser River, and years. Full set of fixed effects is assumed.

2. \( u \sim (\text{fixed}), \text{rand}(\omega_{0j}) \) Random intercepts for watersheds nested within Fraser/non-Fraser River. Full set of fixed effects is assumed.

3. \( u \sim (\text{fixed}), \text{rand}(\gamma_{0k}) \) Random intercepts for years. Full set of fixed effects is assumed.

Second, the best set of random effects in terms of BIC for the containing models was used to then compare models in terms of fixed effects. Various reduced models were considered. For the river dataset, these were:

1. \( u \sim \alpha_0 + \text{spp} + \text{HW} + \text{FnF} + \text{FL}, \text{rand}(\omega_{0j}, \gamma_{0k}) \) Full set of fixed effects on travel speed: species, rearing history, Fraser or non-Fraser origin, fork length, and a FnF:FL interaction. Random intercepts for watersheds nested within Fraser/non-Fraser River, and years.

2. \( u \sim \alpha_0 + \text{spp} + \text{HW} + \text{FnF} + \text{FL}, \text{rand}(\omega_{0j}) \) Fixed effects: species, rearing history, Fraser or non-Fraser origin, and fork length (no interaction). Random intercepts.

3. \( u \sim \alpha_0 + \text{spp} + \text{HW} + \text{FnF}, \text{rand}(\omega_{0j}, \gamma_{0k}) \) Fixed effects: species, rearing history, and Fraser or non-Fraser origin (no fork length or interaction). Random intercepts.

4. \( u \sim \alpha_0 + \text{spp} + \text{FnF} + \text{FL}, \text{rand}(\omega_{0j}, \gamma_{0k}) \) Fixed effects: species, Fraser or non-Fraser origin, and fork length (no rearing history or interaction). Random intercepts.

5. \( u \sim \alpha_0 + \text{HW} + \text{FnF} + \text{FL}, \text{rand}(\omega_{0j}, \gamma_{0k}) \) Fixed effects: rearing history, Fraser or non-Fraser origin, and fork length (no species or interaction). Random intercepts.

6. \( u \sim \alpha_0 + \text{FnF} + \text{FL}, \text{rand}(\omega_{0j}, \gamma_{0k}) \) Fixed effects: Fraser or non-Fraser origin and fork length (no species, rearing history, or interaction). Random intercepts.

The list of candidate models used for the ocean dataset was the same, with one exception: an interaction was not considered between FnF:FL, as mentioned above, so model 1 in this second list was not considered. It was replaced by a model in which speeds after ocean entry were hypothesized to be common for otherwise-similar fish from the Fraser River and other rivers:

1. \( u \sim \alpha_0 + \text{spp} + \text{HW} + \text{FL}, \text{rand}(\omega_{0j}, \gamma_{0k}) \) Fixed effects: species, rearing history, and fork length (no Fraser or non-Fraser origin or interaction). Random intercepts.
Travel speeds were log-transformed prior to analyses since their distributions were typically log-normal (FL was also log-transformed to maintain the assumed linear relationship for conversion to BL·s⁻¹). Comparison of models with differing random effects was done using a restricted maximum likelihood approach, while a maximum likelihood approach was used for comparing models with differing fixed effects (Pinheiro and Bates 2000).

In addition to travel speeds, the time of day that salmon smolts first arrived at a receiver station was compared across different habitats to assess possibilities of diurnal migratory behaviour. Habitats included the Fraser River, other rivers (tidal reaches or estuaries as well as portions upstream of tidal waters), Howe Sound, the northern Strait of Georgia, Queen Charlotte Strait, Juan de Fuca Strait, and other ocean stations (pooled) where smolts were rarely detected. Frequency distributions were plotted to look for species or rearing history differences in diurnal migratory behaviour.

7.2.3 Small-scale movement and mortality patterns in Howe Sound

To complement tag detection from the stationary listening lines, we actively tracked smolt movements and looked for evidence of mortality on finer spatial scales, mostly within Howe Sound. Principle study populations were Tenderfoot Creek hatchery coho and wild and hatchery-reared Cheakamus River steelhead, both of which entered Howe Sound from the Squamish River. When a tag was detected from a vessel using a towed hydrophone and receiver system (methodological details are described in Chapter 5 and Appendix A), it was not usually known at the time whether the smolt was still alive, or where it had previously been. If tags remained in the same location over several days or weeks as verified by repeated triangulations and were not detected thereafter on any stationary receiver, we assumed that fish had died and that the tag was laying on the seabed, either in a dead smolt or previously defecated by a predator. These tag locations were assumed to represent approximate locations of mortality.

Initial goals of the mobile tracking program in 2003–2004 were to quantify fine-scale movements and habitat usage of smolts after ocean entry as well as location and approximate timing of mortality during the migration. By years 2005–2007, focus was placed mostly on the latter goal, and sampling strategies shifted accordingly. Shortest-route distances from the Squamish River mouth to assumed locations of mortality were calculated for all years. These were used in conjunction with estimated numbers of smolts entering Howe Sound to estimate per-distance mortality rates during the migration through Howe Sound.
There were 49 approximate locations of assumed mortality of Tenderfoot Creek Hatchery coho salmon smolts identified in years 2003–2007 by mobile transect surveys. These occurred throughout Howe Sound at a wide range of distances from the Squamish River mouth. These provide a means of estimating an instantaneous mortality rate during the migration through Howe Sound. To estimate mortality, a starting value of the number of fish leaving freshwater alive, $N_i$, is assumed. This was estimated from mark-recapture analyses using stationary receiver stations (Chapter 9), and totalled 329.2 over the years 2003–2007. Assuming a constant mortality rate throughout Howe Sound, i.e., a constant probability of mortality per kilometre travelled, $M$, the expected number still alive after distance $d$ is calculated as a simple exponential decline, i.e., $N_d = N_i e^{-M \cdot d}$. The expected number of smolts that died over some distance $\Delta d$ (e.g., 1-km or 5-km segments) is then calculated by subtracting the expected number alive at the end of the segment from the number alive at the start of the segment. These expectations of numbers dead cannot be compared directly with observed mortality location data because it is unlikely that all mortality locations were identified. A detection efficiency, $p_{\text{mort}}$, for locating stationary tags from fish that died is incorporated into the equation so that expected numbers of detected mortality locations, $D$, can be directly compared with observed numbers detected and assumed to be dead:

$$D_{\Delta d} = p_{\text{mort}}(N_i e^{-M \cdot d} - N_i e^{-M \cdot (d + \Delta d)})$$

For $\Delta d$ of 1 km, observed and expected frequencies were tabulated for each successive kilometre of the migration and the sum of squares was calculated between these vectors. Assuming $N_i$ to be fixed, the sum of squares was minimized by searching over combinations of parameter values $M$ and $p_{\text{mort}}$. We assumed that $M$ and $p_{\text{mort}}$ were constant through Howe Sound. The assumption of constant $M$ allows expected numbers of detected mortality locations to approximate the observed pattern of declining mortalities with distance by an exponential decay, and the assumption of constant $p_{\text{mort}}$ allows the overall scale of expected frequencies to match observed frequencies.

Two measures of $d$ were considered, both of which underestimate the actual distance travelled by smolts. The first measure was the shortest possible route directly from the Squamish River mouth to the triangulated location of the stationary tag. The second measure accounted for all detections of the tag (from stationary lines as well as earlier mobile tracking detections of the smolt while still alive) in the period between ocean entry and detection at the assumed mortality location. This was also a shortest-route measure and likely underestimated the actual travel distance. Minimum known travel distances were generally longer than corresponding direct
distances, especially when smolts (or their tags inside predator stomachs) moved back and forth between stationary receiver lines or periodically moved upstream then downstream in the lower river estuary. Parameters $M$ and $p_{\text{mort}}$ were estimated under both measures of $d$.

**7.3 Results**

Few coho or Chinook smolts from populations entering Georgia Strait were detected after entry to the main body of the Strait. These populations included hatchery-reared Tenderfoot Creek coho entering from Howe Sound as well as mostly hatchery-reared coho and Chinook from lower Thompson River tributaries (middle-Fraser River region; Table A.2) entering the Strait from the Fraser River. In contrast, sockeye and steelhead smolts entering Georgia Strait were consistently detected migrating past ocean receiver stations as they left via either Johnstone and Queen Charlotte Straits to the north, or Juan de Fuca Strait to the south.

**7.3.1 Migration direction after ocean entry**

Within release groups, variation in direction of migration was observed in about one third of smolt populations, as some fish went north while others went south (Fig. 7.1). About half of the populations entering into Georgia Strait had split migration route patterns. All populations entering Queen Charlotte Strait (Fig. 7.1a) and the other half of populations entering Georgia Strait (Fig. 7.1b, c) were only detected moving northwards. There were no consistent differences among species or rearing histories (wild versus hatchery) in $P(N)$. There was some evidence of a latitudinal pattern, as expected, with populations entering Georgia Strait further to the north more likely to migrate northwards (Figs. 1.4, 7.1).

Few fish from mid-Fraser populations survived the downstream and inshore migrations. The four release groups that had ≥5 fish detected on either NSOG or QCS had variable $P(N)$ estimates, ranging from <20% to >80%, but were based on only 6–23 fish detected (Fig. 7.1b). In contrast, Cultus Lake sockeye from the lower Fraser moved almost exclusively northward, with only 8 of 249 detected fish taking the southern route across JDF.

Fish from other rivers adjacent to Georgia Strait showed a range of patterns in $P(N)$. Most fish from south coast Rivers (Cheakamus River, Tenderfoot Creek, Seymour River) migrated northwards, although some wild and some hatchery-reared Cheakamus River steelhead took the southern route (Fig. 7.1c). Sakinaw Lake sockeye and kokanee (a genetically-distinct and generally non-anadromous, freshwater-resident form of sockeye) also moved northward most
often, but $P(N)$ was slightly lower for wild kokanee than for the hatchery-reared sockeye. Englishman River steelhead moved northward almost exclusively, while the group from the Cowichan River, the only study river on southeastern Vancouver Island, was the only one to move predominantly southwards (Fig. 7.1c).

### 7.3.2 Travel speed analysis

Relationships between mean travel time of release groups and the minimum distance they migrate, either downstream or through the Georgia Strait system, show among-group variability in travel speed. Tagged fish generally took <15 d on average to arrive at the river mouth after release (Fig. 7.2a, c). Despite considerably longer distances travelled, mean travel times downstream were not much greater for mid-Fraser River populations (320–410 km) than for populations from other watersheds (<100 km). There was little difference among species in this pattern (Fig. 7.2a), but hatchery-reared fish took about 5 more days to complete the downstream migration than wild fish, consistent across different migration distances (Fig. 7.2c). Two outliers were hatchery-reared steelhead populations from the Cheakamus River in 2008 that took >20 d on average to migrate downstream despite distances of just 19 or 27 km. After ocean entry, species differences were observed in travel speeds. Coho populations took longer on average to reach the NSOG, QCS or JDF stations than steelhead or sockeye/kokanee populations for a similar migration distance (Fig. 7.2b). Regression intercepts were >0 for all species, suggesting that even at relatively short distance from river mouth to ocean stations, smolts took more time on average to reach this distance than would be predicted if they migrated continuously after release. Similar to the downstream migration, hatchery fish took more time on average to reach ocean stations after ocean entry than did wild fish, although variation in travel times was considerable for both rearing history groups (Fig. 7.2d).

Variation in travel speeds also occurs among individuals within a given release group, which is not represented in Fig. 7.2. Considering fish independently, travel speeds, $u$, ranged widely from near 0 to 189 km·d$^{-1}$ or 15.8 BL·s$^{-1}$ during the downstream migration, and from near 0 to 48 km·d$^{-1}$ or 2.9 BL·s$^{-1}$ during the inshore migration. Frequency distributions of travel speeds appeared to be approximately log-normal or exponential (Fig. 7.3; ‘average’ travel speed implies the average speed during an individual’s migration, not an average of individuals). Downstream travel speeds were much faster in the Fraser River ($\bar{u} = 33.6$ km·d$^{-1}$, 2.40 BL·s$^{-1}$) than in other rivers ($\bar{u} = 6.6$ km·d$^{-1}$, 0.50 BL·s$^{-1}$), and the outlying individuals with speeds of >100 km·d$^{-1}$ or >10 BL·s$^{-1}$ tended to be from the Fraser River. Travel speeds during the inshore
migration were intermediate between these \(\left(\bar{u} = 12.8 \text{ km·d}^{-1}, 0.82 \text{ BL·s}^{-1}\right)\). Note these travel speeds are calculated assuming the minimum distance from release to river mouth or river mouth to outer ocean lines, so if actual fish migration routes were longer than this shortest path, actual speeds would be faster.

In rivers other than the Fraser River, one characteristic that stands out is the large proportion of fish that moved <2 km·d\(^{-1}\) or <0.2 BL·s\(^{-1}\) during the downstream migration (Fig. 7.3). Separating the data by species, these slow-moving fish are mostly steelhead (Fig. 7.4), some wild and some hatchery-reared (Fig. 7.5). Across all species, travel speeds during the downstream migration in rivers other than the Fraser were generally similar between wild and hatchery-reared fish (Fig. 7.5). In the Fraser River, Cultus Lake sockeye (from the lower Fraser) had slower travel speeds during the downstream migration than populations of Chinook, coho, or steelhead from the mid-Fraser River (Fig. 7.4), likely just because the portion of their migration in the Fraser occurred where the river was wider and slower. This population difference (Cultus Lake sockeye are hatchery-reared) was the main reason for an observed difference in downstream travel speeds between wild and hatchery fish in the Fraser River (Fig. 7.5). During the inshore migration, the coho smolts that were detected at both river mouth and QCS/JDF stations moved at a slower net rate between these stations \(\left(\bar{u} = 3.8 \text{ km·d}^{-1}, 0.29 \text{ BL·s}^{-1}\right)\) than did steelhead \(\left(\bar{u} = 13.9 \text{ km·d}^{-1}, 0.88 \text{ BL·s}^{-1}\right)\) or sockeye/kokanee \(\left(\bar{u} = 15.9 \text{ km·d}^{-1}, 1.00 \text{ BL·s}^{-1}\right)\) smolts (Fig. 7.4). Travel speeds of wild and hatchery-reared smolts were generally similar after ocean entry (Fig. 7.5). Histograms of travel speeds in BL·s\(^{-1}\) (not shown) have similar shapes to those of km·d\(^{-1}\) shown in Figs. 7.4 and 7.5.

In rivers, fish body length may have little effect on travel speeds if river flows contribute substantially to movement downstream (in contrast to ocean migrations, where most movement results from directed swimming). Relationships between travel speed and body length were generally weak or inconsistent in direction. In the Fraser River, positive relationships between absolute travel speeds and body length were observed for coho and steelhead (Fig. 7.6) and for wild fish in general (Fig. 7.7), but slight negative relationship were seen for sockeye (Fig. 7.6) and hatchery fish in general (Fig. 7.7, which was driven mainly by hatchery-reared Cultus Lake sockeye). In other rivers, travel speed-body length relationships were weak when separated by species (Fig. 7.6) and weak but in opposite directions for wild and hatchery-reared fish (Fig. 7.7).

Under the common assumption that larger fish travel faster than smaller fish, fish travel speeds are often converted from absolute measures (km·d\(^{-1}\)) to length-specific measures (BL·s\(^{-1}\)). This conversion is typically assumed to correct for length-biased variation in travel speeds, such
that fish of different lengths have similar resulting speeds in BL·s\(^{-1}\). If little variation exists among individuals of different body sizes in average absolute travel speeds, however, this conversion may over-correct, resulting in faster length-specific travel speeds in smaller fish. This may be the case for some salmon smolts when grouped by species. For example, during the inshore migration there was relatively little effect of fork length on average absolute travel speeds (slopes were even slightly negative; Fig. 7.6). When adjusted for body length, however, travel speeds in BL·s\(^{-1}\) decreased as fork length increased. This pattern may simply result from the particular range of fork lengths within each species, however, since when fish were instead separated by wild or hatchery rearing history, the BL·s\(^{-1}\) measure did properly correct the positive relationship between absolute speed and length for hatchery fish, and partly correct it for wild fish (Fig. 7.7). As it is unclear which measure is more suitable for quantifying travel speeds in these salmon smolts, both measures of km·d\(^{-1}\) and BL·s\(^{-1}\) were considered in the multiple regression analysis below.

In comparisons of mixed-effects candidate models for variation in travel speed, the best set of random effects included both watershed nested within Fraser/non-Fraser rivers and year. This was true for both river and ocean datasets, as well as for both measures of travel speed (Table 7.1). Of these two effects, \(\omega_{0j}\) was the stronger in terms of explaining variation in \(u\), especially for downstream travel speeds, as expected. These random effects were both included in candidate models for comparing fixed effects.

In terms of fixed effects, ranking of candidate models differed among river and ocean datasets. For downstream travel speeds, the best model by far was the global model (Table 7.2). This was true for both measures of \(u\); since the conversion to BL·s\(^{-1}\) is a simple linear transformation, all models involving FL were identical in terms of likelihood and BIC between the two measures (the only differences between measures lie in the estimates for intercept and slope coefficients for FL). In the one model that did not involve FL, this was closer to the best model for the BL·s\(^{-1}\) measure (\(\Delta\text{BIC} = 16.9\)) than for the km·d\(^{-1}\) measure (\(\Delta\text{BIC} = 44.4\); Table 7.2), simply indicating that the conversion did improve the model fit if FL was not explicitly included as a predictor variable. Looking at the fit of the global model for the absolute travel speed measure, species and rearing history differences were both observed after accounting for other factors. Steelhead travel speeds during the downstream migration were slower on average than those of other species (confidence limits around the estimated coefficient excluded zero; \(\beta_{1, \text{steelhead}} = -0.43; 95\% \text{ c.l., } -0.83 \text{ to } -0.03\), compared to the Chinook reference group). There was some indication that coho were faster than the other species, all else equal (\(\beta_{1, \text{coho}} = 0.38\);
95% c.l., −0.03 to 0.79). Wild fish migrated faster downstream than hatchery-reared fish, all else equal (β_{2, wild} = 0.80; 95% c.l., 0.65–0.96, compared to the hatchery group). There was a large overall difference in \( u \) between Fraser River fish and smolts from other rivers, with greater \( u \) downstream in the Fraser River (β_{3, Fraser} = 17.0; 95% c.l., 11.5–22.5), although this overall difference was dependent on an interaction with body length. The slope of ln(\( u \)) versus ln(FL) was not different from zero in the Fraser River (β_{4, Fraser;FL} = −0.32; 95% c.l., −1.22 to 0.58), but was positive for fish from other rivers (β_{5, nF;FL} = 2.86; 95% c.l., 1.78–3.94).

For inshore travel speeds, the best model differed depending on the measure of \( u \). For absolute travel speeds, the best model included predictor variables of species, wild or hatchery-rearing history, and Fraser or non-Fraser origin, but did not include body length (thus, when the absolute measure in which FL was a poor predictor of \( u \) was converted to BL·s\(^{-1}\), the resulting model fit was poorer, as one might expect; Table 7.2). This model had essentially equal support (\( \Delta BIC = 0.4 \)) as one involving additive effects of spp., FnF, and FL, but not HW, which was the top candidate model for the length-adjusted measure of \( u \) (Table 7.2). For both measures of \( u \), a third model involving additive effects of spp., HW, and FL (but not FnF) also had a considerable amount of support within the dataset (\( \Delta BIC = 2.3–2.8 \)). We look further at the fit of the top model to absolute travel speed estimates (since this did not involve FL, there is little reason to look at fits to length-adjusted \( u \)). Multiple regression results confirm the slower travel speeds of coho during the inshore migration compared to those of steelhead and sockeye (Fig. 7.4; \( \beta_{1, steelhead} = 1.34, 95\% \) c.l., 1.17–1.51; \( \beta_{1, sockeye} = 1.29, 95\% \) c.l., 0.73–1.84, compared to the coho reference group). Despite being factors in the best model, neither HW nor FnF had confidence limits that excluded zero (β_{2, wild} = 0.05, 95% c.l., −0.09 to 0.20, compared to the hatchery group; \( \beta_{3, Fraser} = −0.45, 95\% \) c.l., −0.94 to 0.05, compared to the non-Fraser group). A further reduced model was not part of the original model set, but in a post-hoc comparison, the model \([u–α_0+spp, \text{rand}(ω_0, γ_0)]\) outperformed all others in the original model set (\( k = 7, −2·\ln(L) = 771.2, \text{BIC} = 814.5 \)). Thus, it appears that species is the only fixed effect that explains a sufficient amount of variation in early ocean travel speeds to warrant inclusion as a parameter in the model.

Strong patterns of diurnal behaviour were seen in smolts migrating out of smaller rivers (Fig. 7.8). Smolts were rarely detected moving past river stations (freshwater) or stations near river mouths (tidal) during daylight hours. The May 1 and June 1 reference lines bracket the release dates of most populations released in rivers (Fig. 7.8), but diurnal patterns were robust to possible migration times in April or June also. In contrast, there was only a weak diurnal pattern in smolts passing Fraser River stations, with a very slight tendency of smolts detected less often.
during early evening hours and more often after dusk (to note, this pattern may simply result from daily fluctuations in river flow and velocity in the lower river where receivers were located, as river flow tends to decrease slightly during daylight hours and then increase overnight in response to diurnal patterns of snowmelt further up the valley). There appeared to be a higher frequency of fish detected during daylight hours at Howe Sound stations, but this was likely simply a carry-over effect of smolts leaving the river during night-time hours (the inner Howe Sound station was 11–13 km from the last Squamish River or estuary station, so continually-migrating fish leaving the river under cover of darkness would have arrived some hours later at the first Howe Sound line). At the major ocean stations NSOG, QCS, and JDF, as well as at ocean stations where smolts were detected less often, there was little or no evidence of diurnal migratory behaviour. These frequency distributions were also separated by species and by wild or hatchery-rearing history (not shown), but no differences in diurnal migration patterns were observed among species or among wild and hatchery fish.

7.3.3 Small-scale movement and mortality patterns in Howe Sound

Sampling for salmon smolts in Howe Sound with mobile transect surveys covered a large proportion of the fjord during most sampling trips (Fig. 7.9). In 2003, surveys were limited mainly by boat speeds <7 km·h⁻¹, since the hydrophone was pole-mounted from the boat rather than towed behind it, and most transects were conducted close to shore. In 2004, surveys were conducted near shore and in the middle of channels, and the fjord was fully sampled except for Thornbrough Channel on the west side. Some sampling tracks extended up the Sunshine Coast in Georgia Strait (Fig. 7.10a). Full coverage in Howe Sound was achieved in May 2005 (Fig. 7.9c), but little sampling was done later that year (mainly just to verify whether tags detected in May were still in the same location), since efforts were instead directed toward sampling in Georgia Strait (Fig. 7.10b). In 2006, equipment problems and limited sampling days led to a relatively small proportion of the fjord being sampled in May. The proportion of the fjord sampled in August was higher, although transects were spaced slightly further apart than in other years (Fig. 7.9f). In both the first and second sampling trips of 2007, most of the fjord was covered except around the islands that lie between Howe Sound and Georgia Strait.

There did not appear to be any strong tendency for coho salmon or steelhead smolts to either stay near coastlines or mid-channel during their migration through Howe Sound. Whether smolts were later interpreted to be alive or dead at the time of detection, smolts were detected throughout the fjord along mainland shorelines, island shorelines, and in the middle of various
channels (Fig. 7.11; these detection locations include those heard on stationary receivers deployed temporarily during the mobile tracking program in Squamish Harbour or off Keats Island in lower Howe Sound). In most sampling trips (May 2004, May 2005, Aug. 2006, and both trips in 2007) a large proportion of the fjord was covered with surveys both along shorelines and in open waters (Fig. 7.9), so any positional bias in proximity to shorelines would have indicated behavioural preferences. Such biases were not apparent (Fig. 7.11). Similarly, late-summer sampling for tags still remaining in Howe Sound after completion of the migration occurred only in 2006 and 2007, so these years provide the best opportunity for looking specifically at the distribution of approximate mortality locations (i.e., sampling during May could in theory have missed smolts that delayed migrating until June, although this was rarely observed on stationary receivers). In these years, approximate mortality locations of coho smolts appeared to be randomly scattered throughout the fjord at a range of distances from the river mouth, both along shorelines and mid-channel, both near the river mouth and further south (Fig. 7.11d, e). The other years showed similar patterns for May sampling trips.\(^5\)

Depending on how the distance from the Squamish River mouth to assumed mortality locations is calculated, different per-distance instantaneous mortality rates, \(M\), are inferred for coho smolts (too few steelhead mortality locations were identified to estimate \(M\) for steelhead). Direct, shortest-route distances to approximate mortality locations ranged from 0.35–43.2 km from the river mouth (Fig. 7.12a). Many of the 49 total triangulated mortality locations were <5 km from the river mouth, after which the distribution of distances to mortality locations was more even throughout the Howe Sound migration. Best fit parameter values for the exponential mortality model fit to direct distance data (while accounting for detection efficiency in locating stationary tags) were 0.044 km\(^{-1}\) for constant \(M\) and 0.165 for constant detection efficiency \((p_{\text{mort}})\). These relied on the fixed starting value of 329.2 tagged fish that were estimated to have entered Howe Sound alive from 2003–2007 (Table 7.3). In many cases these direct distances are known to underestimate actual distances travelled because a smolt may be detected at stationary receivers or elsewhere in the fjord with mobile sampling which are not along the shortest-route direct path from the river mouth to the assumed mortality location (in some cases underestimates are severe, with minimum travel path distances known to be at least 2–3 times longer than direct distances). Accounting for these known travel paths, minimum known travel distances to

\(^5\) An exception is in 2003, when only 15 fish were tagged, but all freshwater survivors were accounted for either on HSouter or by the three mortality locations in Squamish Harbour. Restricted sampling did not therefore create a positional bias in this case.
approximate mortality locations ranged from 0.93–78.9 km. The frequency distribution of minimum known travel distances was a more gradual decline (Fig. 7.12b), with parameter values estimated at $M = 0.024$ km$^{-1}$ and $p_{\text{mort}} = 0.177$. While $p_{\text{mort}}$ was similar among measures, direct-distance $\hat{M}$ was nearly twice that of known travel distance $\hat{M}$.

Parameter estimates of $M$ and $p_{\text{mort}}$ of the exponential mortality model are confounded, showing negative correlation (Fig. 7.13). There is considerable uncertainty in the above parameter estimates, with a wide range of $M$ and $p_{\text{mort}}$ values able to fit the distance data almost as well as the best fit values. For the minimum direct distance data, combinations of $[M \approx 0.032$ km$^{-1}, p_{\text{mort}} \approx 0.2]$ or $[M \approx 0.06$ km$^{-1}, p_{\text{mort}} \approx 0.135]$ are nearly as likely as the best fit values (Fig. 7.13a). For the minimum known travel distance data, combinations of $[M \approx 0.017$ km$^{-1}, p_{\text{mort}} \approx 0.22]$ or $[M \approx 0.032$ km$^{-1}, p_{\text{mort}} \approx 0.15]$ are nearly as likely as the best fit values (Fig. 7.13b). Under both measures, combinations of relatively low $p_{\text{mort}}$ and low $M$ or high $p_{\text{mort}}$ and high $M$ are unlikely.

Some movement patterns in the Squamish River estuary were suggestive of tags being inside predator stomachs rather than in live smolts. Receivers in the lower Squamish River were typically >2 km upstream from the actual mouth of the river, so there was an opportunity to detect tags moving between Squamish Harbour (the upper portion of Howe Sound) and river receivers. Tags could be detected in Squamish Harbour either with intensive mobile tracking in the area (2003) or with receivers deployed from navigation buoys, pilings, log boom cans, or tethered to shore (consistently in 2006–2008, and occasionally in 2004–2005). In those years with adequate detection coverage in Squamish Harbour, 3–7 coho tags and 4 steelhead tags were observed to have atypical movement patterns (Table 7.3). These tags moved upstream from Squamish Harbour one or more times (typically detected at night on river receivers), generally over a 2–4 d period but ranging from 1–15 d. These tags occasionally displayed rapid movements between successive detection locations, even when travelling upstream. After these back-and-forth movements, none of these tags were detected leaving Howe Sound or at ocean stations further along migration routes. About half of these tags ended up remaining in one location as verified by repeated triangulations during mobile tracking surveys. The other tags were detected for the last time at either the lower river or Squamish Harbour stations. In 2004 and 2005, when sampling coverage in Squamish Harbour was sparse, movement patterns upstream were rarely observed (Table 7.3).
7.4 Discussion

7.4.1 Migration direction after ocean entry

The proportion of fish within a release group migrating northwards after ocean entry ranged widely among groups. Fish entering saltwater in northern Georgia Strait or Queen Charlotte Strait moved predominantly northwards, while those entering further to the south displayed split migration routes. Even further south, steelhead from five Hood Canal populations (Puget Sound, Washington State) were only detected leaving via JDF (Moore et al. *In press*). In some cases the estimated \( P(N) \) was likely biased due to unequal distances to the northern and southern stations. Since higher total mortality is expected for longer migration distances (assuming a constant mortality rate per unit distance), \( P(N) \) is biased upwards for the populations whose route to the northern station is shorter than the route to the southern station. This is especially true for Sakinaw Lake and Englishman River populations, as the distance to NSOG was much shorter than the distance to JDF (Fig. 1.4). To note, if \( P(N) \) were calculated based on detections at QCS and JDF instead of NSOG and JDF, then for these two populations the five estimates of \( P(N) \geq 90\% \) would change very little, but the \( P(N) \) estimates for 2005 Sakinaw Lake kokanee and 2006 Sakinaw Lake sockeye would decrease from 56% and 84% to 23% and 60%, respectively. In contrast, the bias in \( P(N) \) would be negligible for Fraser and Cowichan River populations, as distances to northern and southern stations were roughly equal. Bias in \( P(N) \) could be reduced by incorporating it directly into mark-recapture models as an estimated parameter and treating survival separately along northern and southern routes (Skalski 2006). For populations with relatively few fish detected at either northern or southern stations, however, such methods are prohibitive if \( P(N) \) tends to vary among populations, as they appear to.

As previously mentioned, very few coho smolts entering the main body of Georgia Strait were detected moving across terminal stations at QCS or JDF, which may have been due to summer residency in the Strait rather than high mortality during a directed migration. The high \( P(N) \) of coho populations (100% for the Tenderfoot Creek release groups and 84% for the Coldwater River group) are based almost exclusively on fish detections at NSOG without subsequent detection at terminal stations. Only five Georgia Strait coho (from Tenderfoot Creek in 2006 and 2007) were detected at QCS, and only one (a Coldwater River coho in 2006) was detected at JDF. It is possible that fish were foraging near NSOG and detected, rather than migrating continuously northward, so these estimates of \( P(N) \) might not actually represent directed migration behaviour. Tag batteries implanted into coho smolts prior to their downstream
migration last only a few months, so if smolts resided in Georgia Strait over the summer and left during the fall or winter, tag batteries would have likely expired so fish would not be detected at QCS or JDF. In a related study, however, coho post-smolts were trawl-caught, tagged, and released in Georgia Strait in July and September of 2006 so that possible out-migration behaviour after the first ocean summer could be assessed (Chittenden et al. In press). Of all the coho post-smolts detected leaving the Georgia Strait system (59 of 173 originally tagged), only 4 fish were detected at QCS, with the other 55 (93%) detected at JDF. The frequency with which coho post-smolts took the southern route increased over time, being low and similar to the proportion taking the northern route from July-September, but increasing thereafter throughout winter months (Chittenden et al. In press). It is also possible that coho and Chinook do not leave Georgia Strait at all. Earlier studies have suggested that some coho spend their entire marine life in the Strait, and this proportion may vary annually with salinity (Godfrey et al. 1975, Hartt and Dell 1986). Differences among salmon species in duration of residence in Georgia Strait likely reflect diet differences, as coho and Chinook are less reliant on small invertebrate prey by June (compared to sockeye, pink, and chum salmon; Healey 1980, Brodeur et al. 2007). Small invertebrate prey abundance declines after May, so other species may not satisfy food requirements if they were to reside in the Strait like coho and Chinook.

Similar arguments of a possible lack of migration out of Georgia Strait may apply to some smolts from Sakinaw Lake kokanee and sockeye release groups. It appears that some fish from these groups have non-migratory behaviours, either remaining in the Strait throughout their ocean lives or returning to Sakinaw Lake. About 20–30% of smolts from 2004 hatchery sockeye and 2005 wild kokanee groups were detected at QCS or JDF stations, but none of these fish were detected thereafter as returning adults (Wood et al. In press; these fish had ‘sleeper’ tags that turned on again during the return migration). In contrast, of the 57% of fish from the 2004 group that were not detected at any station as smolts, 5% of these were detected as adults near the release site or elsewhere in Georgia Strait. Since these fish were detected neither leaving nor returning via Queen Charlotte or Juan de Fuca Straits, this suggests that some fish did not leave Georgia Strait; these large hatchery-reared sockeye had been grown to an artificially large body size, and then happened to be the ones surviving to adulthood (Wood et al. In press). There were also indications that some wild kokanee smolts similarly had non-migratory behaviours, as about 12% of the smolts released in 2006 were detected entering Sakinaw Lake several days after release and remaining there (Wood et al. In press).
It is not clear whether the direction of migration in juveniles may correlate with that of returning adults. Previous studies showed this is not necessarily the case for Fraser River sockeye taking the northern or southern route around Vancouver Island (Groot and Cooke 1987). The direction taken by returning adults has varied under different ocean regimes, with most returning through Juan de Fuca Strait during 1953–1977, and most returning through Queen Charlotte Strait since then (Groot and Quinn 1987, McKinnell et al. 1999). Population-specific migration routes (Rose 1993, Secor 1999) and rearing or foraging grounds (e.g., adult coho, Labelle et al. 1997; and juvenile Chinook, D. Beamish, *pers. comm.*) have been observed in some fish meta-populations. Further, direction of migration of returning adult Fraser River sockeye salmon may be predictable from brain physiology measured during the return migration near the Queen Charlotte Islands, prior to arrival at a bifurcation point north of Vancouver Island (K. Miller-Saunders, *pers. comm.*). Adult sockeye retained the differentiated brain profiles throughout the remainder of their migration up the Fraser River. If direction of travel may be at least in part deterministic several days or weeks ahead of the point where a fish takes the northern or southern route, then it is possible this has a genetic component, in which case the direction taken by smolts may also in part be deterministic. If smolt outmigration and adult return migration route directions are correlated, then quantifying the direction taken by juveniles may help to inform management decisions about area and time fishery closures during the adult return migration. Threatened or at-risk populations that tend to take one particular return route (at a particular time) could be allowed to escape the fishery through closures, allowing fisheries to operate along other migration routes that may not involve as many weak stocks.

If direction of migration has some genetic-based component to it, then populations exhibiting split-route migration paths with some individuals moving north and others moving south are more genetically diverse with respect to this trait. A mix of directional ‘strategies’ among individuals in a population may be maintained in the absence of strong selection against one direction over the other. Similar to different directions taken, recent evidence shows that within coho populations along the outer coast from Oregon to southeast Alaska, fish fall into discrete groups with respect to migration speeds (Morris et al. 2007). There is a fast, northward-migrating component and a slow component in which fish delay migrating until winter and then move northwards more slowly. Populations originating from Georgia Strait and Puget Sound predominantly have the ‘slow’ strategy, with only 3.5% of populations having a fast-migrating component, and with some populations overwintering off the west coast of Vancouver Island rather than migrating further northward (Morris et al. 2007). This is apparent on a regional scale.
as well as on a population scale, and is line with the observations of at least some coho delaying outmigration from Georgia Strait until winter months (Healey 1980, Chittenden et al. *In press*).

### 7.4.2 Travel speeds during downstream and early ocean migration

Observed travel speeds were variable, but generally within the range of those observed in other studies (reviewed in Brodeur et al. 2003). Species differences in travel speeds were observed, but the relationship differed between river and ocean portions of the migration. In rivers, steelhead had slower average travel speeds than other species. This was likely a result of temporary delaying of migrations rather than slower travel while actually migrating. For example, two hatchery-reared steelhead groups from the Cheakamus River in 2008 took a relatively long time on average to migrate a fairly short distance downstream (Fig. 7.2a). Nearly half of all steelhead smolts had very slow average migration speeds of <2 km·d⁻¹ or <0.2 BL·s⁻¹, which was a much higher proportion than those seen in other species (Fig. 7.4). Slow migration speeds were also observed for wild and hatchery-reared steelhead from Hood Canal (3.1 km/day; Moore et al. *In press*). In the Columbia River, in contrast to sockeye and Chinook smolts, an inverse relationship between body length and downstream migration speed was observed for steelhead (Giorgi et al. 1997). Such migratory behaviour differences between steelhead and other species may relate to the propensity for freshwater residualization, i.e., failure to migrate to the ocean (Ricker 1938). Steelhead are closely related genetically to the non-anadromous rainbow trout (Zimmerman and Reeves 2000; they are, in fact, the same species). In a meta-analysis across several watersheds, on average about 2–9% of steelhead smolts from a given cohort have been found to residualize (S. Hausch and M. Melnychuk, *unpubl. data*), either delaying migration for an additional year of freshwater rearing, or permanently, essentially adopting a rainbow trout life history strategy. There may be a period of delayed migration in steelhead smolts even if they do eventually migrate to sea, which would explain the slower average migration speeds downstream.

In rivers, coho were slightly faster on average than other species after accounting for other factors such as wild or hatchery-rearing history, Fraser or non-Fraser watershed, and fork length. After ocean entry, however, coho moved slower on average than steelhead or sockeye smolts. Since ocean travel speeds were defined as from river mouth to exit from Georgia Strait via QCS or JDF, most ocean travel speed data for coho came from Keogh and Nimpkish River populations, which entered Queen Charlotte Strait rather than Georgia Strait proper (as previously mentioned, only a few coho from other populations were detected at QCS or JDF. In
contrast, most steelhead and sockeye/kokanee smolts detected were from populations that entered Georgia Strait directly.) In part, coho travel speeds during the inshore migration were slower simply because of this shorter migration distance for most fish, and any ‘distance-independent’ components of ocean travel time thus being averaged over a shorter total travel time (see below). The few Georgia Strait coho that were detected at terminal stations, however, did have greater average travel times than steelhead and sockeye that migrated similar distances (Fig. 7.2), so shorter distances cannot fully explain the slower average ocean travel speeds of coho smolts. As mentioned above, coho and Chinook smolts entering Georgia Strait were rarely detected, and it is not clear whether this is primarily due to very high mortality after ocean entry or summer residency in the Strait away from detection stations, such as in the Gulf Islands or Fraser plume regions (Healey 1980). The fall and winter emigrations of coho post-smolts out of the Strait, primarily via Juan de Fuca Strait (Chit tenden et al. In press), suggest that at least part of the pattern is due to summer residency. The few coho smolts from Georgia Strait populations detected at QCS or JDF may have spent some time foraging in the Strait before emigration, thus leading to slower average travel speeds than steelhead or sockeye/kokanee, which tended to emigrate from the Strait soon after ocean entry. Average observed speeds of steelhead and sockeye smolts through the Strait (0–2 BL·s\(^{-1}\)) were slower than what are thought to be optimal cruising speeds for small pelagic fish (1-3 BL/s; Weih s 1973, Ware 1978), so at least some portion of their migrations through the Strait were likely not continuous and directed. The observed differences among species in travel speeds are not surprising given previous observations on species differences in foraging behaviour (Healey 1980).

Smolts from the Fraser River had much faster travel speeds downstream than smolts from other rivers, which is largely explained by faster river flow. It is also explained in part by differential proportions of time spent not migrating. Periods of movement interspersed with periods of holding are common during the downstream migration (Moser et al. 1991). In rivers other than the Fraser River, smolts were observed to travel mainly at night, as has been previously observed (Hoar 1951, McDonald 1960). They avoided travel during daylight hours, presumably to reduce the risk of visual predation (Gregory and Levings 1998), and this slowed their average speed over the full downstream migration. This is likely the main reason why downstream migration speeds in these other rivers were slower on average than ocean speeds, even though ocean travel would have little assistance from currents. In the Fraser River, however, the water is siltier and moves at a higher velocity, both of which may reduce the risk of
visual predation during the day. Fraser River smolts did not avoid migrating during daylight hours; migration during both day and night led to faster average travel speeds.

The higher flows in the Fraser River compared to others might also explain why body length had little effect on downstream travel speed in the Fraser River, but had a positive effect in other rivers, with large individuals migrating faster on average. (To note, in the Fraser River, there was actually a weak negative relationship, with larger individuals moving slower on average. In fast-flowing rivers, large individuals may be able to hold better against the current while smaller individuals are swept downstream.) Movement down the Fraser River may be largely passive, whereas more active movement downstream might be required in other rivers to complete the downstream migration quickly. Larger individuals are generally better able to swim faster. Surprisingly, this relationship was not found during the inshore migration; large and small individuals migrated from the river mouth to QCS or JDF lines at similar average absolute travel speeds. One possible explanation for this lack of difference in average speed is foraging activity along migratory routes. Larger individuals may require more time spent foraging to satisfy a higher metabolic demand, and this might compensate for their possible faster speeds while actually migrating. The resolution of receiver stations during the early ocean migration did not allow for the proportion of time spent actively migrating to be quantified.

Travel speed differences were observed between wild and hatchery-reared fish during the downstream migration, with wild fish moving faster than hatchery-reared fish on average. This difference occurred after accounting for species differences. It could have been confounded with species differences, although most steelhead populations were wild and most coho populations were hatchery-reared, whereas steelhead were slower than coho and other species, all else equal. It appears from Fig. 7.2c that this difference is attributed not to slower speeds in hatchery fish while travelling, but to an intercept difference in travel time versus distance, i.e., a distance-independent factor. Even at very short distances downstream, hatchery fish took about 5 d more to complete the downstream migration, and this difference was consistent across the range of downstream distances studied. This difference is likely due to some necessary activity of hatchery fish after release but prior to actively migrating downstream. Such activities could include: seeking refuge for several days while stress levels slowly decrease after release, since creek or river environments are substantially different than hatchery environments; holding in waters near the release site to imprint on the local water (imprinting is common during smoltification and aids in finding the watershed of origin when adults later return to spawn); or holding somewhere during the downstream migration until smoltification is complete, in the case
of hatchery release groups that had forced rather than volitional release strategies used. After ocean entry, wild and hatchery-reared smolts migrated at similar average absolute travel speeds.

Similar to the downstream migration, intercepts >0 in a travel time–distance relationship for the inshore migration were also observed for coho and sockeye/kokanee (Fig. 7.2). Although a simple linear regression through point estimates for steelhead also had an intercept >0, the fit was not convincing as the travel times for migration distances of <20 km were short, suggestive of an actual non-linear intercept close to 0 for these steelhead groups. The intercept of about 10 d for sockeye/kokanee is largely driven by smolts from Sakinaw Lake detected at the NSOG station, 40 km from the release site. These smolts were mostly released directly into the ocean near the lake outlet, so it is reasonable that a saltwater acclimation period could have been necessary before actively migrating. Many Cultus Lake sockeye and Sakinaw Lake smolts were also detected entering Howe Sound (Fig. 1.4) prior to leaving via either QCS or JDF, so this 10-day intercept may have also resulted from time spent searching for migration route cues or even foraging periods shortly after ocean entry. Healey (1980) documented similar migration times of sockeye through Georgia Strait, although found that most sockeye took the Juan de Fuca Strait exit. The difference may relate to watershed of origin, as most sockeye caught were likely from wild Fraser River populations in contrast to the hatchery groups in this study. The intercept for coho was also about 10 d, and this was driven by smolts entering Queen Charlotte Strait from the Keogh and Nimpkish Rivers. This could have resulted from similar explanations of osmotic adjustment, initial estuarine or marine foraging, or migration route-seeking shortly after ocean entry. In other studies, coho smolts have been shown to temporarily reside in estuaries between 1–5 d on average before continuing their migration (Moser et al. 1991, Miller and Sadro 2003). An alternative explanation is that some fish from these populations resided within Queen Charlotte Strait during summer months, similar to how at least a portion of the coho and Chinook that entered into Georgia Strait resided over the summer within the Strait. Coho smolts may have spent several days in Queen Charlotte Strait milling or foraging, after which a portion of fish migrated northwards across QCS and another portion resided for the summer. This possibility is admittedly speculative, but consistent with the observation that apparent survival to QCS was generally lower for Nimpkish and Keogh River coho populations than for Keogh River steelhead populations despite similar migration distances (Chapter 9; low apparent survival can be interpreted not only as mortality but also as residency without possibility of detection).

It is not clear how travel speeds along a migration route may affect the risk of predation. Exposure to predation might be simply proportional to the distance migrated, in which case
speed may have little further effect on predation risk. On the other hand, predation risk within rivers or these inshore waters may be proportional to the amount of time spent there, in which case faster speeds out of these areas would be expected to reduce overall predation risk. The relative importance of these distance-based and travel time-based possibilities may largely depend on foraging strategies of predators. Along a migration route, if only single encounters between a particular smolt and particular predator are predicted (for example, if smolts run a gauntlet of predators that do not chase after smolts that escape through the gauntlet), then theory suggests that only distance should affect predation risk (Anderson et al. 2005). If multiple encounters between a smolt and a predator are predicted (for example, in highly mobile predators that move back and forth along a migration route), then travel time is expected to be a better predictor (Anderson et al. 2005). Although some seal (Olesiuk et al. 1996) or fish (e.g., bull trout or Dolly Varden char) predators in rivers may largely be sit-and-wait types that tend to remain within particular river reaches, many predators of salmon smolts like birds (Wood 1987, Collis et al. 2001), seals (Laake et al. 2002), and dogfish (Beamish et al. 1992) are highly mobile and may encounter a particular smolt repeatedly. It is therefore likely that faster travel speeds reduce predation risk along migration routes at least somewhat, especially during the inshore portion. One further consideration is that, especially in rivers, total travel time may consist of a component of time actually spent migrating (during which smolts are vulnerable) and a component of time spent in refuges where smolts are invulnerable to predators. This is analogous to foraging arena theory (Walters and Juanes 1993), where the vulnerable activity is migrating rather than foraging. Migration could be punctuated, with bouts of (vulnerable) fast travel interspersed by periods of (invulnerable) little net movement. In such a case, predation risk would not be proportional to total travel time since during a portion of that time smolts would be invulnerable. Differences between migration distance and travel time as possible predictors of mortality will be addressed using mark-recapture models in Chapter 9.

### 7.4.3 Small-scale movement and mortality patterns in Howe Sound

There did not appear to be any strong behavioural preferences for coho or steelhead smolts with respect to migrating near or away from coastlines in Howe Sound, as smolts were detected at a wide range of distances from shore. Similarly, no strong preferences were observed with respect to migrating along the western or eastern channels of Howe Sound on the way to Georgia Strait. Coho salmon smolts generally swim in the upper 45 m of the water column, with the majority in the upper 15–25 m (Pearcy and Fisher 1988, Orsi and Wertheimer 1995, Beamish
et al. 2000). Since most of Howe Sound has much deeper bottom depths and steep shorelines, smolts did not likely travel within visual range of coastlines more often than expected from a random distribution. It is therefore unlikely that smolts used coastline cues for navigation during the nearshore migration.

Similarly, there did not appear to be any strong departure from random expectations of where smolts were assumed to have died in Howe Sound, with respect to either proximity to shorelines or distance from the river mouth. There are at least three potential sources of error in considering triangulated locations of stationary tags as locations of mortality. First, locations where tags stopped moving may not represent exact locations where smolts died, since predators may have carried tags inside their guts for considerable times and distances before defecation. Second, it is possible that if a live smolt took up residence in some highly confined area in Howe Sound, it could be detected repeatedly at the same location and could be interpreted as a smolt that died. Such behaviours have not been demonstrated in other studies, and there is no evidence here that smolts temporarily took up residence for some period of time (during which time they were detected repeatedly) before continuing their migration and being detected later at stationary receivers. Third, some tags becoming stationary could be the result of tag expulsion during the migration of a live smolt instead of mortality. It is unclear how serious a factor this could be. In some hatchery tank studies, tag expulsion rates in similarly-sized fish during approximately the first 6 weeks after surgical implantation were only 0% and 2–9% for Chinook smolts tagged with V7 and V9 tags, respectively (Rechisky and Welch In press), or 1.5% for steelhead smolts tagged with V7 and V9 tags (Moore et al. In press). In other tank studies, however, tag shedding rates in the first 6 weeks were much higher, ranging from 0% and 36–54% for similarly-sized coho smolt groups tagged with V7 and V9 tags, respectively (Chittenden et al. 2009). Tag shedding rates tended to increase after this period of about 6 weeks in some tank studies.

Setting aside these caveats, approximate mortality locations of smolts that died appeared to be scattered throughout Howe Sound. Mortality locations were more frequent within 5 km of the river mouth (or, on a per-area basis, were much more concentrated in the narrow, inner part of Howe Sound north of Anvil Island), but they also occurred in other parts of the fjord, wherever sampling occurred. Smolts may be particularly vulnerable to mortality immediately after ocean entry, during their migration through Squamish Harbour. Fish or harbour seal predators may aggregate at the river mouth to coincide with the timing of the annual outmigration of salmon smolts (Greenstreet et al. 1993; in addition to coho, millions of juvenile chum and Chinook salmon are also released from Tenderfoot Creek Hatchery each year).
Although birds are important estuarine predators in other watersheds (Mace 1983, Collis et al. 2001), they were not often observed foraging for salmon smolts in Squamish Harbour, possibly because of the high turbidity of the river and estuary. The transition from freshwater to saltwater may also be physiologically challenging, either making escape from predation more difficult or requiring additional time spent in the lower river or Squamish Harbour until completion of osmotic adjustment. Although mortality locations were somewhat more common in Squamish Harbour, they did still occur lower in the fjord, with nearly 60% of all Howe Sound mortality locations observed >10 km from the river mouth. This suggests two possibilities: (1) predation is common throughout Howe Sound, not just immediately after ocean entry due to aggregations of predators targeting smolts, or (2) factors other than heavy, ‘bottleneck’ predation may also be responsible for early ocean mortality. The possibility of mortality due to physiological impairment will be addressed in Chapter 10.

Movement patterns around the Squamish River estuary that were considered suggestive of tags inside predator stomachs included travel from Squamish Harbour back upriver and/or rapid movements between detection locations, followed by a later absence of detections on any receivers and/or verification of tag stationarity in Howe Sound with mobile tracking surveys. When receiver coverage in Squamish Harbour was adequate to detect upstream movements (years 2003, 2006, 2007), the proportion of tags that showed movement patterns suggestive of being in predator stomachs varied considerably among years. In 2003, this number of suspected depredations on coho as a proportion of fish tagged (3/15, 20%) or of fish surviving the downstream migration (3/11.1, 27%) was higher than in other years for either coho or steelhead (which ranged from 3.3–4.0% as a proportion of fish tagged and from 4.8–11.3% as a proportion of fish surviving the downstream migration; Table 7.3). 2003 was a year of particularly high harbour seal abundance near the Squamish River mouth compared with 2006–2007, based on casual observations. Seals commonly haul out on log booms in Squamish Harbour, and are often observed swimming up the Squamish River several kilometres. Seals were less commonly seen in Squamish Harbour or hauled up on log booms in years after 2003–2004.

Instantaneous rates of mortality are generally treated as time-based parameters. For obligate migrants that consistently travel along some general route, distance-based mortality rates may be more appropriate. The simplest argument is that specific times of mortality are generally less well known than locations of mortality verified by mobile transect surveys since those surveys are often conducted several weeks after the migration pulse. Another possible reason is that some proportion of time is not spent actively migrating and vulnerable to
predators; this will be further discussed in Chapter 9. Estimated mortality rates of coho smolts based on approximate mortality locations in Howe Sound were highly confounded with estimated detection efficiencies, and also depended strongly on which measure of distance from river mouth to triangulated tag location was assumed. Direct distances underestimate actual distance travelled by most fish, so $M$ is likely overestimated. The distance measure that accounts for longer, known travel distances between successive detections predicts a lower $M$, but even this measure underestimates the actual distance travelled, because actual routes from ocean entry to eventual approximate mortality locations are unknown. If actual routes were known, $\hat{M}$ would be lower still. Another reason why $M$ may be overestimated in some portions of Howe Sound relates to its definition as a constant rate under the exponential mortality model. If $M$ were actually higher immediately after ocean entry than later in the migration, this change would not be accounted for and the constant or average $\hat{M}$ would underestimate $M$ immediately after ocean entry and overestimate $M$ later in the migration. A changing time-based $M$ from soon after ocean entry compared to weeks later has been observed in other studies (Parker 1968, Pearcy 1992, Dieperink et al. 2001, Wertheimer and Thrower 2007). In this case, the migration through Howe Sound generally lasted days rather than weeks, but there could still reasonably be a decrease in $M$ over this distance. Finally, the pooling of mortality location data required for achieving a reasonable sample size does not account for year-to-year variability in $M$, so estimates $\hat{M}$ are weighted more towards years in which a larger number of approximate mortality locations was identified, such as 2004, 2006, and especially 2007.

Aside from actual travel distances being unknown and possibilities of $M$ decreasing over distance (or time), $\hat{M}$ is also highly sensitive to $\hat{p}_{\text{mort}}$. A wide range of combinations of $M$ and $p_{\text{mort}}$ parameter values gave nearly the same fit to observed mortality location data, resulting in low precision of $\hat{M}$. Estimated $\hat{p}_{\text{mort}}$ were similar among distance measures, and surprisingly low.\(^6\) One possible explanation is that $p_{\text{mort}}$ was also assumed to be constant throughout Howe Sound, but could actually be heterogeneous. Near the Squamish River mouth, fine silt may cover over tags that have settled to the bottom. There are also shallow areas in the estuary where the tracking vessel could not travel (in contrast to the majority of Howe Sound), so any mortality

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\(^6\) To note, these low $\hat{p}_{\text{mort}}$ are discouraging for future possibilities of conducting mobile transect surveys for stationary tags on the seabed in larger areas such as Georgia Strait, e.g., Figure 7.10. Assuming that 50 stationary tags were randomly distributed throughout Georgia Strait and that they could be detected with an average $p_{\text{mort}}$ of 0.177, under typical transect sampling capabilities the expected number of tags detected per day would be only about 0.08. I.e., the expected number of sampling days required until the very first tag was detected would be 8.5 d to achieve a 50% cumulative probability, or 19.5 d to achieve an 80% cumulative probability.
locations in these areas would be more likely to go undetected. Both factors may result in a lower \( p_{\text{mort}} \) soon after ocean entry than further south away from the river mouth. Assuming a constant \( p_{\text{mort}} \) would fail to detect this change, and this would result in underestimating \( \tilde{M} \) immediately after ocean entry.

For comparison with mobile transect survey estimates, instantaneous distance-based mortality rates for Howe Sound segments were calculated from stationary receiver detection data (independently from mobile data). Mark-recapture survival probabilities for the segments from river mouth to HS\(_{\text{inner}}\) and from HS\(_{\text{inner}}\) to HS\(_{\text{outer}}\) were estimated (Chapter 9), and were converted to instantaneous rates using shortest-route segment distances, i.e., \( M_{\text{seg}} = -\ln(\phi_{\text{seg}})/d_{\text{seg}} \). Estimates \( M_{\text{stationary}} \) were slightly lower than those of \( M_{\text{mobile}} \), and were also observed to decrease during the migration. In the segment from river mouth to HS\(_{\text{inner}}\), \( M_{\text{stationary}} \) for coho ranged from 0.007–0.046 km\(^{-1}\) across years (average 0.024 km\(^{-1}\), weighted by freshwater survivors), while in the segment from HS\(_{\text{inner}}\) to HS\(_{\text{outer}}\), ranged from 0.003–0.022 km\(^{-1}\) (average 0.012 km\(^{-1}\), weighted by survivors to HS\(_{\text{inner}}\)). This suggests that the assumption of constant \( M \) throughout Howe Sound in the exponential mortality model for estimating \( M_{\text{mobile}} \) is probably unreasonable. Despite not accounting for change in \( M \) throughout Howe Sound, the estimate of 0.024 km\(^{-1}\) for \( M_{\text{mobile}} \) using the distance measure which incorporates known smolt locations between ocean entry and eventual triangulated mortality locations was at least comparable to those for \( M_{\text{stationary}} \). These were both much lower than instantaneous distance-based mortality rates estimated for Atlantic salmon (0.15–0.16 km\(^{-1}\)) and sea trout (0.13–0.18 km\(^{-1}\)) in a shallow reservoir 35 km upstream from a Danish fjord, which was attributed to fish and bird predation (Jepsen et al. 1998).

As a result of the above uncertainties and the resulting direction of overall bias in \( M_{\text{mobile}} \) being unknown, it does not appear as if mobile transect surveys by themselves (i.e., without stationary receiver lines) are adequate to properly estimate instantaneous distance-based mortality rates for migrating salmon smolts. Joint analysis of stationary and mobile detection data could provide more reliable estimates of mortality (one such model will be considered in Chapter 10).
Table 7.1. Model selection results for comparison of random effects in travel speed models. Comparison criteria include number of parameters ($k$), negative log-likelihood ($-2\cdot\ln(L)$), and the Bayesian Information Criterion (BIC).

<table>
<thead>
<tr>
<th>Model</th>
<th>Absolute travel speeds, km·d$^{-1}$</th>
<th>Length-adjusted travel speeds, BL·s$^{-1}$</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>$k$</td>
<td>$-2\cdot\ln(L)$</td>
</tr>
<tr>
<td><strong>Downstream travel speeds</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>$u$-(fixed), $\text{rand}(\omega_0, \gamma_0)$</td>
<td>13</td>
<td>5037.5</td>
</tr>
<tr>
<td>$u$-(fixed), $\text{rand}(\omega_0)$</td>
<td>12</td>
<td>5107.2</td>
</tr>
<tr>
<td>$u$-(fixed), $\text{rand}(\gamma_0)$</td>
<td>11</td>
<td>5838.6</td>
</tr>
<tr>
<td><strong>Ocean travel speeds</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>$u$-(fixed), $\text{rand}(\omega_0, \gamma_0)$</td>
<td>10</td>
<td>778.3</td>
</tr>
<tr>
<td>$u$-(fixed), $\text{rand}(\omega_0)$</td>
<td>9</td>
<td>815.7</td>
</tr>
<tr>
<td>$u$-(fixed), $\text{rand}(\gamma_0)$</td>
<td>8</td>
<td>824.7</td>
</tr>
</tbody>
</table>

*In all models, fixed parameters included additive effects of species, wild or hatchery-rearing history, Fraser River or non-Fraser origin (FnF), fork length (FL), and a FnF:FL interaction. Models differ in their random effects considered: $(\gamma_0)$, random intercepts for years; $(\omega_0)$, random intercepts for watersheds nested within Fraser/non-Fraser River; $(\omega_0, \gamma_0)$, random intercepts for both effects.*
Table 7.2. Model selection results for comparison of fixed effects in travel speed models. Comparison criteria include number of parameters \((k)\), negative log-likelihood \((-2 \cdot \ln(L))\), and the Bayesian Information Criterion (BIC). The lowest BIC value in each comparison is boldfaced.

<table>
<thead>
<tr>
<th>Model(^a)</th>
<th>Absolute travel speeds, \text{km} \cdot \text{d}^{-1}</th>
<th>Length-adjusted travel speeds, \text{BL} \cdot \text{s}^{-1}</th>
</tr>
</thead>
<tbody>
<tr>
<td>(k) (-2 \cdot \ln(L)) BIC (\Delta\text{BIC})</td>
<td>(k) (-2 \cdot \ln(L)) BIC (\Delta\text{BIC})</td>
<td></td>
</tr>
<tr>
<td><strong>Downstream travel speeds</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>(u_{\alpha} + \text{spp} + \text{HW} + \text{FnF} + \text{FL} + \text{FnF:FL})</td>
<td>13</td>
<td>5029.0</td>
</tr>
<tr>
<td>(u_{\alpha} + \text{spp} + \text{HW} + \text{FnF} + \text{FL})</td>
<td>12</td>
<td>5056.7</td>
</tr>
<tr>
<td>(u_{\alpha} + \text{spp} + \text{HW} + \text{FnF})</td>
<td>11</td>
<td>5088.5</td>
</tr>
<tr>
<td>(u_{\alpha} + \text{spp} + \text{FnF} + \text{FL})</td>
<td>10</td>
<td>5132.0</td>
</tr>
<tr>
<td>(u_{\alpha} + \text{HW} + \text{FnF} + \text{FL})</td>
<td>9</td>
<td>5121.0</td>
</tr>
<tr>
<td>(u_{\alpha} + \text{FnF} + \text{FL})</td>
<td>7</td>
<td>5231.0</td>
</tr>
<tr>
<td><strong>Ocean travel speeds</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>(u_{\alpha} + \text{spp} + \text{HW} + \text{FnF})</td>
<td>9</td>
<td>767.8</td>
</tr>
<tr>
<td>(u_{\alpha} + \text{spp} + \text{FnF} + \text{FL})</td>
<td>9</td>
<td>768.2</td>
</tr>
<tr>
<td>(u_{\alpha} + \text{spp} + \text{HW} + \text{FL})</td>
<td>9</td>
<td>770.6</td>
</tr>
<tr>
<td>(u_{\alpha} + \text{spp} + \text{HW} + \text{FnF} + \text{FL})</td>
<td>10</td>
<td>767.8</td>
</tr>
<tr>
<td>(u_{\alpha} + \text{FnF} + \text{FL})</td>
<td>7</td>
<td>914.2</td>
</tr>
<tr>
<td>(u_{\alpha} + \text{HW} + \text{FnF} + \text{FL})</td>
<td>8</td>
<td>911.6</td>
</tr>
</tbody>
</table>

\(^a\) In all models, random effect parameters consisted of random intercepts for watersheds nested within Fraser/non-Fraser River and random intercepts for years, i.e., rand(\(\omega_{0j}\), \(\gamma_{0k}\)).
Table 7.3. Summary of tag detections and assumed smolt mortalities in Howe Sound as verified with mobile tracking surveys.

<table>
<thead>
<tr>
<th>Population, year</th>
<th>Number tagged</th>
<th>Estimated number entering Howe Sound</th>
<th>Total number of unique detections</th>
<th>Number of smolts detected in Howe Sound with mobile surveys</th>
<th>Number of identified approximate mortality locations in Howe Sound</th>
<th>Number of tags with estuarine movement patterns suggestive of predation</th>
</tr>
</thead>
<tbody>
<tr>
<td>Tenderfoot Creek Hatchery coho</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>2003</td>
<td>15</td>
<td>11.1</td>
<td>34</td>
<td>6</td>
<td>3</td>
<td>3</td>
</tr>
<tr>
<td>2004</td>
<td>100</td>
<td>44.7</td>
<td>89</td>
<td>34</td>
<td>11</td>
<td>1</td>
</tr>
<tr>
<td>2005</td>
<td>100</td>
<td>82.0</td>
<td>30</td>
<td>19</td>
<td>6</td>
<td>0</td>
</tr>
<tr>
<td>2006</td>
<td>120</td>
<td>84.1</td>
<td>87</td>
<td>64</td>
<td>12</td>
<td>4</td>
</tr>
<tr>
<td>2007</td>
<td>199</td>
<td>107.3</td>
<td>18</td>
<td>18</td>
<td>17</td>
<td>7</td>
</tr>
<tr>
<td>Total</td>
<td>534</td>
<td>329.2</td>
<td>258</td>
<td>141</td>
<td>49</td>
<td>15</td>
</tr>
<tr>
<td>Cheakamus River steelhead</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>2004 (wild)</td>
<td>51</td>
<td>38.1</td>
<td>13</td>
<td>10</td>
<td>2</td>
<td>0</td>
</tr>
<tr>
<td>2005 (wild)</td>
<td>49</td>
<td>42.5</td>
<td>11</td>
<td>6</td>
<td>1</td>
<td>0</td>
</tr>
<tr>
<td>2007 (hatchery)</td>
<td>100</td>
<td>35.1</td>
<td>5</td>
<td>3</td>
<td>2</td>
<td>4</td>
</tr>
<tr>
<td>Total</td>
<td>200</td>
<td>115.7</td>
<td>29</td>
<td>19</td>
<td>5</td>
<td>4</td>
</tr>
</tbody>
</table>

\(^a\) Estimated number entering Howe Sound from the Squamish River was calculated by multiplying the number tagged by the estimated survival for the downstream migration (Chapter 9).

\(^b\) Detections are considered unique if a tag was heard while running blind transects. If the boat returned to a location where a tag was previously identified to check whether it was still there, that was not considered unique. A particular smolt may have several unique detections during its migration. Detections on temporary stationary receivers deployed during mobile sampling are included.

\(^c\) Smolts were considered to have died if a tag was re-located in the same location several days or weeks later, and was not detected thereafter on any stationary receivers.

\(^d\) Movement patterns suggestive of tags inside predator stomachs include travel from Squamish Harbour back upriver and/or rapid movements between detection locations, followed by a later absence of detections on any receivers and/or verification of tag stationarity with mobile tracking surveys. Note that receivers were not consistently in place in Squamish Harbour in 2004–2005, so upstream movements from Squamish Harbour were likely missed.
Figure 7.1. Proportion of fish migrating northward out of the Georgia Strait system (GS) after ocean entry. Fish enter saltwater north of GS and Johnstone Strait (a), into GS from the Fraser River (b), or into GS from other rivers (c). In (a), direction is determined by detection at QCS (north) or NSOG (south). In (b) and (c), direction is determined by detection at NSOG (north) or JDF (south). All estimates are adjusted for station and year-specific detection probability estimates. Estimates are shown by species and wild or hatchery-rearing history. Width of the bars is proportional to the total number of fish detected at northern or southern stations; only populations with $\geq 5$ detections in total are shown.
Figure 7.2. Mean travel time of smolt release groups during downstream migration and inshore migration as a function of minimum distance travelled. Ocean travel times include times from ocean entry to northern Georgia Strait, Queen Charlotte Strait, or Juan de Fuca Strait lines, so each release group may have up to three points in (b) and (d). Travel time estimates are separated by species during the downstream (a) and inshore (b) migration, and separated by wild or hatchery-rearing history (c, d). Lines show linear regressions fit to mean travel time point estimates for each species or rearing history separately.
Figure 7.3. Histograms of travel speeds of tagged fish during the downstream and inshore migrations. Frequency distributions are truncated at 100 km·d$^{-1}$ and 10 BL·s$^{-1}$, as few fish had speeds faster than these. Number of fish is indicated for each category. Dashed red lines show the mean travel speed in each habitat.
Figure 7.4. Histograms of travel speeds of tagged fish during the downstream and inshore migrations, separated by species. Frequency distributions are truncated at 100 km·d$^{-1}$. Number of fish is indicated for each category. Dashed lines show the mean travel speed of each species and habitat combination.
Figure 7.5. Histograms of travel speeds of tagged fish during the downstream and inshore migrations, separated by wild or hatchery rearing history. Frequency distributions are truncated at 100 km·d⁻¹. Number of fish is indicated for each category. Dashed lines show the mean travel speed of each rearing history and habitat combination.
Figure 7.6. Average travel speeds during the downstream and inshore migration vs. body length at time of tagging, separated by species. Travel speed estimates, in units of km-d\(^{-1}\) on the left side and BL·s\(^{-1}\) on the right, represent individual fish. Lines show linear regressions fit to travel speeds for each species separately. Note the different scales on the travel time axes for Fraser River, other river, and ocean segments.
Figure 7.7. Average travel speeds during the downstream and inshore migration vs. body length at time of tagging, separated by wild or hatchery rearing history. Travel speed estimates, in units of km·d\(^{-1}\) on the left side and BL·s\(^{-1}\) on the right, represent individual fish. Lines show linear regressions fit to travel speeds for each rearing history separately. Note the different scales on the travel time axes for Fraser River, other river, and ocean segments.
Figure 7.8. Time of day (Pacific Daylight Time) that smolts originating from B.C. were first detected at a receiver station. Frequency distributions are grouped by habitat type. River mouth stations are those deployed in tidal reaches of rivers or estuaries, and ‘upstream’ stations are upriver of tidal waters. ‘Other ocean stations’ includes receivers deployed in some years in Burrard Inlet, Indian Arm, Point Atkinson, the Fraser River plume, or on the outer coast at Lippy Point or Willipa Bay. Vertical lines show time of sunrise (red) and sunset (black) on May 1 (dashed) and June 1 (dotted) in Vancouver, B.C. Sample size of fish/receiver station combinations are shown for each habitat type (i.e., a smolt may be represented more than once within a histogram.)
Figure 7.9. Boat tracks during mobile transect surveys in Howe Sound. Eight separate survey periods are shown, with the number of sampling days indicated for each trip. Only tracks are plotted (in blue) when hydrophone and receiver were operational. Red circles show stationary receiver locations deployed throughout the sampling year. See Table 5.1 for equipment used and survey distance covered during each sampling trip. Latitude and longitude values are not shown for clarity, but correspond with the map in Fig. 5.1. Shortest-route distance from the Squamish River mouth (near the top of each plot) to exit from Howe Sound is 40 km.
Figure 7.9 cont.
Figure 7.10. Boat tracks during mobile transect surveys in Georgia Strait. Two study periods are shown, with the number sampling days in Georgia Strait indicated. Only tracks are plotted (in blue) when hydrophone and receiver were operational. Red circles show stationary receiver locations deployed throughout the sampling year. The red triangle shows the location of a Cheakamus River steelhead tag.
Figure 7.11. Locations of unique tag detections in Howe Sound heard during mobile transect surveys. Five sampling years are indicated (a-e), and island names are shown in (a). Blue symbols show Tenderfoot Creek Hatchery coho locations and red symbols show Cheakamus River steelhead locations. Fates of fish at the time of detection were alive (○), dead (×), or unknown (Δ). Lines join detections of the same tag.
Figure 7.11 cont.
Figure 7.11 cont.
Figure 7.12. Frequency distributions of distances from the Squamish River mouth to approximate locations of mortality of Tenderfoot Creek Hatchery coho during their migration through Howe Sound. Distances are calculated as: (a) the shortest route directly from the river mouth to mortality locations; and (b) the shortest route travelled by the smolt taking into account all detections by mobile sampling and stationary receivers prior to arrival at the mortality location. Locations are pooled for years 2003–2007 ($n = 49$). Red dashed lines show the best fit predictions of numbers dying under maximum likelihood estimates of: (a) constant per-kilometre mortality rate ($M$) = 0.044, detection efficiency ($p$) = 0.165; and (b) $M = 0.024$, $p = 0.177$. 
Figure 7.13. Surface plots of exponential mortality model fit to distances from the Squamish River mouth to approximate mortality locations, for different combinations of per-kilometre mortality rate ($M$) and detection efficiency ($p$) parameter values. Distances were measured as direct from river mouth to mortality location (a) or accounting for known movements between these locations (b). Different shades represent sums of squares values (SS), ranging from 52 (dark grey) to 132 (light grey), with each change in shade representing a ΔSS of 5. Note the different scales of axes in (a) and (b).
7.5 References


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8 Comparison of survival and residualization rates between wild and hatchery-reared steelhead smolts

8.1 Introduction

A train derailed in the Cheakamus River canyon on August 5th, 2005. From one overturned railway car, about 45,000 L of 73% concentration sodium hydroxide (NaOH, i.e., caustic soda or lye) was spilled into the Cheakamus River. The highly basic (pH > 9) pulse of NaOH travelled downstream, and before reaching the Squamish River where it was further diluted, killed >90% of the free-swimming fish in the mainstem Cheakamus River (McCubbing et al. 2006). Four cohorts of wild juvenile steelhead (*Oncorhynchus mykiss*) were impacted (ages 0* to 3*), with an estimated 90% mortality over all age classes (McCubbing et al. 2006). A conservation concern for the population was immediately recognized by fisheries scientists, anglers, managers, and the public. Following considerable debate over appropriate actions to take (Labelle 2006), a short-term (two years) hatchery supplementation program using native broodstock was implemented in an effort to boost adult steelhead returning to the river from two of the three years of poor forecasted wild smolt yield.

Concerns regarding the effectiveness of this hatchery-based restoration effort include potentially high levels of residualization (i.e., failure to migrate; Ricker 1938) and lower survival of hatchery-reared smolts during the downstream and ocean migration compared with wild smolts. Both factors could reduce adult returns and thus the likelihood of success of the hatchery-rearing program. A review of steelhead residualization rates reported in the literature, theses, or government reports (most from the Columbia River watershed) showed that hatchery-reared steelhead typically residualize at rates between 2–9%, ranging as high as 17% in some studies (S. Hausch and M. Melnychuk, *unpubl. data*). Residualization could be either temporary or permanent, and could serve three purposes: (1) smolts (especially smaller smolts) revert to parr for an additional year of freshwater rearing, and migrate downstream the following year; (2) smolts revert to parr and remain in freshwater thereafter, taking up a similar life history strategy to the non-anadromous (and somewhat genetically distinct, Zimmerman and Reeves 2000) form of *O. mykiss*, rainbow trout; or (3) large male smolts revert to parr but mature rapidly and spawn soon thereafter or the following year (Tipping et al. 2003), after which they may migrate to sea.
or remain in freshwater. Hatchery residuals could potentially compete with wild juvenile steelhead or rainbow trout for space and resources, thereby affecting their growth (McMichael et al. 1997), or directly feed on smaller wild fish.

Few studies have directly compared either residualization or survival of migrating smolts between wild and hatchery-rearing histories. Two studies showed higher detected proportions of wild fish on ocean acoustic receivers than of hatchery fish, implying higher survival of wild steelhead smolts (Welch et al. 2004) and coho salmon smolts (Chittenden et al. 2008). Two studies showed no consistent differences between wild and hatchery-rearing histories for Atlantic salmon smolts (Thorstad et al. 2007, Lacroix 2008). Since the first few weeks of the smolt migration are arguably the most important period determining recruitment in salmon populations, a comparison of survival between wild and hatchery-reared steelhead during the downstream and early ocean migration could provide insight into relative differences of total marine survival, and therefore fitness differences.

To address the hypotheses of (1) lower survival during the migration and (2) higher residualization rates of hatchery-reared steelhead smolts relative to wild smolts, we conducted an acoustic tagging and tracking study. Hatchery-reared smolts were tagged and released into the Cheakamus River watershed in 2007 and 2008. In 2006 and 2007, wild steelhead smolt abundance appeared much reduced (Melville and McCubbing 2008), and insufficient numbers of fish were available for tagging. The 2007 portion of the study therefore represented an initial baseline for survival estimates and migration timing measurements in hatchery-reared smolts. Previous studies in 2004 and 2005 on wild Cheakamus steelhead produced baseline estimates for wild smolts. In 2008, sufficient wild steelhead smolts were caught during the downstream migration for tagging. Having both wild and hatchery-reared smolts tagged in 2008 allowed for a direct comparison of survival and residualization between rearing groups in the same year.

8.2 Methods

8.2.1 Study site and stationary receivers

The Cheakamus River is a 5th order river regulated by a dam, with a mean annual discharge of 31.5 m$^3$·s$^{-1}$. It drains into the Squamish River before reaching Howe Sound. The railway spill occurred upstream of an anadromous fish barrier, and tagged smolts were released at various locations below the barrier (Fig. 8.1). The total distance from smolt release in the Cheakamus River to the mouth of the Squamish River ranged from 15.9–27.5 km, depending on
Prior to releasing smolts, POST staff installed VEMCO Ltd. VR-2 or VR-3 acoustic receivers arranged in listening lines in Howe Sound (HS$_{inner}$ and HS$_{outer}$), the northern Strait of Georgia (NSOG), Queen Charlotte Strait (QCS), and Juan de Fuca Strait (JDF; Fig. 1.4; details in Appendix A). We also installed receivers as single or paired units in the Cheakamus and Squamish Rivers at several locations (Fig. 8.1), as well as one receiver in Tenderfoot Creek (in 2007). Three stations in 2007 and 2008 were located in the Cheakamus River upstream of the Tenderfoot Creek confluence; these were mainly used to monitor for any residualized smolts that moved upstream after release (they were also used to detect fish migrating downstream from the release site furthest upstream in 2008). One station (in 2004, 2005), two stations (2007) or four stations (2008) were located in the Cheakamus River between Tenderfoot Creek and Squamish River confluences; these were used to monitor smolts during their downstream migration, as well as to monitor smolts from all release sites that may have residualized within this portion of the river. Three (in 2004, 2005), five (2007) or two (2008) stations were deployed in the Squamish River in addition to one station (of three receivers) deployed in 2007 and 2008 in Squamish Harbour near the river mouth (Fig. 8.1). These were used to monitor smolts as they completed the downstream migration and entered ocean waters; the concentration of stations near the Squamish River mouth permits the partitioning of survivorship into freshwater and ocean components. Squamish River receivers were in place until at least early June in all years. Cheakamus River receivers were in place until mid-August in 2007 and 2008.

### 8.2.2 Fish release groups

Hatchery steelhead smolts were reared from eggs collected from wild Cheakamus River adult steelhead. Adults were transported and spawned (spring 2006 and 2007) and eggs were incubated (summer 2006 and 2007) at Fraser Valley Trout Hatchery (FVTH). In September of each year, a portion of the fry was transferred to Tenderfoot Creek Hatchery (TCH). Fry were reared until smoltification the following spring at each of the two hatcheries. Smolts were tagged ≥8 d before release. They were either released into Tenderfoot Creek under volitional release (TCH fish) or transported by truck and released into the Cheakamus River at various sites (FVTH fish). Wild (W) smolts were caught during their downstream migration in side channel traps and rotary screw traps in the Cheakamus River. They were held for up to 21 d (2004), 17 d
(2005), or 7 d (2008) in side channel traps until fish could be tagged, and were released 1–5 d after tagging near the original capture sites. In 2008, one tag-related mortality and one tag extrusion were observed in wild smolts prior to fish release, but otherwise there were no signs of tag rejection, infection or altered behaviour in any year. A total of 51, 49, 100, and 198 tagged fish were released in 2004, 2005, 2007, and 2008, respectively. These fell under the two (2004, 2005, 2007) or five (2008) release groups (RG) shown in Table 8.1.

The unbalanced sample sizes among groups in 2007 and 2008 were a result of tag manufacturing logistics and uncertainty in the numbers of wild smolts that would be caught in 2008, after hatchery groups were already tagged. Over all years, release dates ranged from May 5–24 (Table 8.1). Release locations varied among groups, shown in Fig. 8.1. One group (FVTH RG1 in 2008) was released further upstream than others, approx. 15 km upstream of the Cheakamus and Squamish River confluence. Another group (FVTH in 2007) was released further downstream than others, approx. 3.6 km upstream of the Cheakamus and Squamish River confluence. The remaining nine groups were all released within 1.5 km of each other, either at Tenderfoot Creek Hatchery or in a side channel of the Cheakamus River near the confluence with Tenderfoot Creek (Fig. 8.1).

Mean body size varied among years and release groups, but there was no consistent size difference among wild and hatchery-reared groups. Release groups with relatively long mean body length (fork length, FL) included wild fish in 2004, TCH fish in 2007, and FVTH fish in 2008 (Table 8.1). Groups with relatively short mean FL included wild fish in 2005 and 2008 as well as TCH fish in 2008. These differences among groups were relatively small compared to the variation within groups, however (Table 8.1), and there was considerable overlap in FL among all 11 release groups. In 2008, weights of smolts were also measured. The condition factor (K), a scaled ratio of individual body weight to body length $^3$, was lowest in the two W groups, intermediate in the TCH group, and highest in the two FVTH groups (Table 8.1). Larger values of K imply heavier fish for a given body length.

VEMCO V9-6L acoustic tags that transmitted at 69.0 kHz were used for all fish in all years. A variety of pulse rates were used. Tags in 2004 and 2005, as well as 20 of the 100 tags in 2007 (used for the 19 TCH fish and one FVTH fish), had a 30–90 s random delay between transmissions. The other 80 tags in 2007 (all used for FVTH fish) and 19 tags in 2008 (used for W RG2), had a 20–40 s delay. The remaining 179 tags in 2008 (used for the other four groups and the remaining nine fish from W RG2) had a 20–60 s random delay. Shorter average delay intervals between transmissions are expected to slightly increase detection probabilities on
acoustic receivers as fish swim by, but also results in a shorter lifespan from the date of tag activation. In all years, no tags were predicted to stop transmitting before July 19; tag lifespan estimates tend to be conservative so actual tag life is likely at least several weeks longer. The shorter intervals were used for the 2007 and 2008 studies to increase the chance of detecting residualized fish in the first few months after release. The delay interval factor was taken into account when estimating detection probabilities (but was seen to have little effect). Tags were implanted into smolts using standard surgical procedures (details in Appendix A).

8.2.3 Test tag passes in Cheakamus River

To estimate the rate of residualization of tagged steelhead smolts in the Cheakamus River, it was necessary to quantify the probability of detecting a tag at a receiver station for several weeks or months following release. Mark-recapture estimates of detection probability ($p_{mr}$, or from Chapter 2, $p_{mig}$) from tagged fish were possible during the brief in-river migration period, but not afterwards, since detection data were absent. It may not be reasonable to assume that $p_{mr}$ during the smolt migration is the same for the remainder of the summer because river flows change over this period. To estimate a mark-recapture-like probability of detection after the migratory period, we conducted a series of test tag passes past each receiver in 2008. When river discharge was less than 75 m$^3$.s$^{-1}$, multiple passes were conducted by two swimmers, each with a test tag, drifting past a receiver. Due to safety concerns, single passes by raft were used when discharge was 75–150 m$^3$.s$^{-1}$, and passes were not conducted with either method when discharge exceeded 150 m$^3$.s$^{-1}$.

The two swimmers floating down the river attempted to stay approximately one-third river width away from the left and right banks, respectively. Each swimmer dangled a tethered V9-6L transmitter below him and varied the distance at which the tag was held from his body depending on bottom depth, attempting to maintain direct line-of-sight between the tag and receiver at all times. Transmitters remained $\geq$5 cm above the substrate and $\leq$1 m below the swimmer. In shallow areas, the transmitter was dangled beside the swimmer such that his body did not block line-of-sight to the receiver. Swims began and ended about 200 m upstream and downstream of the receiver, respectively. Put-in and pull-out locations were selected to meet at least one of three criteria: (1) both banks were beyond line of sight from the receiver; (2) the pool or run in which the receiver was deployed ended, moving into strong riffles or rapids; or (3) the location reached further than 300 m away from the receiver. Swimmers entered the water together at the start site, from opposite banks where possible, and the time was recorded. For
consistency, one particular transmitter was always on the river side closest to the receiver. Due to heterogeneous water velocity, swimmers ended their passes at different times and the later pull-out time was recorded.

Five swim passes at a receiver on a given test day were typically conducted, though this number ranged from 1–10 (Table 8.2). Both test tags transmitted every 20 s and were activated 10 s apart before each swim pass so their transmissions would not overlap. Before swim passes, each receiver was checked for proper positioning (when flow conditions permitted), and detection data were downloaded. After a set of passes, the receiver was downloaded for test tag data and then re-positioned to continue monitoring for steelhead tags. A set of swim passes was conducted at each receiver on 3 or 4 d (Table 8.2, including the single passes on Aug. 14). If the receiver had moved from where it was last deployed due to river flow, an initial swim was conducted at the altered position to estimate its detection probability since last deployment. The receiver was then re-positioned and the regular set of test tag passes was conducted.

Due to high water velocities mid-study, swim-based passes were not possible. Thus, five raft trips were conducted (Table 8.2), during which most of the Cheakamus River receivers were passed once each. For safety reasons, receivers were not downloaded or checked for upright positioning during raft passes. The criteria for tag put-in and pull-out locations for raft passes were the same as those for swim passes. Time-in and time-out were recorded. The two test tags were kept together on a weighted line ≥5 cm off the substrate and ≤2 m deep, again offset by 10s so their signals would not collide. The raft was kept near the centre of the river moving at the same velocity as the surface water.

8.2.4 Freshwater mobile tracking

Sampling trips for steelhead tags were periodically conducted by raft down the Cheakamus River in 2008 to monitor for tagged steelhead that may have residualized between stationary acoustic receivers where they would not be detected. A VEMCO VR-100 acoustic receiver with an omnidirectional hydrophone was operated by one crew member while the other steered the boat. This receiver can decode tags, and provides sound output through headphones so the user can hear tag pulses even if the tag ID cannot immediately be decoded. The hydrophone was towed behind the raft as it travelled downstream, generally 0.25–0.5 m below the water surface, but raised while crossing rapids or shallow areas. The raft was slowed in calm pools to spend more time listening for tags; audible detection efficiency was assumed to be highest in these areas. Mobile tracking trips were conducted on May 30, June 4, July 3, and Aug.
6, concurrently with raft-lowered test tag passes past stationary receivers. Mobile sampling trips began near the release site for 2008 FVTH RG1 (approx. 1 km downstream of Chk_1 in 2008) and ended in the Squamish River downstream of the Cheakamus River confluence.

Estimating sampling efficiency by raft was largely prohibitive due to swift flow conditions at the time that raft trips were conducted. The raft with VR-100 passed a stationary test tag deployed along a river bank on only one occasion, and the tag was neither decoded nor audibly detected. Instead, maximum detection range during raft trips was estimated using the test tag. Measurements were taken from shore in calm eddies or laminar runs, with one individual holding the hydrophone fully submersed in ≥0.25 m of water while another individual submersed a tag in the water and progressively moved further away from the hydrophone in 1–2 m increments. Two distances were noted: the furthest distance at which the tag was decoded by the receiver on the first or second transmission, and the furthest distance at which the technician could audibly detect the tag. Tags were reliably decoded and audibly detected no further than 5 and 10 m away, respectively, in typical river conditions. As sampling speed by raft averaged 2.9 m·s⁻¹ and most fish tags transmitted, on average, every 40 s, decoding and audible detection efficiencies of mobile tracking were likely low. Absence of detections during mobile monitoring trips was therefore not considered evidence that tags were absent along sampling tracks.

Mobile monitoring was conducted in Tenderfoot Lake, the Tenderfoot Creek Hatchery acclimation lake, on July 6th 2008. In range tests, the VR-100 was shown to have a detection range of >100 m in this relatively still water, so six sites along the length of the lake were selected to provide line-of-site monitoring of the entire lake. At each site, the hydrophone was submersed for 120 s while the user listened for tag pulses through the headphones.

8.2.5 Mark-recapture analysis for survival estimation

During their migration downstream and out of Georgia Strait, tagged smolts passed up to 9–13 detection stations (Figs. 8.1, 1.4). In 2004 and 2005, wild smolts passed up to one station in the Cheakamus River downstream of the release site and three stations in the Squamish River. In 2007, FVTH smolts passed up to six stations in freshwater, all in the Squamish River (including Squamish Harbour), while TCH smolts passed up to nine stations in freshwater (three of those in the Cheakamus River). In 2008, smolts from FVTH RG2, W RG 1, and W RG2 groups passed up to three stations in the Cheakamus River and three stations in the Squamish River, while FVTH RG1 smolts passed an additional three upstream stations in the Cheakamus River (TCH smolts passed one of these additional stations as well; Fig. 8.1). In all groups in all years, tagged
smolts passed up to two stationary lines of receivers in Howe Sound, and one (JDF) or two (NSOG and QCS) lines of receivers covering the southern and northern exit routes from Georgia Strait, respectively (Fig. 1.4).

Mark-recapture models based on the Cormack-Jolly-Seber (CJS) model were used to estimate survival probabilities ($\phi$) in each segment of the migration and detection probabilities ($p$) at each river receiver or line of ocean receivers (see Appendix A for model details and assumptions). One assumption particularly important for this chapter is that fish did not cease their migration prior to encountering any receivers, or between any stationary stations where they would not be detected. I.e., we assume that residualization rates were negligible. The potential for residualization in the 2008 study is considered later, and $\hat{\phi}$ are interpreted with the caveat that residualization may be $>0$. Detections from the outer lines at QCS and JDF were pooled as the final station of the migration to represent exit from the Georgia Strait system. The terminal station detection probability $p_{QCS/JDF}$ was fixed at year-specific values for V9 tags based on year-specific $p_{NSOG}$ estimates with slight adjustment for receiver coverage on each line (see Appendix A). After fixing these values, we used the 14-digit individual detection histories in a CJS recaptures-only model implemented with Program MARK (White and Burnham 1999; version 5) through RMark (Laake and Rexstad 2009; version 1.8.8) to estimate $\phi$ and $p$ parameters. The product of segment-specific $\phi$ represents cumulative survivorship along migration routes.

We used model goodness-of-fit diagnostics in Program RELEASE (Burnham et al. 1987) to assess the fit of the most general mark-recapture model considered, $[\phi(seg \times G), p(S \times G)]$, to detection data, where ‘seg’ represents segment, ‘S’ represents station, and ‘G’ represents release group. There were five levels of ‘G’ in the 2008 analysis and 11 levels in the all-years analysis, while there were 9–13 segments and detection stations. This model implies independence among groups and segments/stations. For the 2008 dataset, the general model had an overall poor goodness-of-fit ($\chi^2 = 83.8$, d.f. = 35, $p < 0.01$), suggesting that model assumptions were possibly not met (Appendix A). This was due to a poor fit for two of the five groups: TCH and W RG1 ($p < 0.01$ for these groups). Sparse data prevented analysis of which assumption(s) were responsible, so survival results for these two groups are interpreted with caution. In the all-years dataset, an additional group, FVTH in 2007, also had poor goodness-of-fit. In the face of poor goodness-of-fit, we estimated an overdispersion parameter, $\hat{\epsilon}$ (Burnham et al. 1987) using the deviance bootstrap simulation method through Program MARK. The estimated values were $\hat{\epsilon} = 1.279$ for the 2008 dataset and $1.263$ for the all-years dataset; to be conservative we simply used the higher value of $1.279$ in both analyses to adjust AIC (Akaike’s Information Criterion) values.
for comparing candidate models (Lebreton et al. 1992), and also for expanding confidence limits on $\phi$ and $p$ parameter estimates (Burnham et al. 1987).

Release groups from all years were combined in the same analysis to provide generality in observed survival patterns. This permitted the effect of covariates on $\phi$ or $p$ to be consistent across years (as well as across segments or stations). I.e., certain relationships were constrained to be shared among years, such as the relationship between $p$ and river level, or the relationship between $\phi$ and body size. Of the 11 release groups, two had very small sample sizes (Table 8.1). General CJS models would be over-parameterized for these groups, but more constrained models borrow information from other groups in the same year or different years in order to estimate shared parameters for these groups (e.g., Chapter 3).

Several factors have been hypothesized to affect juvenile salmon survival. We considered possible effects of rearing history (hatchery vs. wild; hatchery location), body size, release date, migration distance, and bull trout predator abundance on survival. In addition, we considered possible effects of release group and river level on $p$. These factors were included in models directly as covariates; candidate models are treated as competing hypotheses and were compared using information-theoretic methods (i.e., AIC; Burnham and Anderson 2002) on the basis of their goodness-of-fit to the data and the number of parameters in the model required to achieve that fit. Rather than comparing a suite of models at once involving all the above potential factors, we took a sequential approach and compared a small set of related models, selected the best model from that set, then moved to another comparison with a different focus. First, we compared models for $p$ while keeping a constant and general model for $\phi$. Second, having selected the best $[p]$, we compared $[\phi]$ in terms of rearing history effects. Third, we selected the best model from this set and considered body size and release date effects on $\phi$. Fourth, we selected the best model from this set and made one final comparison of $[\phi]$ that included migration distance-based models. Sequential approaches of first comparing $p$ sub-models and then comparing $[\phi]$ have been used in similar studies (e.g., Zabel and Achord 2004).

Detection probability models

In river systems like the Fraser River, water level (or discharge) has a strong influence on $p$ at river stations (Chapter 3). Higher river levels and faster flows, typically later in the migration season, generally result in decreased $p$ due to greater background noise, and/or smolts spending less time within detection range of a given receiver as they travel downstream. The 11 release groups were released at different times (Table 8.1), and consequently faced different flow conditions.
conditions in the Cheakamus and Squamish Rivers (Fig. 8.2). Water levels are correlated with discharge measurements \((r > 0.99)\), with approximate equivalence of \(1.0 \text{ m} = 39 \text{ m}^3\cdot\text{s}^{-1}\) and \(2.0 \text{ m} = 180 \text{ m}^3\cdot\text{s}^{-1}\) in the Cheakamus River. For example, in 2008 the earliest four groups released faced relatively low water levels in the Cheakamus River, while FVTH RG2 encountered higher river levels. We accounted for potential effects of river level on \(p\) at river stations by constraining \(p\) in some models to be functions of river level (likelihoods are evaluated in logit-space, so the constrained linear relationship is actually \(\text{logit}(p)\) vs. river level). At each station in the Cheakamus or Squamish Rivers, the mean arrival time of each group was calculated (from the first time that each individual fish was detected at a particular station), and the corresponding river level at that mean arrival time was used as the group-specific covariate value. Separate covariates were used for Cheakamus River and Squamish River stations, as an increase in one unit of water level does not necessarily translate into the same decrease in \(p\) in both rivers.

Detection probabilities were modelled as common across release groups at ocean receivers. Fish from 6 of the 11 release groups showed evidence of split-route migration patterns, with some fish moving north and crossing QCS, and others moving south and crossing JDF: the two wild groups in 2004, the two hatchery groups in 2007, and the two wild groups in 2008. To remove the bias associated with collapsing these split forks into a CJS analysis, four extra \(p\) parameters were incorporated to allow for group-specific movement probabilities to the NSOG station (Chapter 3). The two wild groups from 2004 were made to share one such extra parameter (assuming the proportion would be similar among release groups for this wild population in the same year) and the two hatchery groups from 2007 were made to share another parameter because of small sample sizes of fish detected at QCS and JDF in three of these four release groups. The pooled sample size of hatchery fish in 2007 was still fairly small but the estimated proportion moving northwards was not out of line with estimates for wild populations in 2004 or 2008. The two wild groups from 2008 each had their own estimated movement parameter. These four extra movement parameters were incorporated into the \([p]\) below, except the general \([p]\) which already allows group-specific \(p\) at each station.

Across comparisons of \([p]\), the \([\phi]\) held constant was composed of interactions between groups (\(G\)) and segments of the migration, i.e., \([\phi_{\text{seg}G}]\), allowing the 11 release groups to be considered independent in terms of \(\phi\). Four \([p]\) were considered:

1. \(\phi_{\text{seg}G}, p(S;G)\),
   - fully-independent \(p\) estimates for each group in each year at each station
   - (no main effects of station, year, or group)
2. \( \phi(\text{seg}:G), p(S:Y) \) fully-pooled \( p \) estimates across groups in each year at each station; station and year combinations are independent

3. \( \phi(\text{seg}:G), p(S:Y+\text{lev}_{\text{Cheam}}) \) \( p \) constrained by an additive effect of river level (Cheakamus River only) at the mean arrival time of a group at a station; station and year combinations are independent

4. \( \phi(\text{seg}:G), p(S:Y+\text{lev}_{\text{Cheam}}+\text{lev}_{\text{Squam}}) \) \( p \) constrained by additive effects of river level (separate effects for Cheakamus River and Squamish River) at the mean arrival time of a group at a station; station and year combinations are independent.

We selected one \([p]\) on the basis of AIC scores, and used this for comparing \([\phi]\). We also considered the potential effect of average tag delay interval on \( p \) in similar analyses.

**Survival probability models: effects of rearing history and stock**

A particular segment digit (e.g., a group’s 1\textsuperscript{st} or 2\textsuperscript{nd} segment after release) may represent different physical portions of the migration for different release groups, even if they are all released in the same river. This can occur either if some groups are released later along a migration route than earlier groups, or if groups are released mid-way between receiver stations. For example, the 2008 segment from station Chk_4 to station Chk_5 for group FVTH RG1 is a physically different route than the segment from release to station Chk_5 for group FVTH RG2. One way of dealing with this is to assume conditional independence of survival among segments: smolts from an upstream release location are no more or less susceptible to mortality in some river segment than are smolts in that same segment that were released further downstream (Skalski et al. 2001). This may bias results, however, if any portion of mortality is attributed not only to the particular segment that smolts migrate along, but to how far upstream of this segment they were released. Instead, these differences in physical migration routes were explicitly accounted for in some candidate models: we used additive parameters to represent mortality during the first segment, wherever the first segment may physically occur for a release group. It is appropriate to maintain differences in this initial mortality between wild (\( M_{i,W} \)) and hatchery-reared (\( M_{i,H} \)) groups, since the hatchery-reared fish have not been exposed to natural selection prior to release and therefore, on average, may be more susceptible to initial predation mortality. These initial mortality parameters also provide a distance-independent initial mortality level for distance-based models considered later.

All models assumed independence among segments and years. The effect of wild or hatchery-rearing history (HW) was incorporated as an additive covariate on survival in some
models (i.e., a consistent effect of HW across all segments of the monitored migration). Since hatchery-raised fish were reared at two different hatcheries, we also considered additive effects of stock within HW in some models. In total, seven $[\phi]$ were hypothesized:

1. $\phi$(seg:G), $p(S:Y+\text{lev}_{\text{Cth}}+\text{lev}_{\text{Sqm}})$
   each of the 11 release groups and each of their own segments are fully-independent

2. $\phi$(seg:Y), $p(S:Y+\text{lev}_{\text{Cth}}+\text{lev}_{\text{Sqm}})$
   fully-pooled $\phi$ estimates across release groups in each segment and year; segment and year combinations are independent

3. $\phi$(seg:Y+HW), $p(S:Y+\text{lev}_{\text{Cth}}+\text{lev}_{\text{Sqm}})$
   additive effect of HW, consistent across all segments and years

4. $\phi$(seg:Y+HW+stock), $p(S:Y+\text{lev}_{\text{Cth}}+\text{lev}_{\text{Sqm}})$
   additive effects of HW and hatchery stock within HW, consistent across all segments and years

5. $\phi$(seg:Y+$M_{i,H}$+$M_{i,W}$), $p(S:Y+\text{lev}_{\text{Cth}}+\text{lev}_{\text{Sqm}})$
   like (2), with additive initial mortality (separate for W and H fish, consistent across all years); implies the only survival difference among wild and hatchery-reared fish occurs in the first segment after release

6. $\phi$(seg:Y+HW+$M_{i,H}$+$M_{i,W}$), $p(S:Y+\text{lev}_{\text{Cth}}+\text{lev}_{\text{Sqm}})$
   like (3), with additive initial mortality (separate for W and H fish, consistent across all years)

7. $\phi$(seg:Y+HW+stock+$M_{i,H}$+$M_{i,W}$), $p(S:Y+\text{lev}_{\text{Cth}}+\text{lev}_{\text{Sqm}})$
   like (4), with additive initial mortality (separate for W and H fish, consistent across all years)

We selected one $[\phi]$ on the basis of AIC scores, and used this for evaluating body size and release date effects on $\phi$.

**Survival probability models: effects of body size and release date**

Body size at release and release or migration date are often thought to affect smolt and post-smolt survival, and we considered these in models as factors possibly affecting survival during the downstream and inshore migration. We only considered models with additive effects in this section, assuming the relative effect of FL on $\phi$ or release date on $\phi$ would be similar for wild and hatchery-reared fish (we relax this assumption in the next section). It is possible that observed HW effects from the previous section were simply the result of body size and/or release date differences among groups and not wild vs. hatchery-rearing *per se*, so we considered some models with effects of body size and/or release date without the HW term. In total, we considered seven $[\phi]$:
1. $\phi(\text{seg} : Y+HW+M_{i,H}+M_{i,W})$, $p(S : Y+\text{lev}_{\text{Chk}}+\text{lev}_{\text{Sqm}})$, additive effect of HW, consistent across all segments and years; additive initial mortality (separate for W and H fish)

2. $\phi(\text{seg} : Y+HW+RD+M_{i,H}+M_{i,W})$, $p(S : Y+\text{lev}_{\text{Chk}}+\text{lev}_{\text{Sqm}})$, like (1), with additive effect of release date, consistent across all segments and years

3. $\phi(\text{seg} : Y+HW+FL+M_{i,H}+M_{i,W})$, $p(S : Y+\text{lev}_{\text{Chk}}+\text{lev}_{\text{Sqm}})$, like (1), with additive effect of fork length, consistent across all segments and years

4. $\phi(\text{seg} : Y+HW+RD+FL+M_{i,H}+M_{i,W})$, $p(S : Y+\text{lev}_{\text{Chk}}+\text{lev}_{\text{Sqm}})$, like (1), with additive effects of release date and fork length, both consistent across all segments and years

5. $\phi(\text{seg} : Y+RD+M_{i,H}+M_{i,W})$, $p(S : Y+\text{lev}_{\text{Chk}}+\text{lev}_{\text{Sqm}})$, additive effect of release date, consistent across all segments and years; additive initial mortality (separate for W and H fish); no HW effect

6. $\phi(\text{seg} : Y+FL+M_{i,H}+M_{i,W})$, $p(S : Y+\text{lev}_{\text{Chk}}+\text{lev}_{\text{Sqm}})$, additive effect of fork length, consistent across all segments and years; additive initial mortality (separate for W and H fish); no HW effect

7. $\phi(\text{seg} : Y+RD+FL+M_{i,H}+M_{i,W})$, $p(S : Y+\text{lev}_{\text{Chk}}+\text{lev}_{\text{Sqm}})$, additive effects of release date and fork length, consistent across all segments and years; additive initial mortality (separate for W and H fish); no HW effect

We selected one $\phi$ on the basis of AIC scores, and used this to compare segment-independent $\phi$ with distance-based $\phi$.

**Survival probability models: distance-based models**

Distance-based models for $\phi$ may be especially parsimonious in a multi-year analysis. Rather than estimating separate parameters for each segment in each year, the series of $\phi_{\text{seg}}$ may be related to one another through segment-specific attributes. For example, the migration distance through each segment may be a reasonable predictor of mortality within segments if per-distance mortality rates are constant across segments. In some models, we constrained logit($\phi$) of each segment to be linearly related to the length of the segment (the relationship was indirectly proportional due to the presence of a common intercept from other additive terms). These models require fewer parameters to be estimated than the fully segment-specific models, so may be more parsimonious in explaining detection data. Segment distances were measured with mapping software as shortest-route distances between receiver stations. Some hypothesized models assumed a common effect of distance on $\phi$ across habitats, while others allowed separate effects among Cheakamus River, Squamish River, and ocean segments.
In some of these distance-based models, we included ‘year’ as an additive effect (rather than an interacting effect, like in segment-independent models), allowing overall survival across all segments to vary among years. ‘Year’ was treated as a categorical rather than numerical covariate, so no continuous trend over 2004–2008 was assumed. Even though release date was not an important factor in segment-independent models of the previous section (see Results), we again considered the additive effect of release date in distance-based models. In these simpler, more constrained models the single extra parameter for release date could be relatively more important. Finally, we consider an interaction effect between HW and body size in this section, for both the best model carried forward from the previous set as well as distance-based models. These models allow the effects of body size on $\phi$ to be independent between wild and hatchery-reared fish (i.e., the relative survival advantage of a big fish vs. a little fish might be less for wild fish that for hatchery fish, or vice-versa). In this final set, we considered the following 10 $[\phi]$: 

1. $\phi$(seg:Y+HW+FL+M$_{i,H}$+M$_{i,W}$), $p$(S:$Y$+lev$_{Chk}$+lev$_{Sqm}$) 
   additive effects of HW and fork length, consistent across all segments and years; additive initial mortality (separate for W and H fish)

2. $\phi$(seg:Y+HW$\times$FL+M$_{i,H}$+M$_{i,W}$), $p$(S:$Y$+lev$_{Chk}$+lev$_{Sqm}$) 
   like (1), with an interaction between HW and FL, consistent across all segments

3. $\phi$(d+HW+FL+M$_{i,H}$+M$_{i,W}$), $p$(S:$Y$+lev$_{Chk}$+lev$_{Sqm}$) 
   $\phi_{seg}$ constrained to segment distance; additive effects of HW and FL, consistent across all segments; additive initial mortality (separate for W and H fish)

4. $\phi$(d+HW+FL+RD+M$_{i,H}$+M$_{i,W}$), $p$(S:$Y$+lev$_{Chk}$+lev$_{Sqm}$) 
   like (3), with additive effect of release date, consistent across all segments

5. $\phi$(d+HW+FL+Y+M$_{i,H}$+M$_{i,W}$), $p$(S:$Y$+lev$_{Chk}$+lev$_{Sqm}$) 
   like (3), with additive effect of year, consistent across all segments

6. $\phi$(d+HW$\times$FL+M$_{i,H}$+M$_{i,W}$), $p$(S:$Y$+lev$_{Chk}$+lev$_{Sqm}$) 
   like (3), with an interaction between HW and FL, consistent across all segments

7. $\phi$(d$_{Chk}$+d$_{Sqm}$+d$_{sw}$+HW+FL+M$_{i,H}$+M$_{i,W}$), $p$(S:$Y$+lev$_{Chk}$+lev$_{Sqm}$) 
   $\phi_{seg}$ constrained to segment distance, with separate relationships for Cheakamus River, Squamish River, and ocean segments; additive effects of HW and FL, consistent across all segments; additive initial mortality (separate for W and H fish)

8. $\phi$(d$_{Chk}$+d$_{Sqm}$+d$_{sw}$+HW+FL+RD+M$_{i,H}$+M$_{i,W}$), $p$(S:$Y$+lev$_{Chk}$+lev$_{Sqm}$) 
   like (7), with additive effect of release date, consistent across all segments

9. $\phi$(d$_{Chk}$+d$_{Sqm}$+d$_{sw}$+HW+FL+Y+M$_{i,H}$+M$_{i,W}$), $p$(S:$Y$+lev$_{Chk}$+lev$_{Sqm}$) 
   like (7), with additive effect of year, consistent across all segments
As in previous steps, we compared $[\phi]$ on the basis of AIC scores.

**Analyses specific to 2008 study**

Combining all years in the same dataset provides generality through the joint analysis of multiple hatchery and wild steelhead release groups. On the other hand, it is possible that inter-annual variation in survival could be confounded with rearing history effects, as only wild fish were released in 2004 and 2005 and only hatchery fish were released in 2007. Both rearing histories were released in 2008, so this provides a more direct comparison of the ‘HW’ effect on survival. We conducted a similar analysis of sequential model comparisons for 2008 only, first comparing $[p]$, then $[\phi]$ in terms of rearing histories, body size effects, and finally distance-based models. We do not present the entire analysis here since the results were similar to the all-years comparison, but we highlight two aspects that were specific to the 2008 study. The full analysis was presented in a report by Melnychuk et al. (2009).

Body weights of smolts from all release groups were recorded in 2008 (in addition to fork length, which was recorded in all years). Body weight was loosely correlated with length (Fig. 8.3), but there was some variation among rearing histories in this relationship. A body condition factor (K, a scaled ratio of weight to length$^3$) permits a second type of size effect evaluation. We considered candidate models with an additive effect of FL, K, or both factors.

In the Cheakamus River, periodic snorkel surveys to estimate the abundance of steelhead spawners and adult bull trout have been conducted from January-June for >10 years (data from J. Korman, Ecometric Research). A count-per-river-reach stratification has been consistently employed since 2003. The area surveyed begins above the location of Chk_1 in 2008 and ends below the confluence of the Cheekeye River, just downstream of station Chk_6 in 2008 (Fig. 8.1). As bull trout are potentially predators of outmigrating steelhead smolts, these count data were used to represent two indices of potential predation risk. The number of snorkel survey days that occurred between May 5–24 (representing the range of smolt release dates) ranged from 1–4 in most years since 2003 (with none in 2004; Fig. 8.4). Bull trout were relatively scarce in reaches upstream of Chk_4. Average counts each year were variable, with lower counts in 2005 and 2006 and higher counts in 2007. In all years, however, a fairly consistent spatial distribution was observed, with some reaches having consistently higher bull trout counts than...
others (Fig. 8.4). The first index considered was the average per-reach count with all years combined (a 2008-specific index was also considered, but this had similar results to the all-years index). The second index considered involved a smoothed fit to the bull trout count data. Initially, a bivariate fit was considered, with effects of both snorkel reach and day in May (Fig. 8.5). Since there was relatively little change in Lowess-fit predicted counts over the period of May 5–24, a univariate fit involving just river reach was used. The sum of the reach-specific average counts or Lowess-predicted counts was taken for each acoustic-tracking segment of the 2008 study (e.g., the covariate value for the segment from Chk_2 to Chk_3 is equal to the sum of counts in reaches 5–18; Fig. 8.4). This was only possible for the following segments: release to Chk_2 (FVTH RG1), Chk_2 to Chk_3 (FVTH RG1), Chk_3 or release to Chk_4 (FVTH RG1 and TCH), Chk_4 or release to Chk_5 (all groups), and Chk_5 to Chk_6 (all groups). The segment Chk_6 to Chk_7 was not fully monitored by snorkel surveys, and segments beyond Chk_7 had no associated bull trout counts. One or the other bull trout density index was considered in some distance-based candidate models as an additive effect for the appropriate segment. The spatial resolution of receivers in the Cheakamus River was too coarse prior to 2008 to permit mapping bull trout densities onto acoustic tracking segments for migrating steelhead.

8.2.6 Detection probability projections for residualization estimation

To estimate the rate of residualization of smolts in the Cheakamus River, we predicted mark-recapture-like detection probabilities over the period of several months after the brief steelhead migration. Mark-recapture detection probabilities \( p_{mr} \) were not directly estimable at river stations for the remainder of the summer because smolts had already left the river. To predict \( p_{mr} \), we used detection indices derived from test tag passes \( p_{test} \) as an intermediate measure of detection probability. Unlike mark-recapture estimates, test tag passes were conducted over a wide range of time and river levels. We related \( p_{test} \) to river level measured the day of the passes, and then subsequently related \( p_{mr} \) to \( p_{test} \) at the same station \( (i) \) and river level \( (RL) \). We combined these components using regressions and bootstrapping in order to predict a mark-recapture-like \( p \) as a function of river level. River levels measured over time in the Cheakamus River (by Environment Canada) were used to generate a time series of predicted \( p_{mr,i} \) while receivers were deployed, a span of several months after the steelhead migration.

Detection data from test tag passes were summarized as a series of detection indices that ranged from 0–1. We considered several different indices, and compared them according to their relationship with river level and their predictive ability of \( p_{mr} \). Some indices were based on
single passes of test tags, while others were based on a set of passes (generally five) that occurred on the same day. Some were specific to each of the two test tags, while others considered both tags together. Indices fell into four categories: a binary outcome of a tag detected or not as it passed a receiver station; proportion of transmissions that were detected; ratio of time between the first and last detections to the duration of the pass; and indices based on VR-2 receiver metadata logged during the test tag passes (detections, pulses, and syncs received). These are summarized in Table 8.3.

The first three categories of detection indices each contained three levels of aggregation (Table 8.3). Per-tag indices involved calculating a separate index value for each test tag during each pass. Per-pass indices involved pooling the two tags and calculating an index value for each pass. Per-set indices were assessed by averaging these per-pass values across all passes in the set. In the fourth category, two indices based on receiver meta-data were calculated over a set of passes only when receivers were downloaded before and after a set of passes. The small number of these occurrences (Table 8.3) limited their usefulness. The first was a ratio of tag detections to syncs (the first part of a pulse train), and the second was a ratio of tag detections to pulses, corrected by the number of pulses in a pulse train (8). Since all indices were on the (0–1) scale, values were logit-transformed for regressions with river level and $p_{mr}$. Index values of 0 and 1 were set to 0.01 and 0.99, respectively, prior to transformation and regression, for numerical estimation purposes. Two regressions were conducted, which mirrored the nature of the index as an intermediate step between river level and $p_{mr}$. The first involved the transformed index, logit($p_{test,i,day}$), regressed against river level measured on the day of the passes:

$$ (8.1) \quad \text{logit}(p_{test,i,day}) = \beta_i + \beta_8 \cdot RL_{day}, $$

The effects of receiver station ($i$) and river level (RL) were treated as additive, assuming that the effect of river level on $p_{test}$ was consistent across all stations and test tag days. All stations shared the same slope ($\beta_8$), but separate intercepts ($\beta_1$...$\beta_7$) corresponding with stations Chk_1...Chk_7. The second regression involved logit($p_{mr}$) against the logit-transformed index, accounting for variation among stations and river levels in both detection probability types. Mark-recapture $p_{mr}$ represents a single (or average) estimate of a smolt release group at a station, even though the probability of detecting individual fish within that group may vary over the run timing span of the group due to variation in river level. The river level corresponding with the average arrival time of each release group at each station was accounted for in the estimation of $p_{mr}$ (the model
used was \([\phi\text{(seg+HW)}, p(S+\text{levChk})]\) from the 2008-only dataset. This \(p_{\text{mr},\text{RL}}\) was paired with the predicted \(p_{\text{test}_{i,RL}}\) (from the first regression) at the corresponding river level:

\[
(8.2) \quad \text{logit}(p_{\text{mr}_{i,RL}}) = \beta_9 + \beta_{10} \cdot \text{logit}(p_{\text{test}_{i,RL}})\text{pred}.
\]

The model involved a single slope (\(\beta_{10}\)) and intercept (\(\beta_9\)), such that \(p_{\text{mr}}\) was assumed to be proportional to \(p_{\text{test}}\) across all stations. The effect of station is implicit, with some stations having lower values of both \(p_{\text{mr}}\) and \(p_{\text{test}}\), and other stations having higher values of these.

The indices shown in Table 8.3 were compared in terms of fit to river level data and ability to predict \(p_{\text{mr}}\). Coefficients of determination (\(R^2\)), slopes, and intercept parameters were calculated for both regressions. Two indices from Table 8.3 stood out as having relatively high \(R^2\) values in both regressions. We used each of these indices in turn for the basis of \(p_{\text{mr}}\) predictions \(p_{\text{mr}^*}\) across the range of river levels (0.9–1.9 m; data from Environment Canada) measured during the period that Cheakamus River receivers were deployed and test tag passes were conducted in 2008 (Melnychuk et al. 2009). As these two indices gave similar \(p_{\text{mr}^*}\) predictions, we present only one of them here (proportion of transmissions detected per pass; see results). We divided this range of river levels into 100 equal bins, and predicted \(p_{\text{mr}^*,i}\) in each bin. First, we used the best-fit \(\beta_8\) and \(\beta_1…\beta_7\) parameters from regression 1 (Eq. 8.1) to predict \(p_{\text{test}_{i,RL}}\) at each river level. This value of \(p_{\text{test}_{i,RL}}\) was treated as fixed and, in turn, used in regression 2 (Eq. 8.2) to predict \(p_{\text{mr}^*,i,RL}\) at the corresponding river level.

The uncertainty in \(p_{\text{mr}^*}\) was quantified using a bootstrapping approach which accounted for three sources of variation: (a) error in regression 1, (b) error in regression 2, and (c) uncertainty in \(p_{\text{mr}}\) assessed from mark-recapture models fit to steelhead detection data during their migration. We assumed these three sources of error were independent, and that each was normally distributed in logit space. At a particular river level and station, a random draw from the distribution of \(\text{logit}(p_{\text{test}_{i,RL}})\) was taken, based on the estimated standard error of regression 1 at that river level and station. This value of \(\text{logit}(p_{\text{test}_{i,RL}})\) was then treated as fixed, and used in regression 2 to take a random draw from the distribution of \(\text{logit}(p_{\text{mr}_{i,RL}})\) at that value of \(\text{logit}(p_{\text{test}_{i,RL}})\). The third component of uncertainty, CJS model error in \(p_{\text{mr}}\), further expanded the error around this random draw of \(\text{logit}(p_{\text{mr}_{i,RL}})\). In logit space, \((p_{\text{mr}})_{\text{CJS}}\) for a particular station and release group can be considered as the mean of a normal distribution with spread characterized by \(\text{SE}(p_{\text{mr}_{i,\text{group}}})_{\text{CJS}}\). The average \(\text{SE}(p_{\text{mr}_{i,\text{group}}})_{\text{CJS}}\) across all release groups was calculated for each of the six stations to give \(\text{SE}(p_{\text{mr}_{i}})_{\text{CJS}}\), which was used to characterize a
distribution centered on the second random draw of \( \text{logit}(p_{mr\_i,RL}) \). (CJS estimates were not possible for Chk_1 since fish migrating downstream did not pass this station. The largest average \( \overline{SE}(p_{mr\_i,\text{group}})_{\text{CJS}} \) from the other six stations was assumed for Chk_1 to be conservative.) A third random draw was taken from this distribution and was then back-transformed to the probability scale, representing a predicted value of \( p_{mr\_i,RL} \). At each of the 100 river level values and seven receiver stations, 10,000 such sets of three random draws were taken. The 5\(^{th}\) and 95\(^{th}\) percentiles of this resulting distribution represented 95\% bootstrap confidence bands of \( p_{mr\_i,RL} \) over the river level range considered.

The final step in meeting the goal of predicting \( p_{mr\_i,RL} \) throughout the study was straightforward. At each day during the period that receivers were deployed, the values and confidence intervals of \( p_{mr\_i,RL} \) corresponding to that day’s average measured river level were taken. These generated a time series of \( p_{mr\_i} \) at each station \( i \), representing the probability of detecting a residualized fish that swam past a given station on a given day. We used this time series of \( p_{mr\_i,RL} \) in conjunction with detection data at Cheakamus River stations from possible steelhead residuals to estimate a likely range for residualization probability, as follows.

The times of fish detections on each river receiver were inspected to assess any evidence of fish residualizing after the initial downstream migration pulse. If a fish was detected either (a) upstream of its release site, or (b) on any Cheakamus River receiver \( >4 \) weeks after release, and was not detected thereafter on Squamish River or ocean receiver stations, we considered it to be a likely residual. We inspected detection patterns to verify whether tag detections were continual, perhaps suggestive of a tag laying on the riverbed near a receiver rather than being in a residualized smolt; these were excluded from the count of residualized smolts. When patterns suggestive of possible residualization were observed at station \( i \), the \( p_{mr\_i,RL} \) corresponding to the average river level over all days where the tag was detected was used to estimate the unknown number of residualized fish. Typically, a number present \( (D) \) is estimated as the ratio of the number observed \( (d) \) to the detection probability, i.e., \( D = dl/p \). In this case, \( p_{mr\_i} \) varies by \( i \) and river level, so we used a modified approach:

\[
D_{\text{Chk}} = \sum_{\text{tag}} \left( \frac{d_{i,\text{tag}}}{p_{mr\_i,RL}} \right),
\]

where \( d_{i,\text{tag}} \) represents a possible residualized fish detected at \( i \) on one or more days with an average river level \( RL \) over those day(s). \( D_{\text{Chk}} \) represents the total estimated number of tagged steelhead from a particular provenance or release group residualizing in the Cheakamus River.
This is divided by the number of fish released to estimate the proportion residualizing. Uncertainty around this estimate is derived by replacing the lower and upper 95% confidence limits of \( p_{mr^{*},i,RL} \) in place of \( p_{mr^{*},i,RL} \) in Eq. 8.3. These return the upper and lower confidence limits of \( D_{Chk} \), respectively, which account for multiple error sources in \( p_{mr^{*},i,RL} \). This method of estimating \( D_{Chk} \) relies on two main assumptions:

- \( d \) observed fish are actually residualized steelhead, and not any of the following: tags in predator stomachs, tags in smolts delaying their migration, tags laying on the river bed after being extruded or having passed through a predator gut, or tags inside dead smolts.
- Residualizing fish move sufficiently within the river to pass at least one Cheakamus River receiver station during the period from release to mid-August.

Violation of the first assumption would lead to over-estimation of residualization rate, while violation of the second would lead to under-estimation. Through use of the intercept parameters in regression 2, we assumed that \( \hat{p}_{mr} \) is not directly proportional to \( p_{test} \). Therefore, it is not necessary to assume the following in predicting \( p_{mr^{*}} \):

- fish detected at receivers (whether moving upstream or downstream) travelled at a similar speed past receivers as test tags during passes.
- Acoustic output and tag delay intervals are the same for test tags as for steelhead tags.

We estimated the 2008 residualization rate separately for wild and hatchery-reared smolts in the Cheakamus River.

### 8.3 Results

#### 8.3.1 Sampling effort with stationary and mobile receivers

Over the course of the 3+ month study in 2008, each receiver was the subject of 11–22 swim passes and 4–5 raft passes, with the majority of passes occurring in May and the first half of June (Table 8.2). The receiver at Chk_1 did not initially detect tags during swim passes, so it was temporarily removed for assessing its functionality. It was re-deployed downstream approx. 1 km on June 17th, near the FVTH RG1 release site, into what was hoped was a quieter section of the river where detections of residualized fish passing the station would be more likely.

Supplemental sampling using the mobile receiver led to the detection of a single tag, from the 2008 TCH group on July 3. This tag was detected upstream of the Tenderfoot Creek and Cheakamus River confluence (~49.82642°N, 123.15078°W). It had been detected previously 4 d after release at Chk_4, but was not detected on stationary receivers thereafter. At the time of
detection, the raft was stationary, with technicians in the process of measuring detection range to a test tag. No fish were detected during sampling trips by raft when the raft was moving, nor during sampling on foot around Tenderfoot Lake.

8.3.2 Fish detections and migration patterns

Deploying several receiver stations in the Cheakamus and Squamish Rivers, as well as in Howe Sound and beyond, allowed survivorship and travel speed during the juvenile migration to be quantified for each group of tagged steelhead. Tagged fish generally moved downstream immediately after release (Fig. 8.6). On average, the time from release until detection at the first station was ≤2 d for most groups, although some groups were not detected until several days after release (e.g., TCH in 2007 and FVTH RG2 in 2008). Once fish did commence migrating downstream, travel speed was generally rapid, especially for wild fish. Fish that survived to the mouth of the Squamish River were heard on average 1.9 d after release for W RG2 in 2004, and on average 21.4 d after release for TCH in 2008; other groups were intermediate within this range (Fig. 8.6). There was no consistent pattern among hatcheries in the rate of migration downstream: fish from TCH were generally slower in 2008 than in 2007; fish from the upper FVTH release site in 2008 were also relatively slow, even taking into account their longer distance travelled, and fish from the lower release site in both years were nearly as fast as wild groups. Some hatchery release groups took a relatively long time to travel from the river mouth to the inner Howe Sound line, while other hatchery groups and all wild groups took less time (the variation around average travel times was also generally less for wild groups; Fig. 8.6). This pattern continued for travel through Howe Sound to the NSOG line, with average travel times since release of 8–20 d for the wild groups and 23–47 d for the hatchery-reared groups. There were relatively few detections of hatchery-reared fish on the outer lines at QCS and JDF.

Despite only minor variation among wild and hatchery-reared groups in travel speeds to successive detection stations (especially in rivers), there was considerable variation in the number of fish detected at stations along the migration. These numbers for 2008, where wild and hatchery fish were both tagged, are listed in Table 8.4. Blank cells indicate that the group of fish was released below that particular station. There appear to be differences between wild and hatchery-reared groups in the proportion of fish reaching the lower Squamish River, Howe Sound, and outer line (QCS, JDF) receiver stations. This could be the result of lower survival and/or a higher rate of residualization in hatchery-reared fish.
8.3.3 Survival during the smolt migration

General model predictions

A general CJS model assumes complete independence among release groups and among each of their migration segments (for \( \phi \)) or stations (for \( p \)). Without accounting for heterogeneity among individuals, the general model \([\phi \text{seg}_G, P_{S:G}]\) is very flexible and provides the best possible fit to the detection data of ‘1’s and ‘0’s. Survival probabilities are estimated for each segment of each group, and the product of a group’s \( \hat{\phi} \) is the estimate of survivorship from release to a particular station, shown in Fig. 8.7. Two patterns seem immediately evident: (1) there is considerable mortality during the downstream migration, with steep declines in survivorship with increasing distance, and (2) in general, wild groups tended to have higher overall survival than hatchery-reared fish, a difference that was established early, soon after release.

A simpler, more constrained model may be preferred to the general model even if parameter estimates are not as accurate given the data. Reducing the number of parameters typically leads to improved precision in the estimate of any one parameter, and less chance of over-fitting to sparse data (Chapter 3). Two release groups (W RG2 2004 and W RG2 2005) had <10 fish tagged (let alone detected), so the model is clearly over-parameterized for these groups. Similar arguments can be made for two groups which had <20 fish tagged (Table 8.5). We turn to comparisons of candidate models to evaluate whether other models may be more parsimonious than the general model in the balance of bias and precision.

Detection probability models

The comparison of \([p]\) while keeping a general \([\phi]\) constant resulted in a preference for the model with (separate) water level covariates for Cheakamus and Squamish River stations, \([\phi(\text{seg}_G), p(S:Y+\text{lev}_{\text{Chek}}+\text{lev}_{\text{Sqm}})]\), in terms of QAICc scores (Table 8.5). Despite involving only a single extra parameter for the Squamish River covariate, the goodness-of-fit was much better compared to model \([\phi(\text{seg}_G), p(S:Y+\text{lev}_{\text{Chek}})]\), which had a \(\Delta\text{QAICc}\) of 14.8. The general CJS model required estimating many more parameters. It had a correspondingly lower negative log-likelihood, but overall was less parsimonious, with \(\Delta\text{QAICc}\) of 6.8. Beta coefficients for the best model showed a stronger relationship between \(p\) and river level at Cheakamus River stations \((\beta = -4.08, 95\% \text{ c.l., } -5.19 \text{ to } -2.97)\) than at Squamish River stations \((\beta = -0.62, 95\% \text{ c.l., } -0.88 \text{ to } -0.35)\), although this may have been confounded by absolute water level differences between rivers. For both rivers, \(p\) decreased as water level increased.
Apart from AIC scores, there are reasons for preferring \([p]\) that use environmental covariates. The group-independent model is associated with small sample sizes for some groups (Table 8.5), especially at later stations during the migration route. Over-fitting biases are likely, so the \(\hat{p}\) at a given station vary considerably among groups (even at ocean stations where little variation is expected), and confidence intervals are wide (e.g., for 2008, Fig. 8.8a). In contrast, the environmental covariate models constrain \(\hat{p}\) to be equal among release groups, apart from differences in \(p\) among groups due to river level differences at group-specific migration times (Fig. 8.8b). This seems reasonable since all groups used V9 tags and should therefore have similar probabilities of detection as they migrate past receiver stations. Detection probabilities varied widely across receiver stations, for example in 2008, from 0.5–12.9\% at Chk_7 to ~90\% at Chk_4, HS inner, and HS outer (Fig. 8.8b). All \([p]\) besides the general model were given four extra terms to represent group-specific \(p_{NSOG}\) for groups that demonstrated split-route behaviour after entry into Georgia Strait. This effect is seen in Fig. 8.8 for the two wild groups in 2008. At NSOG, the estimates shown for these two groups are not true detection probabilities, but rather joint probabilities of movement and detection.

Although all tags were assumed to have the same acoustic output, they differed in average delay intervals between transmissions: 30, 40, or 60 s. This factor was considered in other \([p]\) (results not shown), but the effect was in the opposite direction than expected (higher \(p\) associated with tags with longer intervals), so appears to be a spurious result. The tag delay effect was not considered in subsequent analyses. We proceed to comparing \([\phi]\) while assuming the detection model \([p(S:Y+lev_{Chk}+lev_{Sqm})]\).

**Survival probability models: effects of rearing history and release date**

There was a strong overall effect of wild or hatchery-rearing history on survival, with higher survival in wild fish than in hatchery-reared fish (‘HW’ coefficient for best model, \(\beta_W = 0.75, 95\%\) c.l., 0.25–1.26). Compared to the best model \([\phi(seg:Y+HW+M_{i,H}+M_{i,W}), p(S:Y+lev_{Chk}+lev_{Sqm})]\), the corresponding model without this effect had a \(\Delta QAICc\) of 4.5 (Table 8.6). In addition to an overall ‘HW’ (hatchery vs. wild) effect, the best model also included two extra parameters that allowed for wild-specific and hatchery-specific mortality in the first segment of each release group, irrespective of where that segment is. These parameters were warranted due to the associated decrease in negative log-likelihood (Table 8.6). The top three models all involved these initial mortality parameters, and \(\Delta QAICc\) for the fourth-best model, similar to the best model but without these initial mortality parameters, was 5.1. Beta coefficients
for these parameters under the best model showed that the initial mortality effect was greater for hatchery fish ($\beta_{M_i,H} = -1.53, 95\% \text{ c.l., } -2.45 \text{ to } -0.62$) than for wild fish ($\beta_{M_i,W} = -0.30, 95\% \text{ confidence limits, } -1.63 \text{ to } 1.02$).

The additive ‘stock’ effect nested within ‘HW’ was weak. Two extra parameters were estimated for model $[\phi(\text{seg:} Y + \text{HW} + \text{stock} + M_{i,H} + M_{i,W}), p(S:Y + \text{lev}_{\text{Chek}} + \text{lev}_{\text{Sqm}})]$ compared with the best model, but the gain in goodness-of-fit was relatively small (Table 8.6). The most general model, with segments and release groups fully-independent, was over-parameterized for some release groups and had no support in the data relative to other models. We carry forward the best model from this set and next evaluate effects of body size and release date.

**Survival probability models: effects of body size and release date**

There was a strong effect of body size on survival, with the top four models all containing this covariate (Table 8.7). The best model, $[\phi(\text{seg:} Y + \text{HW} + \text{FL} + M_{i,H} + M_{i,W}), p(S:Y + \text{lev}_{\text{Chek}} + \text{lev}_{\text{Sqm}})]$, had a QAICc that was 7.0 lower than the corresponding model without the fork length effect once wild or hatchery-rearing history was already accounted for. The beta coefficient for ‘FL’ under this best model showed positive size-dependence, with higher predicted survival of larger fish than of smaller fish when other factors were accounted for ($\beta_{\text{FL}} = 0.021, 95\% \text{ c.l., } 0.009–0.033$).

There was no effect of release date on survival under this segment-based model formulation. The second-best model differed from the best model by only one parameter, ‘RD’, but improvement in the goodness-of-fit was negligible by including it (Table 8.7). Models $[\phi(\text{seg:} Y + \text{FL} + M_{i,H} + M_{i,W})], [\phi(\text{seg:} Y + \text{RD} + M_{i,H} + M_{i,W})]$, and $[\phi(\text{seg:} Y + \text{RD} + \text{FL} + M_{i,H} + M_{i,W})]$ were considered to examine whether the effect of ‘HW’ observed in the previous section may have been the result of body size or release date differences between wild and hatchery release groups, and not effects of wild vs. hatchery rearing *per se*. There was little support for these models ($\Delta\text{QAICc} = 6.2, 13.3, \text{ and } 7.9$, respectively; Table 8.7), confirming the overall ‘HW’ effect on $\phi$ was well-supported. We carry the best model forward to the final set to consider effects of migration distance, and nested effects within this of year and release date.

**Survival probability models: distance-based models**

Distance-based models had considerably more support than the more flexible $[\phi]$ that allowed for independent $\hat{\phi}$ in each segment in each year (Table 8.8). The distance-based models that allowed separate effects of distance on $\phi$ among Cheakamus River, Squamish River, and
ocean segments had more support than the more constrained models in which the effect of
distance on $\phi$ was constant across these habitats. For example, the best model,
$[\phi(d_{Chk}+d_{Sqm}+d_{sw}+HW+FL+M_{i,H}+M_{i,W})]$, has only two more parameters than model
$[\phi(d+HW+FL+M_{i,H}+M_{i,W})]$, but a much lower negative-log-likelihood, resulting in $\Delta QAICc = 4.4$ (Table 8.8).

The effect of release date on survival was fairly weak, but not negligible as in the
previous section with segment-based models. Estimation of the extra ‘RD’ parameter reduced the
negative log-likelihood by >2 from that of the best model (Table 8.8). These factors balanced
out, such that the top two models in Table 8.8 had essentially equal support. The beta coefficient
for ‘RD’ under this model $[\phi(d_{Chk}+d_{Sqm}+d_{sw}+HW+FL+RD+M_{i,H}+M_{i,W})]$ had confidence limits
that did not exclude zero, but was at least suggestive of later release dates being associated with
lower overall survival than earlier release dates ($\beta_{RD_{date}} = -0.018, 95\%$ c.l., $-0.040$ to $0.004$). With
a more constrained sub-model as the basis for comparison, $[\phi(d+HW+FL+M_{i,H}+M_{i,W})]$, the effect
of release date on survival was stronger (incorporation of ‘RD’ reduced the negative log-
likelihood by >5; Table 8.8).

The interaction effect of ‘HW’ and ‘FL’ on survival was weak. Compared with the best
model, $[\phi]$ involving this extra ‘HW:FL’ parameter (implied by HW×FL) resulted in only a
slight improvement in goodness-of-fit (Table 8.8). The effect of ‘FL’ on $\phi$ was slightly stronger
for hatchery fish ($\beta_{FL_{H}} = 0.025, 95\%$ c.l., 0.008–0.042) than for wild fish ($\beta_{FL_{W}} = 0.015, 95\%
c.l., -0.007$ to $0.038$), although in both groups, increased body size was associated with higher
survival. Predicted $\phi$ over a range of fork lengths are shown in Fig. 8.9 for one wild and one
hatchery-reared group under the model that assumes this ‘HW:FL’ interaction (i.e., in logit-
space, predicted lines for these groups are not parallel). The slope of the predicted line for
hatchery fish is slightly greater than that for wild fish, and the intercept difference is large
enough such that over the full range of fork lengths considered over all years, predicted survival
of wild fish was higher than that of hatchery-reared fish, especially at smaller body size.

There was essentially no support for an effect of year per se on survival under the
distance-based models. Inclusion of this effect required three extra parameters to be estimated,
but the increase in goodness-of-fit compared to the best model was marginal (Table 8.8). This
suggests that survival trends tended to be consistent across years once the factors contained in
the best model (e.g., ‘HW’, ‘FL’) were already accounted for.
Of the top two models with nearly equal support, the one that includes a release date effect allows for more variability among release groups in $\hat{\phi}$. Survivorship declines under this model $[\phi(d_{Chk} + d_{Sqm} + d_{sw} + HW + RD + M_{i,H} + M_{i,W}), p(S:Y + lev_{Chk} + lev_{Sqm})]$ are shown in Fig. 8.10a, plotted against minimum cumulative distance travelled. Under this assumed model, survivorship from release to the river mouth was estimated to be 69–82% for the wild groups and 23–36% for the hatchery-reared groups (Table 8.9). The decline of survivorship in the first 20 km of the migration was very steep in hatchery fish, already <50% by 20 km in many groups. The survival decline in freshwater was less precipitous for wild groups, which is more easily seen in a plot of ln(survivorship) vs. distance (Fig. 8.10b). After ocean entry, proportional mortality in the remainder of the monitored migration was more similar between wild and hatchery-reared fish (i.e., slopes in Fig. 8.10b are more similar in ocean segments compared with freshwater segments). By the point of exit from the Georgia Strait system via QCS or JDF, the survival difference was large, with survivorship of wild groups at 21–33% and that of hatchery-reared groups at 3–6% (Table 8.9; Fig. 8.10a).

For reference, we also provide survivorship estimates assuming the general model, $[\phi(seg;G), p(S;G)]$, with fully-independent segments (or stations) and release groups (Table 8.9). The goodness-of-fit was poor for three groups under the general model (FVTH 2007, TCH 2008, W RG1 2008), so we interpret their results with caution, but the survivorship declines of these groups at least appear to be similar to those of other hatchery and wild groups (Fig. 8.7). Ignoring the two wild groups with insufficient sample sizes to properly estimate parameters, wild survivorship estimates ranged from 65–84% to the Squamish River mouth and 18–39% to the outer ocean lines (Table 8.9). Ignoring the two hatchery groups with <20 fish tagged that were also susceptible to over-fitting, hatchery survivorship estimates ranged from 32–43% from release to the Squamish River mouth and 3% to the outer ocean lines (Table 8.9). Thus, despite the potential for over-fitting, the survivorship estimates to the three stations in Table 8.9 under this general model are in line with those under the AIC-best model. Uncertainty in survivorship estimates was much higher under the general model (Fig. 8.7) than the more constrained and more parsimonious distance-based model (Fig. 8.10), largely a result of having more parameters estimated and thus less certainty in the estimated value of any one parameter. Survivorship declines assuming the more parsimonious distance-based model (Fig. 8.10a) by and large captured the trends of the general model (Fig. 8.7), with steeper declines in freshwater and higher survival in wild fish, so survival estimates are quite robust to model choice.
Analyses specific to 2008 study

In the 2008-only analysis, when wild and hatchery-reared steelhead were both tagged, a strong effect of rearing history was again observed, with wild fish having higher overall survival than hatchery-reared fish during the migration (not shown). Similarly, the initial mortality in the first segment after release was higher for hatchery smolts than for wild smolts. Differing from the all-years analysis, a segment-independent model with these additive factors of ‘HW’, ‘M_{i,w}’, and ‘M_{i,h}’ had more support than a distance-based model with these factors. With only a single year, the reduction in the number of parameters moving from a segment-independent model to a distance-based model is considerably less than the reduction in a multi-year analysis. This is a result of distance-based models involving consistent effects of distance on $\phi$ across years, whereas in segment-independent models, years are independent because the physical segments delimited by receiver stations changed from year to year.

There was no support for an additive effect of condition factor, ‘K’, on survival in candidate models, either when included by itself or when ‘FL’ was already accounted for. The inclusion of this extra parameter led to no improvement in terms of goodness-of-fit. Body length (or weight) combined with ‘HW’ seem able to account for variation among individuals in the probability of survival, without having to incorporate ‘K’.

Comparing distance-based models for the 2008 study alone, the observed effect of bull trout density on steelhead smolt survival was weak. Models that involved an average of raw bull trout count data over all years performed similarly to those with a smoothed Lowess fit to count data. Despite the lack of a strong effect, we examined the possibility further. Of the five release groups, three were released in a side channel adjacent to the Cheakamus River, and one was released into Tenderfoot Creek. The majority of the first segment of these four groups was either in this channel or this creek and not in the mainstem river, where bull trout typically reside. We thus excluded the first segment, and considered all remaining Cheakamus River segments up to Chk_6 (where bull trout surveys ended) for all groups together. Survival probabilities by segment from the general model, [$\phi(\text{seg}\times G)$, $p(S\times G)$], and bull trout counts by segment were converted to survival rates and bull trout densities per unit length (km$^{-1}$). The relationship between these suggests a slight decrease in steelhead survival rates as bull trout density increased (Fig. 8.11). There were not sufficient numbers of segments monitored to evaluate whether the relationship differed by wild and hatchery rearing histories.
8.3.4 Residualization and projected detection probability

Few steelhead smolts were detected in 2007 or 2008 at either: (1) receivers upstream of their release site, or (2) any Cheakamus River receivers >4 weeks past their release date and not thereafter at Squamish River or ocean receivers (Table 8.10). In 2008, the observed proportion of released fish meeting either of these criteria was slightly higher in hatchery-reared fish (4 of 98, excluding the tag that was more likely stationary than in a live, residualized smolt) than in wild fish (1 of 100). In 2007, no fish from either group were detected upstream of their release site. No fish were detected >4 weeks after release in 2007 either, although the number of stations operated was fewer in 2007, there were no Cheakamus River stations downstream of the FVTH release site, receivers were checked and maintained less frequently, and no mobile sampling was conducted in 2007. The overall sampling efficiency was therefore likely less than in 2008. In-river monitoring effort in 2004 and 2005 was considerably less than 2007 and 2008 in terms of both locations (Fig. 8.1) and duration (Fig. 8.2) of receiver operation, but in each year one wild smolt was detected at the station upstream of the release site and not thereafter on any receivers, so fits the criteria of a likely residual.

On the basis of $R^2$ values for regressions between test tag pass indices and river level (Eq. 8.1), as well as between mark-recapture detection probability estimates, $p_{mr}$, and test tag pass indices (Eq. 8.2), we selected two indices that outperformed others (Table 8.11). Both indices involved aggregating the two test tags together, but not aggregating passes within a set. These indices described whether test tags were detected or not during a pass [$P/A$ (per-pass)], and the proportion of signals transmitted that were detected during a pass [$\%\text{Det}$ (per-pass)]. These were attractive compared to other types of indices in that they had more values estimated than temporal range or receiver meta-data indices (Table 8.11). Use of these two indices results in similar predicted $p_{mr}$ time series (Melnychuk et al. 2009). We consider only one of these for the remainder of this chapter, the index [$\%\text{Det}$ (per-pass)], which we prefer because it provides more information than simply a binary outcome during each test tag pass.

Changes in water level of the Cheakamus River during the study (Fig. 8.2a) caused variation in detection probabilities at Cheakamus River stations over this period (Fig. 8.8). This was evident in the variation of test tag pass index values with river level (Figs. 8.12, 8.13), where pass index values tended to be higher during periods of lower river levels. It was also evident from one tag from FVTH RG1, which was detected at Chk_4 during several periods in 2008: fairly consistently from May 9–15, June 4, June 6, sporadically from June 12–30, fairly consistently from July 12–Aug. 7, and sporadically from Aug. 8–14. These periods coincide with
relatively low water levels in the Cheakamus River (Fig. 8.2a). During the period from May 9–Aug. 14, there were no detections of this tag during the times when water level was >1.6 m. It is possible this tag was stationary, laying on the river bed some distance from Chk_4 (either in a fish that died, after being defecated from a smolt predator, or after being extruded from the smolt). During periods of low water level and thus low acoustic background noise, the tag was occasionally detected; during periods of high water level and noise, it was not.

Mark-recapture estimates \( \hat{p}_{mr} \) were only possible during the smolt migration, which for Cheakamus River receivers, occurred only in May, and only at certain river levels (Fig. 8.12). The test tag pass indices, \( p_{test} \), that were used to estimate a mark-recapture-like detection probability, were assessed over wider ranges of time and river level (Fig. 8.12). There was a negative relationship between the test tag index value and river level during the passes (Fig. 8.13). Variation among stations was observed, similar to that seen for \( \hat{p}_{mr} \) (Fig. 8.8): the highest \( p_{test} \) values occurred at Chk_4, while the lowest values occurred at Chk_7 (as well as at Chk_1, for which \( \hat{p}_{mr} \) were not possible).

Test tag pass indices were not evaluated at the exact mean arrival time of each release group at each Cheakamus River detection station, as these were unknown at the time of conducting test tag passes. This would ideally be the appropriate comparison between \( p_{test} \) and \( \hat{p}_{mr} \), since river level affects both types of \( p \). Instead, the predicted logit(\( p_{test,i,RL} \)) at the corresponding river level for \( \hat{p}_{mr,i,RL} \) (i.e., the predicted value along the best fit line in Fig. 8.13 at the appropriate river level and station) was calculated to compare with \( \hat{p}_{mr,i,RL} \). There is a reasonably strong relationship between \( \hat{p}_{mr} \) and predicted \( p_{test} \) for both indices (Fig. 8.14; Table 8.11). Values of predicted \( p_{test} \) tended to be lower than \( \hat{p}_{mr} \) values at the corresponding river level (Figs. 8.12, 8.14), and the slope between them was >1 (\( \beta_{10} \) coefficient in Table 8.11).

The established relationships between river level and \( p_{test} \) (Fig. 8.13; Eq. 8.1) and between \( \hat{p}_{mr} \) and \( p_{test} \) (Fig. 8.14, Eq. 8.2) allow \( p_{mr} \) to be predicted (\( p_{mr*} \)) for any given river level at any Cheakamus River receiver station. These predictions are shown by the lines in Fig. 8.15, back-transformed to the probability scale (slopes of the predicted line are equal among stations in logit-space, but not after back-transformation). These show a general decrease in \( p_{mr*} \) with increasing river level. Variation among stations is predicted, in line with the observed variation among stations in \( \hat{p}_{mr} \) estimated from steelhead detection data and \( p_{test} \). Bootstrapped 95% confidence limits around these best-fit predictions are quite wide, as they take into account multiple error sources involved with estimating \( p_{mr} \) through the intermediate step of \( p_{test} \). In general, \( p_{mr*} \) fit \( \hat{p}_{mr} \) from steelhead detections reasonably well (as they should, since they were
partly based on these). In three cases, however, \( p_{mr^*} \) was not very close to \( \hat{p}_{mr} \) (Chk_3 at low river level, Chk_6 at low and high river level, and Chk_7 at low river level; Fig. 8.15). This is a result of the constraint on the slope \( \beta_8 \) in Eq. 8.1 being equal among stations; consequently, slopes (in logit-space) are also equal in Fig. 8.15. Predicted fits are not flexible enough to ‘chase’ all these estimates, but rather, the constrained best fit is achieved over all stations together.

Predicted \( p_{mr} \) varied throughout the study from May to mid-August, and was inversely related to river level (Fig. 8.16). Two main pulses of high river flow, in mid-May to mid-June and in late June to early July, resulted in relatively low \( p_{mr^*} \) during these times. Relatively low river level periods occurred in early to mid-May, mid to late June, and early July to the end of the study period in mid-August. During these periods, \( p_{mr^*} \) was relatively high (Fig. 8.16), so any steelhead potentially residualizing in the Cheakamus River would have been more likely to be detected at these times. There was also variation among stations in \( p_{mr^*} \): it was generally >80% at Chk_4 at all but the highest river levels, and was generally <30% at Chk_1 and Chk_7.

We now return to the detections at Cheakamus River stations that were suggestive of possible residualization (Table 8.10), and use these to estimate residualization rates. Because detections were so few, we group them by wild and hatchery-reared categories rather than by release group for estimating residualization. Tags were detected at both high and low river levels (Table 8.10), so we assume it was possible for tagged fish to be detected throughout the May to mid-August study period. The five fish that were detected as possible residuals were detected on different days and at different stations (Table 8.12). The average river level during the day(s) that fish were detected at a station was used to calculate the corresponding \( p_{mr^* \cdot i, RL} \) and its 95% confidence limits. These were used to predict the number of fish that actually passed station \( i \) based on the number detected there \( (d_{i, tag}) \); the sum of these extrapolated numbers gave a group-specific estimate of the number of tagged fish residualizing in the Cheakamus River \( (D_{Chk}; \) Eq. 8.3). The resulting estimated residualization rates were 0.02 (95% c.l., 0.01–0.04) for wild fish and 0.09 (0.05–0.20) for hatchery-reared fish in 2008. The confidence limits for these estimates are a direct inversion of the confidence limits for \( p_{mr^* \cdot i, RL} \), and therefore incorporate multiple sources of error associated with test tag passes and estimated \( \hat{p}_{mr} \) during the steelhead migration.

**8.4 Discussion**

In this study, we tested two main hypotheses and found: (1) survival of hatchery-reared smolts from wild Cheakamus River steelhead broodstock was lower overall than survival of wild smolts, a difference that was established early during the downstream migration; and (2) there
was some indication that residualization was higher for hatchery-reared smolts than for wild smolts in 2008, although estimates for both groups were <10% and had wide confidence limits. These results are related; $\hat{\phi}$ in each segment and overall (cumulative) survivorship since release are actually estimates of ‘apparent survival’, which assumes that no residualization occurs (i.e., fish do not cease migrating before arriving at Cheakamus River receiver stations or in between stations where they would not be detected). We discuss the potential for residualization later, but the conclusion of survival differences between wild and hatchery-reared fish appears to be robust to the estimated residualization rates of <10%.

8.4.1 Survival differences among wild and hatchery-reared steelhead smolts

Despite similar broodstock origins, survival during the smolt migration was clearly higher for wild smolts than for hatchery-reared steelhead. This difference was consistent in both the 2008-only analysis, when rearing histories were compared in the same year, and in the all-years analysis, which provided generality through incorporation of wild-only or hatchery-only studies in previous years. It was also consistent across different assumptions of mark-recapture model structures.

Studies of salmonids from two other B.C. watersheds showed some indication of higher survival in wild fish than hatchery-reared fish during the smolt migration (Welch et al. 2004, Chittenden et al. 2008). In contrast, Atlantic salmon showed either no difference during the smolt migration (Thorstad et al. 2007) or higher survival in wild smolts during an earlier (estuarine) portion of the migration but not during a later (coastal inshore) portion (Lacroix 2008). More commonly, studies have compared survival between wild and hatchery-reared smolts over the full ocean life (i.e., smolt-to-adult survival). Recapture rates of Atlantic salmon tagged as smolts and caught as adults in fishing gear were 2–3 times higher for wild fish than hatchery-reared fish in southwestern Norway (Jonsson et al. 2003) and in the Baltic Sea (Kallio-Nyberg et al. 2004, Saloniemi et al. 2004, Jokikokko et al. 2006). However, survival of sea-ranched Atlantic salmon offspring in the Baltic Sea was higher for fish with hatchery-reared parents than fish with wild parents, likely due to the heritability of higher growth rates in hatchery fish and size-related advantages for survival (Kallio-Nyberg et al. 2007). In the Columbia River basin, a short review of comparative differences in steelhead found that total marine survival was consistently higher for wild than for hatchery-reared smolts (Reisenbichler and Rubin 1999). In Chinook salmon from the Columbia River basin, survival was higher in wild smolts than in hatchery-reared smolts of the same size, but the larger average body size of hatchery-reared smolts compensated
for this. As a result, return rates of hatchery fish were higher than of wild fish (Zabel and Williams 2002). Earlier, Raymond (1988) had found higher survival of wild fish for both steelhead and stream-type Chinook. Across Oregon State watersheds, productivity of mixed populations of wild and hatchery-reared steelhead (in terms of both ln(recruits/spawners) and the Ricker $a$ parameter) was correlated with the proportion of wild fish in each population (Chilcote 2003). In New Zealand, fry-to-adult survival of Chinook salmon was higher in wild than hatchery-reared fish when standardized to a similar body size, but hatchery-reared fish were much larger so total survival was higher (Unwin 1997). Finally, in one study that similarly compared wild steelhead smolts with smolts from a newly-implemented hatchery program on the Hood River, OR, which used wild broodstock for eggs, wild smolts had 7-fold higher average smolt-to-adult survival than hatchery smolts (6.1% and 0.9% survival, respectively; Kostow 2004). A large survival difference was also observed in the present study, and the fine-scale resolution of receiver stations in the Cheakamus and Squamish Rivers showed that this difference was established primarily during the in-river migration, immediately after release.

The most likely explanation for the lower observed survival of hatchery-reared fish is a higher vulnerability to predation (reviewed in Mesa et al. 1994, and Olla et al. 1998) due to their lack of substantial exposure to natural selection pressures prior to release from a hatchery. Populations are comprised of a wide range of individuals with differing traits as early as the egg stage, some of which may affect survival. Most wild fish smolt after 2 or 3 years. During this period between emergence and smoltification, the wild population was subjected to predation pressures and environmental stressors that likely resulted in a smaller, ‘more-fit’ subset of the population remaining at the time of tagging and release. In contrast, hatchery-reared fish were not exposed to such pressures, so a higher proportion of ‘less-fit’ individuals was likely tagged compared to the wild population. The initial mortality component in the first migration segment following release was greater in hatchery-reared fish, supporting the assertion that the ‘less-fit’ individuals would be more likely to die soon after release. Possible mechanisms of higher mortality in hatchery fish include increased predation risk from feeding at the surface more often (Vincent 1960), having lighter skin colouration (Donnelly and Whoriskey 1991), or having reduced escape responses when faced with predators (Woodward and Strange 1987).

Fitness, of course, is a lifetime reproductive measure, but if later ocean survival and fecundity are similar among wild and hatchery-reared fish, survival estimated in this study is a reasonable correlate. Others have described this ‘fitness’ correlate over a short portion of an individual’s lifespan as ‘vitality’ (Anderson, 2000).
Cheakamus River segments of the migration of each release group contained variable numbers of bull trout, potential predators of steelhead smolts. There were few bull trout in the first segment of FVTH RG1 compared with the first segment experienced by the other four groups in 2008, but mortality was still relatively high for this group in the first segment (Fig. 8.7). In segments following the first, there was slight evidence that bull trout density had a negative effect on steelhead survival rate (Fig. 8.11), but the effect was not strong enough for the bull trout covariate in candidate models to be supported by the data. Other predators including merganser ducks have been known to aggregate and feed on outmigrating salmonid smolts (Wood 1987), and are commonly observed on the Cheakamus River. They may have taken advantage of ‘naïve’ hatchery smolts soon after release. Higher avian predation rates on hatchery smolts than on wild smolts have been observed in other salmonids soon after release (e.g., in predation of sea trout smolts by cormorants and herons in a Baltic Sea fjord estuary; Dieperink et al. 2001). In contrast, predation rates on wild and hatchery Atlantic smolts by fish predators (Atlantic cod and saithe) were not different during the estuarine migration (Hvidsten and Lund 1988). In early ocean migration segments, the difference in mortality between wild and hatchery-reared steelhead was less compared to segments during the downstream migration (Fig. 8.10).

Survival differences occurred despite hatchery-reared smolts being slightly larger than wild smolts on average (Table 8.1). Size-dependent mortality has been observed in other salmonid populations over total ocean life, with larger smolts generally having higher survival than smaller fish (see Chapter 9), perhaps due to improved predator avoidance capacity and/or greater energy stores. It has been observed less commonly during the short window of the smolt migration (see Dieperink et al. 2001 for an exception). Since positive size-dependent mortality during the first few weeks of the smolt migration was also observed here, if we were to standardize survival to a common body length (Fig. 8.9) and compute the product of these segment-specific predicted survival probabilities, the resulting survivorship difference between wild and hatchery-reared fish would be even greater. The interaction effect of ‘HW’ and fork length in model \( \phi(d_{\text{Clk}}+d_{\text{Sqm}}+d_{\text{sw}}+\text{HW}\times FL+M_{i,H}+M_{i,W}) \) was weak (Table 8.8), but nonetheless suggestive that the effect of fork length on survival was stronger for hatchery fish than wild fish. That is, in both groups larger body sizes were associated with increased survival, but an increase of 1 mm in length resulted in a greater increase in survival of hatchery fish than it did for wild fish (Fig. 8.9). Size dependence in survival due to predation may have already occurred in wild pre-smolt stages (fry or parr) prior to the time of capture, so may be weaker after tagging and release. The stronger size-dependence in mortality of hatchery fish seems reasonable considering
initial mortality after release was higher in hatchery fish; some degree of size-dependence in mortality of hatchery smolts likely occurred in the first few segments when overall mortality rates were higher. I.e., there was likely a greater opportunity for size-dependent mortality to occur in hatchery smolts since there had been less opportunity for the smaller hatchery individuals to be ‘weeded out’ prior to release. Condition factor was found to have little predictive ability for survival, which has also been observed elsewhere (Zabel and Achord 2004).

Difference in release date does not appear to be a likely explanation for survival differences. In the all-years comparison, there were some early and some late releases of both wild and hatchery fish. Overall the ‘RD’ factor had a fairly weak effect, with later release dates associated with decreased survival (once other factors of distance, ‘HW’, ‘FL’ and ‘Mi’ were already accounted for). The negative correlation between release date and survival is somewhat in line with results found in other studies (Bilton et al. 1982, where the observed relationship for coho was actually dome-shaped) and supports hypotheses relating to shifting advantages of earlier migrants in the face of climate change (Beamish et al. 2008). If hatchery fish had smolted and were released later than physiologically optimal, there could have been survival consequences from being held back. Smolts from TCH were released under volitional release, however, so this appears unlikely, as their survival was comparable to smolts from FVTH that were transported by truck and released (Fig. 8.10). Wild fish were caught during their migration and held for up to 3 (2004), 2.5 (2005) or 1 (2008) weeks prior to tagging; this interruption to the migration could have equally been physiologically stressful, slowing the process of smoltification (Zaugg et al. 1985). The data suggest that the overall wild vs. hatchery-rearing effect was much stronger than a possible release date effect on survival.

8.4.2 Distance-based survival models

Some [\( \phi \)] were based on \( \phi \) being independent in different segments (and years), while others were distance-based, in which segments were related to one another (across years) through the distance covariate on \( \phi \). In these distance-based models, the interest is not particularly in whether increased migration distance results in decreased probability of survival—that is perhaps obvious (although not so obvious that the relationship between distance and \( \phi \) differs across habitats). The issue, rather, is to consider which mark-recapture model structure, segment-independent or distance-based, is more suitable as a framework on which to build hypothesized models of interest involving potential effects on \( \phi \) such as body size, release date, or initial
mortality. Segment-independent models involve more parameters and consequently allow more flexibility in fitting detection data. Distance-based models are constrained to the assumption that logit(\(\phi\)) is indirectly proportional to segment distance, but estimation precision under this framework is typically higher than in segment-independent models. Model selection criteria like AIC can assist in arbitrating between these trade-offs to achieve greater parsimony.

Distance-based models had considerably more support than independent segment-based models in the all-years analysis (Table 8.8), but not in the 2008-only analysis. This is easily explained by the number of years in the dataset. With only a single year, independent segment models required estimating only 11 parameters more than the corresponding, heavily-constrained distance-based models. With multiple years, we assumed that the relationship between segment distance and segment survival was consistent across all years. The distance-based models are no more constrained in the all-years analysis than in the single-year analysis (apart from the relationship being consistent across years), but they required estimating 39 fewer parameters than the corresponding independent segment models, in which years were also independent. The assumption of consistent effects of distance on survival across years may not be realistic due to interannual variation in density of bull trout or other predators, but sample sizes may not be adequate to detect differences among years. Indeed, the additive ‘year’ effect was weak when incorporated into distance-based models (Table 8.8), suggesting that other factors (distance, ‘HW’, ‘FL’, and ‘\(M_i\)’) were more important in accounting for variation in survival among release groups in different years than was the effect of ‘year’ per se.

The distance-based models that allowed for separate relationships of segment distance and \(\phi\) among the three habitats (Cheakamus River, Squamish River, ocean) were better supported than models assuming a common effect of distance on \(\phi\) across these habitats (Table 8.8). Estimated model coefficients showed the decrease in survival for an increase of one unit of distance was greatest in the Cheakamus River, followed by the Squamish River, and least in ocean segments. This ranking could reflect differential predation pressures among habitats. The Cheakamus River above the confluence with the Cheekye River generally exhibits relatively low turbidity during the smolt migration, and smolts may be highly susceptible to visual predators, either fish or birds. The Squamish River in comparison has a higher turbidity, perhaps reducing predation risk. In the ocean, predator densities may be lower, and smolts could travel at different depths (Orsi and Wertheimer 1995, Beamish et al. 2000) to reduce exposure to possible predators, unlike in the two rivers where depth refugia are likely less common. Aside from physical characteristics of these three habitats, all releases occurred in the Cheakamus River. The
initial period after tagging and release is likely associated with higher mortality due to new predation pressures (for hatchery fish) and/or adjusting to swimming with an implanted tag (both wild and hatchery fish) regardless of where fish are released. These adjustment factors could reasonably be least in ocean segments, and intermediate in Squamish River segments. This ‘order of habitats’ hypothesis could therefore also explain why per-distance mortality was higher in the Cheakamus River than the other two habitats.

The assumptions of mark-recapture models for survival outlined in Appendix A could have resulted in biases in parameter estimates if they were violated. The possibility of tag-related mortality or tag shedding exists (see Chapter 9). Even if tag-related mortality was higher in migrating smolts than in tank studies, as long as the effect was similar for wild and hatchery-reared fish, the conclusion of survival differences among them remains robust. Tag failure may have occurred for one late-migrating group, FVTH in 2007, as some fish could have crossed ocean lines after tag batteries expired. Tags in this group were predicted to shut off around July 23, but three different fish were detected on the HSouter, NSOG, and QCS lines between July 22–24. Survivorship to the outer QCS or JDF lines may therefore have been somewhat underestimated for this group (although tag batteries tend to last at least several weeks beyond their predicted expiry dates). No other release group in any year appeared to cross ocean lines after or around the time of tag expiry.

8.4.3 Potential for higher rates of residualization in hatchery-reared smolts

We now turn to the assumption that fish did not cease their migration prior to encountering any receivers, or between any stationary river stations, where they would not be detected. In a mark-recapture framework, if fish are not detected at a station during their migration but \( p \) at the station is reasonably high (as estimated from other fish detected at and after that station), the most likely explanation under the assumption of no residualization is that fish died prior to arriving at the station. Mark-recapture \( \hat{\phi} \) are thus ‘apparent survival’, which are essentially joint probabilities of migration and survival to the station. If some fish from a release group residualized in freshwater, survivorship (Figs. 8.7, 8.10, Table 8.9) would be underestimated for the group.

The method developed of using test tag passes as an intermediate step for predicting mark-recapture-like detection probabilities (during times when \( p_{mr} \) cannot be estimated) allowed residualization rates of tagged fish to be estimated. It seems reasonable that \( p_{test} \) can serve as an index of \( p_{mr} \); test tag pass indices are on the 0–1 scale, like \( p_{mr} \); \( p_{test} \) and \( p_{mr} \) both varied
inversely with river level, independently; and test tags were similar in acoustic power to steelhead tags. Values of $p_{\text{test}}$ for the [%Det (per-pass)] index tended to be lower than $p_{\text{mr}}$ (Figs. 8.12, 8.14) despite test tag transmissions being more frequent than steelhead tags. This does not present a problem since the second regression (Eq. 8.2) allowed an intercept to be estimated, but is interesting biologically as it might be explained by fish behaviour. Test tags drifted downstream at the speed of river flow. Since $p_{\text{mr}}$ tended to be higher, this implies fish may have travelled more slowly past receivers, or travelled in short distance increments, temporarily stopping often enough that they would be likely to stop within range of a receiver station where detection would be more likely than if travelling continuously at the speed of the water. Diurnal timing arguments seem unlikely to be an explanation for the $p_{\text{mr}} > p_{\text{test}}$ difference. Both wild and hatchery smolts were observed travelling past river stations more frequently during night time hours (data not shown, but patterns are similar to those in Melnychuk et al. (2007) and to those for small rivers in Chapter 7), while test tag passes were conducted in daylight. River level and discharge tended to be higher at night (following the day’s snowmelt from the upper watershed), so lower $p$ would be expected at night than during the day.

Detections providing evidence of residualization behaviour were very few: only one wild fish and four hatchery-reared fish were detected either upstream of the release site or anywhere in the Cheakamus River >4 weeks after release in 2008 (Table 8.10). The estimated residualization rates of 2% and 9%, respectively, are therefore very sensitive to this small number of ‘suspected’ residualized steelhead. The confidence limits around these estimates, despite being conservative by accounting for multiple sources of error independently, may not provide adequate coverage as a result. We illustrate this with two examples, the first involving the possibility of not detecting residualized fish, and the second involving the possibility that ‘suspected’ residuals might not actually be live, residualized steelhead smolts.

(i) As there was only a single wild ‘suspected’ residual in 2008, the estimated rate for wild fish would approximately double if a single other wild residual had been detected. This doubled rate would be very close to the current upper confidence limit of 4%. (Conversely, the estimated rate and confidence limits would all be zero if this fish had not been detected.)

(ii) One ‘suspected’ residual, the FVTH RG1 tag detected at Chk_1 beginning June 17 (when the receiver was relocated to this position; Table 8.10) displayed consistent diurnal movements. For several days during the period from June 17–27, the tag was detected several hundred times during night time hours, but not at all during daylight hours. As river levels were typically higher during night time hours than daylight hours, this suggests one of two
possibilities: (a) the tag was on a river bank or bar, and submerged during night time hours but exposed to the air during daylight hours (when it would not be detected). This seems unlikely, however, since detections trailed off in early July when river levels rose. Alternatively, (b) the tag was inside a fish that exhibited diurnal movements, often within detection range of Chk_1 at night but either upstream or downstream out of range during the day. This fish could be either a residualized smolt or a predator that had previously eaten the smolt. Case (b, smolt) was assumed in the residualization rate estimation, but if either cases (a) or (b, predator) were instead true, then one of the four ‘suspected’ steelhead residuals would not actually be a live, residualized smolt. The estimated hatchery residualization rate would in this case be 0.04 (95% c.l., 0.03–0.07), a considerable change from the case where this tag is assumed to be a residualized smolt, and outside this current lower 95% confidence limit (Table 8.12).

Other studies have also found that residualization rate estimates were possibly inaccurate when based on a small number of recaptures estimates (Viola and Schuck 1991, Cannamela 1993). In this estimation method we assumed that residualizing fish pass at least one Cheakamus River receiver station during the period from release to mid-August, so that any fish that do residualize have the opportunity to be detected at a station. The detection with mobile tracking allowed us to identify one fish with likely residualization behaviour that was not detected at any receiver station suggestive of residualization, and we incorporated this into the analysis.

Despite residualization rate estimates being relatively imprecise and sensitive to the small number of ‘suspected’ residuals, it is at least true that very few tags were detected over a period of several months while multiple receivers in the Cheakamus River were operational, as verified by test tag passes. Whether or not residualization estimates are accurate largely depend on the possible scale of movement associated with residualization. If the possibility of residualization is associated with in-river movement of several kilometres by smolts (as it was in other rivers; McMichael and Pearsons 2001, Werlen 2003, Walters 2005), then it is unlikely that many other tagged smolts would have residualized in the Cheakamus River and not been detected during this period. If the possibility of residualization is associated with shorter distances of in-river movement or more localized habitat use, then we cannot exclude the possibility that additional fish residualized in the river but did not move far enough to be detected on receiver stations during the survey period. In this case, estimated residualization rates would be biased low. Of the five ‘suspected’ residuals (Table 8.12), three were detected at a receiver either immediately upstream or immediately downstream of the release site, so may have only travelled short distances. The other two ‘suspected’ residuals passed either the immediate upstream or
immediate downstream station after release without being detected. They were later detected at a different station or with mobile tracking, so may have travelled longer actual distances. The possibility of bias in estimated residualization exists, but the estimate of 9% for hatchery-reared smolts is well within the range of those estimated for hatchery-reared steelhead in other systems, which averaged about 6% (S. Hausch and M. Melnychuk, *unpubl. data*). We were not able to find any published estimates of residualization rate in wild steelhead, although the frequency of upstream travel was higher in hatchery steelhead than in wild steelhead from the Snake River (Plumb et al. 2006), which is suggestive of residualization differences.

Residualization rates in the Cheakamus River appear to have been higher for hatchery-reared fish than for wild fish in 2008. This implies that estimated survivorship was likely underestimated for hatchery fish more so than for wild fish, as residualization and mortality were not distinguished in the mark-recapture analysis. A larger portion of the initial decline in apparent survivorship after release of hatchery fish is therefore explained by residualization, compared with wild fish. Since few of the ‘suspected’ residual fish were detected travelling downstream before showing evidence of residualization behaviour, this would most likely be interpreted as mortality during the first segment after release. This partly explains why the extra initial mortality parameter for hatchery-reared smolts was higher than that for wild smolts. Given the large estimated survivorship differences and the smaller residualization differences between wild and hatchery-reared fish, however, there still appear to be considerable survival differences among them even after accounting for differences in residualization rate. It is noted that residualization does not necessarily imply a fish will never migrate, as smolts could revert to parr and residualize for a year but then smolt and migrate to the ocean the following year. Variation in the extent and timing of migration within salmonid populations is very common (Jonsson and Jonsson 1993), resulting mainly from tradeoffs of growth potential and survival probability in different habitats. Some hatchery-reared steelhead smolts that were released in either 2007 or 2008 with a clipped adipose fin were caught in May 2009 migrating downstream (D. McCubbing, *pers. comm.*), but the proportion of smolts that temporarily residualized vs. permanently residualized is not currently known.

Management interest is not in residualization rate *per se*, but rather the combined rates of permanent residualization and mortality, since both possibilities result in fewer adult steelhead returning from the ocean as adults. Both factors are implicit in the estimates of ‘apparent survival’ presented here. The proportion of hatchery-reared steelhead smolts surviving to successive stations during the migration was in general much lower than that of wild smolts.
(Table 8.9), regardless of whether the assumed mark-recapture model had the most parsimonious fit to the data (Fig. 8.10) or the best fit without regard for pitfalls of over-parameterization (Fig. 8.7). The greatest differences in survival between wild and hatchery-reared fish occurred soon after release, during the downstream migration. Survival differences were much less during the inshore segments, so survival during the remainder of ocean life after leaving Queen Charlotte Strait may be reasonably similar for the subset of wild and hatchery-reared smolts that survived to the outer QCS line. This is supported by evidence for coho salmon that overwinter mortality (from September/November following outmigration to the following summer or fall of the return year) was not selective for rearing history. Wild and hatchery-reared fish returned at a similar rate (Beamish et al. 2004).
Table 8.1. Release groups of Cheakamus River steelhead smolts tagged in 2004, 2005, 2007 and 2008. Size criteria include fork length (FL) and condition factor (K).

<table>
<thead>
<tr>
<th>Release year</th>
<th>Rearing history</th>
<th>Release group</th>
<th>Release date</th>
<th>Release location</th>
<th>Mean FL [SD]</th>
<th>Range FL (mm)</th>
<th>Mean weight [SD]</th>
<th>Range weight (g)</th>
<th>Mean K [SD]</th>
<th>Range K</th>
<th>Number released</th>
</tr>
</thead>
<tbody>
<tr>
<td>2004 W</td>
<td>1</td>
<td>08 May</td>
<td>NVOS side channels</td>
<td>185.1 [16.8]</td>
<td>148–226</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>42</td>
<td></td>
</tr>
<tr>
<td>2004 W</td>
<td>2</td>
<td>24 May</td>
<td>NVOS side channels</td>
<td>181.3 [20.1]</td>
<td>153–215</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>9</td>
<td></td>
</tr>
<tr>
<td>2005 W</td>
<td>1</td>
<td>06 May</td>
<td>NVOS side channels</td>
<td>177.5 [14.2]</td>
<td>153–212</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>44</td>
<td></td>
</tr>
<tr>
<td>2005 W</td>
<td>2</td>
<td>19 May</td>
<td>NVOS side channels</td>
<td>177.8 [13.4]</td>
<td>160–197</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>5</td>
<td></td>
</tr>
<tr>
<td>2007 H (TCH)</td>
<td>1</td>
<td>06 May</td>
<td>Tenderfoot Hatchery</td>
<td>186.4 [9.6]</td>
<td>172–206</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>19</td>
<td></td>
</tr>
<tr>
<td>2007 H (FVTH)</td>
<td>1</td>
<td>23 May</td>
<td>Below Cheekye R. confluence</td>
<td>182.6 [11.6]</td>
<td>163–210</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>81</td>
<td></td>
</tr>
<tr>
<td>2008 W</td>
<td>1</td>
<td>06 May</td>
<td>NVOS side channels</td>
<td>177.6 [12.7]</td>
<td>149–209</td>
<td>56.6</td>
<td>34.9–100.0</td>
<td>0.84–1.27</td>
<td>72</td>
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<tr>
<td>2008 W</td>
<td>2</td>
<td>12 May</td>
<td>NVOS side channels</td>
<td>178.8 [9.5]</td>
<td>158–203</td>
<td>59.1</td>
<td>41.0–103.0</td>
<td>0.92–1.17</td>
<td>28</td>
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<td></td>
</tr>
<tr>
<td>2008 H (TCH)</td>
<td>1</td>
<td>05 May</td>
<td>Tenderfoot Hatchery</td>
<td>176.7 [8.7]</td>
<td>158–192</td>
<td>59.7</td>
<td>41.8–108.7</td>
<td>0.93–1.17</td>
<td>40</td>
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<td></td>
</tr>
<tr>
<td>2008 H (FVTH)</td>
<td>1</td>
<td>08 May</td>
<td>Upstream of Culliton Cr.</td>
<td>183.7 [13.6]</td>
<td>155–206</td>
<td>74.4</td>
<td>42.2–108.7</td>
<td>1.08–1.33</td>
<td>40</td>
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<td></td>
</tr>
<tr>
<td>2008 H (FVTH)</td>
<td>2</td>
<td>22 May</td>
<td>NVOS Gorbuscha channel</td>
<td>188.4 [10.0]</td>
<td>167–205</td>
<td>79.3</td>
<td>53.2–101.1</td>
<td>1.10–1.34</td>
<td>18</td>
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</tr>
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</table>
Table 8.2. Date and number of test tag passes conducted in 2008 at each receiver station in the Cheakamus River. Swim passes are boldfaced and passes by raft are italicized.

<table>
<thead>
<tr>
<th>Date</th>
<th>Chk_1</th>
<th>Chk_2</th>
<th>Chk_3</th>
<th>Chk_4</th>
<th>Chk_5</th>
<th>Chk_6</th>
<th>Chk_7</th>
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<td>May 08</td>
<td>-</td>
<td>-</td>
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<tr>
<td>May 09</td>
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<td>5</td>
<td>-</td>
<td>5</td>
<td>5</td>
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<tr>
<td>May 13</td>
<td>5</td>
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<td>Jun 09</td>
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<td>Aug 06</td>
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<td>8</td>
<td>1</td>
<td>1</td>
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</table>
Table 8.3. Detection probability indices considered for test tag passes at Cheakamus River receiver stations in 2008. The number of values for which the index could be calculated across all stations is indicated by $n$.

<table>
<thead>
<tr>
<th>Index</th>
<th>Description</th>
<th>$n$</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Presence or absence of any detections</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>P/A (per-tag)</td>
<td>Boolean value, equals 1 if the tag was detected at least once, and 0 otherwise</td>
<td>248</td>
</tr>
<tr>
<td>P/A (per-pass)</td>
<td>Boolean value, equals 1 if either tag was detected at least once, and 0 otherwise</td>
<td>131</td>
</tr>
<tr>
<td>P/A (per-set)</td>
<td>Average of the P/A (per-pass) index values</td>
<td>52</td>
</tr>
<tr>
<td><strong>Proportion of transmissions detected</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>%Det (per-tag)</td>
<td>Proportion of signals transmitted by a given tag between time-in and time-out that were detected</td>
<td>248</td>
</tr>
<tr>
<td>%Det (per-pass)</td>
<td>Proportion of signals transmitted by both tags between time-in and time-out that were detected</td>
<td>131</td>
</tr>
<tr>
<td>%Det (per-set)</td>
<td>Average of the %Det (per-pass) index values</td>
<td>52</td>
</tr>
<tr>
<td><strong>Ratio of temporal range of detections to the temporal range of transmissions</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>%Time (per-tag)</td>
<td>Time between the first and last detection of a given tag as a proportion of the time between time-in and time-out</td>
<td>101</td>
</tr>
<tr>
<td>%Time (per-pass)</td>
<td>Time between the first and last detection of either tag as a proportion of the time between time-in and time-out</td>
<td>66</td>
</tr>
<tr>
<td>%Time (per-set)</td>
<td>Average of the %Time (per-pass) index values</td>
<td>16</td>
</tr>
<tr>
<td><strong>Receiver meta-data during a set of passes</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Det:Sync</td>
<td>Number of tag detections divided by the number of syncs during the period of the set of passes</td>
<td>15</td>
</tr>
<tr>
<td>Det:Pulse</td>
<td>Number of tag detections divided by the number of (pulses/8) during the period of the set of passes</td>
<td>19</td>
</tr>
</tbody>
</table>
Table 8.4. Number (and percent) of tagged steelhead smolts detected at receiver stations during the 2008 smolt migration.

<table>
<thead>
<tr>
<th>Rearing history</th>
<th>RG</th>
<th>Number released</th>
<th>CHK_2</th>
<th>CHK_3</th>
<th>CHK_4</th>
<th>CHK_5</th>
<th>CHK_6</th>
<th>CHK_7</th>
<th>SQM_11</th>
<th>SQM_12</th>
<th>SQM_H</th>
<th>Hinner</th>
<th>Houter</th>
<th>NSOG</th>
<th>QCS</th>
<th>QCS</th>
<th>IDF</th>
<th>QCS + IDF</th>
</tr>
</thead>
<tbody>
<tr>
<td>W</td>
<td>1</td>
<td>72</td>
<td>66 (92)</td>
<td>62 (86)</td>
<td>9 (13)</td>
<td>49 (68)</td>
<td>48 (67)</td>
<td>42 (58)</td>
<td>46 (64)</td>
<td>38 (53)</td>
<td>26 (36)</td>
<td>10 (14)</td>
<td>2 (3)</td>
<td>2 (3)</td>
<td>12 (17)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>W</td>
<td>2</td>
<td>28</td>
<td>14 (50)</td>
<td>16 (57)</td>
<td>0 (0)</td>
<td>9 (32)</td>
<td>9 (32)</td>
<td>11 (39)</td>
<td>16 (57)</td>
<td>14 (50)</td>
<td>10 (36)</td>
<td>6 (21)</td>
<td>4 (14)</td>
<td>10 (35)</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>H (TCH)</td>
<td>1</td>
<td>40</td>
<td>25 (63)</td>
<td>16 (40)</td>
<td>14 (35)</td>
<td>1 (3)</td>
<td>12 (30)</td>
<td>13 (33)</td>
<td>12 (30)</td>
<td>11 (28)</td>
<td>7 (18)</td>
<td>1 (3)</td>
<td>0 (0)</td>
<td>1 (3)</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>H (FVTH)</td>
<td>1</td>
<td>40</td>
<td>22 (55)</td>
<td>13 (33)</td>
<td>18 (45)</td>
<td>13 (33)</td>
<td>5 (13)</td>
<td>0 (0)</td>
<td>9 (23)</td>
<td>12 (30)</td>
<td>12 (30)</td>
<td>5 (13)</td>
<td>4 (10)</td>
<td>3 (8)</td>
<td>1 (3)</td>
<td>0 (0)</td>
<td>1 (3)</td>
<td></td>
</tr>
<tr>
<td>H (FVTH)</td>
<td>2</td>
<td>18</td>
<td>0 (0)</td>
<td>1 (6)</td>
<td>2 (11)</td>
<td>5 (28)</td>
<td>2 (11)</td>
<td>5 (28)</td>
<td>4 (22)</td>
<td>5 (28)</td>
<td>5 (28)</td>
<td>2 (11)</td>
<td>0 (0)</td>
<td>2 (11)</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>


Table 8.5. Model selection results for detection probability ($p$) sub-models. $^a$

<table>
<thead>
<tr>
<th>Model</th>
<th>$k$</th>
<th>$-2\cdot\ln(L)$</th>
<th>QAICc</th>
<th>ΔQAICc</th>
</tr>
</thead>
<tbody>
<tr>
<td>$\phi$(seg:G), $p(S:Y+\text{lev}<em>{\text{Chek}}+\text{lev}</em>{\text{Sqm}})$ $^b$</td>
<td>149</td>
<td>2794.3</td>
<td>2512.2</td>
<td>0.0</td>
</tr>
<tr>
<td>$\phi$(seg:G), $p(S:G)$</td>
<td>201</td>
<td>2636.8</td>
<td>2519.0</td>
<td>6.8</td>
</tr>
<tr>
<td>$\phi$(seg:G), $p(S:Y+\text{lev}_{\text{Chek}})$ $^b$</td>
<td>148</td>
<td>2816.3</td>
<td>2527.0</td>
<td>14.8</td>
</tr>
<tr>
<td>$\phi$(seg:G), $p(S:Y)$ $^b$</td>
<td>147</td>
<td>2867.8</td>
<td>2564.8</td>
<td>52.6</td>
</tr>
</tbody>
</table>

$^a$ Quantities shown are number of parameters ($k$), log-likelihoods, and QAIC$_c$ values (adjusted for small sample sizes and extra-binomial variation with $\hat{\epsilon} = 1.279$). Sub-models for $p$ are compared while the fully time- (‘seg’) and group-varying CJS sub-model for $\phi$ (without main effects) is held constant, $[\phi$(seg:G)]$. The final station $p$ is fixed for all groups and models according to year-specific predictions ranging from 0.855 to 0.923. S = station; seg = segment; G = release group; Y = year; lev$_{\text{Chek}}$ = water level in the Cheakamus River at the mean arrival time of a particular release group at a particular station.

$^b$ Models contain group-specific $p$ parameters for the NSOG station for groups that showed split-route migration patterns beyond Howe Sound (a total of four parameters for six such groups, as two pairs of groups were pooled due to few detections at outer lines).

Table 8.6. Model selection results for survival ($\phi$) sub-models, focusing on rearing history effects. $^a$

<table>
<thead>
<tr>
<th>Model</th>
<th>$k$</th>
<th>$-2\cdot\ln(L)$</th>
<th>QAICc</th>
<th>ΔQAICc</th>
</tr>
</thead>
<tbody>
<tr>
<td>$\phi$(seg:$Y+\text{HW}+M_{i,H}+M_{i,W}$)</td>
<td>87</td>
<td>2861.5</td>
<td>2421.0</td>
<td>0.0</td>
</tr>
<tr>
<td>$\phi$(seg:$Y+\text{HW}+\text{stock}+M_{i,H}+M_{i,W}$)</td>
<td>89</td>
<td>2860.0</td>
<td>2424.3</td>
<td>3.3</td>
</tr>
<tr>
<td>$\phi$(seg:$Y+M_{i,H}+M_{i,W}$)</td>
<td>86</td>
<td>2870.1</td>
<td>2425.4</td>
<td>4.5</td>
</tr>
<tr>
<td>$\phi$(seg:$Y+\text{HW}$)</td>
<td>85</td>
<td>2873.7</td>
<td>2426.1</td>
<td>5.1</td>
</tr>
<tr>
<td>$\phi$(seg:$Y+\text{HW}+\text{stock}$)</td>
<td>87</td>
<td>2869.5</td>
<td>2427.2</td>
<td>6.2</td>
</tr>
<tr>
<td>$\phi$(seg:$Y$)</td>
<td>84</td>
<td>2887.2</td>
<td>2434.4</td>
<td>13.4</td>
</tr>
<tr>
<td>$\phi$(seg:$G$)</td>
<td>149</td>
<td>2794.3</td>
<td>2512.2</td>
<td>91.2</td>
</tr>
</tbody>
</table>

$^a$ Quantities shown are number of parameters ($k$), log-likelihoods, and QAIC$_c$ values (with $\hat{\epsilon} = 1.279$). Sub-models for $\phi$ are compared while the sub-model for $p$ is held constant at $[p(S:Y+\text{lev}_{\text{Chek}}+\text{lev}_{\text{Sqm}})]$ (not shown for clarity), in which four group-specific $p$ parameters for the NSOG station are included for groups that showed split-route migration patterns beyond Howe Sound. The final station $p$ is fixed for all groups according to year-specific predictions ranging from 0.855 to 0.923. seg = segment; G = release group; Y = year; HW = rearing history (hatchery or wild); stock = rearing hatchery (TCH or FVTH); $M_{i,H}$, $M_{i,W}$ = initial mortality in the first segment after release, common across all hatchery groups or wild groups, and additive to the ‘baseline’ mortality within each segment.
Table 8.7. Model selection results for survival (φ) sub-models, focusing on body size and release date effects.\textsuperscript{a}

<table>
<thead>
<tr>
<th>Model</th>
<th>$k$</th>
<th>$-2\cdot\ln(L)$</th>
<th>QAICc</th>
<th>ΔQAICc</th>
</tr>
</thead>
<tbody>
<tr>
<td>φ(seg;Y+HW+FL+$M_{i,H}$+$M_{i,W}$)</td>
<td>88</td>
<td>2849.7</td>
<td>2414.0</td>
<td>0.0</td>
</tr>
<tr>
<td>φ(seg;Y+HW+RD+FL+$M_{i,H}$+$M_{i,W}$)</td>
<td>89</td>
<td>2849.5</td>
<td>2416.0</td>
<td>2.0</td>
</tr>
<tr>
<td>φ(seg;Y+FL+$M_{i,H}$+$M_{i,W}$)</td>
<td>87</td>
<td>2860.5</td>
<td>2420.2</td>
<td>6.2</td>
</tr>
<tr>
<td>φ(seg;Y+HW+$M_{i,H}$+$M_{i,W}$)</td>
<td>87</td>
<td>2861.5</td>
<td>2421.0</td>
<td>7.0</td>
</tr>
<tr>
<td>φ(seg;Y+RD+FL+$M_{i,H}$+$M_{i,W}$)</td>
<td>88</td>
<td>2859.8</td>
<td>2421.9</td>
<td>7.9</td>
</tr>
<tr>
<td>φ(seg;Y+HW+RD+$M_{i,H}$+$M_{i,W}$)</td>
<td>88</td>
<td>2861.4</td>
<td>2423.1</td>
<td>9.1</td>
</tr>
<tr>
<td>φ(seg;Y+RD+$M_{i,H}$+$M_{i,W}$)</td>
<td>87</td>
<td>2869.6</td>
<td>2427.3</td>
<td>13.3</td>
</tr>
</tbody>
</table>

\textsuperscript{a} Quantities shown are number of parameters ($k$), log-likelihoods, and QAIC\textsubscript{c} values (adjusted for small sample sizes and extra-binomial variation with $\hat{\epsilon} = 1.279$). Sub-models for φ are compared while the sub-model for $p$ is held constant at $[p(S;Y+\text{lev}_{\text{Chk}}+\text{lev}_{\text{Sqm}})]$ (not shown for clarity), in which four group-specific $p$ parameters for the NSOG station are included for groups that showed split-route migration patterns beyond Howe Sound. The final station $p$ is fixed for all groups according to year-specific predictions ranging from 0.855 to 0.923. seg = segment; Y = year; HW = rearing history (hatchery or wild); FL = fork length; RD = release date; $M_{i,H}$, $M_{i,W}$ = initial mortality in the first segment after release, common across all hatchery groups or wild groups, and additive to the ‘baseline’ mortality within each segment.
Table 8.8. Model selection results for survival ($\phi$) sub-models, focusing on migration distance and its nested effects of year and release date.\(^a\)

<table>
<thead>
<tr>
<th>Model</th>
<th>$k$</th>
<th>$-2\cdot \ln(L)$</th>
<th>QAICc</th>
<th>$\Delta$QAICc</th>
</tr>
</thead>
<tbody>
<tr>
<td>$\phi(d_{Chk} + d_{Sqm} + d_{sw} + HW + FL + M_{i,H} + M_{i,W})$</td>
<td>51</td>
<td>2930.7</td>
<td>2396.7</td>
<td>0.0</td>
</tr>
<tr>
<td>$\phi(d_{Chk} + d_{Sqm} + d_{sw} + HW + FL + RD + M_{i,H} + M_{i,W})$</td>
<td>52</td>
<td>2928.2</td>
<td>2396.9</td>
<td>0.2</td>
</tr>
<tr>
<td>$\phi(d_{Chk} + d_{Sqm} + d_{sw} + HW \times FL + M_{i,H} + M_{i,W})$</td>
<td>52</td>
<td>2930.1</td>
<td>2398.3</td>
<td>1.6</td>
</tr>
<tr>
<td>$\phi(d + HW + FL + RD + M_{i,H} + M_{i,W})$</td>
<td>50</td>
<td>2936.7</td>
<td>2399.3</td>
<td>2.6</td>
</tr>
<tr>
<td>$\phi(d + HW + FL + M_{i,H} + M_{i,W})$</td>
<td>49</td>
<td>2941.8</td>
<td>2401.1</td>
<td>4.4</td>
</tr>
<tr>
<td>$\phi(d_{Chk} + d_{Sqm} + d_{sw} + HW + FL + Y + M_{i,H} + M_{i,W})$</td>
<td>54</td>
<td>2929.8</td>
<td>2402.4</td>
<td>5.7</td>
</tr>
<tr>
<td>$\phi(d + HW \times FL + M_{i,H} + M_{i,W})$</td>
<td>50</td>
<td>2941.3</td>
<td>2402.8</td>
<td>6.2</td>
</tr>
<tr>
<td>$\phi(d + HW + FL + Y + M_{i,H} + M_{i,W})$</td>
<td>52</td>
<td>2940.3</td>
<td>2406.4</td>
<td>9.7</td>
</tr>
<tr>
<td>$\phi(\text{seg}: Y +HW + FL + M_{i,H} + M_{i,W})$</td>
<td>88</td>
<td>2849.7</td>
<td>2414.0</td>
<td>17.3</td>
</tr>
<tr>
<td>$\phi(\text{seg}: Y +HW \times FL + M_{i,H} + M_{i,W})$</td>
<td>89</td>
<td>2849.1</td>
<td>2415.8</td>
<td>19.1</td>
</tr>
</tbody>
</table>

\(^a\) Quantities shown are number of parameters ($k$), log-likelihoods, and QAIC\(_c\) values (adjusted for small sample sizes and extra-binomial variation with $\hat{c} = 1.279$). Sub-models for $\phi$ are compared while the sub-model for $p$ is held constant at $\{p(S:Y+lev_{Chk}+lev_{Sqm})\}$ (not shown for clarity), in which four group-specific $p$ parameters for the NSOG station are included for groups that showed split-route migration patterns beyond Howe Sound. The final station $p$ is fixed for all groups according to year-specific predictions ranging from 0.855 to 0.923. seg = segment; $d$ = distance of the segment, used to constrain $\phi$ across all segments; $d_{Chk}$, $d_{Sqm}$, $d_{sw}$ = distance of segments in the Cheakamus River, Squamish River, and ocean that are used to constrain $\phi$ with habitat-specific relationships; $Y$ = year; HW = rearing history (hatchery or wild); FL = fork length; RD = release date; $M_{i,H}$, $M_{i,W}$ = initial mortality in the first segment after release, common across all hatchery groups or wild groups, and additive to the ‘baseline’ mortality within each segment.
Table 8.9. Estimated survivorship from release to three detection points during the steelhead smolt migration, under two different model assumptions.

<table>
<thead>
<tr>
<th>Model</th>
<th>Release group</th>
<th>Survivorship (S.E.)</th>
<th>to Sqm H or lowest Squamish River station</th>
<th>to HSOuter</th>
<th>to QCS/JDF</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>( \phi(d_{Chk}+d_{Sqm}+d_{sw}+HW+FL+RD+M_{1,t}+M_{1,W}) ), ( p(S:Y+lev_{Chk}+lev_{Sqm}) )</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>W RG1 2004</td>
<td>0.766 (0.034)</td>
<td>0.706 (0.035)</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>W RG2 2004</td>
<td>0.704 (0.061)</td>
<td>0.633 (0.070)</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>W RG1 2005</td>
<td>0.824 (0.028)</td>
<td>0.763 (0.032)</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>W RG2 2005</td>
<td>0.784 (0.036)</td>
<td>0.712 (0.044)</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>W RG1 2008</td>
<td>0.720 (0.034)</td>
<td>0.666 (0.039)</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>W RG2 2008</td>
<td>0.694 (0.037)</td>
<td>0.637 (0.043)</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>TCH 2007</td>
<td>0.364 (0.055)</td>
<td>0.303 (0.056)</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>TCH 2008</td>
<td>0.358 (0.048)</td>
<td>0.299 (0.048)</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>FVTH 2007</td>
<td>0.308 (0.047)</td>
<td>0.241 (0.045)</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>FVTH RG1 2008</td>
<td>0.233 (0.046)</td>
<td>0.192 (0.046)</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>FVTH RG2 2008</td>
<td>0.279 (0.052)</td>
<td>0.219 (0.050)</td>
</tr>
<tr>
<td></td>
<td></td>
<td>( \phi(seg:G), p(S:G) )</td>
<td>W RG1 2004</td>
<td>0.739 (0.077)</td>
<td>0.643 (0.084)</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>W RG2 2004 *</td>
<td>0.778 (0.157)</td>
<td>0.778 (0.157)</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>W RG1 2005</td>
<td>0.843 (0.063)</td>
<td>0.773 (0.071)</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>W RG2 2005 *</td>
<td>1 (0)</td>
<td>1 (0)</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>W RG1 2008</td>
<td>0.768 (0.057)</td>
<td>0.595 (0.068)</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>W RG2 2008</td>
<td>0.646 (0.104)</td>
<td>0.571 (0.106)</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>TCH 2007 *</td>
<td>0.579 (0.128)</td>
<td>0.510 (0.130)</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>TCH 2008</td>
<td>0.427 (0.089)</td>
<td>0.300 (0.082)</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>FVTH 2007</td>
<td>0.328 (0.066)</td>
<td>0.149 (0.049)</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>FVTH RG1 2008</td>
<td>0.325 (0.098)</td>
<td>0.150 (0.098)</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>FVTH RG2 2008 *</td>
<td>0.393 (0.131)</td>
<td>0.336 (0.127)</td>
</tr>
</tbody>
</table>

* Two wild release groups were over-parameterized under the general model with <10 fish tagged, and two hatchery groups had <20 tagged, so estimates for these groups under the general model are likely inaccurate.
Table 8.10. Detections providing potential evidence of residualized steelhead in the Cheakamus River in 2008. Listed in either detection category are fish that were not detected thereafter at Squamish River or ocean stations.

<table>
<thead>
<tr>
<th>Release group</th>
<th>Number released</th>
<th>Number detected &gt;4 weeks after release</th>
<th>Number detected upstream of release site</th>
<th>Range of dates detected</th>
<th>Range of river level (m)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>2007</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>FVTH</td>
<td>81</td>
<td>0</td>
<td>0</td>
<td></td>
<td></td>
</tr>
<tr>
<td>TCH</td>
<td>19</td>
<td>0</td>
<td>0</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Total 2007</td>
<td>100</td>
<td>0</td>
<td>0</td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>2008</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>W RG1</td>
<td>72</td>
<td>0</td>
<td>0</td>
<td></td>
<td></td>
</tr>
<tr>
<td>W RG2</td>
<td>28</td>
<td>1</td>
<td>0</td>
<td>July 2–5, 10–12, 14</td>
<td>1.05 – 1.85</td>
</tr>
<tr>
<td>FVTH RG1</td>
<td>40</td>
<td>2 §,*</td>
<td>1 *</td>
<td>June 6–Aug. 14; June 17–27, July 1</td>
<td>0.93 – 1.58; 0.96 – 1.84</td>
</tr>
<tr>
<td>FVTH RG2</td>
<td>18</td>
<td>1</td>
<td>0</td>
<td>July 28–29, Aug. 2–3</td>
<td>1.04 – 1.08</td>
</tr>
<tr>
<td>TCH</td>
<td>40</td>
<td>0</td>
<td>2 †</td>
<td>May 9; July 3</td>
<td>0.92; 1.84</td>
</tr>
<tr>
<td>Total 2008</td>
<td>198</td>
<td>3 §,*</td>
<td>3 *</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

§ One of the FVTH RG1 fish was detected nearly continuously from June 6–Aug 14 during periods of river levels <1.6 m. This is suggestive of a stationary tag near the receiver rather than in a live, residualized fish, so this fish is not considered a likely residual.

* The other FVTH RG1 fish met both criteria and is listed under both columns.

† One of the TCH fish was detected by mobile sampling upstream of the release site.
Table 8.11. Regression results for detection probability indices fit to river level measurements (reg 1), and for mark-recapture $p$ estimates fit to detection indices (reg 2). Criteria for comparing indices include $R^2$ values for regressions, slope ($\beta_8$) of reg 1, and intercept ($\beta_9$) and slope ($\beta_{10}$) of reg 2. The index selected for subsequent analyses is boldface italicized.

<table>
<thead>
<tr>
<th>Index</th>
<th>$n$</th>
<th>$\beta_8$</th>
<th>$R^2_{\text{reg 1}}$</th>
<th>$\beta_9$</th>
<th>$\beta_{10}$</th>
<th>$R^2_{\text{reg 2}}$</th>
</tr>
</thead>
<tbody>
<tr>
<td>Presence or absence of any detections</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>P/A (per-tag)</td>
<td>248</td>
<td>–6.39</td>
<td>0.36</td>
<td>0.38</td>
<td>0.44</td>
<td>0.77</td>
</tr>
<tr>
<td>P/A (per-pass)</td>
<td>131</td>
<td>–5.64</td>
<td>0.43</td>
<td>0.18</td>
<td>0.41</td>
<td>0.74</td>
</tr>
<tr>
<td>P/A (per-set)</td>
<td>52</td>
<td>–2.78</td>
<td>0.33</td>
<td>0.66</td>
<td>0.49</td>
<td>0.56</td>
</tr>
<tr>
<td>Proportion of transmissions detected</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>%Det (per-tag)</td>
<td>248</td>
<td>–1.38</td>
<td>0.29</td>
<td>8.64</td>
<td>2.22</td>
<td>0.79</td>
</tr>
<tr>
<td>%Det (per-pass)</td>
<td>131</td>
<td>–1.78</td>
<td>0.37</td>
<td>5.63</td>
<td>1.57</td>
<td>0.78</td>
</tr>
<tr>
<td>%Det (per-set)</td>
<td>52</td>
<td>–1.07</td>
<td>0.31</td>
<td>6.65</td>
<td>1.79</td>
<td>0.60</td>
</tr>
<tr>
<td>Ratio of temporal range of detections to the temporal range of transmissions</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>%Time (per-tag)</td>
<td>101 *</td>
<td>–2.36</td>
<td>0.11</td>
<td>4.81</td>
<td>1.02</td>
<td>0.74</td>
</tr>
<tr>
<td>%Time (per-pass)</td>
<td>66 *</td>
<td>–2.71</td>
<td>0.28</td>
<td>2.08</td>
<td>0.45</td>
<td>0.30</td>
</tr>
<tr>
<td>%Time (per-set)</td>
<td>16 *</td>
<td>–2.28</td>
<td>0.47</td>
<td>2.04</td>
<td>0.57</td>
<td>0.43</td>
</tr>
<tr>
<td>Receiver meta-data during a set of passes</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Det:Sync</td>
<td>15</td>
<td>–0.68</td>
<td>–0.03</td>
<td>0.93</td>
<td>0.43</td>
<td>0.31</td>
</tr>
<tr>
<td>Det:Pulse</td>
<td>19</td>
<td>0.32</td>
<td>0.54</td>
<td>0.86</td>
<td>0.40</td>
<td>0.22</td>
</tr>
</tbody>
</table>

* Note: at Chk_7 station, no tags were detected during passes, so %Time indices could not be calculated for this station.
Table 8.12. Estimation of residualization rate in the Cheakamus River for steelhead smolts in 2008. Detections of steelhead tags that were suggestive of possible residualization behaviour were combined with detection probability estimates ($p_{mr^*,i,RL}$) at the appropriate station and river level (RL) to predict the total number of tagged fish that residualized in the river. Estimates of $p_{mr^*,i,RL}$ are based on the test tag pass index [%Det (per-pass)].

<table>
<thead>
<tr>
<th>Release group</th>
<th>Station</th>
<th>Detection date(s)</th>
<th>Average RL during days detected</th>
<th>Corresponding $p_{mr^*,i,RL}$ (95% c. l.)</th>
<th>Extrapolated number of fish passing $i$ (95% c. l.)</th>
<th>Estimated residualization rate (95% c. l.)</th>
</tr>
</thead>
<tbody>
<tr>
<td>W RG2</td>
<td>Chk_5</td>
<td>July 2–5, 10–12, 14</td>
<td>1.40</td>
<td>0.47 (0.26 – 0.70)</td>
<td>2.14 (1.44 – 3.92)</td>
<td></td>
</tr>
<tr>
<td>FVTH RG1</td>
<td>Chk_1</td>
<td>June 17–27, July 1</td>
<td>1.11</td>
<td>0.22 (0.08 – 0.53)</td>
<td>4.55 (1.89 – 12.50)</td>
<td></td>
</tr>
<tr>
<td>FVTH RG2</td>
<td>Chk_6 $\dagger$</td>
<td>July 28–29, Aug. 2–3</td>
<td>1.06</td>
<td>0.58 (0.26 – 0.85)</td>
<td>1.73 (1.18 – 3.85)</td>
<td></td>
</tr>
<tr>
<td>TCH</td>
<td>Chk_3</td>
<td>May 8</td>
<td>0.92</td>
<td>0.85 (0.61 – 0.96)</td>
<td>1.18 (1.05 – 1.65)</td>
<td></td>
</tr>
<tr>
<td>TCH</td>
<td>mobile*</td>
<td>July 3</td>
<td>1.84 *</td>
<td>0.83 (0.62 – 0.94) *</td>
<td>1.21 (1.06 – 1.61)</td>
<td></td>
</tr>
</tbody>
</table>

$$D_{Chk,W} = 2.14 \ (1.44 - 3.92) \ 0.02 \ (0.01 - 0.04)$$

$$D_{Chk,H} = 8.66 \ (5.18 - 19.61) \ 0.09 \ (0.05 - 0.20)$$

$\dagger$ The fish passed Chk_5 undetected sometime between May 22–July 28. The average river level during this period was 1.29 m, and an extrapolated number calculated from this corresponding $p_{mr^*,i,RL}$ gives a similar result to that calculated for Chk_6 at 1.06 m.

* Detection probabilities during mobile sampling raft trips were not estimated. The fish was detected 4 d after release at Chk_4, presumably moving downstream. Since the mobile detection location was upstream of Chk_4, this implies the fish moved upstream past Chk_4 sometime between May 9–July 3 without being detected. The average river level during this period was 1.35 m, so $p_{mr^*,i,RL}$ is calculated for Chk_4 at 1.35 m.
Figure 8.1. Map of the portions of the Cheakamus and Squamish Rivers and inner Howe Sound monitored in years 2004, 2005, 2007, and 2008. Release sites are shown by X’s for wild groups (blue) and hatchery-reared groups (yellow). Red circles indicate locations of in-river acoustic receiver stations, and are labelled for Cheakamus River stations in the 2008 study. Red lines indicate the inner Howe Sound receiver line (HS_{inner}, composed of four receivers).
Figure 8.2. Daily means of water level in (a) the Cheakamus River and (b) the Squamish River during studies in 2004, 2005, 2007, and 2008. Water levels were measured at the Environment Canada gauge station near the Chk_5 (2008) station (Cheakamus River) and near Brackendale, downstream of the Cheakamus River confluence (Squamish River). Release times of tag groups are indicated for each year. The range of dates in each time series corresponds to when receivers were operational.
Figure 8.3. Length-weight relationships for tagged fish from wild groups and the two hatcheries (Tenderfoot Creek Hatchery and Fraser Valley Trout Hatchery) in 2008. Lengths are fork lengths.
Figure 8.4. Average counts of adult bull trout during snorkel surveys in the Cheakamus River during the period May 5–24 in years 2003–2008. Counts are averaged within each snorkel reach, and shown as year-specific as well as year-pooled. Locations of acoustic receiver stations in 2008 are shown, paired with the appropriate snorkel reach. Data provided by J. Korman.
Figure 8.5. A Lowess bivariate fit to bull trout counts during Cheakamus River snorkel surveys, by snorkel reach and day of month during the period May 1–24. All years (2003, 2005–2008) are pooled. A smoothing parameter value of 0.15 was assumed. Contours show average counts and shading is overlaid, ranging from low (dark) to high (light) counts. Raw data provided by J. Korman.
Figure 8.6. Migration timing and travel speed of release groups in 2004, 2005 and 2007 (a) and 2008 (b) past detection stations up to and including the inner Howe Sound line. Data points show cumulative travel time estimates since release plotted against cumulative distance travelled. Wild groups are shown by blues and purple while hatchery groups are shown by red, pink and oranges. Error bars show 1 S.E.
Figure 8.7. Survivorship estimates from release to successive detection stations during the steelhead migration. Different numbers and locations of receiver stations were used in different years. Estimates are shown for the model $\phi (\text{seg}; G), p(S; G)$, plotted against minimum migration distance from the point of release for each group. Wild groups are shown by blues and purple while hatchery groups are shown by red, pink and oranges. Error bars show 1 S.E. Note that models for four release groups are over-parameterized (see Table 8.9).
Figure 8.8. Estimated detection probabilities at receiver stations in the Cheakamus River, Squamish River, and early ocean portions of steelhead smolt migration routes in 2008. Estimates were generated under the assumed models: (a) \( \phi(\text{seg}:G), p(S:G) \), and (b) \( \phi(d_{\text{Chk}}+d_{\text{Sqm}}+d_{\text{sw}}+\text{HW}+\text{FL}+\text{RD}+M_{\text{HF}}+M_{\text{W}}), p(S:Y+\text{lev}_{\text{Chk}}+\text{lev}_{\text{Sqm}}) \), shown by release group. Error bars show 95% confidence limits.
Figure 8.9. Predicted survival probabilities in successive segments of the migration as a function of body size. Predictions are shown for one wild group (WRG2 2008, in blue) and one hatchery-reared group (FVTH RG2 2008, in red) under the model $[\phi(d_{\text{Chk}}+d_{\text{Sqm}}+d_{\text{sw}}+HW\times FL+M_{i,H}+M_{i,W})$, $p(S;Y+\text{lev}_{\text{Chk}}+\text{lev}_{\text{Sqm}})]$. Dotted lines show 95% confidence bands around best-fit predictions.
Figure 8.10. Survivorship estimates (a) and ln(survivorship) (b, next page) from release to successive detection stations during the steelhead migration. Different numbers and locations of receiver stations were used in different years. Estimates are shown for the model 
\[ \phi(d_{chk}+d_{sqm}+d_w+HW+FL+RD+M_{ii}+M_{iw}) \cdot p(S;Y+lev_{chk}+lev_{sqm}) \], plotted against minimum migration distance from the point of release for each group. Wild groups are shown by blues and purple while hatchery groups are shown by red, pink and oranges. Error bars in (a) show 1 S.E.
Figure 8.10 cont.  Part (b).
Figure 8.11. Survival rate (km$^{-1}$) of steelhead during the 2008 migration in Cheakamus River segments plotted against average bull trout density (km$^{-1}$) in the corresponding segment. Estimates are shown by release group under models \( \phi(\text{seg};G), p(S;G) \) (a) and \( \phi(\text{seg}+\text{HW}+\text{RD}+\text{FL}+M_{i,H}+M_{i,W}), p(S+\text{levChk}) \) (b). The first segment of each release group is excluded. Survival rates in the segment from Chk_5 to Chk_6, at 12.2 bull trout km$^{-1}$, are purposely offset to show 95% confidence limit error bars for each release group. Line shows the best-fit logistic curve through all points.
Figure 8.12. Mark-recapture detection probability estimates ($\Delta$) from 2008 model [$\phi$(seg+HW), $p$(S+lev Chk)] (with 95% confidence limits), and test tag pass index values (●) under the index [%Det (per-pass)] during the 2008 study. Estimates are plotted for each station in the Cheakamus River at the mean arrival time of a release group at a station. Area of the index points is proportional to the number of test tag passes with the same index value during that set of passes. River level is shown over the same period (grey line).
Figure 8.13. Regression of logit-transformed test tag pass index values under the index [%Det (per-pass)] against river level measured the day of the passes. Index values of 0 and 1 were set to 0.01 and 0.99, respectively, prior to transformation and regression. Slopes are constrained to be equal among the seven stations, but intercepts vary freely. Area of the index points is proportional to the number of test tag passes with the same index value and river level. Bands show 95% confidence limits of the best-fit regression line.
Figure 8.14. Regression of logit-transformed mark-recapture estimates from 2008 model [$\phi$(seg+HW), $p$(S+levChk)] against logit-transformed test tag pass index predictions under the index [%Det (per-pass)]. Index predictions were taken from the best-fit line of regression 1 at the same river level corresponding to the mark-recapture estimates. Bands show 95% confidence limits of the best-fit regression line.
Figure 8.15. Predicted detection probability (from best-fit lines of regression 1 and regression 2) and 95% bootstrap confidence interval bands as a function of river level. Predictions are shown for the seven Cheakamus River receiver stations under the index [%Det (per-pass)]. Mark recapture detection probability estimates (Δ) from 2008 model [φ(seg+HW), p(S+levChk)], with 95% confidence limits as error bars, are overlaid for comparison.
Figure 8.16. Predicted daily mark-recapture detection probability at seven Cheakamus River receiver stations from early May to mid-August. Thick black lines show the best-fit predictions, with thin black lines as 95% bootstrap confidence intervals. Predictions are shown using test tag pass index [%Det (per-pass)]. River level during this period is shown for comparison, overlaid as grey lines.
8.5 References


Multi-stock analysis of salmon smolt survival during the downstream and early ocean migration

9.1 Introduction

Pacific salmon exhibit tremendous variability in morphology, behaviour, and life history strategies both among and within populations (Groot and Margolis 1991, Taylor 1991, Bradford 1995, Quinn 2005). The smolt and post-smolt periods of salmon are thought to be particularly important in determining recruitment (Ricker 1976, Pearcy 1992), so factors affecting survival during these stages likely have a large impact on overall fitness. Joint analysis of survival data for multiple populations during the smolt migration may reveal patterns that would not be apparent at the level of a single population.

Several factors have been examined or proposed in previous studies that may affect survival during the smolt migration (Walters et al. 1978). Fish body size typically affects the probability of survival within a population, with larger individuals enjoying a survival advantage over smaller individuals (Lorenzen 1996, Sogard 1997). Larger fish are generally faster so can escape from predators more easily, may be above a critical size threshold for gape-limited predators, and with greater energy stores can better buffer against periodic food shortages compared with smaller fish. Smaller fish might also take longer on average to leave inshore areas, exposing them to more accumulated predation risk over this time.

To reach marine foraging areas, smolts must migrate downstream and through inshore waters. Distances during these portions of the migration vary among populations, with some travelling long distances during the downstream and early ocean migration before leaving the Georgia Strait system (e.g., mid-Fraser River populations, Fig. 1.4), and others travelling much shorter distances (e.g., Keogh and Nimpkish River populations). Since migration necessarily exposes salmon smolts to some degree of predation risk, it is expected that mortality should be higher for populations with further distances to migrate. Similarly, smolts that spend more time within the river environment or Georgia Strait system during the migration period may be more likely to suffer higher mortality than smolts that travel through these areas more quickly, due to a greater cumulative exposure to predation risk (unless the greater amount of time spent within these environments occurs in refuges where smolts are invulnerable to predators). The relative importance of migration distance and travel time as predictors of mortality may depend on
foraging strategies of predators and the resulting potential for repeat encounters between smolts and their predators (Anderson et al. 2005).

Migration date has been shown to affect survival of salmon smolts (e.g., Bilton et al. 1982, Scheuerell et al. 2009), and for the past several decades hatcheries have attempted to release their smolts at optimal times for survival. The optimal window of ocean entry may have recently shifted as a result of climate change (Beamish et al. 2008), so current hatchery release times are potentially sub-optimal, and changes in release date may affect survival in unpredictable ways.

Comparisons of survival during freshwater and/or marine phases of the life cycle have been made between different species of salmon (Bradford 1995) as well as between wild and hatchery rearing histories (Chapter 8; Reisenbichler and Rubin 1999). These differences are often confounded with other population differences like body size or migration distance, but by combining multiple populations in a single analysis and considering these many possible factors affecting survival together, effects of these factors may be teased apart.

In this chapter, we present the results of a joint survival analysis of 22 salmon smolt populations tagged and released across 13 watersheds in southern British Columbia under the Pacific Ocean Shelf Tracking Project (POST) in 2004–2007 (Fig. 1.4). In total, 44 ‘release groups’, or unique combinations of species, watershed, wild or hatchery rearing history, and release year were analyzed (Table A.2 in Appendix A). We use models developed in Chapter 3 to combine populations sharing the same tag type in terms of common detection probabilities at shared detection stations along migration routes. We hypothesize several factors that could affect survival of smolts, and formulate these as candidate models to be compared using model selection methods. We present results from a general, complex statistical model for survival probabilities, and then explore simpler models to evaluate which factors best explained variation in survival within and among populations.

9.2 Methods

In this chapter, we consider ‘population’ to be a group of fish of the same species from the same watershed (Table A.1) with the same rearing history (wild or hatchery). Not all populations were tagged in each year; fish from the same population that smolt and migrate in the same year are considered a ‘release group’. Note that within a release group, fish may be tagged and released over several days (Table A.2). Further descriptions about the populations included in this analysis, as well as tagging and receiver deployment procedures, are in Appendix
A. Some POST populations, in contrast, were not included in this analysis (Table A.3). Reasons for excluding these populations included small sample sizes, freshwater residency of the population, different acoustic output or average pulse interval of tags, fall releases, suspected poor physical condition, and absence of receiver stations at which to detect migrating smolts.

9.2.1 Survival and detection probability estimation

Spatial forms of Cormack-Jolly-Seber (CJS) models, where tagged animals are detected at fixed locations along a migration route rather than re-captured at fixed sampling times, are widely used for modelling survival in migrating salmon smolts (e.g., Burnham et al. 1987, Skalski et al. 2001, Zabel and Achord 2004). Sampling at successive detection stations 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 (Table A.2) so that populations could be linked where appropriate to compensate for small sample sizes of fish from some populations at some stations. Some stations were shared among all populations while others were unique to one or a few populations. The number and location of stations varied among years for some populations. Detection probabilities ($p$, the probability that a tag is detected at least once while passing a station) were generally treated as shared among populations with similar tag types experiencing similar environmental conditions. Survival probabilities ($\phi$) were treated as independent among populations in some models, but related through additive ‘effects’ of species, rearing history, release date, body size, segment distance or travel time in other more constrained models. These combined factors resulted in more intricate models than typical CJS models, and development of these required several steps and assumptions that are described in Chapter 3 and Appendix A. All mark-recapture models were implemented with Program MARK (ver. 5.1; White and Burnham 1999) through the R package RMark (ver. 1.8.8; Laake and Rexstad 2009).

Briefly, variations on the classic CJS model were based on several major assumptions that shaped model construction: (1) $p$ at a station was pooled across populations with the same tag type; (2) at Fraser River stations, $p$ was modelled as a function of the water level at the mean time of population crossing; (3) some populations exhibited split-route migration patterns in Georgia Strait so extra parameters were incorporated to allow for this flexibility and reduce the bias in $\phi$ estimates; (4) $p$ at the terminal detection stations (QCS and JDF) was predicted from $\hat{p}$ on other ocean lines and was assumed as a fixed value to untangle the confounded $\phi$ and $p$ parameters in the final segment/station.
We determined the detection history of individual fish at receiver stations (Chapter 3). Tagged smolts potentially passed between 2–12 stations during their migration (for a maximum of 13 digits in the detection history). The number of freshwater or estuary stations 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 lines potentially crossed was only one (at QCS) for Nimpkish and Keogh River populations leaving freshwater north of NSOG (these fish were only detected moving northward). The number of ocean lines potentially crossed for populations entering Georgia Strait south of NSOG was one (JDF) or two (NSOG and QCS) depending on the direction taken. Prior to entering Georgia Strait, some populations potentially crossed an additional one (across Burrard Inlet) or two (in Howe Sound) ocean lines.

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 station varied widely. Many populations had few detections at some stations, and \( \phi \) or \( \hat{p} \) would not have been reliable for these populations if separate CJS models were constructed for each population in each year (Chapter 3). Instead, the populations and years listed in Table A.2 were included in one of two datasets (17 groups for the Fraser River and 27 groups from other watersheds). Combining populations in the same analysis had three main advantages: (1) sample sizes of detected smolts from some populations at receiver stations were often small, so ‘borrowing’ information from other populations with the same tag type at the same station can result in more reliable parameter estimates (Chapter 3); (2) this allows a common relationship between model parameters (especially \( p \)) and environmental covariates like river level or day of year, since this relationship is expected to be consistent across populations and years; and (3) similarly, this allows estimation of a common effect of individual covariates across populations, such as the effect of tag type on \( p \) or body size on \( \phi \). We assume that the same tag type (and therefore acoustic power) passing over a river receiver line around the same time has the same probability of being detected regardless of the species or population from which the tagged smolts originated (apart from run timing differences between populations at Fraser River stations, Chapter 3.5). It was computationally infeasible to combine all 44 release groups in the same analysis, as run time of models increased closer to exponentially than linearly with the number of groups included.

Tagged salmon smolts originated from diverse locations in southern B.C. (Fig. 1.4). Along the migration route of a population, some detection stations were shared with other populations and some were unique. To analyze multiple populations and years together in the same model, this required appropriately pairing the detection history digit for each population.
with those from other populations. In other cases, particular stations at a given digit of the
detection history were not common to all populations. This was not an issue for the Fraser River
dataset since, at least within each year, all populations shared the same receiver stations along
migratory routes. For the non-Fraser dataset, having different receiver stations represented at a
given digit was dealt with by incorporating extra parameters to represent the interaction of
stations, years, and general migration route clusters (Chapter 3.3). These parameters were
additive components of all $p$ sub-models ($[p]$). They ensured that $\hat{\phi}$ were common for
populations with the same tag type at some station in some year, but were independent from
populations with migration routes that brought them past different stations at the same given
detection history digit. Eleven such parameters were required to specify such distinctions over all
stations, years, and populations outside of the Fraser River.

A variance inflation factor ($c$) was estimated to compensate for overdispersion in
detection data (Burnham et al. 1987). This was used to expand variances and covariances of
parameter estimates. Estimated $c$ values were also used for model comparisons, with computed
QAICc values corrected for both extra-binomial variation (Lebreton et al. 1992) and small
sample sizes (Burnham and Anderson 2002). We estimated $c$ assuming the general CJS model
$[\phi_{\text{seg} \times (G:Tag)} p_{S \times (G:Tag)}]$, where ‘seg’ represents segment of the migration, ‘S’ represents
detection station, ‘Tag’ represents tag type, and ‘G’ represents release group. We used two
bootstrapping methods implemented through Program MARK. 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 about $\hat{c} = 1.245$ using the deviance ratio method).

In this chapter, we present survival results as ‘downstream’ (from release to river mouth
or lowest in-river receiver station) and ‘total’ (downstream+inshore; from release to terminal
stations) components. The product of segment-specific $\hat{\phi}$ during either the downstream or ‘total’
migration of each population was calculated as an estimate of ‘downstream’ or ‘total’
survivorship, respectively. The variances of these products were calculated using the Delta
method. Additionally, we present instantaneous mortality rate estimates, both distance-based
($M_d$, km$^{-1}$) and time-based ($M_{TT}$, d$^{-1}$) for the downstream and inshore components. These were
calculated for each release group $i$ simply as $M_{d,i} = -\ln(\hat{\phi}_i)/d_i$ or $M_{TT,i} = -\ln(\hat{\phi}_i)/TT_i$, where $\hat{\phi}$ is
estimated survival (with release groups fully-independent) for either the downstream or the
inshore (excluding downstream) portion of the migration, \( d \) is minimum travel distance, and TT
is the average travel time of smolts that were detected. To represent exit from Georgia Strait
regardless of the particular direction that fish took after ocean entry, detections at the terminal
stations (QCS and JDF) were pooled in the final digit of detection history sequences. This
pooling somewhat complicates estimates of \( \phi \) to NSOG and \( p \) at NSOG, but this was easily
resolved by incorporating population-specific parameters for NSOG that represented joint
probabilities of detection and northward movement (Chapter 3.4). 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.

The large number of possible factors considered here that may affect \( p \) and \( \phi \) can result in
a set of hundreds of candidate models containing various combinations of these factors. This is
undesirable in model selection procedures (Burnham and Anderson 2002). Others have used
sequential model comparisons, first comparing a small number of candidate models for \( p \), and
then selecting the best model(s) for a subsequent comparison(s) of a small number of candidate
models for \( \phi \) (Lebreton et al. 1992, Zabel et al. 2005, Keeler et al. 2007). We took a similar
approach, using four steps: (1) comparing \([p]\) while holding constant a general \([\phi]\); (2)
comparing reduced \([\phi]\) in terms of rearing history while holding constant the best \([p]\) from the
previous step; (3) comparing \([\phi]\) in terms of body size, tag size, and release date effects, building
on the \([\phi]\) from the previous step; and (4) comparing distance- and travel time-based \([\phi]\),
building on the best \([\phi]\) from the previous step.

9.2.2 Comparison of detection probability models

Several candidate models representing hypotheses of how \( p \) is affected by factors such as
tag type and river flow were fit to the detection data. In all models, \( p \) was specified as station-
specific and year-specific. In some models considered, \( p \) was specified as tag type-specific, since
V9 tags (142 dB re 1\( \mu \)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 station 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; see below). We also constrained the relative difference in \( \hat{p} \)
between tag types to be additive (i.e., constant in logit space) across years and detection stations.
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.

In the Fraser River, multiple release groups were tagged and released at varying times throughout the migratory season (Fig. 3.4), so the potential effect of increasing water level on \( p \) was considered in some candidate models. This effect is observed by initially treating groups independently. Figure 9.1 shows fully-independent \( \hat{p} \) for all Fraser River populations, i.e., model \([\phi_{\text{seg},G}, p_{\text{S},G:\text{Tag}}]\), where ‘G’ is a unique combination of species, watershed, hatchery or wild-reared provenance, and year. The number and locations of receiver stations in the Fraser River varied among years, so the first station encountered in one year is not necessarily the same as the first station in another year. Estimates of \( p \) for a particular group and tag type are plotted against the water level measured at the mean arrival time of that group at a particular station, as in Fig. 3.5. On average, and within each tag type, these stock-specific \( \hat{p} \) 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 higher 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.

Modelling \( p \) as fully-independent among populations results in several \( \hat{p} \) that are imprecise and susceptible to over-fitting (Fig. 9.1), while at the other extreme, fully pooling populations at a given station in a given year results in an average \( \hat{p} \) that does not capture any seasonal trend (Chapter 3.5). To achieve a good balance in this trade-off between bias and precision, models incorporating an environmental covariate were considered for the Fraser River dataset. These \([p]\) 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 station. Daily water level data from two Environment Canada gauge stations in the lower Fraser River (at Mission and Port Mann) were matched to the DOY of mean arrival time at each receiver station; these provided two other models. A fourth model incorporated both water level covariates, with the measure for each detection station taken from a combination of both gauge stations. This fourth model was hypothesized because \( p \) at Mission receiver stations likely correlates best with the Mission water level, but increased inflow from tributaries downstream of this station are such that \( p \) at lines

\[\text{8} \] The Mission gauge was closest to the first detection station in 2004 and 2007, but to avoid over-fitting to only two stations, the water level at Mission was used as a covariate for all stations and years. In addition to this, the water level at Port Mann was used as another additive covariate at all later river stations in all years.
Further downstream may correlate better with water level at the Port Mann gauge, further downstream. These covariate effects were additive: slopes of \( p \) vs. DOY or water level were assumed to be constant across years, stations, and tag types, but the intercepts were permitted to vary for year/station 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 four years 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 station 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.

**List of candidate models: detection probabilities**

To compare \([p]\), we assumed a general CJS \([\phi]\) where segment-specific \( \hat{\phi} \) varied freely for each release group. Main effects of segment and group *per se* were not of interest, especially since the \( n^{th} \) segments of different groups were often in different geographic locations.

Models for \( p \) allowed independent estimates for each particular combination of station and year, i.e., \([p_{S,Y}]\), and most \([p]\) involved additional parameters that increased the flexibility of \( \hat{p} \). In all models, tags of the same acoustic output crossing a particular receiver station around the same time were assumed to have a common \( p \) even if they were implanted into smolts from different populations. For the non-Fraser dataset, this required including additional ‘cluster’ parameters to ensure that fish crossing the same station had a common \( \hat{p} \) for that station, while \( \hat{p} \) were different for fish crossing different stations at the same digit of their detection history sequence (i.e., this maintained appropriate structures of nested migration routes; Chapter 3). In some models, \( \hat{p}_{V7} \) and \( \hat{p}_{V9} \) were allowed to differ (consistently across stations and years), and in other more constrained models, a common \( \hat{p} \) was assumed with tag types pooled. In the Fraser River dataset, various run timing or river flow covariates were used to characterize seasonal changes in \( p \). Finally, in all models \( p_{\text{final}} \) was fixed at a value derived from an isolated analysis of \( p \) on ocean receiver lines, adjusting for geometrical properties of individual receiver lines (Appendix A). Fixing this parameter allowed estimation of \( \phi_{\text{final}} \) (conditioned on the fixed value assumed for \( p_{\text{final}} \)), which would otherwise be confounded with \( p_{\text{final}} \).
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) and five possibilities for environmental covariates during mean arrival time at detection stations, for a total of 10 candidate models:

1. \( \phi(\text{seg}; G), p(S; Y) \)  
   \( p \) estimates independent among stations and years, but all populations are pooled at each station/year combination

2. \( \phi(\text{seg}; G), p(S; Y + \text{DOY}) \)  
   \( p \) estimates for Fraser River stations related among stations and years by an additive effect of the average release date (day of year) of each group

3. \( \phi(\text{seg}; G), p(S; Y + \text{lev}_{\text{mis}}) \)  
   \( p \) estimates for Fraser River stations related among stations and years by an additive effect of water level at the Mission gauge station measured at the mean arrival time of each group at each station/year

4. \( \phi(\text{seg}; G), p(S; Y + \text{lev}_{\text{pm}}) \)  
   \( p \) estimates for Fraser River stations related among stations and years by an additive effect of water level at the Port Mann gauge station measured at the mean arrival time of each group at each station/year

5. \( \phi(\text{seg}; G), p(S; Y + \text{lev}_{\text{mis}} + \text{lev}_{\text{pm}}) \)  
   \( p \) estimates for Fraser River stations related among stations and years by additive effects of water level at the Mission gauge station (for all stations) and the Port Mann gauge station (for stations downstream of Mission) measured at the mean arrival time of each group at each station/year

6. \( \phi(\text{seg}; G), p(S; Y + \text{Tag}) \)  
   like (1), with an additive effect of tag type (i.e., separate \( p \) estimates for V7 and V9 tags, with a constant difference in logit space across all stations and years)

7. \( \phi(\text{seg}; G), p(S; Y + \text{DOY} + \text{Tag}) \)  
   like (2), with an additive effect of tag type

8. \( \phi(\text{seg}; G), p(S; Y + \text{lev}_{\text{mis}} + \text{Tag}) \)  
   like (3), with an additive effect of tag type

9. \( \phi(\text{seg}; G), p(S; Y + \text{lev}_{\text{pm}} + \text{Tag}) \)  
   like (4), with an additive effect of tag type

10. \( \phi(\text{seg}; G), p(S; Y + \text{lev}_{\text{mis}} + \text{lev}_{\text{pm}} + \text{Tag}) \)  
    like (5), with an additive effect of tag type

In the non-Fraser dataset, there were two possibilities for tag type:

1. \( \phi(\text{seg}; G), p(S; Y + \text{Clusters}) \)  
   \( p \) estimates independent among stations and years, but populations are pooled at each station/year combination that they share along their migration routes

2. \( \phi(\text{seg}; G), p(S; Y + \text{Clusters} + \text{Tag}) \)  
   like (1), with an additive effect of tag type (i.e., separate \( p \) estimates for V7 and V9 tags, with a constant difference in logit space across all stations and years)
9.2.3 Comparison of survival probability models

“All models are wrong, but some are useful”

George E. P. Box

This chapter does not pretend to find a single ‘best’ model to describe variation in survival and estimate parameters \( p \) and \( \phi \) with an optimal trade-off of bias and precision. Beginning with the general \( \phi \), the number of biologically reasonable reduced models involving various subsets of factors of interest (species, watershed, rearing history, year, body size, tag type, release date, and migration distance or travel time) could be overwhelming, especially with interactions considered. Instead, with a goal of identifying which factor(s) are most important overall in explaining variation in survival, we start with a simple framework for specifying \( \phi \), and mainly just consider additive effects on survival. For example, rather than considering large multiplicative models with separate effects for each release group, we consider the overall effect of these factors in simpler models. In such an approach, it is entirely possible that an AIC-best model could fall somewhere between the general CJS \( \phi \) and this set of simpler, more reduced models, so there is admittedly a higher chance of under-fitting models to detection data and missing some sources of variation. As we will see, however, this potential for increased bias in parameter estimates (from under-fitting) probably pales in comparison to other sources of bias where a group of tagged fish may not be representative of the population of interest.

The first step of comparing \( \phi \) involved looking at effects of watershed of origin, species, and wild or hatchery rearing history. In all segment-based \( \phi \) (as opposed to distance- or travel time-based models), \( \phi \) was modelled as independent among unique combinations of segment and year (since stations were usually in different locations in different years). In some models, watershed of origin was incorporated as an additive effect (i.e., \( \phi_{\text{seg}:Y+W+...} \)), with a constant effect of watershed of origin across all segment-year combinations of the migration. In other models it was incorporated as part of the unique combinations of segment, year and watershed (i.e., \( \phi_{\text{seg}:Y:W+...} \)), where the effect of watershed of origin may differ across segments (for example, there may be differences among watersheds in some shared segments of survival, but in other segments survival may be similar among different watersheds of origin). Added to this framework were overall effects of species (‘spp’; Fraser River dataset: Chinook, coho, sockeye, steelhead; non-Fraser dataset: these same four as well as kokanee; Table A.2), wild or hatchery rearing history (‘HW’; including one ‘unknown’ group in each of the datasets in which fish were
caught in rotary screw traps downstream of a hatchery release site where not all hatchery fish had adipose fins clipped), or both species and HW.

In multi-stock analyses where populations have nested migration route structures, some segments of migration routes may be common among populations while others may be in geographically distinct locations, even if those segments are represented by the same digit of a detection history sequence. Similar to how ‘cluster’ parameters were used in the previous section and Chapter 3 for modelling $p$, parameters involving interactions of segment, year, and general migration route cluster (seg; $Y_j; C_m$) were used for $[\phi]$ to ensure that populations sharing a segment of their migration routes were grouped appropriately at their $n^{th}$ detection history digit, and were separated from other populations that crossed a different station at their $n^{th}$ digit. In the non-Fraser dataset, 28 such additive cluster parameters (‘CP’) were required to differentiate segments in this complex structure of nested migration routes (Fig. 1.4). In the Fraser River dataset, although all release groups shared the same first detection station, the physical routes of this first segment were often very different depending if fish were released in the lower Fraser, Deadman, Nicola, Spus, or Coldwater watersheds, or even at different locations within each watershed (Fig. 1.4). Cluster parameters (9 in total; additive) were also used to differentiate different migration routes in the first segment of these Fraser River populations. These CP parameters in both datasets were only required when watershed of origin was modelled as an additive effect. They were not necessary in models where watershed of origin was part of an interaction with segment and year, since these models already provide sufficient independence of clusters in each segment and year.

The first segment after release may have particularly high mortality rates (per unit distance or time travelled) compared to other segments as a result of ‘distance-independent’ factors like tagging effects or predator aggregations at release locations. This initial mortality may reasonably differ for wild and hatchery reared fish, since the latter have not generally been exposed to selective predation pressures prior to release. Additive effects of initial mortality ($M_{i,W}$ and $M_{i,H}$; separate for wild and hatchery reared fish) were incorporated into models for the non-Fraser dataset, allowing for flexibility in survival in the first segment after release (as in Chapter 8). $M_{i,W}$ and $M_{i,H}$ were not necessary in segment-based models used for the Fraser River dataset, since the CP parameters happened to provide all necessary differentiation among wild and hatchery fish in their first segment after release in a given year.

The second step of comparing $[\phi]$ involved considering effects of individual covariates, that is, factors that varied within release groups. Body size (measured by fork length, FL) was
considered in some models as a continuous covariate. In models with FL, some further included an additive effect of tag size (‘Tag’) or a multiplicative effect of FL×Tag on survival. Tag size was treated as a discrete (i.e., group) covariate, with V7-2L and V9-6L tag models used in the non-Fraser dataset, and these as well as V9-1L and V9-2L tag models used in the Fraser dataset. In some models, release date (measured as day since 1 Jan of that year) was considered as a continuous covariate.

The third comparison of $\phi$ involved distance-based and travel time-based model specifications. Rather than separate $\hat{\phi}$ in each segment, $\phi_{\text{seg}}$ was constrained to be a linear function (in logit space) of the segment distance (‘$d$’) or the average travel time (‘TT’) of detected fish in the segment. Average travel times within a segment were estimated as differences between cumulative travel times from release to adjacent stations (Appendix A). In some models, the relationship between $\phi_{\text{seg}}$ and $d$ (or TT) was assumed to apply across all segments of the migration. In other models, separate relationships were assumed for freshwater segments and inshore segments.

These distance-based or time-based models were not considered simply to assess the overall effect of distance or travel time on survival. The main reasons for using these model structures are: (1) they allow a comparison of whether distance-based or time-based models are better at explaining variation in survival. (2) They permit a framework involving fewer numbers of parameters than if separate $\phi_{\text{seg}}$ were estimated independently. Other possible effects on survival (body size, species, rearing history) can be incorporated into this framework, and the importance of these factors in explaining variation in survival may differ whether they are considered under more constrained distance- (or time-) based models or more complex segment-based models. (3) Distance-based or travel time-based survival rate estimates (per unit distance or time) can be allowed to vary across segments or habitats. This provides a straightforward means of assessing whether instantaneous mortality rates change during the migration.

List of candidate models for survival: watershed, species, and rearing history effects

Survival models considered had either a base of unique combinations of segment and year (with an additive effect of watershed of origin), or unique combinations of segment, year, and watershed. Under these frameworks, additive effects of species and rearing history were also considered (specified as group covariates, meaning all individuals of the group share the same trait, or level of the factor effect). For each dataset, the best $[p]$ from the previous model
comparison was held constant. In total, eight models were considered for the Fraser River analysis:

1. \( \phi(\text{seg}:Y+W+CP), \)
   \( p(S:Y+\text{lev}_{\text{mis}}+\text{lev}_{\text{PM}}+\text{Tag}) \)
   \( \hat{\phi} \) related among unique combinations of segments and years by an additive effect of watershed of origin (i.e., species and wild/hatchery rearing histories are pooled); additive initial mortality by release location clusters

2. \( \phi(\text{seg}:Y+W+CP+spp), \)
   \( p(S:Y+\text{lev}_{\text{mis}}+\text{lev}_{\text{PM}}+\text{Tag}) \)
   \( \hat{\phi} \) related among segments and years by additive effects of watershed of origin and species (HW rearing histories are pooled); additive initial mortality by release location clusters

3. \( \phi(\text{seg}:Y+W+CP+HW), \)
   \( p(S:Y+\text{lev}_{\text{mis}}+\text{lev}_{\text{PM}}+\text{Tag}) \)
   \( \hat{\phi} \) related among segments and years by additive effects of watershed of origin and HW rearing histories (species are pooled); additive initial mortality by release location clusters

4. \( \phi(\text{seg}:Y+W+CP+spp+HW), \)
   \( p(S:Y+\text{lev}_{\text{mis}}+\text{lev}_{\text{PM}}+\text{Tag}) \)
   \( \hat{\phi} \) related among segments and years by additive effects of watershed of origin, species, and HW rearing histories; additive initial mortality by release location clusters

5. \( \phi(\text{seg}:Y:W), \)
   \( p(S:Y+\text{lev}_{\text{mis}}+\text{lev}_{\text{PM}}+\text{Tag}) \)
   \( \hat{\phi} \) fully independent among unique combinations of segments, years, and watershed of origin (species and HW rearing histories are pooled)

6. \( \phi(\text{seg}:Y:W+spp), \)
   \( p(S:Y+\text{lev}_{\text{mis}}+\text{lev}_{\text{PM}}+\text{Tag}) \)
   \( \hat{\phi} \) related among unique combinations of segments, years, and watershed of origin by an additive effect of species (HW rearing histories are pooled)

7. \( \phi(\text{seg}:Y:W+HW), \)
   \( p(S:Y+\text{lev}_{\text{mis}}+\text{lev}_{\text{PM}}+\text{Tag}) \)
   \( \hat{\phi} \) related among unique combinations of segments, years, and watershed of origin by an additive effect of HW rearing histories (species are pooled)

8. \( \phi(\text{seg}:Y:W+spp+HW), \)
   \( p(S:Y+\text{lev}_{\text{mis}}+\text{lev}_{\text{PM}}+\text{Tag}) \)
   \( \hat{\phi} \) related among unique combinations of segments, years, and watershed of origin by additive effects of species and HW rearing histories

A similar set of eight models were compared in the non-Fraser analysis, which differed in some respects: a different \( [p] \) was held constant; different cluster parameter for \( \phi \) were used, and initial mortality parameters for wild and hatchery fish were necessary.

1. \( \phi(\text{seg}:Y+W+CP+M_{\text{sw}}+M_{\text{sh}}), \)
   \( p(S:Y+\text{Clusters}+\text{Tag}) \)
   \( \hat{\phi} \) related among unique combinations of segments and years by an additive effect of watershed of origin (i.e., species and wild/hatchery rearing histories are pooled); additive initial mortality by release location clusters and by HW rearing history

2. \( \phi(\text{seg}:Y+W+CP+M_{\text{sw}}+M_{\text{sh}}+spp), \)
   \( p(S:Y+\text{Clusters}+\text{Tag}) \)
   \( \hat{\phi} \) related among segments and years by additive effects of watershed of origin and species (HW rearing histories are pooled); additive initial mortality by release location clusters and by HW rearing history
3. \( \phi(\text{seg}: Y+W+CP+M_{i,w}+M_{i,h}+HW), \)
\( p(S: Y+\text{Clusters}+Tag) \)
\( \hat{\phi} \) related among segments and years by additive effects of watershed of origin and HW rearing history (species are pooled); additive initial mortality by release location clusters and by HW rearing history

4. \( \phi(\text{seg}: Y+W+CP+M_{i,w}+M_{i,h}+spp+HW), \)
\( p(S: Y+\text{Clusters}+Tag) \)
\( \hat{\phi} \) related among segments and years by additive effects of watershed of origin, species, and HW rearing history; additive initial mortality by release location clusters and by HW rearing history

5. \( \phi(\text{seg}: Y+W+CP+M_{i,hl}), \)
\( p(S: Y+\text{Clusters}+Tag) \)
\( \hat{\phi} \) independent among unique combinations of segments, years, and watershed of origin (species and HW rearing histories are pooled); additive initial mortality by HW rearing history

6. \( \phi(\text{seg}: Y+w+spp+M_{i,w}+M_{i,hl}), \)
\( p(S: Y+\text{Clusters}+Tag) \)
\( \hat{\phi} \) related among segment, year, and watershed of origin combinations by an additive effect of species (HW rearing histories are pooled); additive initial mortality by HW rearing history

7. \( \phi(\text{seg}: Y+HW+M_{i,w}+M_{i,hl}), \)
\( p(S: Y+\text{Clusters}+Tag) \)
\( \hat{\phi} \) related among segment, year, and watershed of origin combinations by an additive effect of HW rearing history (species are pooled); additive initial mortality by HW rearing history

8. \( \phi(\text{seg}: Y+w+spp+HW+M_{i,w}+M_{i,hl}), \)
\( p(S: Y+\text{Clusters}+Tag) \)
\( \hat{\phi} \) related among segment, year, and watershed of origin combinations by additive effects of species and HW rearing history; additive initial mortality by HW rearing history

For both datasets, the general CJS model \([\phi_{\text{seg}: G}]\) does not appear in the model set since the intention is to evaluate simpler models and compare which factors have the greatest effect on variation in survival. These reduced models were compared to the general model for reference.

**List of candidate models for survival: body size, tag size, and release date effects**

For each dataset, the AIC-best \([\phi]\) from the model set in the previous comparison was carried forward to evaluate effects of fork length, tag size, and release date on survival. In total, eight models were considered for the Fraser River dataset:

1. \( \phi(\text{seg}: Y+W+CP+spp), \)
\( p(S: Y+\text{lev}_{\text{Mis}}+\text{lev}_{\text{PM}}+\text{Tag}) \)
\( \hat{\phi} \) related among unique combinations of segments and years by additive effects of watershed of origin and species (i.e., HW rearing histories are pooled); additive initial mortality by release location clusters

2. \( \phi(\text{seg}: Y+W+CP+spp+FL), \)
\( p(S: Y+\text{lev}_{\text{Mis}}+\text{lev}_{\text{PM}}+\text{Tag}) \)
\( \hat{\phi} \) related among segments and years by additive effects of watershed of origin, species, and fork length (HW rearing histories are pooled); additive initial mortality by release location clusters
A similar set of eight models was considered for the non-Fraser dataset, the difference being in the base model that was carried forward from the previous model comparison:

1. \(\phi(seg:Y+W+HW-M_{i,w}+M_{i,h}),\)  
   \(p(S:Y+Clusters+Tag)\)  
   \(\phi\) related among unique combinations of segment, year, and watershed of origin by an additive effect of HW rearing history (i.e., species are pooled); additive initial mortality by HW rearing history

2. \(\phi(seg:Y+W+HW-M_{i,w}+M_{i,h}+FL),\)  
   \(p(S:Y+Clusters+Tag)\)  
   \(\phi\) related among segment, year, and watershed combinations by additive effects of HW and fork length; additive initial mortality by HW rearing history

3. \(\phi(seg:Y+W+HW-M_{i,w}+M_{i,h}+FL+Tag),\)  
   \(p(S:Y+Clusters+Tag)\)  
   \(\phi\) related among segment, year, and watershed combinations by additive effects of HW, fork length, and tag size; additive initial mortality by HW rearing history

4. \(\phi(seg:Y+W+HW-M_{i,w}+M_{i,h}+FL\times Tag),\)  
   \(p(S:Y+Clusters+Tag)\)  
   \(\phi\) related among segment, year, and watershed combinations by additive effects of HW, fork length, and tag size, with an interaction between FL and Tag; additive initial mortality by HW rearing history

5. \(\phi(seg:Y+W+HW-M_{i,w}+M_{i,h}+RD),\)  
   \(p(S:Y+Clusters+Tag)\)  
   like (1), with additive effect of release date

6. \(\phi(seg:Y+W+HW-M_{i,w}+M_{i,h}+FL+RD),\)  
   \(p(S:Y+Clusters+Tag)\)  
   like (2), with additive effect of release date
7. $\phi(\text{seg}; Y; W + HW + M_{i,w} + M_{i,h} + \text{FL} \times \text{Tag} + \text{RD})$, like (3), with additive effect of release date $p(S; Y + \text{Clusters} + \text{Tag})$

8. $\phi(\text{seg}; Y; W + HW + M_{i,w} + M_{i,h} + \text{FL} \times \text{Tag} + \text{RD})$, like (4), with additive effect of release date $p(S; Y + \text{Clusters} + \text{Tag})$

Again, the general CJS $[\phi]$ (or any intermediate models) is not present in this model set, but is compared to these reduced models for reference.

**List of candidate models for survival: distance and travel time-based models**

Segment-based models for $\phi$ are generally more complex and flexible than models constrained by distance or average travel time of each segment. It is possible that a dataset would support more additive effects under distance- or travel time-based models than would be warranted under segment-based models. Since the interest here is in identifying important factors affecting survival, however, there is little concern about under-fitting distance-based models to detection data relative to segment-based models (i.e., if an additive factor is important, it should be obvious in either a segment-based model or a distance-based model). The additive parameters from the best $[\phi]$ for each dataset from the previous comparison were therefore carried forward and incorporated into distance- or travel time-based model structures for the final model comparison. In total, five models were considered for the Fraser River dataset:

1. $\phi(\text{seg}; Y; W + CP + \text{spp} + \text{FL} \times \text{Tag})$, $p(S; Y + \text{lev}_{\text{Mis}} + \text{lev}_{\text{PM}} + \text{Tag})$ $\phi$ related among unique combinations of segment and year by additive effects of watershed of origin, species, fork length, and tag size, with an interaction between FL and Tag; additive initial mortality by release location clusters

2. $\phi(d + W + M_{i,w} + M_{i,h} + \text{spp} + \text{FL} \times \text{Tag})$, $p(S; Y + \text{lev}_{\text{Mis}} + \text{lev}_{\text{PM}} + \text{Tag})$ $\phi_{\text{seg}}$ constrained to segment distance; additive effects of watershed of origin, species, FL, and Tag, with an interaction between FL and Tag; additive initial mortality by HW rearing history

3. $\phi(d_{f,w} + d_{o,w} + W + M_{i,w} + M_{i,h} + \text{spp} + \text{FL} \times \text{Tag})$, $p(S; Y + \text{lev}_{\text{Mis}} + \text{lev}_{\text{PM}} + \text{Tag})$ $\phi_{\text{seg}}$ constrained to segment distance, with separate relationships for freshwater and ocean segments; additive effects of watershed, species, FL, and Tag, with an interaction between FL and Tag; additive initial mortality by HW rearing history

4. $\phi(\text{TT} + W + M_{i,w} + M_{i,h} + \text{spp} + \text{FL} \times \text{Tag})$, $p(S; Y + \text{lev}_{\text{Mis}} + \text{lev}_{\text{PM}} + \text{Tag})$ $\phi_{\text{seg}}$ constrained to average segment travel time for each group; additive effects of watershed of origin, species, FL, and Tag, with an interaction between FL and Tag; additive initial mortality by HW rearing history
5. \( \phi(T_{fw} + TT_{sw} + W + M_{i,w} + M_{i,H} + \text{spp} + FL \times \text{Tag}), \quad p(S; Y + \text{lev}_{mis} + \text{lev}_{PM} + \text{Tag}) \)

\( \phi_{seg} \) constrained to average segment travel time for each group, with separate relationships for freshwater and ocean segments; additive effects of watershed, species, FL, and Tag, with an interaction between FL and Tag; additive initial mortality by HW rearing history

A similar set of five models was considered for the non-Fraser dataset, with the only difference being a different set of additive factors from the base model that was carried forward from the previous model comparison. These factors were incorporated into the distance- and travel time-based model formulations:

1. \( \phi(\text{seg}; Y; W + HW + M_{i,w} + M_{i,HT} + \text{FL} + \text{Tag}), \quad p(S; Y + \text{Clusters} + \text{Tag}) \)

\( \phi_{seg} \) constrained to segment distance; additive effects of watershed of origin, HW rearing history, FL, and Tag; additive initial mortality by HW rearing history

2. \( \phi(d + W + HW + M_{i,w} + M_{i,HT} + \text{FL} + \text{Tag}), \quad p(S; Y + \text{Clusters} + \text{Tag}) \)

\( \phi_{seg} \) constrained to segment distance; additive effects of watershed of origin, HW rearing history, FL, and Tag; additive initial mortality by HW rearing history

3. \( \phi(d_{fw} + d_{sw} + W + HW + M_{i,w} + M_{i,HT} + \text{FL} + \text{Tag}), \quad p(S; Y + \text{Clusters} + \text{Tag}) \)

\( \phi_{seg} \) constrained to segment distance, with separate relationships for freshwater and ocean segments; additive effects of watershed of origin, HW rearing history, FL, and Tag; additive initial mortality by HW rearing history

4. \( \phi(TT + W + HW + M_{i,w} + M_{i,HT} + \text{FL} + \text{Tag}), \quad p(S; Y + \text{Clusters} + \text{Tag}) \)

\( \phi_{seg} \) constrained to average segment travel time for each group; additive effects of watershed of origin, HW rearing history, FL, and Tag; additive initial mortality by HW rearing history

5. \( \phi(TT_{fw} + TT_{sw} + W + HW + M_{i,w} + M_{i,HT} + \text{FL} + \text{Tag}), \quad p(S; Y + \text{Clusters} + \text{Tag}) \)

\( \phi_{seg} \) constrained to average segment travel time for each group, with separate relationships for freshwater and ocean segments; additive effects of watershed of origin, HW rearing history, FL, and Tag; additive initial mortality by HW rearing history

For all sets of candidate models, AIC values were calculated and used to compare models in terms of parsimony—the goodness-of-fit of the model to detection data balanced with the number of parameters required to achieve that fit (Burnham and Anderson 2002; Appendix A).

### 9.2.4 Selection differentials for body size

If size-dependent survival within populations occurs during the migration, we should expect a different size distribution of smolts before and after some portion of the migration.
Positive size dependence in survival (i.e., larger individuals having a higher survival probability) should result in a larger mean body length of fish detected (the survivors of selection) compared with the mean body length of fish tagged. Standardized directional selection differentials ($\delta$) on body length were calculated to assess the relative strength of selection (Endler 1986) as:

\[
\delta = \frac{\bar{FL}_{det} - \bar{FL}_{rel}}{s(FL_{rel})},
\]

where $\bar{FL}_{det}$ is the mean fork length at release of fish that were detected at either: (1) the lowest in-river receiver (or second lowest receiver, if <10 fish were detected at the lowest receiver but $\geq$10 fish were detected at the second lowest), or (2) the outer ocean stations QCS or JDF. $\bar{FL}_{rel}$ and $s(FL_{rel})$ are the sample mean and standard deviation of fork lengths of fish from a release group that were tagged and released. The larger the magnitude of $\delta$, the greater the strength of selection, with $\delta > 0$ implying positive size-dependence in survival. We did not calculate $\delta_{fw}$ or $\delta_{tot}$ if the number of detected fish was <10 at a river station or the outer QCS/JDF stations, respectively, to reduce inaccuracy in $\bar{FL}_{det}$ due to small sample sizes. If a release group was tagged with >1 tag type, we calculated $\delta$ separately for each tag type (this often meant that combinations of release group and tag type did not meet the criterion of $\geq$10 detected fish). For release groups meeting criteria of $\geq$10 detected fish at both an in-river station and the outer QCS/JDF stations, we compared $\delta_{fw}$ and $\delta_{tot}$ to assess the relative strength of size-dependent selection during the downstream and inshore migration. Since $\delta$ is often sensitive to sample size (Kingsolver et al. 2001), we also looked at the relationship between $\delta$ and the number of detected fish at the river station or outer ocean stations. Note that this approach does not involve mark-recapture models, so provides an independent means of assessing the effect of body size on survival within release groups, whereas the mark-recapture analysis (as specified) combines within and among-group effects.

9.3 Results

9.3.1 Parameter estimates under general survival model

Detection probability estimates

Estimates of $p$ were independent among stations and years in all models, but the remaining components of $[p]$ were incorporated as additive effects. Of the 10 $[p]$’s fit to the
Fraser River dataset, the strongest support was found in $[p]$ that involved tag type and two river level covariates (Table 9.1). This model, with the greatest number of parameters of all models considered, had a much lower QAICc value than the second and third-best models ($\Delta$QAICc = 12.0 and 16.3), which did not involve a tag type effect or a second river level covariate, respectively. The top eight $[p]$’s all involved at least one flow or day of year covariate corresponding with the mean arrival time of a population at a detection station (the bottom two did not), demonstrating the importance of incorporating seasonal decreases in $p$ among populations as a result of increasing river flows over the salmon migration season. 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 five of the models that incorporated the extra parameter having lower QAICc values than their corresponding models which did not. The difference between logit-link model coefficients for $\beta_{V9}$ and $\beta_{V7}$ 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.

Of the two $[p]$’s fit to the non-Fraser dataset, the strongest support was again seen in the model that incorporated an effect of tag type (Table 9.1), with a QAICc value 23.6 lower than the model without this effect. The difference between $\beta_{V9}$ and $\beta_{V7}$ coefficients was $>0$ (0.71; 95% CL, 0.46–0.97), again with $\hat{p}$ higher for V9 tags than for V7 tags. This constant difference among tag types on the logit scale becomes a variable difference on the probability scale, dependent on the magnitude of $\beta$. Differences in $\hat{p}$ on the probability scale are shown in Fig. 9.2 (river stations) and Fig. A.6 (ocean stations).

Mark-recapture $\hat{p}$ varied widely across stations as well as between tag types. In general, $\hat{p}$ at ocean stations NSOG, HSinner and HSouter were consistently high, typically ranging from 85–95% for V9 tags and 60–85% for V7 tags (Fig. A.6a). The variation that did occur on these ocean lines was partly explained by slight year-to-year variation in receiver geometry, and this was taken into account when making predictions of $p$ at the outer QCS and JDF stations (Fig. A.6b; Appendix A).

In the Fraser River, $\hat{p}$ at stations decreased sharply over the migration season as a result of increased river flow, with earlier-migrating groups facing lower flows typically having higher $\hat{p}$ (Fig. 9.1). The best model from Table 1, which accounts for this seasonal variation by constraining $\hat{p}$ to be a function of the river water level corresponding with the mean arrival time.
of each release group at each station, was assumed for the \( \hat{\phi} \) shown in Fig. 9.2a. These estimates show considerable variation within each year-station combination due to the river level effect, in some cases with >60% difference in \( \hat{\phi} \) between early and late-migrating release groups. On average, there was less variation among years and stations, despite the assumed model being flexible in terms of separate intercepts for these year-station combinations.

In the lower Squamish and Englishman Rivers, \( \hat{\phi} \) varied widely among years (Fig. 9.2b). This is partly the result of different locations of receivers in different years (e.g., in the Englishman River, \( \hat{\phi} \) was 59% in 2004 when a single station was deployed at the river mouth, but ranged from 79–99% in 2005 and 2006 when two stations in each year were deployed in the lower river). It may also result from fine-scale receiver orientation differences or river flow differences among years (e.g., in the Squamish River, the receiver in 2004, 2005, and 2006 was at the same location to within a few metres, but \( \hat{\phi} \) was much lower in 2005). Receiver stations in the Nimpkish, Cowichan, and Seymour Rivers as well as at the Keogh River mouth had very high \( \hat{\phi} \) for both tag types (typically >85%; Fig. 9.2b). High \( \hat{\phi} \) at river mouth station(s) are particularly important for partitioning downstream from inshore \( \hat{\phi} \). The relative difference of \( \hat{\phi}_{V7} < \hat{\phi}_{V9} \) was fairly consistent between the two datasets (Fig. 9.2).

### Survival probability estimates

The general CJS [\( \phi \)] allows for independent \( \hat{\phi} \) for each release group in each segment of the migration, i.e., [\( \phi_{segG} \)] (this becomes possible for these release groups with relatively small sample sizes when more constrained [\( p \)]’s are assumed). The summarized \( \hat{\phi} \) for the downstream migration and total migration (using products of segment-specific \( \hat{\phi} \)) are shown in Fig. 9.3, generated under the best [\( p \)] for each dataset (Table 9.1). Survival varied among populations especially during the downstream migration, but also during the portion through Georgia Strait. Some of this variation is evidently due to differences among populations in body size and migration distance (see below).

For the downstream migration, \( \hat{\phi} \) was typically lower for lower Thompson River populations than for other populations with shorter distances to migrate. Within watersheds, there did not appear to be strong differences between species in \( \hat{\phi} \) for the downstream migration. In contrast, there were strong species differences in \( \hat{\phi} \) after the total migration, with much lower survival for coho and Chinook populations than for steelhead and sockeye/kokanee populations (Fig. 9.3). (An exception for coho and Chinook populations are those from northeast Vancouver...
Island, which do not actually migrate through Georgia Strait.) It is important to note that survival estimates assume continuous migration past stations. The possibility of residency of coho and Chinook in Georgia Strait (Chapter 7) would violate this assumption and cause total survival to be underestimated. Aside from Keogh River steelhead, which have <20 km to migrate before arriving at the terminal QCS station (Fig. 1.4), most steelhead and sockeye/kokanee release groups had similar \( \hat{\phi} \) by the end of the total migration despite the large differences in downstream \( \hat{\phi} \) (or in the case of Sakinaw Lake sockeye and kokanee, no downstream migration).

Surprisingly, visual inspection of the estimates does not reveal consistent differences in \( \hat{\phi} \) between wild and hatchery-reared fish. In this 2004–2007 analysis, the only watershed-species combination with a wild-hatchery comparison in the same year was Keogh River steelhead in 2004, where no differences were observed after downstream or inshore portions\(^9\) (Fig. 9.3; but migration distances were very short, as mentioned above). Rearing history effects may be confounded with body size (hatchery fish tended to be larger, Table A.2) and also with species differences (most steelhead populations were wild and most coho and Chinook populations were hatchery-reared). We will attempt to tease these factors apart in the following section.

Uncertainty in \( \hat{\phi} \) arises from two different sources. First, there is uncertainty because detection data can often be explained by many possible combinations of \( p \) and \( \phi \) values under some assumed model. This error is typical of mark-recapture models, and is shown as green or blue error bars in Fig. 9.3. For the total migration \( \hat{\phi} \), recall that a value of \( p_{\text{final}} \) was held fixed for the terminal stations QCS/JDF in order to untangle the confounded parameters \( p_{\text{final}} \) and \( \phi_{\text{final}} \). Since uncertainty in this fixed value causes the uncertainty of \( \phi_{\text{final}} \) to be underestimated (and therefore also the product of \( \hat{\phi} \)'s for the total migration), a second component of uncertainty is represented by black bars in Fig. 9.3. These are high- and low-bounded \( \hat{\phi} \) when \( p_{\text{final}} \) is fixed at its lower and upper 95% confidence limits, respectively, rather than at the maximum likelihood estimate of \( p_{\text{final}} \). This component of uncertainty due to fixed values of \( p_{\text{final}} \) was typically negligible for downstream migration \( \hat{\phi} \), but for the total migration \( \hat{\phi} \), it was sometimes greater than the parameter uncertainty component (Fig. 9.3). This is especially true for Keogh River and Nimpkish River smolts, where the only ocean segment of their migration is from the river mouth to QCS, so \( \phi_{\text{ocean}} \) is entirely dependent on the fixed value for \( p_{\text{final}} \). This component of uncertainty was also typically greater in 2004 than in other years, as indicated by 95%

\(^9\) In contrast, a 2008 study showed strong wild vs. hatchery differences in survival for Cheakamus River steelhead, as described in Chapter 8.
confidence intervals for $p_{\text{final}}$ being wider that year (Fig. A.6) as a result of substantial
equipment loss at JDF in 2004 (Fig. A.3). In general, inshore $\hat{\phi}$ (and therefore total migration $\hat{\phi}$)
are sensitive to assumptions about $p_{\text{final}}$.

In the following sections, variation in survival during both the downstream and total
migration will be attributed to several biological factors within and among populations.

9.3.2 Effects of watershed, species, and rearing history on survival

The importance of ‘species’ and wild or hatchery rearing history (‘HW’) factors, as well
as whether ‘watershed’ is best implemented as an additive or interaction effect with segment-
year combinations, differed between populations from the Fraser River and those from other
rivers. In the Fraser River dataset, $[\phi]$’s in which watershed was considered as an additive effect
were much more parsimonious than corresponding $[\phi]$’s in which watershed was part of the
interaction terms with migration segment and year ($\Delta QAICc > 18$; Table 9.2; watersheds are
Coldwater River, Spius Creek, Nicola River, Deadman River, and Cultus Lake). There were
strong overall effects of species and HW (or both) compared to $[\phi]$’s without these effects
($\Delta QAICc$ range, 23.3–29.3). Of these three top $[\phi]$’s, the one involving a species effect but not a
HW effect was the best overall. The species effect involves a ranking of Chinook $<$ coho $\approx$
sockeye $<$ steelhead in terms of overall survival, but this ranking will be assessed again below,
after accounting for differences in body size and migration distance among groups.\footnote{Note: the absence of a HW effect was largely the result of including the 2005 Coldwater Chinook release group of unknown wild or hatchery-rearing provenance. This group increased the number of levels within HW to 3 (wild, hatchery, unknown), so required 2 parameters to distinguish between these levels. The decrease in negative log-likelihood associated with incorporating the HW effect was 2.0 (Table 9.2), so if the unknown group had not been included and only 1 parameter were required to distinguish between wild and hatchery rearing histories, the $\Delta QAICc$ would have been close to zero rather than 2.7.}

In the non-Fraser dataset, $[\phi]$’s in which watershed was part of the interaction terms with
migration segment and year were more parsimonious than corresponding $[\phi]$’s in which
watershed was considered as an additive effect (Table 9.2). Compared to the sub-watersheds
within the mid-Fraser River, from which populations all shared the same migration route down
the mainstem Fraser River, there was greater variation among non-Fraser watersheds in factors
likely to affect survival, since populations generally did not share the same migration routes.
There were again strong overall effects of species or HW compared to $[\phi]$’s without these effects
($\Delta QAICc$ range, 9.0–9.3). The top two $[\phi]$’s had similar levels of support. These were $[\phi]$ involving a HW effect but not a species effect (despite there being one release group of unknown
wild or hatchery origin in this dataset as well—2006 Nimpkish River Chinook—and therefore one extra parameter to estimate to distinguish among levels of HW), and \([\phi]\) involving a species effect but not a HW effect. The \([\phi]\) including both these effects was less parsimonious (\(\Delta QAIC = 4.2\) or 3.9), suggesting at least a moderate degree of covariation among species and HW factors in their effect on survival. The HW effect involved a ranking of \(H < W\) in the first segment and \(H \approx W\) in following segments in terms of survival, but again this ranking will be assessed later after accounting for body size and migration distance differences among release groups.

Model sets for both Fraser River and non-Fraser datasets did not include a general CJS \([\phi]\) or any models intermediate between the general model and these more constrained models. For the Fraser River dataset, the best \([\phi]\) in this current model set (Table 9.2) was more parsimonious than the general CJS \([\phi]\) (Table 9.1; \(\Delta QAICc = 5.0\)). In the non-Fraser dataset, however, the general CJS \([\phi]\) was better than the best \([\phi]\) in the current set of more constrained survival models (\(\Delta QAICc = 34.8\)).

**9.3.3 Effects of body size and tag size on survival**

**Within-population selection for larger body sizes**

Mean body length of release groups (containing fish tagged with the same tag type and having \(\geq 10\) fish detected at \(\geq 1\) station, \(n = 40\)) ranged from 117.1–208.0 mm (Table A.2; Fig. 9.4a). The average size of fish detected in the lower river (Fig. 9.4b) did not differ much from the average size of tagged fish. Most release groups had mean body lengths ranging from 125–195 mm at both these sampling occasions, and overall means (\(FL_{rel} = 161.5\) mm, \(FL_{det,river} = 162.1\) mm) and medians (\(FL_{rel} = 162.0\) mm, \(FL_{det,river} = 165.8\) mm) across release groups were similar among sampling occasions. A paired t-test for the 39 release groups in common showed no significant difference in the overall mean between these sampling occasions at \(\alpha = 0.05\) (2-tailed, d.f. = 38, \(p = 0.058\)). In contrast, mean body lengths at the last sampling occasion (fish detected at QCS or JDF) were larger (\(FL_{det,QCS/JDF} = 179.3\) mm, \(FL_{det,QCS/JDF} = 182.4\) mm; Fig. 9.4c); note that \(FL_{det}\) here is length at tagging, hence is not larger because of growth during the migration. This is partly a result of a smaller subset of groups \((n = 17)\) meeting the criterion of \(\geq 10\) fish detected, as the groups that met that criterion tended to have larger mean body lengths. However, if only these 17 groups are considered across all three sampling occasions, overall means and medians at the last occasion were still larger than the subset of release groups
at the earlier two sampling occasions (FL_{rel} = 176.3 mm, FL_{det,river} = 176.9 mm, FL_{rel} = 177.6 mm, FL_{det,river} = 177.9 mm, n = 17). A paired t-test for the 17 groups in common showed a difference in the overall mean between the first (tagging/release) and third (detection at QCS/JDF) occasions (d.f. = 16, p = 0.001).

The change in mean fork length within release groups during the migration is most easily seen by plotting FL for the river and outer ocean detection occasions vs. FL (Fig. 9.5a,b). Although the increase in FL was significant for QCS/JDF and nearly significant for the in-river station, the magnitude of mean body length increases (river, 0.9 mm; QCS/JDF, 3.0 mm) were small compared with the among-group range of body sizes (Fig. 9.5a,b). There was also some indication of a reduction in variance of body lengths of fish detected at QCS/JDF compared with those tagged and released (Fig. 9.5d), but no change comparing the tagging/release and in-river sampling occasions (Fig. 9.5c). Paired t-tests support this observation (s(FL_{det,river}) vs. s(FL_{rel}), d.f. = 38, 2-tailed p = 0.579; s(FL_{det,QCS/JDF}) vs. s(FL_{rel}), d.f. = 16, p = 0.007).

Standardized directional selection differentials (δ) account for both the change in mean value of a trait and variation in the trait prior to selection. From release to a lower in-river receiver, δ_{fw} ranged from –0.36 to 0.72 (n = 39), with most values falling between –0.25 to 0.25 (Fig. 9.6a). The distribution of δ_{fw} was centered around zero (overall mean, \bar{\delta}_{fw} = 0.04; overall median, \tilde{\delta}_{fw} = 0.02) indicating no consistent directional selection (95% confidence limits of \delta_{fw} did not exclude zero, –0.03 to 0.11). In contrast, calculated values of δ_{tot} from release to QCS/JDF were generally >0 (Fig. 9.6b), with δ_{tot} ranging from –0.20 to 0.66 (n = 17) and most values falling between –0.05 to 0.45. The overall mean (\bar{\delta}_{tot} = 0.22; 95% c.l., 0.10–0.34) and median (\tilde{\delta}_{tot} = 0.23) were >0, indicating positive directional selection. The overall difference between δ_{fw} and δ_{tot} does not simply result from a different subset of release groups that met the criterion of ≥10 fish detected at the in-river station or QCS/JDF stations. If only the subset of 17 groups in common are considered, δ_{fw} was generally small in magnitude and centered around zero, while δ_{tot} was generally positive with larger coefficient values (Fig. 9.6c). Paired values were generally above the 1:1 line, indicating that the positive size-dependent selection within release groups that did occur during the smolt migration generally occurred after ocean entry rather than during the downstream migration (values on the 1:1 line would indicate that δ_{tot} is fully explained by δ_{fw} at the time of ocean entry).

Calculated δ differentials were inaccurate due to small sample sizes. Although the criterion of ≥10 fish detected was used to guard against this problem, the threshold used may
have been too low. Figure 9.7 shows δ\text{fw} and δ\text{tot} plotted against the number of fish detected at the station in question. Clearly, the variation in δ around the overall mean values of $\bar{\delta}_{\text{fw}}$ and $\bar{\delta}_{\text{tot}}$ was higher when δ was based on fewer fish contributing to $\overline{FL}$ than when more fish contributed to $\overline{FL}$. A threshold of $\geq20$ fish detected, for example, would not alter the average relationship much for $\delta_{\text{fw}}$ ($\bar{\delta}_{\text{fw}} = 0.03$ based on the 27 $\delta_{\text{fw}}$ values with $\geq20$ fish detected), but would reduce the variation around this overall mean (Fig. 9.7a). For $\delta_{\text{tot}}$, a threshold of $\geq20$ fish detected would similarly reduce the variation around the overall mean $\bar{\delta}_{\text{tot}}$, and in this case would also decrease it slightly ($\bar{\delta}_{\text{tot}} = 0.16$ based on the 9 $\delta_{\text{tot}}$ values with $\geq20$ fish detected).

**Within and among-population size-dependent survival**

The among-population effect of body length on survival can be seen by initially plotting $\hat{\phi}$ from the general CJS [$\phi$] against the mean body length of release groups (Fig. 9.8). For each species or rearing history, there appear to be positive trends in body length and among-group survival during both the downstream migration and the total migration from release to QCS/JDF stations.\textsuperscript{11} Positive trends are strengthened by separation of survival estimates by species or rearing history. For example, coho and Chinook tended to be smaller than steelhead or sockeye smolts, and within only coho release groups the increase in survival with mean body length was greater than if all species were pooled together (Fig. 9.8a,b). Although the range of sockeye/kokanee mean body lengths was limited, at a given size survival appeared to be higher for steelhead groups than for sockeye/kokanee groups. There was considerable overlap in mean body lengths of wild and hatchery-reared release groups (even though only wild populations with mean size $>145$ mm were tagged), which permits a more direct comparison among groups. Survival increased with mean body length for both wild and hatchery fish during both the downstream and total migration, but at a given body length survival of wild fish tended to be higher than that of hatchery-reared fish (Fig. 9.8c,d).

Consistent with the within-group size-selection results and the among-group patterns of increased survival with increased mean size, body length (‘FL’) had an overall strong effect on survival in both the Fraser River and non-Fraser datasets (Table 9.3). As implemented in these models, FL involves both within-group and among-group effects. In both datasets, incorporating an effect of tag size (‘Tag’) in addition to body size was further supported by the detection data.

\textsuperscript{11} Note that logistic curves were fitted to point estimates for visual reference only, and do not account for uncertainty in $\hat{\phi}$ or within-group variation in body length. These will be accounted for below with body length as a covariate.
In the non-Fraser dataset, the best $[\phi]$ involved FL and Tag each as additive factors, while in the Fraser River dataset, the best $[\phi]$ also involved a FL:Tag interaction on survival (Table 9.3).

The best $[\phi]$ for the Fraser River dataset, $[\phi(\text{seg:}Y+W+CP+spp+\text{FL}\times\text{Tag})]$, had a QAICc that was 9.0 less than $[\phi]$ without FL or Tag effects (Table 9.3). The effect of FL on survival was weak for fish tagged with V7-2L tags ($\beta_{\text{FL:V72L}}$ coefficient, –0.009 with 95% confidence limits of –0.025 to 0.006), but was stronger for fish tagged with V9-6L ($\beta_{\text{FL:V9-6L}}$, 0.036, 95% c.l. 0.017 to 0.054), V9-1L ($\beta_{\text{FL:V91L}}$, 0.023, 95% c.l. 0.0004 to 0.045), or V9-2L tags ($\beta_{\text{FL:V9-2L}}$, 0.046, 95% c.l. 0.005 to 0.087). These $\beta_{\text{FL:Tag}}$ coefficients represent the slopes of logit($\phi$) vs. FL for each tag type. The intercepts of this relationship also determine the relative effects of tag type on survival for a given body length. Compared with V7-2L tags, there was a strong reduction in survival at a hypothetical FL = 0 mm for smolts tagged with the larger V9-6L, V9-1L, or V9-2L tags (differences in $\beta_{\text{V9XL}}$ and $\beta_{\text{V72L}}$ all had 95% c.l. that fell <0).

The best $[\phi]$ for the non-Fraser dataset, $[\phi(\text{seg:}Y+W+\text{HW}+M_{i,W}+M_{i,H}+\text{FL}+\text{Tag})]$, was strongly supported compared to $[\phi]$ without FL or Tag effects ($\Delta$QAIC = 30.3; Table 9.3). The slope of logit($\phi$) vs. FL was the same for fish tagged with V7-2L and V9-6L tags ($\beta_{\text{FL}}$, 0.017, 95% c.l. 0.010 to 0.024), indicating positive size-dependence in survival. The intercepts of this relationship were different for V7 and V9 tags, with V7-tagged fish having higher survival than V9-tagged fish of the same body length (difference in $\beta_{\text{V96L}}$ and $\beta_{\text{V72L}}$ had 95% c.l. that fell <0).

These relationships between $\phi$ and FL are more easily seen by using estimated parameters from the best $[\phi]$ for each dataset to generate predictions of survival at a given body length for each tag type. Three release groups from the Fraser River dataset and two from the non-Fraser dataset had $\geq$2 tag types used, in which $\geq$20 fish were tagged with each tag type (Table A.2). Within these groups, there was some degree of overlap in the body lengths of fish tagged with different tag types, which allows survival at a given body length to be compared among fish tagged with different tag sizes. For example, the fate of each tagged smolt from the 2005 Tenderfoot Creek Hatchery coho release group to each successive detection station was ‘manually’ assessed (i.e., not using mark-recapture methods) by identifying the last station at which a smolt was detected during its migration. The fates of fish were then binned into 5-mm fork length categories to permit comparison of tag size effects on survival for fish of the same body length (Fig. 9.9). From release to the last in-river receiver station and to HS$_{outer}$ (about 28

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12 Note that most smolts were tagged with either V7-2L or V9-6L tags (Table A.2). Only Cultus Lake sockeye were tagged with V9-1L (2005, 2006, 2007) or V9-2L (2005) tags.
km south of the river mouth), the proportion of fish in the two overlapping size bins that survived the downstream migration or left Howe Sound was higher for V7-tagged fish than V9-tagged fish.\textsuperscript{13} Incorporating body length and tag size as covariates into mark-recapture models is an analogous approach to assessing their effects on survival, but this approach accounts for differences in \( p \) among tag types, and also accounts for overall effects across all release groups, including but not limited to the release groups in which \( \geq 2 \) tag types were used.

Predicted values of survival at a given body length and tag size are shown in Fig. 9.10 for the five release groups, generated under the best models from Table 9.3 (as specified, these patterns incorporate both within-group and among-group effects). In Fraser River groups, a FL:Tag interaction on \( \phi \) was supported, so slopes differ among tag sizes (Fig. 9.10a, b, c). In non-Fraser groups, an interaction was not as well supported as a simpler additive model, so slopes are parallel in logit-space (Fig. 9.10d, e). For each group, slopes of \( \phi \) vs. FL as well as intercept differences between tag sizes were constant across all segments. Absolute intercepts differed across segments, and a single segment was selected for each group which best showed the relationship between \( \phi \), FL, and tag size. For 2005 Cultus Lake sockeye (a) and 2005–2006 Tenderfoot Creek coho (d, e), there were clear differences in survival at a given FL between tag sizes, in each case with larger tags leading to lower survival. In the Fraser River dataset, a slight negative relationship between \( \phi \) and FL was observed for V7-tagged fish (although 95\% confidence limits of the slope did not exclude zero). However, average fork lengths of these two groups of fish tagged with V7 tags were less than the point of intersection between the V7 and V9 predicted fits in Figure 9.10b and c, so in the FL region with the highest density of V7 tags, higher survival is still predicted than for V9-tagged fish of the same size. Additionally, the V7 relationship is based on more limited data (V7 tags, 512 released and 142 detected on any receiver; V9 tags, 1317 released and 575 detected). In the model where the slope of \( \phi \) and FL is constrained to be similar for V7 and V9 tags, the common slope is positive \((\beta_{\text{FL}}, 0.015, 95\% \text{ c.l.} 0.008 \text{ to } 0.024)\).

\textbf{9.3.4 Effects of release date on survival}

In both datasets, the effect of day-of-year released (‘RD’) on survival was only moderately supported. Many release groups were tagged and released over several days rather

\textsuperscript{13} Since \( p \) was not accounted for in this simple example, survival is probably underestimated more for V7-tagged fish than V9-tagged fish, especially at HS\textsubscript{outer}, so this would only exaggerate observed survival differences between tag types. Also, sample sizes of some length classes are small, so these results are interpreted with caution.
than all at the same time. As specified, the effect of RD on $\phi$ incorporated both within-group and among-group effects. $\Delta$QAIC between the best $[\phi]$ and the corresponding model involving RD as an additive covariate was 0.5 and 0.7 for the Fraser River and non-Fraser datasets, respectively (Table 9.3). For both datasets, the RD effect size was $>0$ but confidence limits of effect sizes did not exclude zero, suggesting a weak, positive relationship between RD and survival (Fraser River, $\beta_{RD} = 0.008$, 95% c.l. –0.003 to 0.020; non-Fraser, $\beta_{RD} = 0.011$, 95% c.l. –0.006 to 0.028).

The among-group effect of RD on survival can further be seen by plotting $\hat{\phi}$ from the general CJS $[\phi]$ against the release date of each group (or for groups with $>1$ release date, the weighted average of RD). When separated by species or by wild or hatchery rearing history, most patterns were inconsistent (i.e., in opposite directions), especially during the downstream migration (Fig. 9.11). This inconsistency was observed among species or rearing history as well as between the downstream and inshore migration portions (e.g., steelhead showed a slight decrease in survival after the downstream migration but an increase in survival after the total migration as release date increased). The lack of a consistent relationship among release groups suggests that the weak, positive overall effect of RD on survival occurred largely within groups.

### 9.3.5 Comparison of distance- and travel time-based models

The effect of migration distance or travel time on survival can be seen by initially plotting $\hat{\phi}$ from the general CJS model against these variables (Figs. 9.12 and 9.13, respectively). Since minimum migration distance is the same for all individuals within a release group and travel time estimates are implemented as means of detected fish in the release group, there is no within-group variation in $\hat{\phi}$. In general, $\hat{\phi}$ declined as cumulative distances or travel times increased, but many interesting patterns also emerge.

After the downstream migration, some intercepts of $\hat{\phi}$ vs. distance or $\hat{\phi}$ vs. travel time were near 1 (or, $\ln(\hat{\phi})$ near 0). An intercept $\ln(\hat{\phi}) = 0$ with a negative slope would suggest that survival rates per unit distance or travel time are constant. This is apparent, for example, for wild smolts in the distance-based relationship (Fig. 9.12c) and for both wild and hatchery smolts in the travel time-based relationship (Fig. 9.13c). In contrast, the intercept for hatchery smolts in the distance-based relationship is –0.418 (corresponding to 0.66 on the probability scale). I.e., even at very short migration distances after release, about 33% mortality is expected for hatchery fish (and for reference, 17% mortality for wild fish). This can be interpreted either as ‘distant-independent’ mortality or, more realistically, that per-unit-distance mortality rates were higher in
the first few kilometres after release than they were for the remainder of the downstream migration, especially for hatchery fish. In the species comparisons, slopes and intercepts of $\ln(\hat{\phi})$ vs. distance or travel time relationships were more variable. Some seemed to be spurious as a result of narrow ranges of downstream distances and travel times (e.g., four $\hat{\phi}$ for Cultus Lake sockeye; Figs. 9.12a, 9.13a).

After the total migration, intercepts of $\ln(\hat{\phi})$ vs. distance were generally less than those observed after the downstream migration. This suggests a further component of ‘distance-independent’ mortality associated with ocean entry. The intercept for steelhead and sockeye/kokanee was about $-1$ (Fig. 9.12b; or 0.37 on the probability scale). Onto this ‘base’ mortality of about 63%, smolts incurred additional mortality as distance increased. The furthest-migrating steelhead from the lower Thompson River, for example, suffered about 93% mortality after their 750 km migration downstream and through Georgia Strait. Coho and Chinook populations had a much higher basal mortality rate; the intercept of about $-2$ corresponds to about 86% mortality on average. This greater ‘basal mortality’ associated with ocean entry for coho and Chinook may not actually be higher mortality, but rather the result of residency in Georgia Strait being interpreted as mortality (discussed later). When separated by wild and hatchery smolts instead of by species, the different rearing histories had fairly similar intercepts, but the slope of $\ln(\hat{\phi})$ vs. distance was steeper for hatchery fish than for wild fish (Fig. 9.12d). The slope for hatchery fish over the total migration was similar to the one over the downstream migration, suggesting similar per-distance mortality rates between habitats after accounting for intercept differences. In contrast, the slope for wild fish over the total migration was lower than the slope over the downstream migration, and lower than both hatchery slopes. Although the combined ‘distance-independent’ effects associated with release and ocean entry were similar between wild and hatchery fish (Fig. 9.12d), the reduction in survival after ocean entry for release groups with further distances to travel was therefore not as great for wild groups as it was for hatchery groups. Again, there is likely some confounding between species and rearing history separations, as most steelhead populations were wild and most coho populations were hatchery-reared.

Relationships between $\hat{\phi}$ after the total migration and travel time differed from the distance-based relationships, especially for separations by rearing history (Fig. 9.13c, d). There was less evidence of intercepts $<0$ during either the downstream or total migration, for either wild or hatchery populations (even though the best fit line for hatchery fish in Fig. 9.13d shows an intercept of about $-2$, inspection of the data points shows that the linear fit is probably not appropriate and a broken regression model would have an intercept closer to zero. A broken
regression may be reasonable, where the slope would be similar to that for wild smolts for the
group of \( \ln(\hat{\phi}) \) approximately <40 d travel time, and a second portion would be shallower for the
group of \( \ln(\hat{\phi}) \) approximately >50 d travel time. Most of these estimates in the >50 d group were
for coho and Chinook, which may have temporarily resided in Georgia Strait rather than
migrated continually during this time, possibly resulting in reduced per-time mortality rates).
This suggests that mortality was roughly proportional to travel time, and there were no ‘travel
time-independent’ components of mortality, like those in the distance relationship. This is
supported by the relationship between travel time and migration distance (Fig. 7.2), where even
at short migration distances, there were still travel time intercepts >0 for both the downstream
and inshore migration, for both wild and hatchery fish, implying that on average smolts spent
some time in freshwater (soon after release) and in ocean segments (soon after ocean entry)
without actively migrating. Despite considerable variation in \( \ln(\hat{\phi}) \) at a given travel time, the
generally proportional relationship between mortality and travel time (Fig. 9.13c, d) suggests that
smolts were susceptible to mortality during these periods soon after release and soon after ocean
entry even if their net distance travelled was generally short. Similar patterns are seen when
estimates are separated by species, since most wild populations were steelhead and most
hatchery populations were coho (Fig. 9.13a, b).

Relationships between survival and migration distance or duration can also be considered
on a per-unit-distance or per-unit-time basis. Instantaneous distance-based mortality rates \( (M_d) \)
were highly variable among release groups, especially during the downstream migration of
populations outside of the Fraser River (Fig. 9.14). In these smaller rivers, \( M_d \) ranged as high as
0.44 km\(^{-1}\). Most estimates of \( M_d \), however, including those for the Fraser River downstream
migration and the migration through Georgia Strait for steelhead and sockeye/kokanee were
between 0–0.025 km\(^{-1}\) (i.e., up to 2.5% mortality per kilometre of the migration). \( M \) was not
calculated for coho and Chinook release groups because of the likely confounding of residency
and mortality in the Strait. Instantaneous time-based mortality rates \( (M_{TT}) \) also varied among
release groups. In the Fraser River, \( M_{TT} \) during the downstream migration ranged from 0.02–0.47
d\(^{-1}\), with a fairly uniform distribution (Fig. 9.14d). During the downstream migration in other
rivers, and also during the inshore migration of steelhead and sockeye/kokanee, most estimates
of \( M_{TT} \) ranged from 0.01–0.16 d\(^{-1}\).

Conversion of survival estimates during downstream and inshore portions of the
migration (\( \hat{\phi}_{\text{river}} \) and \( \hat{\phi}_{\text{ocean}} \); Fig. 9.3) into the instantaneous mortality rates \( (M_{d,\text{river}}, M_{d,\text{ocean}},
M_{TT,\text{river}}, M_{TT,\text{ocean}}; \) Fig. 9.14) implies that mortality rates are constant within either the
downstream or the inshore migration. This is clearly not the case (Fig. 9.15), so these mortality rates should be interpreted with caution. In particular, the highest $M$ were only estimated for release groups that had relatively short minimum migration distances or average travel times. This is simply a result of the ‘distance-independent’ or ‘travel time-independent’ components of mortality being distributed over a short distance or time, thereby resulting in higher $M$. For release groups with longer migration distances or travel times, this component of mortality is distributed over a longer distance or duration, so on average the per-unit mortality is less. For example, migration distances of Keogh River groups are about 0.75 km for the downstream migration and 19.5 km for the inshore migration. When these relatively small values are used in the denominator of $M = -\ln(\hat{\phi})/d$, the distance-independent components of $\hat{\phi}_{\text{river}}$ and $\hat{\phi}_{\text{ocean}}$ sometimes result in large $M$ (Fig. 9.15b,c). The pattern is not as strong for the Fraser River, as there were no release groups with downstream migration distances <50 km or travel times <2 d, so the denominator values are not particularly small. Excluding the values of $M$ for migration distances <20 km and travel times <5 d, remaining values of $M$ were on average 0.0061 km$^{-1}$ and 0.148 d$^{-1}$ for the Fraser River downstream migration, 0.0095 km$^{-1}$ and 0.099 d$^{-1}$ for the downstream migration in other rivers, and 0.0042 km$^{-1}$ and 0.080 d$^{-1}$ for steelhead and sockeye/kokanee during the inshore migration.

Estimates of $M$ are separated by species and rearing history in Table 9.5. In general, $M_d$ was lower for wild than for hatchery fish, but $M_{TT}$ was similar among rearing histories. During the inshore migration, $M_d$ was similar for steelhead and sockeye/kokanee groups, but $M_{TT}$ was higher for steelhead than for sockeye/kokanee. The cut-off criteria of 20 km and 5 d are arbitrary, based on visual inspection. In some cases lower thresholds would appear to be acceptable (e.g., >1 d, Fig. 9.15e), while in other cases these thresholds may not be stringent enough (e.g., Fig. 9.15f). Ranges of distances travelled or durations of migration for release groups are not wide enough in all habitats to assess whether habitat-specific thresholds would be more appropriate.

We now consider the relationship between survival and distance or travel time with model selection criteria. For both the Fraser River and non-Fraser datasets, the distance- and travel time-based models had much higher QAICc values than the best segment-based model carried forward from the previous comparison (Table 9.4). Segment-based models had a much better goodness-of-fit, and this was not compensated by the ‘penalties’ associated with using 29–97 more parameters than distance- or time-based models. Nonetheless, the more constrained model structures are useful in two ways: (1) for comparing distance- vs. travel time-based effects
on survival, and (2) for looking at the effects on survival of other factors such as species, HW, and FL after accounting for variation in migration distance or travel time among release groups.

In the Fraser River dataset, the best of the four constrained models was a distance-based model, while in the non-Fraser dataset, the best constrained model was travel time-based (Table 9.4). In all cases, models which permitted separate slopes of $\phi$ vs. distance or travel time between river and ocean segments were strongly supported compared with models in which the slope was constrained to be common across river and ocean segments. However, the ranking of river and ocean slopes of logit($\phi$) vs. distance or travel time differed between datasets. In the Fraser River, there was very little effect of travel distance on survival during the downstream migration as confidence limits for the slope did not exclude zero ($\beta_{d_{fw}} = 0.0012, 95\% \text{ c.l.} -0.0006$ to $0.0029$), but during the inshore migration survival declined with increasing migration distances ($\beta_{d_{sw}} = -0.0163, 95\% \text{ c.l.} -0.0187$ to $-0.0140$). In other rivers, survival per unit travel time was less during the downstream migration ($\beta_{TT_{fw}} = -0.341, 95\% \text{ c.l.} -0.421$ to $-0.261$) than during the inshore migration ($\beta_{TT_{sw}} = -0.120, 95\% \text{ c.l.} -0.131$ to $-0.109$).

Inspection of model coefficients under the best of the four constrained sub-models in each dataset (Fraser River, [$\phi(d_{fw} + d_{sw} + W + M_{i,W} + M_{i,H} + \text{spp} + \text{FL x Tag})$]; other rivers, [$\phi(TT_{fw} + TT_{sw} + W + HW + M_{i,W} + M_{i,H} + \text{FL} + \text{Tag})$]; Table 9.4) allows us to see the effect of different predictor variables on survival once the other factors (including migration distance or travel time) are accounted for. Larger fish at time of tagging generally had higher survival than smaller fish. This was seen for fish tagged with V9-6L tags in the Fraser River (the majority of Fraser River fish; $\beta_{FL:V9-6L} = 0.0354, 95\% \text{ c.l.} 0.0050$ to $0.0659$) and fish from other rivers (tag sizes pooled; $\beta_{FL} = 0.0113, 95\% \text{ c.l.} 0.0057$ to $0.0169$). The 95% confidence limits for slopes of logit($\phi$) vs. FL did not exclude zero for Fraser River fish tagged with V9-1L tags ($\beta_{FL:V9-1L} = 0.0252, 95\% \text{ c.l.} -0.0091$ to $0.0596$), or V9-2L tags ($\beta_{FL:V9-2L} = 0.0422, 95\% \text{ c.l.} -0.0118$ to $0.0962$), suggesting weak effects of FL on $\phi$ (Cultus Lake sockeye was the only Fraser River population implanted with these two tag types). There was actually a weak negative relationship between survival and body size for Fraser River fish tagged with V7-2L tags ($\beta_{FL:V7} = -0.0140, 95\% \text{ c.l.} -0.0283$ to $-0.0003$; Fig. 9.10b, c). In addition to different slopes of the $\phi$ vs. FL relationship for different tag sizes in the Fraser River, the intercepts for tag sizes also differed. Compared to V7 tags, $\beta_{V9-XL}$ coefficients for all three V9 tag sizes were <0 and their 95% confidence limits excluded zero, so survival at a theoretical FL = 0 mm was lower for fish with
larger tags. Similar patterns were seen in the non-Fraser dataset between V7 and V9-6L tags \( (\beta_{V9-6L} = -0.700, 95\% \text{ c.l.} -0.936 \text{ to } -0.444). \)

In the Fraser River dataset, a species effect was observed, with higher survival in steelhead populations compared to Chinook, coho, and Cultus Lake sockeye populations once the other factors (migration distance, FL, tag size) were accounted for (i.e., \( \beta_{\text{steelhead}} \) was >0 with 95\% confidence limits that excluded zero, compared with the other species). Compared with segment-independent model structures, effects of rearing history were weak in distance-based or travel time-based frameworks. In the Fraser River, a strong reduction in survival in the first segment following release was observed for both wild and hatchery fish, with little difference among these groups \( (\beta_{M_{i,W}} = -3.29, 95\% \text{ c.l.} -4.08 \text{ to } -2.49; \beta_{M_{i,H}} = -3.05, 95\% \text{ c.l.} -3.61 \text{ to } -2.49). \) The best \( \phi \) from the previous step did not include a HW parameter, so any differences between wild and hatchery-reared fish would be absorbed by these \( M_i \) parameters. In the non-Fraser dataset, the best \( \phi \) did include a HW parameter, and in the travel time-based framework there was some indication that hatchery fish actually survived better than wild fish in segments after the first one when other factors were accounted for, although 95\% confidence limits of the model coefficient did not exclude zero \( (\beta_W = -0.233, 95\% \text{ c.l.} -0.513 \text{ to } 0.047, \) compared to the H reference group). In the first segment after release, however, initial survival was higher in wild fish than in hatchery-reared fish \( (\beta_{M_{i,W}} = 1.208, 95\% \text{ c.l.} 0.844 \text{ to } 1.572; \beta_{M_{i,H}} = 0.295, 95\% \text{ c.l.} -0.049 \text{ to } 0.639). \) The \( \beta_{M_{i}} \) coefficients >0 were surprising, although this may simply be a result of the steep slope of \( \text{logit}(\phi) \) vs. travel time during the downstream migration, such that initial mortality is largely absorbed by this time-based parameter rather than by the \( M_i \) parameters.

9.4 Discussion

9.4.1 Mortality during successive portions of smolt-to-adult life

Considerable variation in survival estimates \( (\phi) \) was observed among species, populations and years during both the downstream and inshore migration. Portions of the total variation were explained by differences in body size, migration distance (or travel time), and rearing history; these factors will be considered below. Across all release groups, downstream survival of tagged fish was estimated to be 58\% on average (51\% for coho and Chinook, 63\% for steelhead and Cultus Lake sockeye). Excluding coho and Chinook that likely resided in Georgia Strait to some extent, survival through the Strait was estimated to be 32\% (i.e., the proportion of freshwater survivors leaving the Strait). After both components of the migration, an estimated 22\% of
tagged steelhead and sockeye survived to leave the Strait. Since smolt-to-adult survival has typically been <5% since the 1990s (Chapter 1), this implies that survival for the remainder of ocean life, outside the area and time framed by the POST array, is also about 10–20% overall. There is much variation in these simple averages of survival during different portions of smolt-to-adult life, but it at least seems safe to conclude that considerable mortality occurs in all three portions: the downstream migration, inshore migration, and the remainder of ocean life.

Different portions of the migration have different distances or travel times associated with them. Accounting for these differences, instantaneous mortality rates were generally higher during the downstream migration than during the inshore migration on either a per-distance or per-time basis. These inshore estimates suggest that on average, steelhead and sockeye die at an average rate of 0.42% km\(^{-1}\) or 8.0% d\(^{-1}\) during the migration through Georgia Strait. The time-based estimates are on the high end compared with previous mortality rate estimates during early ocean life, of 2–8% d\(^{-1}\) for coho (Pearcy 1992), 2–4% d\(^{-1}\) for pink (Parker 1968), and 3.9–8.1% d\(^{-1}\) for chum (Wertheimer and Throver 2007). These estimates are much lower than have been estimated for chum, of 31–46% d\(^{-1}\) (Bax 1983), and sea trout, of 20–34% d\(^{-1}\) (Dieperink et al. 2001), although those were based on just the initial 4 or 2 d after ocean entry, respectively, so are likely sensitive to this short duration, as we found for \(\bar{M}_{TT}\) that were eventually excluded. In the latter study, after the first two days, predation rates on sea trout decreased to 0.5–2.6% d\(^{-1}\) (Dieperink et al. 2001). Estimates of \(M\) are likely biased high for two reasons. First, there is likely some amount of tagging-related mortality (see below). Second, any ‘distance-independent’ or ‘travel time-independent’ component of mortality (see below) is incorporated within \(M_d\) or \(M_{TT}\). Release groups with short distances or travel times were excluded from calculations of mean \(M\), and this reduced but did not eliminate the sensitivity of mean \(\bar{M}\) to these components of mortality that are independent of distance or travel time. If these ‘independent’ components of mortality could be isolated, \(M_d\) or \(M_{TT}\) for the remainder of the migration through the Strait would be lower. Even if actual \(M_d\) or \(M_{TT}\) were only half of the estimated values, however, mortality rates for the remainder of ocean life beyond the area and time framed by the POST study (likely >2000 km and 2–3 years) would still be much lower\(^\text{14}\) than those estimated for the migration through Georgia Strait. Others have found similar declines in \(M_{TT}\) during ocean life (Parker 1968, Pearcy 1992), typically attributed to lower risk of predation as fish grow.

\(^{14}\) e.g., approximately 2–5 times lower across a range of assumptions of migration distance, adult return timing and remaining ocean survival
The relationship between the Fraser River and other rivers in terms of $M$ for the downstream migration differed between distance-based and time-based rates. Average $M_d$ was lower for Fraser River groups than for groups from other rivers, but the opposite was true for $M_{TT}$ (Table 9.5). This seems reasonable considering that downstream migration distances were much longer for Fraser River groups than for other rivers (Fig. 1.4), but downstream travel times were not much different (Fig. 7.2). Any ‘distance-independent’ component of mortality will be averaged over much shorter distances in the smaller rivers, so $M_d$ may simply be sensitive to these shorter migration distances for the other rivers (i.e., if downstream migration distances for these other rivers were also hundreds of kilometres, $M_d$ would hypothetically be lower). Since downstream travel times were similar between Fraser and non-Fraser Rivers, then assuming that any ‘travel time-independent’ component of mortality would also be similar, these watershed groups should be similar in terms of their sensitivity of $M_{TT}$ to short travel times. Even if overall biases in $M_{TT}$ exist, it appears that $M_{TT}$ for Fraser River groups are on average 1.5 times higher than $M_{TT}$ for groups from other rivers. This could be attributable to differences in diurnal migration behaviour, as Fraser River smolts passed the lower river stations at all times of the day, but smolts from other rivers generally did not pass river stations during daylight hours, presumably to reduce the risk of visual predation (Chapter 7). Water velocity and visibility in the Fraser River may be such that visual predation is not a major concern for smolts, however (in terms of local adaptation, this may reasonably be why no pattern of nocturnal migration was observed). Alternatively, the higher $M_{TT}$ in the Fraser River may relate to tagging effects being greater in the faster, more turbulent waters of the mid-Fraser River (i.e., lower Thompson River populations) compared with smaller rivers. In contrast to these mid-Fraser populations, Cultus Lake sockeye entered the lower Fraser River where water velocities and turbulence were lower; $M_{TT}$ for this sockeye population was much lower than those of the mid-Fraser populations and similar to $M_{TT}$ of populations from smaller rivers (Table 9.5).

$M$ could not be estimated for coho or Chinook during the migration through Georgia Strait due to apparent non-continuous or non-directional migration patterns. Tenderfoot Creek Hatchery coho do migrate consistently through Howe Sound, however. Estimates of $M_d$ and $M_{TT}$ for coho and Cheakamus River steelhead are shown in Table 9.5 for reference. Estimates $\bar{M}_d$ for both populations were higher through Howe Sound than were $\bar{M}_d$ for sockeye and steelhead through Georgia Strait, likely because any initial mortality after ocean entry was spread over a relatively short distance of <30 km from river mouth to the outer Howe Sound line. Estimates $\bar{M}_{TT}$ for coho through Howe Sound were similar to those for sockeye and steelhead through
Georgia Strait, but those of steelhead through Howe Sound were lower. Although 2 of the 3 steelhead groups would have been excluded under the criterion of travel times through Howe Sound of <5 d, such exclusions would be expected to decrease, not increase mean $M_{TT}$. Two wild steelhead populations had high survival (90–92%) and short travel times (2.4–2.8 d) through Howe Sound while a hatchery population had lower survival (48%) and a long travel time (27.5 d) through Howe Sound; calculated $M_{TT}$ were relatively low for all three groups.

While ultimate causes of mortality are likely numerous and may vary among years, species, watersheds, and different portions of the migration, predation is generally thought to be the proximate cause of most deaths. There are many predators in the study area, several of which have been found to feed heavily on salmon smolts. During the downstream migration, bird predators including common mergansers (Wood 1987), gulls (Ruggerone 1986), and Caspian terns (Antolos et al. 2005), fish predators including bull trout or Dolly Varden (Thompson and Tufts 1967, Beauchamp and Van Tassell 2001) and pike (Jepsen et al. 1998), as well as river otters (Dolloff 1993) have been found to feed on outmigrating salmon smolts. In estuaries, a variety of bird predators may feed on smolts including Bonaparte gulls, glaucous-winged gulls, Arctic loons, and harlequin ducks (Mace 1983), murres (Bayer 1986), and terns or cormorants (Collis et al. 2001, Collis et al. 2002, Ryan et al. 2003, Schreck et al. 2006). Other predators in estuaries or lower rivers may include seals (Greenstreet et al. 1993, Olesiuk et al. 1996, Laake et al. 2002), and lamprey (Beamish and Neville 1995). These may continue to be important predators during the inshore migration, in addition to other fish predators such as spiny dogfish (Beamish et al. 1992), cutthroat trout (Duffy and Beauchamp 2008), Pacific hake (Hargreaves et al. 1990—cited in Wood et al. 1993, Emmett and Sampson 2007), jack mackerel (Emmett and Krutzikovsky 2008) and sablefish (Orsi et al. 2000, Sturdevant et al. 2009).

9.4.2 Survival estimation and model assumptions

If survival estimates for the total migration are unbiased, it appears that a large portion of total smolt-to-adult natural mortality occurs during the short migration window of a few weeks over a few hundred kilometres downstream and through Georgia Strait. Even if $\hat{\phi}$ are unbiased with respect to detection data, however, there are several reasons to suspect these $\hat{\phi}$ are biased for other reasons. These biases relate to the possible violation of mark-recapture CJS model assumptions and the application of these models to a spatial context using biotelemetry. Potential biases are often in opposite directions, so the direction and magnitude of overall bias in survival estimates are unclear.
Several typical assumptions of classic CJS models are listed in Appendix A, and some of these were likely violated. First, tagged animals may not be representative of the population of interest. To meet minimum body size guidelines for a particular tag size, the upper size distribution of smolts was often tagged. Since larger fish generally have higher survival than smaller fish, survival may therefore be overestimated. Capture processes may also cause the subset of tagged smolts to not be representative of a population of interest: catching hatchery fish in a dipnet or wild fish in rotary screw traps or side channel traps during their downstream migration may result in slower or weaker fish being over-represented in the tagged sample. Second, tagged animals seem to be certainly affected by tagging procedures or implanted tags, which would lead to survival being underestimated. The absolute effect of implanted tags on survival cannot easily be assessed because survival is unknown for fish not tagged. The relative effects of two different tag sizes on survival of fish of the same body length, however, showed that larger implanted tags led to lower survival than smaller tags. These relative effects led to survival differences of up to about 10–15 percentage points in each segment of the migration over the range of body sizes that overlapped between different transmitter sizes (Fig. 9.10). The absolute effects are likely to be larger than this, since the smaller tag size itself is likely associated with some degree of tag-related mortality (see below). Third, tag loss or failure are likely not negligible, both of which would lead to underestimating survival. Some hatchery tank studies have shown tag expulsion rates of 0–9% after 6 weeks (Moore et al. In press, Rechisky and Welch In press), while others have shown expulsion rates as high as 7–20% (Welch et al. 2007) or 36–54% (Chittenden et al. 2009) after ≥6 weeks with similar fish and tag sizes. Shedding rates tend to increase after about 6 weeks, so fish with slow average migration speeds might be more likely to lose tags or die before reaching detection stations. Since migrating smolts are likely more active than fish in a hatchery tank, it is possible that tag shedding rates are higher for migrating smolts. Tag failure before expected duration appears to occur in about 7.5% of tags tested (Appendix A). Premature tag failure would lead to underestimating survival (but if the failure rate is known, survival estimates can be corrected; Townsend et al. 2006).

Tagging-related mortality and shedding may depend on the sizes of fish and tags. Most smolts used in this study were below the tag length:body length ratio of 16% recommended by Lacroix et al. (2004; this is typically similar to an 8% tag mass:body mass ratio) for juvenile Atlantic salmon. The development of such thresholds is somewhat subjective; others have recommended 2.2–5.6% of body weight for similarly-sized juvenile salmon (Adams et al. 1998) or 2% for fish in general (Winter 1983). These recommendations have typically been assessed
based on fish in swimming troughs or hatchery tanks. Migrating fish faced with an implanted tag may face further challenges, and manoeuvrability to escape from predation may be impaired even if a tagged fish can swim as fast as an untagged fish of the same size in a swim chamber. For example, in tank trials with a smallmouth bass predator, juvenile Chinook salmon with radio tags implanted were eaten more frequently than control fish on the day following surgeries (Adams et al. 1998). These tag size:body size recommendations do not ensure that fish below these thresholds will not suffer tag-related effects. Rather, it seems more plausible that tagging effects might be proportional to tag size:body size ratios instead of indirectly proportional with no tagging effect below some body size threshold (Perry et al. In review).

Other assumptions of CJS models are more likely to be met. First, fates of individuals were likely independent of all other individuals with respect to \( \phi \) and \( p \), since there is little evidence that tagged smolts schooled with each other during their migration, and detection processes are primarily determined by tag and receiver characteristics. Second, sampling locations were short (in detection range) relative to the distance intervals between sampling stations. Third, it is reasonably likely that \( \phi \) in each segment and \( p \) at each station were homogenous among individuals, with three exceptions: (1) \( p \) may vary systematically over a migration season at a receiver station due to consistent changes in environmental conditions like river flow, so later-migrating fish may consistently have a lower \( p \) than earlier-migrating fish in the same release group (this possibility was accounted for explicitly in the Fraser River); (2) \( p \) may vary consistently among individuals across receiver stations as a result of variation in acoustic tag strength and related detection ranges (Chapter 6; this possibility was not accounted for since tag output measurements were not routinely performed, but the predicted effect is minor); and (3) \( \phi \) may vary among individuals of a release group consistently across migration segments due to variation in body size or other correlates of survival (body size was accounted for explicitly).

Other model assumptions are specific to spatial migration forms of tag-detection studies like the present one. First, it is assumed that detected tags are in live smolts, not in predator stomachs or in dead fish floating downstream past receivers. This seems likely to usually be true

\[ 15 \] I.e., the outcome of whether one individual lives or dies in a particular segment is not expected to impact the probability of survival for other individuals of the same group in the same segment, since there is no strong evidence that fish cluster together spatially during the migration. We do note, however, that individuals in a group may be more likely to behave similarly than individuals in different groups. In terms of \( \phi \), this is accounted for in some models by overall group effects on \( \phi \). In terms of \( p \), behavioural differences among groups (e.g. nocturnal travel patterns at different river flows) could lead to true differences in \( p \) among groups, so in models where \( p \) is pooled among groups, the common \( \hat{p} \) may be overestimated for some groups and underestimated for others.
considering that survival estimates were based on tags that were detected at successive receiver stations along typical salmon migration routes up to a few hundred kilometres long. In a few cases, however, tag movement patterns were observed that were suggestive of tags being inside predator stomachs (Chapter 7). The spatial resolution of receivers for most watersheds was sparse compared to the Squamish River mouth where these tag movement patterns were observed, so it is possible that similar predation events occurred but went unnoticed for lack of receiver coverage. Detecting a tag from a smolt no longer alive and interpreting it as a live smolt would lead to overestimating survival up to the detection station in question, although such a pattern occurring at river mouths would generally only bias downstream survival, not survival to terminal stations at QCS or JDF. Second, it is assumed that tags do not change predator foraging effectiveness through ‘dinner bell’ effects. Transmissions at 69 kHz can be heard by several marine mammals including harbour seals, so it is possible that predators could follow a sound trail to a tagged fish. Tag pulse rates are generally only 30–90 s\(^{-1}\), however, so honing in on infrequent pulses may be challenging. Even if predators could successfully track a tag, the reward of a single smolt at the end is likely not great enough to associate tag pings with fruitful foraging opportunities. We did not find evidence of smolts schooling during the migration, at least for tagged fish. Third, it is reasonable to assume that tag detections in the final dataset were legitimate, not false positives. An extensive filtering process was applied to all detections of B.C. salmon smolts tagged under POST in an effort to screen for possible false detections (Appendix A). The detections thought to be false accounted for only 0.02–0.2% of all detections in these years despite detection filters being fairly conservative in erring on the side of excluding suspect detections. Fourth and most importantly, it is assumed that smolts do not permanently reside between successive receiver stations—they either die during the migration or continually migrate past receiver lines. 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 stations. Residualization rates of steelhead smolts are typically estimated to range from 1–15% (S. Hausch and M. Melnychuk, unpubl. data), and in this study, residualization was observed in the only two populations where a targeted effort was made to sample for residual fish: Cheakamus River steelhead (in 2008; Chapter 8), and Cultus Lake sockeye in 2005 and 2007 (Welch et al. 2009). Residualization would likely not be identified for other populations due to lack of sampling effort. Similarly, it seems likely that at least some coho and Chinook smolts (as well as Sakinaw sockeye/kokanee) entering Georgia Strait resided in the Strait during summer months (Healey 1980, Chittenden et al. In press;
Chapter 7). The areas they may have used (e.g., Gulf Islands or Fraser River plume; Healey 1980) appear to have been away from receiver stations, and without detecting these fish they were considered to have died during their migration. Most tag batteries would have expired before any of these smolts could have emigrated from the Strait during winter months.

Finally, some assumptions of model construction are specific to this multi-stock analysis where survival is estimated to terminal detection stations. The first three are discussed at length in Chapter 3: (1) it seemed reasonable to pool $\hat{p}$ at a station across populations with the same tag type, since $p$ is assumed to be determined primarily by tag and receiver characteristics; (2) at Fraser River stations, specifying $\hat{p}$ as a function of the water level at the mean time of population crossing seemed to be a reasonable compromise between capturing the general form of the decline in $p$ during the migration season and avoiding over-fitting to sparse data for some release groups; and (3) the extra parameters incorporated into the model for stock-specific $\hat{p}$ at the NSOG station (joint probabilities of detection and northward movement) were seen to remove the bias in $\hat{\phi}$ due to split-route migration patterns in Georgia Strait. The last assumption is discussed in Appendix A: (4) $p$ at the terminal detection stations (QCS and JDF) was predicted from $\hat{p}$ on other ocean lines and was assumed as a fixed value to untangle the confounded $\phi$ and $p$ parameters in the final segment/station. Although $\hat{\phi}_{\text{final}}$ and therefore total survival since release were conditioned on this fixed value, the bracketed 95% confidence limits of total $\hat{\phi}$ for quantifying the sensitivity of total $\hat{\phi}$ to this fixed value of $p_{\text{final}}$ were generally small compared with the CJS-based standard errors of total $\hat{\phi}$.

Even though biases exist and affect absolute $\hat{\phi}$ (in an unknown direction overall), variation in survival among populations can still be considered in relative terms, and effects of different predictor variables in explaining variation in survival can be assessed.

9.4.3 Distance-based versus travel time-based survival models

It was not surprising that longer migration distances or greater time spent migrating generally led to lower probability of survival, although the specific relationship was unexpected. If mortality were directly proportional to distance travelled or time spent migrating, we would expect a simple exponential decline in survival from 100% at the release point, with constant rate of decline (or, on a log scale, a linear decline from 0 at the release point with increasing distance or time). Among groups, the relationship between fully-independent estimates of $\ln(\hat{\phi})$ and mean travel time for each release group appeared to be roughly proportional, with $\ln(\hat{\phi})$ declining from
0 with increased mean travel time (Fig. 9.13). In contrast, the relationship between $\ln(\hat{\theta})$ and minimum distance travelled was not directly proportional. After the downstream migration, intercepts were lower than would be expected, especially for hatchery fish. After the migration through Georgia Strait, intercepts were much lower than would be expected, especially for coho and Chinook but also for sockeye and steelhead (Fig. 9.12). The intercepts $<0$ could be interpreted as a component of mortality that is independent of migration distance, but is more reasonably described as per-km instantaneous mortality rates being much higher soon after release or soon after ocean entry than further along each of these portions of the migration. This could be the result of several factors for the downstream migration: high predation soon after release, especially in naïve hatchery fish which had not been exposed to predation pressures prior to release, so ‘weaker’ individuals had not been ‘weeded out’; tagging-related mortality, which would be more likely to occur soon after release than later in the migration; and freshwater residualization after release, which would be interpreted as apparent mortality. For the inshore migration, this could result from high mortality immediately after ocean entry. Exposure to saltwater is physiologically demanding even for fully-smolted fish, and short-term osmotic stress can increase the vulnerability of smolts to predation (Jarvi 1989, Handeland et al. 1996). The additional intercept difference of coho and Chinook relative to that of steelhead and sockeye after the total migration is likely the result of summer residency within Georgia Strait being interpreted as mortality, as suggested above. Patterns of high initial freshwater mortality were seen for Cheakamus River steelhead (Chapter 8), where survival declined more steeply with increasing distance in the Cheakamus River segments than in the Squamish River segments, and were least steep in ocean segments (Fig. 8.10b). In the more highly summarized figures shown in this chapter (involving just downstream and total survival estimates), relationships between survival and migration distance are instead observed among groups.

To address the discrepancy between relationships of survival with travel time and minimum distance, we consider the relationship between cumulative travel time and cumulative migration distance (Fig. 7.2). Intercepts in this relationship among release groups were $>0$ during both downstream and inshore portions of the migration, especially for hatchery fish. This means there was ‘extra’ time spent in both downstream and inshore portions of the migration, likely soon after release and soon after ocean entry, respectively, which did not contribute to much net distance travelled over these periods. The question of whether minimum distance travelled or mean travel time is the better predictor of survival depends on what this ‘extra’ time consists of; it could be any number of activities including foraging, moving upstream and downstream in
estuaries to acclimate to saltwater, searching for navigational cues, or seeking refuge from predation risk. Most of these activities (as well as actively migrating) expose a fish to predation risk, but hiding does not. If time spent hiding represents a large proportion of the total travel time (for example, in-river movement at night and hiding during daylight hours), we might expect that mortality should be proportional to migration distance rather than travel time. The observation that this ‘extra’ time contributes to mortality (since ln(survival) is roughly directly proportional to travel time, not to distance) suggests that it was generally spent on activities which made smolts vulnerable to predation. Mortality resulted from this ‘extra’ time, just as it did from the time actively migrating along assumed minimum-distance routes. From an among-group perspective, it appears that travel time might therefore be a better predictor of survival than minimum migration distance, especially for hatchery fish. A full assessment of whether distance or travel time best accounts for variation in smolt survival involves comparing mark-recapture models with these effects incorporated as covariates.

The ranking of distance-based and travel time-based models for explaining variation in survival was not consistent between datasets. In the Fraser River, distance was a better predictor, similar to findings from other large rivers during the downstream migration (Muir et al. 2001, Smith et al. 2002). Downstream migration distances (Fig. 1.4) were more variable among populations than travel times (Fig. 7.2) since average water velocities encountered were typically higher for populations entering the mid-Fraser mainstem than for Cultus Lake sockeye entering the lower Fraser mainstem. However, the additional effect of distance on mortality during the downstream migration was negligible—it was stronger during the inshore migration. This seems to simply result from the additive $M_i$ parameters ‘absorbing’ the mortality information in the first segment after release instead of the variation being absorbed by the freshwater distance slope parameter. In-river segments after the first one were much shorter, so most in-river mortality would be estimated to have occurred in the first segment under either case. The observation that distance was a better overall predictor of survival may also be a result of $\phi$ in inshore segments fitting better to distances than to travel times of segments, as the relationship between survival and distance was strongest for the inshore migration. In the non-Fraser dataset, travel time was the better predictor. This occurred despite the pattern of in-river nocturnal migration behaviour in non-Fraser rivers (Fig. 7.8), where presumably fish holding during daylight hours were in microhabitats where they were invulnerable to predation risk (thus, one may have expected distance to have been a better predictor at least for the downstream migration since time spent in refuges should not contribute to mortality incurred). In addition to the possible activities
mentioned above that may constitute ‘extra’ travel time not contributing to net distance travelled, this may also be the result of steelhead smolts migrating slowly downstream on average compared with other species (Fig. 7.4). At least some steelhead populations tended to spend several days somewhere around the release site before actively migrating (Chapter 8). If smolts were vulnerable to predation during this period, the mortality experienced during this period would likely be better correlated with the time spent than with the little net distance moved.

Aside from compared fits to detection data, distance-based and travel time-based models each have pros and cons. Distance-based models have the advantage that minimum distance of each segment is known, and is the same for all fish in a release group. Actual distances travelled are not known, however, and may be considerably higher than minimum possible distances (Chapter 7), so mortality may not be proportional to minimum distances (Fig. 9.12). Travel time-based models have the advantage that the actual travel time to a particular station is known from detection data. However, unlike minimum distances, travel times of fish not detected are unknown (i.e., in cases where it is known that a fish passed a station undetected because it was detected later further along the migration route). In this analysis, travel time covariates used for release groups were averages of fish that were detected at successive stations. We assumed that fish not detected would have similar travel times to fish that were detected. These average travel times underestimate the actual travel time for some individuals and overestimate it for other individuals in the release group. For relatively simple analyses of one or a few release groups, models incorporating travel time measures on individual fish could be used (e.g., a Bayesian implementation by Muthukumarana et al. 2008), but these methods are likely to be prohibitively complex and computationally demanding for multi-stock analyses. Finally, whether distance-based or travel time-based models are more appropriate may depend on foraging strategies of predators that feed on migrating salmon smolts. Theory predicts that distance-based models are more appropriate if predators are typically stationary, employing ‘sit and wait’ strategies, such that a migrating smolt passes each predator only once (Anderson et al. 2005). If predators are highly mobile such that during its migration a smolt encounters an individual predator on multiple occasions, a travel time-based model is more appropriate (Anderson et al. 2005).

9.4.4 Effects of body size and tag size on survival

Directional selection within release groups

Within release groups, directional selection against smaller body sizes was observed during the inshore migration, but not the downstream migration. This difference may reflect the
importance of body size to predator avoidance in different habitats. In rivers, travel is likely at least partly passive, with downstream movement assisted by river flow. Under these conditions, swimming ability may be less important for escaping from predators, since smolts could be carried downstream past sit-and-wait predators with little or no burst swimming energy expenditures. After ocean entry, however, net flows are much less, so swimming ability is likely more important for being able to bypass or escape from predators. Larger fish typically swim faster over a short period of time (in contrast to average travel speeds through Georgia Strait over a longer time period, which did not vary with body length, Chapter 7), so would be better able to escape from predators.

Standardized directional selection differentials after the inshore migration ranged from –0.20 to 0.66 but most values were >0. These values are within typical ranges of $\delta$ for various traits affecting survival (Endler 1986, Kingsolver et al. 2001). These values are lower than those calculated for the full ocean life of wild Keogh River steelhead from 1977 to 1982 (ranging from 0.54 to 1.47). A weir near the Keogh River mouth permitted outmigrating smolts and returning adults to be trapped. Means and standard deviations of smolt fork lengths in these years were calculated ($n = 840–6246$). When adults returned, scale samples were taken ($n = 65–303$) and circuli intervals on the scales were used to back-calculate the lengths of those fish when they entered the ocean as smolts several years previous. This method is well-established and scale circuli are generally highly correlated with body length (Ricker 1975, Fisher and Pearcy 2005). The back-calculated smolt lengths of these adults provided the post-selection part of Eq. 9.1 (s.d. of pre-selection smolt lengths, $s(FL_{rel})$, were not available for later years to calculate $\delta$, but back-calculated mean lengths at ocean entry from scales of the fish that returned as adults were greater than mean lengths of all smolts entering the ocean, so it is at least known that $\delta > 0$ in the later four years as well; Fig. 9.16a). The larger values of $\delta$ over the full ocean life compared with those during the smolt migration suggest that additional size-selective mortality still occurs beyond the area and time framed by the POST study. This supports the hypothesis of a second critical period of size-selective mortality during the first marine winter, related to growth and food limitation (Beamish and Mahnken 2001), with the first critical period being soon after ocean entry, related to predation. This assumes, of course, that size at the onset of selection periods is correlated with size at outmigration. As greater lipid stores are typically associated with larger body size, larger fish are better able to buffer against temporary food shortages.

It is possible that the magnitudes of $\delta_{fw}$ or $\delta_{tot}$ are overestimated because $s(FL_{rel})$ of tagged fish were less than those of the populations of inference, at least for smaller body sizes.
Due to minimum body length thresholds for tagging, often the upper end of the size distribution of fish was tagged, especially in populations with shorter FL. A lower $s(\text{FL}_{\text{rel}})$ in the denominator of Eq. 9.1 could therefore inflate estimates of $\delta$. Regressions of $\delta$ against mean fork length at time of tagging, however, showed weak and inconsistent relationships for $\delta_{\text{fw}}$ ($r^2 = 0.02$, slope < 0, $n = 17$) or $\delta_{\text{tot}}$ ($r^2 = 0.11$, slope > 0, $n = 17$). Reduced variation in fork length of release groups due to non-random tagging of the population of interest does not therefore appear to have much influence on estimates of $\delta$. This is likely because by tagging the upper end of the size distribution of a release group, there is less variation within that group on which size-dependent selection can act, so differences between mean fork lengths of detected fish and fish originally tagged are also expected to be less.

It is also possible that some values of $\delta_{\text{fw}}$ or $\delta_{\text{tot}}$ are poorly estimated due to chance. The criterion of having only $\geq 10$ fish detected at the river mouth station or at QCS/JDF stations appears to have led to some outliers in $\delta$ estimates. If a criterion of $\geq 20$ detected fish had instead been used, the distribution of $\delta_{\text{fw}}$ values would still be centered near zero, but magnitudes of the $n = 27$ $\delta_{\text{fw}}$ values would generally be smaller, ranging from about –0.2 to 0.2. Similarly, a new distribution of $\delta_{\text{tot}}$ values would be centered around 0.16, not far from the original mean of 0.22, but the $n = 9$ values of $\delta_{\text{tot}}$ would range from –0.04 to 0.39, no longer including the tails of the original distribution. Both criteria of minimum number of fish detected support the conclusion that directional selection did not occur during the downstream migration, but on average was positive during the inshore migration.

**Effects of body size within and among release groups**

The overall effect of body length on survival, considering not only variation within release groups but among groups as well, clearly showed that larger fish had higher survival than smaller fish. The relationship among groups was strong after both the downstream and the total migration whether separated by species or rearing history (Fig. 9.8), even though these fully-independent survival estimates could be confounded by other differences like migration distance, rearing history, or species. When these other factors were accounted for, the isolated effect of fork length on survival was still strong, where for a given tag size an increase in length of 1 cm generally led to a survival increase of about 3–7% in each segment of the migration (Fig. 9.10; in the case of V7-2L tags in the Fraser River, the best fit to detection was actually a decrease in survival). This is essentially an average effect of fork length on survival across all segments of the migration of all release groups, combining both within and among-group variation in fork
length. Considering that smolt release groups typically had anywhere between 2–10 segments in their migration, these per-segment differences in survival at a given size generate substantial size-related survival differences by the end of the migration downstream (among groups) or through Georgia Strait (among and within groups). Other studies have found similar results, with small differences in body length leading to large differences in survival (Healey 1982).

There are at least three possible explanations why the Fraser River smolts tagged with V7-2L tags showed a negative size-selective survival relationship. This result may simply be spurious. V9-6L tags were much more numerous in Fraser River studies, and under models with additive effects of body length and tag size without the interaction effect, the survival relationship for V7-2L tags was higher but parallel to that of V9-6L tags exhibiting positive size-dependence, similar to the relationship in Figure 9.10d and e. Second, size-selective mortality may be absent or weak in general during the migration down the Fraser River, but this relationship may be altered when fish are tagged, depending on the size of tag used. The smaller V7-2L tag may provide negligible tag burden such that the weak size-dependent survival relationship is not affected. The larger V9-6L tag, however, may provide a greater tag burden especially in smaller fish, such that a negligible size-dependent survival relationship in untagged fish becomes a strong positive relationship in fish tagged with larger tags. Third, in some studies of juvenile fishes, a negative size-survival relationship has been observed as a result of birds preferentially targeting larger fish (Wood and Hand 1985, Sogard 1997, Collis et al. 2001). However, the opposite pattern has also been seen in some salmon smolt studies, with birds eating smaller smolts on average (Feltham 1990, Dieperink et al. 2001). Similar patterns of negative size-dependent survival were not seen in the Fraser River for fish tagged with other tag sizes or for fish from other rivers, so size-selective avian predation is probably not a likely explanation.

There are at least five advantages of larger body size for salmon smolts. Larger fish typically have faster burst swimming speeds, so can more easily escape from predators. Second, larger fish may be invulnerable to some gape-limited predators compared to smaller fish. Third, metabolic demands typically scale allometrically (Winberg 1960), such that if prey size is proportional to body size and different sizes of prey are equally obtainable in terms of energy expended, larger fish may have to spend less time foraging than smaller fish to satisfy metabolic demands. Fourth, larger body sizes may be associated with greater energy stores which can buffer against temporary food shortages. None of these four possibilities can be evaluated from detection data here, but for steelhead and sockeye, possibly only the first two apply since fish tended to leave the inshore area rapidly so likely did not spend considerable time feeding there.
Coho and Chinook may have resided in Georgia Strait to feed, so size-dependent foraging requirements could play a role, but detection data are not informative in terms of survival or size-dependence in survival if they did in fact reside. A fifth possibility is that larger fish may have faster average travel speeds, which could allow them to leave rivers and inshore areas sooner than smaller fish. The density of predators (Huato 2001) or susceptibility of smolts to predators may be higher in rivers and inshore areas than in offshore areas outside of Georgia Strait, so leaving these areas as fast as possible could lead to a higher probability of total marine survival. This possibility is not supported by the data, however, as average downstream or inshore travel speeds did not vary with body length (Chapter 7). It appears as if burst swimming capability to escape from predators or invulnerability to gape-limited predators are overall the most likely mechanisms for observed survival advantages of larger smolts.

Size-dependence in survival is common across various fish taxa, life stages, and habitats (McGurk 1986, Lorenzen 1996, Sogard 1997). In salmon, several studies have considered smolt-to-adult survival over the full ocean life and have generally found size-survival relationships (either within a cohort, or within a population among cohorts) to be positive for coho (Mathews and Ishida 1989 for one hatchery, Holtby et al. 1990), Chinook (Reimers 1971, Bilton 1984, Zabel and Williams 2002), sockeye (Henderson and Cass 1991, Koenings et al. 1993, McGurk 1996, Farley et al. 2007), steelhead (Ward and Slaney 1988, Ward et al. 1989, Tipping 1997), pink (Mortensen et al. 2000, Moss et al. 2005), masu salmon (Miyakoshi et al. 2001), Atlantic salmon (Farmer 1994, Salminen 1997, Kallio-Nyberg et al. 2004, 2006, 2009), Baltic salmon (Lundqvist et al. 1994), and several Pacific salmon species pooled together (McGurk 1996). One study found that smolt-to-adult survival of hatchery Chinook depended more on spring growth prior to release than on smolt size at release (Beckman et al. 1999). Fewer studies have shown either no consistent evidence of size-selective survival (Holtby and Healey 1986, Mathews and Ishida 1989 for another hatchery, Quinn et al. 2005) or a negative relationship (Ewing and Ewing 2002; although adult scales were not collected in earlier years when precocious males may have returned, so these largest smolts surviving to adults may not have been accounted for). Few studies have explicitly considered non-monotonic relationships between smolt size and survival, such as dome-shaped functions (Bilton et al. 1982; in this case, covarying with release date). The POST data don’t support proper consideration of dome-shaped relationships since in many populations only the upper portion of the size distribution was often tagged. If dome-shaped relationships do actually exist, this means that within a release group the fish tagged may be on the downward slope of a size-survival relationship. This is a possible reason for the few values of
δ_{fw} and δ_{tot} < 0 observed within populations, and would lead to underestimating the actual effect of body size on survival in mark-recapture analyses.

During the short window of the smolt migration or early ocean residence, several other studies have also shown evidence of positive size-selective survival for larger body sizes of smolts or post-smolts (Healey 1982, Hargreaves and Lebrasseur 1986, Feltham 1990, Dieperink et al. 2001, Willette 2001, Duffy and Beauchamp 2008). In contrast, some studies show little effect of body size on smolt survival during the downstream (Sawada 1993, Hyvarinen and Vehanen 2004) or early ocean (Fisher and Pearcy 1988) migration, which in some cases may result from the range of body sizes studied being above a threshold where size-selective processes operate (Holtby et al. 1990). Zabel and A chord (2004) found that positive within-population effects of body size on downstream survival of Columbia River Chinook salmon were stronger than among-population effects. Size-survival relationships are not always consistent within a study; of the 11 release groups of Columbia River Chinook and steelhead smolts that exhibited significant size-selective survival relationships during the downstream migration, eight were positive and three were negative (Zabel et al. 2005). Lacroix (2008) found, similar to this study, that the effect of body length on survival of Atlantic salmon smolts became more important after ocean entry.

The strength of size-dependent selection may be mediated by environmental conditions. Holtby et al. (1990) found a positive relationship for coho in years of poor ocean conditions, when growth and subsequent survival were relatively poor, but no relationship in good years. Smolts and post-smolts may not have to spend as much time foraging to satisfy metabolic and growth demands in good years, so the overall intensity of predation may be less across all size classes. Similar arguments may be made for the limited years of data from the Keogh River, since size-selective survival varied inversely with overall survival ($r^2 = 0.68, n = 6$, Fig. 9.16b). During the period 1977–1982, in years when overall survival was poor, the strength of selection for larger smolt body sizes was considerably stronger. In years when overall survival was better, selection for body size was weaker. Body size, growth, and survival are tightly interconnected through risk-sensitive foraging mechanisms (Walters and Juanes 1993) and have even been termed a ‘single process’ (Cushing 1975) due to the difficulty (or even inappropriateness) of separating these measures.
Effects of tag size within and among release groups

The among-group effect of body size on survival occurred largely during the downstream migration (Fig. 9.8), in contrast to size-selective mortality within groups, which occurred only during the inshore migration. This among-group effect may be partly a result of tag-related mortality after release, and not of any particular differences between habitats. It seems reasonable that if tag-related mortality exists, it would occur soon after release rather than later in the migration, and the portion of the migration soon after release happens to be in rivers rather than inshore areas. In both datasets, larger tags generally led to lower survival of fish of the same body size (the exception being V7-2L tags in the Fraser River, as already mentioned; Fig. 9.10). These five release groups in Fig. 9.10 were otherwise similar in terms of release date(s) and locations. Even though tagging effects may be more likely to occur earlier rather than later in the migration, tag size was considered as an additive effect across all segments of the migration and all release groups (not just these five), so represents an average relative effect on survival across all segments and groups.

Perhaps the greatest possible bias in survival estimates is summarized by Lebreton (1992): “It is important that the act of marking does not affect $\phi$ because such an effect cannot be tested for.” It is true that absolute effects of a particular tag size on survival could not be established. Relative effects of different tag sizes on survival, however, were generally clear, with larger tags typically leading to lower survival of fish of the same body length. These relative effects likely underestimate absolute effects, because there is probably at least some tag-related mortality for the smallest tag used (V7-2L). Absolute effects of tags and tag implantation on survival of a freely-migrating fish are only possible to assess if a second type of tag or tracking technology can be used which has no effect on survival. This may be impossible to achieve for migrating fishes, but approximations of absolute effects of acoustic tags would be possible through comparisons with smaller tags assumed to have negligible effects on survival: (1) the Columbia River has an extensive system of dams that house PIT (passive integrated transponder) tag detectors in fish bypass facilities. Some fish could be tagged with V7-2L acoustic tags (or any other tag model of interest) and others with PIT tags. Survival of these two groups could be estimated during the migration downstream to successive dams, accounting for the much lower detection probability typically observed for PIT tags compared with acoustic tags. Recent studies have attempted such comparisons (Welch et al. 2008, Rechisky and Welch In press), but PIT-tagged fish were released at different times, locations, and in one case had shorter mean body lengths, thereby confounding any observed effect of tag size. Future studies
could control for these differences to isolate the effect of tag size. (2) Similarly, in previous studies one group of Columbia River fish was tagged with PIT tags, and another was tagged with dummy radio tags (7.3 mm diameter) containing PIT tags within them (Hockersmith et al. 2003). Survival to successive dams was estimated, and this eliminated the confounding of detection probability between different tag types, making a more straightforward comparison of survival effects. Higher survival was observed for PIT-tagged smolts than for dummy radio/PIT-tagged smolts (Hockersmith et al. 2003) even though tag length:body length ratios were slightly less (average, 11.2%) than those generally used in the present study (Fig. A.1). (3) Some rivers have weirs near the river mouth where outmigrating smolts are caught before being released on the downstream side. Fish could be split in several groups, with a different type of tag applied to each group (e.g., coded wire tags (CWT), PIT tags, acoustic tags), and could be released upstream at the same location and time, also controlling for body size differences among groups. After recapture at the weir, downstream survival could be estimated for each tag size assuming that variation in tag size does not affect the probability of residualizing in freshwater. These first three comparisons would only evaluate tag type effects during the downstream migration. (4) At rivers with weirs, large batches of fish could be tagged, some with CWTs (which are assumed to have less effect on survival than PIT or acoustic tags), and others double-tagged with acoustic tags and a different batch of CWT codes. Fish could be recaptured several years later at the weir during the return migration of adults, and after detecting CWTs, return rates could be compared between CWT (control) and double-tagged fish. The sample size required would be large since smolt-to-adult survival is typically <5%, so dummy acoustic tags could be used instead of electronic tags to reduce costs. Assuming that acoustic tags do not affect the probability of straying (i.e., returning to a different river from which the smolt originated), differences between groups in return rate would approximate an absolute effect of acoustic tags on survival over the entire smolt-to-adult period.

The possibility of having underestimated survival is likely (for either downstream or total migration components) due to tag-related mortality, so $\hat{\phi}$ in Fig. 9.3 should be interpreted with caution (the same can be said for other possible biases also, although tag-related mortality is likely the most severe of these). Despite the possibility of biases in absolute $\hat{\phi}$, relative survival comparisons between different groups of interest should be robust to tag-related effects assuming these effects are similar among groups. For example, survival comparisons between wild and hatchery-reared steelhead smolts (Chapter 8) or UVB-exposed and UVB-shaded coho or sockeye smolts (Chapter 10) are legitimate if different treatment groups use similar fish and tag sizes.
9.4.5 Effects of release date on survival

No overall effect of release date on survival was detected, although this effect is difficult to properly assess in a multi-stock analysis. Optimal release dates of some species or for some regions may differ from those of other species or regions. The effect of release date was modelled across all release groups and segments in each dataset because there were insufficient tag numbers or contrast in release dates within release groups to consider the within-group component independently (for most groups, tagged smolts were released together; Table A.2). Similarly, other than the Fraser River, no watershed had a wide enough range of release dates of tagged smolts to properly assess effects within watersheds. Subtle patterns of release date effects on survival within a particular species or watershed would therefore likely go undetected in this analysis. Two other factors confound the interpretation of release date effects: (1) volitional migration timing of wild fish is often confounded with body size, as larger smolts tend to migrate earlier (Irvine and Ward 1989, Zabel and Achord 2004). Both factors were considered in the model comparisons, however, so the effects of each factor should in theory have been isolated. (2) Release dates of tagged fish did not always reflect actual attempted migration dates. Wild fish were often held for several days or >1 week before tagging crews could arrive to tag fish, so this may have disrupted their migration timing, possibly altering the smoltification process (Zaugg et al. 1985). Tagged hatchery smolts were in most cases released along with the production stock, but in some cases releases of tagged fish were delayed either for logistics reasons or to allow a short period of additional growth prior to tagging. In these cases, release dates of tagged fish may be sub-optimal compared with release dates of the production stock.

Previous studies have shown different effects of release or migration date on survival. For the smolt-to-adult period, Bilton et al. (1982) showed there was an optimal release date (as well as an optimal size at release, covarying with date), with total marine survival of coho increasing with later release dates from mid-April to mid-June, until some point when survival decreased steeply for releases after mid-June. Mathews and Ishida (1989) showed there was a similar dome-shaped relationship for coho from one hatchery, but a linear relationship for another hatchery with higher survival at later release dates. Labelle et al. (1997) also showed that later releases or migration dates resulted in higher survival for coho from the east coast of Vancouver Island. Conversely, Scheuerell et al. (2009) showed that smolt-to-adult survival of Chinook and steelhead from the Snake River generally declined with later migration dates, although in some years survival was greatest at intermediate migration dates. Similar patterns of decreasing survival with increasing release date were observed for Snake River fall Chinook during just the
downstream migration, which Smith et al. (2003) attributed to possibilities of lower discharge later in the season (which could increase exposure to predators, potential for residualization, or susceptibility to disease), warmer temperatures (which increase metabolic costs of rearing and migration as well as metabolic demands of their predators), or higher water transparency (which could increase vulnerability to visual predators). Finally, survival of hatchery-reared Atlantic salmon during the inshore migration decreased with increasing release date (Lacroix 2008), which may be partly associated with increased residency in inshore waters for later releases.

Most release dates of hatchery fish around Georgia Strait have been relatively static over the past several decades (Beamish et al. 2008). Since the time when release group experiments were conducted to quantify optimal release times (e.g., Bilton et al. 1982), there is some evidence to suggest that the optimal window of ocean entry to coincide with zooplankton availability has shifted to earlier dates in recent decades as a result of climate change (Beamish et al. 2008), as it has for pink salmon in Alaska (Taylor 2008). Another series of experimental releases from multiple hatcheries may be warranted to evaluate the current effect of release date on survival of Georgia Strait populations, whether it is assessed with acoustic telemetry during the downstream and early ocean migration or with CWTs over the smolt-to-adult period.

9.4.6 Effects of species and rearing history on survival

Survival estimates assuming independence in $\phi$ among release groups were variable among species, populations and years, especially during the downstream migration (Fig. 9.3). Total $\phi$ of coho and Chinook populations are confounded with the possibility of residency in Georgia Strait, so these are likely underestimated to some unknown degree. Total $\phi$ for steelhead and sockeye/kokanee, however, were more similar among populations and years. Some populations had relatively high downstream survival but low inshore survival (e.g., Englishman River steelhead), while others showed the opposite pattern (e.g., lower Thompson River steelhead), such that by the end of the inshore migration, total survival was similar on average. Likewise, Cultus Lake sockeye had moderate downstream survival, but by the end of the total migration, had similar survival to Sakinaw Lake sockeye and kokanee groups, which did not even have a downstream component and had a shorter migration distance out of the Strait. This suggests that the timing of mortality varied among years and populations, but the proportion of a release group leaving the Strait seemed to be fairly consistent, regardless of where or when fish

16 Note that kokanee are typically regarded to be the non-anadromous form of sockeye, although here these fish confirmed by genetic samples to be kokanee (C. Wood, pers. comm.) were detected leaving the Strait.
died prior to leaving. Distance-based mortality rates $M_d$ were similar for steelhead and sockeye/kokanee during the inshore migration, but since steelhead moved faster on average through the Strait (Fig. 7.2), travel time-based mortality rates $M_{TT}$ were higher for steelhead than for sockeye/kokanee (Table 9.5). There is some indication that wild groups had higher survival on average than hatchery groups, but due to the considerable variability in these fully-independent estimates among release groups (Fig. 9.3), the pattern is not very clear. Within species and watersheds, wild Cheakamus River steelhead had higher survival than their hatchery counterparts in different years, but survival differences were smaller or nil for wild and hatchery Keogh River steelhead as well as Sakinaw Lake sockeye (hatchery) and kokanee (wild).

Treating species and rearing history as covariates in mark-recapture models allowed for the evaluation of isolated effects of species or rearing history per se, when other factors like body size, watershed, migration distance, and release date were also accounted for. In Fraser River populations, steelhead survival was higher than that of other species after accounting for other differences. Unlike in smaller rivers, it does not appear as if steelhead smolts delayed their migration for a few days after release. Their average downstream migration speeds were faster than those of other species, and they continued to migrate rapidly though Georgia Strait (similar to sockeye, and faster than coho and Chinook). Survival estimates after the total migration were similar for steelhead and sockeye (Fig. 9.3), but tagged sockeye smolts tended to be larger than other species (Table A.2), so the size-adjusted species effect on survival was greatest for steelhead. There was no effect of rearing history per se detected in the Fraser River, although steelhead were wild and the other species were of hatchery or mixed origin, so the rearing history effect is confounded with the species effect. Wild steelhead had higher survival than hatchery-reared groups of other species after accounting for other differences.

In the non-Fraser dataset, an effect of rearing history was detected after accounting for other factors. This was only observed for the first segment after release, with survival of wild fish higher than that of hatchery fish ($\beta_{M_{i,W}} > \beta_{M_{i,H}}$). After the first segment, no difference was observed between wild and hatchery-reared fish. As discussed above, it seems reasonable that naïve hatchery fish may suffer particularly high mortality from predators soon after release (Olla et al. 1998) since weaker individuals would not have been ‘weeded out’ prior to release due to a lack of selective predation pressures during hatchery rearing. Across 14 coho populations from the east coast of Vancouver Island, smolt-to-adult survival was inversely related to the duration that juvenile fish spent in a hatchery environment while rearing (ranging from 0-18 months; Labelle et al. 1997). Complex interactions may exist between the different factors considered and
affect survival, but the lack of full experimental crosses and relatively small sample sizes used for most populations in this multi-stock analysis makes it likely that detection data would not be informative with respect to such complex effects. For example, different species may have different relationships between survival and migration distance during the downstream migration, or wild and hatchery fish may have different body size-survival relationships, but only overall additive effects were considered. Similarly, because watersheds were included as additive factors in distance and travel time-based models, years could not be considered as factor variables. There was not enough crossing between watersheds and years to properly evaluate these factors separately, so the year effect was not explicitly considered in distance and travel time-based models.

Pacific salmon species show considerable variation in life history strategies (Groot and Margolis 1991, Quinn 2005), and this results in survival differences among species during freshwater and ocean phases of their life cycle (Bradford 1995, Quinn 2005). These survival differences largely have to do with the size of fish at different points in the life cycle and the amount of time spent in each habitat, but could also reflect other ecological differences. Since a large proportion of total marine mortality is thought to occur soon after ocean entry, species differences in survival during this short period could conceivably contribute largely to overall species differences in total marine mortality. No consistent differences among species were found (with the exception of Fraser River steelhead) after accounting for other factors, but some species or populations could not be monitored. Due to body size thresholds for current tag sizes available, we did not tag pink or chum salmon, which have much different life history strategies than the species we could tag, which were primarily stream-rearing wild fish or hatchery fish. Across all release groups, it appears as if wild fish generally had higher survival than hatchery fish after accounting for other factors. This was actually seen as a species effect (for wild steelhead) in the Fraser River, and in other rivers was established soon after release, in the first segment of the downstream migration. This result across multiple watersheds supports the pattern observed in Chapter 8 between wild and hatchery steelhead from a single watershed, where a high resolution of receiver stations during the downstream migration allowed the initial steep decline in survival of hatchery fish to be quantified.
Table 9.1. Model selection results for detection probability \((p)\) sub-models.  

<table>
<thead>
<tr>
<th>Model</th>
<th>(k)</th>
<th>(-2\cdot\ln(L))</th>
<th>QAIC(_c)</th>
<th>(\Delta)QAIC(_c)</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Fraser River dataset</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>(\phi(\text{seg};G), p(S;Y+\text{lev}<em>{\text{Mis}}+\text{lev}</em>{\text{PM}}+\text{Tag}))</td>
<td>118</td>
<td>5,734.7</td>
<td>4,340.5</td>
<td>0.0</td>
</tr>
<tr>
<td>(\phi(\text{seg};G), p(S;Y+\text{lev}<em>{\text{Mis}}+\text{lev}</em>{\text{PM}}))</td>
<td>117</td>
<td>5,754.5</td>
<td>4,352.5</td>
<td>12.0</td>
</tr>
<tr>
<td>(\phi(\text{seg};G), p(S;Y+\text{lev}_{\text{Mis}}+\text{Tag}))</td>
<td>117</td>
<td>5,760.6</td>
<td>4,356.8</td>
<td>16.3</td>
</tr>
<tr>
<td>(\phi(\text{seg};G), p(S;Y+\text{lev}_{\text{Mis}}))</td>
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<td>5,772.6</td>
<td>4,363.3</td>
<td>22.8</td>
</tr>
<tr>
<td>(\phi(\text{seg};G), p(S;Y+\text{lev}_{\text{PM}}+\text{Tag}))</td>
<td>117</td>
<td>5,783.3</td>
<td>4,373.1</td>
<td>32.6</td>
</tr>
<tr>
<td>(\phi(\text{seg};G), p(S;Y+\text{lev}_{\text{PM}}))</td>
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<td>5,789.8</td>
<td>4,375.6</td>
<td>35.1</td>
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<td>(\phi(\text{seg};G), p(S;Y+\text{DOY}+\text{Tag}))</td>
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<td>5,794.7</td>
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<td>40.7</td>
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<td>52.9</td>
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<td>5,956.1</td>
<td>4,494.4</td>
<td>153.9</td>
</tr>
<tr>
<td>(\phi(\text{seg};G), p(S;Y))</td>
<td>115</td>
<td>6,008.5</td>
<td>4,529.6</td>
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<td><strong>Non-Fraser dataset</strong></td>
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<td></td>
</tr>
<tr>
<td>(\phi(\text{seg};G), p(S;Y+\text{Clusters}+\text{Tag}))</td>
<td>202</td>
<td>7,618.1</td>
<td>6,865.7</td>
<td>0.0</td>
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<tr>
<td>(\phi(\text{seg};G), p(S;Y+\text{Clusters}))</td>
<td>201</td>
<td>7,645.9</td>
<td>6,889.3</td>
<td>23.6</td>
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</tbody>
</table>

\(^a\) Quantities shown are number of parameters \((k)\), log-likelihoods, and QAIC\(_c\) values (adjusted for small sample sizes and extra-binomial variation with \(\hat{c} = 1.400\) for the Fraser River dataset and \(\hat{c} = 1.177\) for the non-Fraser dataset). Sub-models for \(p\) are compared while the fully time- (‘seg’) and group-varying CJS sub-model for \(\phi\) (without main effects) is held constant, \([\phi(\text{seg};G)]\). The final station \(p\) is fixed for all groups and models according to year- and tag-type specific predictions ranging from 0.534 to 0.923 (Appendix A). In all models, additional parameters for \(p\) at NSOG were used for populations that exhibited split-route migration patterns after ocean entry. \(S =\) station; \(\text{seg} =\) segment; \(G =\) release group; \(Y =\) year; \(\text{DOY} =\) mean day of year of arrival of a particular release group at a particular station; \(\text{lev}_{\text{Mis}}(\text{lev}_{\text{PM}}) =\) Fraser River water level at the Mission (Port Mann) gauge station at the mean arrival time of a particular release group at a particular station; \(\text{Tag} =\) tag type (V7 or V9 model).

\(^b\) In non-Fraser models, because smolt migration routes are nested, additive parameters (‘Clusters’) were used in all sub-models for \(p\) 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.
Table 9.2. Model selection results for survival ($\phi$) sub-models, focusing on watershed, species, and rearing history effects. 

<table>
<thead>
<tr>
<th>Model</th>
<th>$k$</th>
<th>$-2\cdot \ln(L)$</th>
<th>QAICc</th>
<th>$\Delta$QAICc</th>
</tr>
</thead>
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<tr>
<td><strong>Fraser River dataset</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>$\phi$(seg;Y+W+CP+spp)</td>
<td>71</td>
<td>5,866.1</td>
<td>4,335.1</td>
<td>0.0</td>
</tr>
<tr>
<td>$\phi$(seg;Y+W+CP+spp+HW)</td>
<td>73</td>
<td>5,864.1</td>
<td>4,337.8</td>
<td>2.7</td>
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<tr>
<td>$\phi$(seg;Y+W+CP+HW)</td>
<td>70</td>
<td>5,877.4</td>
<td>4,341.1</td>
<td>6.0</td>
</tr>
<tr>
<td>$\phi$(seg;Y+HW)</td>
<td>95</td>
<td>5,829.0</td>
<td>4,358.9</td>
<td>23.9</td>
</tr>
<tr>
<td>$\phi$(seg;Y+spp+HW)</td>
<td>98</td>
<td>5,824.6</td>
<td>4,362.1</td>
<td>27.0</td>
</tr>
<tr>
<td>$\phi$(seg;Y+CP)</td>
<td>96</td>
<td>5,832.2</td>
<td>4,363.1</td>
<td>28.3</td>
</tr>
<tr>
<td>$\phi$(seg;Y)</td>
<td>93</td>
<td>5,898.8</td>
<td>4,404.5</td>
<td>69.5</td>
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<tr>
<td><strong>Non-Fraser dataset</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>$\phi$(seg;Y+HW+M_{i,W}+M_{i,H})</td>
<td>184</td>
<td>7,676.0</td>
<td>6,900.5</td>
<td>0.0</td>
</tr>
<tr>
<td>$\phi$(seg;Y+spp+M_{i,W}+M_{i,H})</td>
<td>186</td>
<td>7,671.3</td>
<td>6,900.8</td>
<td>0.3</td>
</tr>
<tr>
<td>$\phi$(seg;Y+spp+HW+M_{i,W}+M_{i,H})</td>
<td>188</td>
<td>7,670.9</td>
<td>6,904.7</td>
<td>4.2</td>
</tr>
<tr>
<td>$\phi$(seg;Y+M_{i,W}+M_{i,H})</td>
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<td>7,692.0</td>
<td>6,909.8</td>
<td>9.3</td>
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<td>$\phi$(seg;Y+CP+M_{i,W}+M_{i,H}+spp+HW)</td>
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<td>7,735.3</td>
<td>6,927.3</td>
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<td>$\phi$(seg;Y+CP+M_{i,W}+M_{i,H}+HW)</td>
<td>169</td>
<td>7,751.0</td>
<td>6,932.1</td>
<td>31.7</td>
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</table>

* Quantities shown are number of parameters ($k$), log-likelihoods, and QAICc values (adjusted for small sample sizes and extra-binomial variation with $\hat{c} = 1.400$ for the Fraser River dataset and $\hat{c} = 1.177$ for the non-Fraser dataset). Sub-models for $\phi$ are compared while the sub-model for $p$ is held constant at $[p(S;Y+\text{lev}_{\text{min}}+\text{lev}_{\text{max}}+\text{Tag})]$ for the Fraser River dataset and $[p(S;Y+\text{Clusters}+\text{Tag})]$ for the non-Fraser dataset (not shown for clarity). The final station $p$ is fixed for all groups and models according to year- and tag-type specific predictions ranging from 0.534 to 0.923 (Appendix A). In all models, additional parameters for $p$ at NSOG were used for populations that exhibited split-route migration patterns after ocean entry. seg = segment; Y = year; W = watershed of origin; spp = species, HW = wild or hatchery rearing history; CP = geographic ‘cluster’ parameters that differentiate between migration segments which are not in common among release groups; $M_{i,W}$, $M_{i,H}$ = initial mortality in the first segment after release, common across all hatchery groups or wild groups, and additive to the ‘baseline’ mortality within each segment.

* See Table 9.1 footnote b.
Table 9.3. Model selection results for survival ($\phi$) sub-models, focusing on body size, tag size, and release date effects.\(^a\)

<table>
<thead>
<tr>
<th>Model</th>
<th>$k$</th>
<th>$-2\cdot\text{ln}(L)$</th>
<th>QAICc</th>
<th>$\Delta$QAICc</th>
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<tr>
<td><strong>Fraser River dataset</strong></td>
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<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>$\phi$(seg:Y+W+CP+spp+FL×Tag)</td>
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<td>5,833.0</td>
<td>4,326.0</td>
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<tr>
<td>$\phi$(seg:Y+W+CP+spp+FL×Tag+RD)</td>
<td>79</td>
<td>5,830.8</td>
<td>4,326.5</td>
<td>0.5</td>
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<td>$\phi$(seg:Y+W+CP+spp+FL+Tag)</td>
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<td>4,331.3</td>
<td>5.3</td>
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<tr>
<td>$\phi$(seg:Y+W+CP+spp+FL×Tag+RD)</td>
<td>76</td>
<td>5,847.2</td>
<td>4,332.0</td>
<td>6.0</td>
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<tr>
<td>$\phi$(seg:Y+W+CP+spp+FL+RD)</td>
<td>72</td>
<td>5,859.8</td>
<td>4,332.6</td>
<td>6.6</td>
</tr>
<tr>
<td>$\phi$(seg:Y+W+CP+spp)</td>
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<td>5,866.1</td>
<td>4,335.1</td>
<td>9.0</td>
</tr>
<tr>
<td>$\phi$(seg:Y+W+CP+spp+RD)</td>
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<td>5,865.7</td>
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<td>10.8</td>
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<td><strong>Non-Fraser dataset(^b)</strong></td>
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<td></td>
<td></td>
</tr>
<tr>
<td>$\phi$(seg:Y+W+HW+M(<em>{i,W})+M(</em>{i,HT})+FL×Tag)</td>
<td>186</td>
<td>7,635.3</td>
<td>6,870.2</td>
<td>0.0</td>
</tr>
<tr>
<td>$\phi$(seg:Y+W+HW+M(<em>{i,W})+M(</em>{i,HT})+FL×Tag+RD)</td>
<td>187</td>
<td>7,633.6</td>
<td>6,870.9</td>
<td>0.7</td>
</tr>
<tr>
<td>$\phi$(seg:Y+W+HW+M(<em>{i,W})+M(</em>{i,HT})+FL×Tag)</td>
<td>187</td>
<td>7,633.6</td>
<td>6,870.9</td>
<td>0.8</td>
</tr>
<tr>
<td>$\phi$(seg:Y+W+HW+M(<em>{i,W})+M(</em>{i,HT})+FL×Tag+RD)</td>
<td>187</td>
<td>7,632.1</td>
<td>6,871.8</td>
<td>1.6</td>
</tr>
<tr>
<td>$\phi$(seg:Y+W+HW+M(<em>{i,W})+M(</em>{i,HT})+FL)</td>
<td>185</td>
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<td>6,888.3</td>
<td>18.2</td>
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<td>$\phi$(seg:Y+W+HW+M(<em>{i,W})+M(</em>{i,HT})+FL+RD)</td>
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<td>6,888.5</td>
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<td>$\phi$(seg:Y+W+HW+M(<em>{i,W})+M(</em>{i,HT})+RD)</td>
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<td>6,897.3</td>
<td>27.1</td>
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<tr>
<td>$\phi$(seg:Y+W+HW+M(<em>{i,W})+M(</em>{i,HT}))</td>
<td>184</td>
<td>7,767.0</td>
<td>6,900.5</td>
<td>30.3</td>
</tr>
</tbody>
</table>

\(^a\) Quantities shown are number of parameters ($k$), log-likelihoods, and QAIC\(_c\) values (adjusted for small sample sizes and extra-binomial variation with $\hat{\sigma} = 1.400$ for the Fraser River dataset and $\hat{\sigma} = 1.177$ for the non-Fraser dataset). Sub-models for $\phi$ are compared while the sub-model for $p$ is held constant at $[p(S:Y+lev_{min}+lev_{max}+Tag)]$ for the Fraser River dataset and $[p(S:Y+Clusters+Tag)]$ for the non-Fraser dataset (not shown for clarity). The final station $p$ is fixed for all groups and models according to year- and tag-type specific predictions ranging from 0.534 to 0.923 (Appendix A). In all models, additional parameters for $p$ at NSOG were used for populations that exhibited split-route migration patterns after ocean entry. seg = segment; Y = year; W = watershed of origin; spp = species, HW = wild or hatchery rearing history; FL = fork length; Tag = tag size; RD = release date; CP = geographic ‘cluster’ parameters that differentiate between migration segments which are not in common among release groups; $M_{i,HT}$, $M_{i,W}$ = initial mortality in the first segment after release, common across all hatchery groups or wild groups, and additive to the ‘baseline’ mortality within each segment.

\(^b\) See Table 9.1 footnote b.
Table 9.4. Model selection results for survival ($\phi$) sub-models, focusing on distance- and travel time-based model structures. 

<table>
<thead>
<tr>
<th>Model</th>
<th>$k$</th>
<th>$-2\ln(L)$</th>
<th>QAICc</th>
<th>$\Delta$QAICc</th>
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</thead>
<tbody>
<tr>
<td>Fraser River dataset</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>$\phi$(seg;Y+W+CP+spp+FLxTag)</td>
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<td>Non-Fraser dataset $^b$</td>
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<td>$\phi$(seg;Y:W+HW+M$<em>{i,W}$+M$</em>{i,HT}$+FL+Tag)</td>
<td>186</td>
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<td>89</td>
<td>8,356.1</td>
<td>7,278.2</td>
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$^a$ Quantities shown are number of parameters ($k$), log-likelihoods, and QAIC$_c$ values (adjusted for small sample sizes and extra-binomial variation with $\hat{c} = 1.400$ for the Fraser River dataset and $\hat{c} = 1.177$ for the non-Fraser dataset). Sub-models for $\phi$ are compared while the sub-model for $p$ is held constant at $[p(S;Y+lev_{min}+lev_{max}+Tag)]$ for the Fraser River dataset and $[p(S;Y+Clusters+Tag)]$ for the non-Fraser dataset (not shown for clarity). The final station $p$ is fixed for all groups and models according to year- and tag-type specific predictions ranging from 0.534 to 0.923 (Appendix A). In all models, additional parameters for $p$ at NSOG were used for populations that exhibited split-route migration patterns after ocean entry. seg = segment; Y = year; W = watershed of origin; spp = species, HW = wild or hatchery rearing history; FL = fork length; Tag = tag size; d = distance of segment, with either an overall relationship of survival and distance, or separate relationships in freshwater ($d_{fw}$) and ocean ($d_{sw}$) segments; TT = average travel time in segment for a group, with either an overall relationship of survival and TT, or separate relationships in freshwater (TT$_{fw}$) and ocean (TT$_{sw}$) segments; CP = geographic ‘cluster’ parameters that differentiate between migration segments which are not in common among release groups; $M_{i,HT}$, $M_{i,W}$ = initial mortality in the first segment after release, common across all hatchery groups or wild groups, and additive to the ‘baseline’ mortality within each segment.

$^b$ See Table 9.1 footnote b.
Table 9.5. Instantaneous distance-based \((M_d, \text{km}^{-1})\) and travel time-based \((M_{TT}, \text{d}^{-1})\) mortality rates of salmon smolts during the downstream and inshore migration. Sample size, mean \(M\), and standard error of \(M\) are shown for estimates separated by species and wild or hatchery-rearing history.  

<table>
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<tr>
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<th>Travel time-based (M)</th>
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<tr>
<td></td>
<td>(n)</td>
<td>(M_d)</td>
<td>se((M_d))</td>
</tr>
<tr>
<td><strong>Downstream – Fraser River</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Species</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Chinook (lower Thompson, H &amp; mixed)</td>
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<td>0.0054</td>
<td>0.0015</td>
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<tr>
<td>Coho (lower Thompson, H)</td>
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<tr>
<td>Steelhead (lower Thompson, W)</td>
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<td>Rearing history</td>
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<tr>
<td>Wild</td>
<td>5</td>
<td>0.0032</td>
<td>0.0006</td>
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<tr>
<td>Hatchery</td>
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<td>0.0020</td>
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<tr>
<td><strong>Total</strong></td>
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<td><strong>0.0061</strong></td>
<td><strong>0.0014</strong></td>
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<td>se((M_d))</td>
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<tr>
<td><strong>Downstream – other rivers</strong></td>
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<tr>
<td>Species</td>
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<tr>
<td>Chinook (Nimpkish River, mixed)</td>
<td>0</td>
<td>0.0095</td>
<td>0.0054</td>
</tr>
<tr>
<td>Coho (Nimpkish River, W &amp; H)</td>
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<td>0.0095</td>
<td>0.0054</td>
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<tr>
<td>Steelhead (Cheakamus River, H)</td>
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<td>0.0054</td>
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<tr>
<td>Rearing history</td>
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<td>Wild</td>
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<tr>
<td>Hatchery</td>
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<td>Hatchery</td>
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<th>Travel time-based (M)</th>
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<tbody>
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<td></td>
<td>(n)</td>
<td>(M_d)</td>
<td>se((M_d))</td>
</tr>
<tr>
<td><strong>Inshore, Howe Sound</strong></td>
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<td></td>
<td></td>
</tr>
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<td>Coho (Tenderfoot Creek, H)</td>
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<td>0.0165</td>
<td>0.0024</td>
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<tr>
<td>Steelhead (Cheakamus River, W &amp; H)</td>
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<td>0.0118</td>
<td>0.0084</td>
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<tr>
<td><strong>Total</strong></td>
<td><strong>7</strong></td>
<td><strong>0.0145</strong></td>
<td><strong>0.0036</strong></td>
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*\(M\) values were calculated for each release group from survival estimates during the downstream or inshore migration (fully-independent among release groups) and either the minimum distance or average travel time of fish that were detected. Values of \(M\) for which distance was <20 km or average travel time was <5 d within either downstream or inshore components were excluded (estimates for Howe Sound are an exception). Coho and Chinook release groups were not calculated for inshore \(M\) (except for Howe Sound). If a particular species group is composed of release groups from only one watershed, the watershed and rearing history (wild (W), hatchery (H), or mixed origin) are indicated in parentheses. Inshore \(M\) values are calculated from the point of ocean entry to the terminal detection stations in Queen Charlotte Strait and Juan de Fuca Strait (or from ocean entry to HSouter).*
Figure 9.1. Stock-specific detection probability estimates ($\hat{p}$) at Fraser River detection stations vs. relative river level at the mean arrival time of a release group at a detection station. Survival and detection probability models are fully independent among release groups and segments/stations; tag types are also fully independent in terms of $p$, i.e., model [$\phi$(seg;G), $p$(S;G;Tag)]. Error bars show 95% confidence intervals and are thick for V7 tags and thin for V9 tags. River levels were measured at the Mission gauge by Environment Canada.
Figure 9.2. Detection probability estimates ($\hat{p}$) at freshwater receiver stations in the Fraser River (a) and near mouths of other rivers (b). Estimates were generated under model $[φ(\text{seg:}G), p(\text{S:}Y+\text{lev:}+\text{Tag})]$ for the Fraser River and $[φ(\text{seg:}G), p(\text{S:}Y+\text{Clusters:}+\text{Tag})]$ for other rivers. In (a), $\hat{p}$ are grouped by year of study and order of stations encountered (e.g., $S_1$), although stations were not always in the same locations among years. Within each year-station grouping, $\hat{p}$ are ordered by average arrival date of release groups, with early-arriving groups shown first. Note that some release groups would not have sufficient fish detected at and after a particular station to estimate $p$ independently, but since $\hat{p}$ are constrained among release groups, they are estimable. In (b), $\hat{p}$ are shown by watershed and year for either the single station or two stations near the river mouth (e.g., 2004a, 2004b). Additional receiver stations were deployed in the Squamish and Cheakamus Rivers upstream of the ones shown, but only the lower 1–2 stations each year near the Squamish River mouth are shown. Error bars show 95% confidence intervals.
Figure 9.3. Estimated survival ($\hat{\phi}$) of tagged B.C. salmon smolt populations from release to the lowest in-river receiver station (green) and from release to exit from the Georgia Strait system via either northern or southern routes (blue). $\hat{\phi}$ were generated under $\phi(\text{seg}G)$. Triangles show wild populations, circles show hatchery-reared populations, and squares show populations of unknown or mixed rearing histories. Two sources of uncertainty are shown: green and blue error bars show ± 1 s.e. for the best fit parameter estimates (fixing the terminal station $p$ at the best predicted value). Black bars above and below these estimates show bounded survival estimates from fixing the terminal station $p$ at lower and upper 95% confidence limits of the predicted value, respectively (Appendix A). Footnotes beneath years represent: a, Nicola River; b, Coldwater River; c, Spius Creek; d, Deadman River; e, FVTH release group of $n = 81$; f, 2nd release group of $n = 200$; g, sockeye; h, kokanee. Region abbreviations beneath watershed names represent: MFR, middle Fraser River; LFR, lower Fraser River; SC, south mainland coast; ECVI, east coast Vancouver Island.
Figure 9.4. Histograms of mean body lengths at tagging of smolt release groups measured at: time of tagging (a), the subset of fish detected at the lowest (or second lowest) in-river receiver (b), and the subset of fish detected at QCS or JDF stations (c). Only release groups where ≥10 smolts were detected at any one station were included for (a) \( (n = 40) \). Only release groups where ≥10 smolts were detected at a single station in the lower river were included for (b) \( (n = 39) \). Only release groups where ≥10 smolts were detected at QCS or JDF were included for (c) \( (n = 17) \). Vertical lines show the overall mean (red) or median (blue) of release group mean body lengths. Release groups in which >1 tag type was used were separated.
Figure 9.5. Comparison of mean or standard deviation of body length before and after portions of the smolt migration. Mean body length of smolt release groups at time of tagging is plotted against the mean body length of fish detected at the in-river receiver furthest (or second furthest) downstream (a; $n = 39$), or detected at QCS or JDF stations (b; $n = 17$). Only those release groups that met the criterion of $\geq 10$ detected smolts are shown in (a) or (b). Similar criteria apply to (c) and (d), where the standard deviation of body length of detected fish is plotted against the standard deviation of body length of tagged fish. Dashed black lines show a 1:1 relationship and solid red lines show the best linear fit.
Figure 9.6. Standardized directional selection differentials on body length ($\delta$) for the downstream migration and total migration (downstream+SOG). Histograms show distributions of $\delta_{fw}$ (a, $n = 39$) and $\delta_{tot}$ (b, $n = 17$) for release groups in which fish shared the same tag type. Vertical lines show the overall mean (red) and median (blue) of the distribution. $\delta$ was only calculated when $\geq 10$ fish were detected at a lower river station or outer ocean QCS/JDF stations. For release group/tag type combinations in which $\delta_{fw}$ and $\delta_{tot}$ were both calculated, they are plotted against each other (c, $n = 17$). The black dashed line shows the 1:1 relationship, along which would fall point estimates if there was no size-based selection after ocean entry.
Figure 9.7. Standardized directional selection differentials on body length ($\delta$) for the downstream migration (a) and total migration (b, downstream+SOG) vs. sample size of fish detected at the in-river receiver or at outer QCS/JDF stations. Dashed black line shows the $\delta = 0$ reference. Dashed red line shows the average $\delta_{fw}$ or $\delta_{tot}$ under the criterion of $\geq 10$ fish in a release group detected at the station.
Figure 9.8. Estimated survival ($\hat{\phi}$) of smolt release groups vs. mean body length of fish in the group. Estimates are separated by species (a, downstream migration; b, total migration (downstream+SOG)) as well as by wild or hatchery rearing history (c, downstream migration; d, total migration). $\hat{\phi}$ were generated under $[\hat{\phi}_{segG}]$. Error bars show ± 1 s.e. Plotted lines show best logistic fit to the equally-weighted point estimates, separately for each species or rearing history.
Figure 9.9. Proportion of smolts from the 2005 Tenderfoot Creek Hatchery coho release group surviving the migration downstream and through Howe Sound, grouped by body length classes and tag sizes. Estimates are based on assessing the fate of each tagged fish to successive detection stations, but do not correct for detection probabilities. The number of fish tagged in each body length and tag size group are indicated below the estimates in (a), totalling $n = 50$ for V7 tags and $n = 50$ for V9 tags.
Figure 9.10. Predicted survival as a function of body length and tag size for five release groups of salmon smolts. Only release groups in which >1 tag sizes were used and in which ≥20 fish were tagged with each tag size are shown. Only a single segment is shown for each group (slopes and relative distance between lines are consistent across segments). Groups and segments shown are: (a) 2005 Cultus Lake hatchery sockeye, river mouth to NSOG; (b) 2006 Coldwater River wild steelhead, release to Fra_1; (c) 2006 Deadman River wild steelhead, release to Fra_1; (d) 2005 Tenderfoot Creek Hatchery coho, HSinner to HSouter; and (e) 2006 Tenderfoot Creek Hatchery coho, Chk_3 to Sqm_4 segment. Models assumed are \[ \phi(\text{seg}: Y + W + CP + spp + FL x Tag), p(S: Y + lev\text{Mis} + lev\text{PM} + Tag) \] for the Fraser River (a, b, c) and \[ \phi(\text{seg}: Y + W + HW + M_{i,W} + M_{i,HT} + FL + Tag), p(S: Y + Clusters + Tag) \] for other rivers (d, e). Solid lines show best fit predictions and dashed lines show 95% confidence bands. The body size range of predictions is limited to the size range of fish that were tagged with a particular tag size. Tag sizes are shown to scale.
Figure 9.11. Estimated survival ($\hat{\phi}$) of smolt release groups vs. weighted average release date of fish in the group. Estimates are separated by species (a, downstream migration; b, total migration (downstream+SOG)) as well as by wild or hatchery rearing history (c, downstream migration; d, total migration). $\hat{\phi}$ were generated under $[\hat{\phi}_{seg,G}]$. Error bars show ± 1 s.e. Plotted lines show best logistic fit to the equally-weighted point estimates, separately for each species or rearing history.
Figure 9.12. Natural logarithm of estimated survival, \( \ln(\hat{\phi}) \), of smolt release groups vs. minimum distance migrated. Estimates are separated by species (a, downstream migration; b, total migration (downstream+SOG)) as well as by wild or hatchery rearing history (c, downstream migration; d, total migration). \( \hat{\phi} \) were generated under \( [\phi_{seg-G}] \). Estimates of \( \ln(\hat{\phi}) < -5 \) (i.e., \( \hat{\phi} < 0.007 \)) were set to \(-5\) for clarity. Error bars show ± 1 s.e. Plotted lines show best linear fit to the equally-weighted \( \ln(\hat{\phi}) \) point estimates, separately for each species or rearing history.
Figure 9.13. Natural logarithm of estimated survival, ln(\(\hat{\phi}\)), of smolt release groups vs. average travel time of detected fish from each release group. Estimates are separated by species (a, downstream migration; b, total migration (downstream+SOG)) as well as by wild or hatchery rearing history (c, downstream migration; d, total migration). \(\hat{\phi}\) were generated under \([\hat{\phi}_{seg,G}\]). Estimates of \(\ln(\hat{\phi}) < -5\) (i.e., \(\hat{\phi} < 0.007\)) were set to –5 for clarity. Error bars show ± 1 s.e. Plotted lines show best linear fit to the equally-weighted ln(\(\hat{\phi}\)) point estimates, separately for each species or rearing history. Note the scale break for travel time in each plot before the last data point in the total migration.
Figure 9.14. Instantaneous distance-based ($M_d$, km$^{-1}$) or time-based ($M_{TT}$, d$^{-1}$) mortality rates of salmon smolts during the downstream and inshore migration. Downstream mortality rate estimates are separated for Fraser River (a, d) and other river (b, e) populations. Mortality rate estimates through the Georgia Strait system (c, f) are shown only for steelhead and sockeye/kokanee. $M$ were calculated from $\phi_{\text{seg:G}}$ that were generated under $[\phi_{\text{seg:G}}]$. Note the largest value of $M_{TT}$ in (e) is indicated in parentheses as it is not on the same scale as other values (i.e., histogram axis is broken).
Figure 9.15. Instantaneous mortality rates of salmon smolts during the downstream and inshore migration vs. the cumulative distance or duration of the migration. Distance-based mortality rates ($M_d$, km$^{-1}$) are shown in (a-c) vs. minimum distance travelled, and time-based mortality rates ($M_{TT}$, d$^{-1}$) are shown in (d-f) vs. average travel time. Downstream mortality rate estimates are separated for Fraser River (a, d) and other river (b, e) populations. Mortality rate estimates through the Georgia Strait system (c, f) are shown only for steelhead and sockeye/kokanee. Distances and travel times for inshore $M$ do not include the downstream portion of the migration.
Figure 9.16. Size-selective smolt-to-adult survival of wild Keogh River steelhead. (a) Mean fork lengths at time of ocean entry back-calculated from scale samples of adults returning to the Keogh River versus mean fork lengths of all smolts at ocean entry in the corresponding year (10 years during 1977–1998). Only years when ≥10 back-calculated smolt lengths were calculated are shown. (b) Standardized directional selection differentials for fork length from smolt release to return of adults versus overall estimated smolt-to-adult survival for smolt years 1977–1982. Earlier data (1977–1982) from Ward and Slaney (1988) and Ward et al. (1989). Recent data (1987–1998) provided by B. Ward.
9.5 References


Chittenden, C.M., Beamish, R.J., Neville, C.M., Sweeting, R.M., and McKinley, R.S. In press. The use of acoustic tags to determine the timing and location of the juvenile coho salmon migration out of the Strait of Georgia, Canada. Trans. Am. Fish. Soc.


10 Effects of solar ultraviolet radiation exposure on early ocean survival and fry-to-smolt growth of juvenile salmon

10.1 Introduction

Many Pacific salmon populations in British Columbia declined over the last several decades, largely as a result of decreased marine survival exclusive of fishing. Large-scale geographic coherence in trends of marine (smolt-to-adult) survival and abundance suggest that factors at the regional scale are responsible for the declines (Coronado and Hilborn 1998, Peterman et al. 1998, Welch et al. 2000; but see Bradford 1999 for exceptions in terms of covariation in smolt abundance at smaller scales). These trends are not exclusive to B.C., as similar ones have been observed simultaneously in Atlantic salmon on the east coast of North America (Friedland 1998). Patterns of decline tended to occur at southerly latitudes first and progressively move northward, and also tended to occur predominantly in rain shadow areas with high exposure to sunlight (Walters and Ward 1998).

Anadromous salmonids exhibit tremendous diversity in life history strategies. Populations that exhibited declines in marine survival and abundance were of species that rear in shallow streams for one or more years, like coho, steelhead, and stream-type Chinook salmon (Walters and Ward 1998). Several hypotheses were suggested as possible causes of these declines, including shifts in ocean climate regimes, density dependent survival at sea due to increased hatchery smolt production, disease, freshwater habitat loss, fishing mortality (in the case of abundance), and shifts in the abundance and distribution of predators. Food limitation in the first year of ocean life and concentrations of predators that feed on outmigrating salmon smolts at river mouths were leading hypotheses in this debate. The hypothesis of food limitation predicts that mortality should occur whenever post-smolts are faced with food shortage, either in summer (Pearcy 1992) or in winter (Beamish and Mahnken 2001). The hypothesis of predator concentrations predicts that mortality should predominantly occur during the smolt migration, especially at river mouths, estuaries, or immediately after ocean entry (Fisher and Pearcy 1988, Greenstreet et al. 1993, Olesiuk et al. 1996, Collis et al. 2002).

Patterns of mortality observed in the first few years of the POST Project, in particular those observed with the mobile tracking component in Howe Sound (Chapters 5, 7), did not
clearly support either leading hypothesis. Mortality rates of Tenderfoot Creek coho salmon were relatively high during their migration though Howe Sound, but mortality locations were not uniquely clustered around the river mouth (Fig. 7.11), as expected under a ‘bottleneck’ predation hypothesis. Rather, mortality locations were scattered throughout Howe Sound, and the rate of mortality appeared to be relatively constant during the migration through Howe Sound (Fig. 7.12). This pattern led us to re-consider a hypothesis proposed 10 years ago, that elevated mortality may occur soon after ocean entry due to osmotic adjustment failure.

One potential cause of elevated mortality is ultraviolet-B radiation (UVB) from sunlight during freshwater life, which could result in DNA damage with physiological and survival consequences once juvenile salmon undergo smoltification and enter saltwater (Walters and Ward 1998). This hypothesis was proposed after observing as noted above that marine survival declines occurred simultaneously on both coasts, started earlier at more southerly latitudes, occurred primarily in sunny areas, and were most often seen in populations that rear in shallow streams ≥1 year. The common factor in all these cases is elevated exposure to UVB in streams or hatchery tanks. While juveniles rear in freshwater, solar UVB may damage DNA which codes for enzymes that are needed for saltwater life. This damage may not be immediately repaired since such enzymes are not induced or actively produced until ocean entry (Walters and Ward 1998). Due to atmospheric ozone depletion at North American latitudes (Fig. 10.1a), levels of incident UVB reaching the ground have gradually increased (Fig. 10.1b, c) over the same period as salmon marine survival declined. These increases in UVB occurred across a wide range of latitudes in both summer (average 3.3–4.4% increase per decade) and winter (average 6.2–7.9% increase per decade) months (Tarasick et al. 2003).

To address the hypothesis that UVB exposure during freshwater rearing causes reduced survival at the time of smoltification and ocean entry, we conducted a UVB shading experiment with two hatchery-reared populations during their outdoor rearing life. We evaluated possible effects on survival of fish under shaded and sunlight-exposed treatments during the smolt migration by tagging fish from treatment groups and using the POST tracking array. Hatchery-reared Tenderfoot Creek coho salmon exhibited marine survival declines, especially during the 1990s (Fig. 10.2a), and are a shallow stream-rearing species in the wild. Marine survival estimates are not available for Cultus Lake sockeye salmon, but this population showed pronounced declines in adult returns over time (Fig. 10.2b; like some other Fraser River sockeye populations, Cultus Lake sockeye have a 4-year abundance cycle, and declines occurred in all four cycle lines). Although wild juvenile sockeye salmon are primarily lake-dwelling fish where
the effect of UVB may be comparably minor due to depth refugia in most lakes, their hatchery-reared counterparts could be susceptible to UVB. While this UVB shading experiment is logistically feasible only in a hatchery, the effects of UVB radiation are predicted to be similar for wild salmonids that rear in shallow freshwater streams ≥1 year.

10.2 Methods

10.2.1 UVB filtering experiment

In early summer 2006, we started UVB exposure experiments at Tenderfoot Creek Hatchery with juvenile coho and at Inch Creek Hatchery with Cultus Lake sockeye (Table 10.1). In the case of Tenderfoot Creek coho, soon after production stock fry were transferred to a rearing pond, a sample of these fish were netted and randomly divided into either side of a smaller divided tank (each half about 3 m long × 1 m wide × 0.45 m deep; about 300 fish in each side). One side of the tank contained the control group, where fish were exposed to sunlight. The other side contained fish that were screened from above by a Dupont-Teijin Melinex® 943 plastic film (125 µm thickness) that filtered UVB wavelengths but allowed photosynthetically active radiation to penetrate to the water (Fig. 10.3). The two groups of fish were otherwise treated identically in terms of the water flowing through the tanks, the feed type and quantity, and tagging procedures. In mid-July 2006, the partition between treatment groups accidentally detached in the tank, and fish mixed between them. This first experiment was abandoned, with fish returned to the rearing pond. A second experiment was started on July 20 with fish again taken from the rearing pond (they were taken before fish from the first experiment were returned to the pond). In the case of Cultus Lake sockeye, fry were initially kept in small circular rearing tanks (1 m diameter) beginning in mid-June, with three tanks shaded by the UVB filter and three tanks exposed to sunlight (i.e., the production stock itself was shaded or exposed to sunlight). Several weeks later, fish were aggregated into larger circular tanks (about 3 m diameter × 1 m deep), maintaining the same treatments. Water at both hatcheries was clear, so at these tank depths little attenuation of UVB would be expected (Kirk 1994). Screening at both hatcheries continued until smolts were tagged in 2007 before their release and downstream migration.

In Tenderfoot coho, stunted growth was observed in the UVB-exposed group 6 weeks prior to tagging and there was concern over whether there would be enough smolts ≥125 mm, the fork length threshold required for tagging (at time of tagging, only 34 fish were of adequate size instead of the desired 100). Dorsal pigmentation differences were also observed between the
production stock and both treatment groups (UVB-shaded and UVB-exposed). The production stock reared in a long hatchery channel 1 m deep, and fish were darker in colour. Both treatment groups reared in smaller, shallower tanks 45 cm deep (which were more amenable to experimental shading), and fish were lighter in colour (tanks were also lighter in colour than the deeper rearing channel). To control for these growth and colouration differences, a second, shorter-term UVB shading experiment was implemented starting April 3 2007. This 5-week exposure experiment was used to evaluate whether, if a UVB radiation effect on survival did exist, the sensitive period to exposure was immediately (~1 month) before the downstream migration. Thus, the experiment became a 2 × 2 crossed design, with 9-month UVB-exposed, 9-month UVB-shaded, 1-month UVB-exposed, and 1-month UVB-shaded treatment groups. Tagged fish were released into Tenderfoot Creek on May 10 along with the hatchery production stock.

Cultus Lake sockeye smolts were much larger and there was no concern about smolts meeting size thresholds for tagging (the fish were part of an accelerated-growth rearing program). Two different tag types were used, each with a different manufacturing timeframe. The first group of fish (containing both UVB-shaded and UVB-exposed sockeye) was released along with most of the Cultus Lake production stock on April 26 into Sweltzer Creek. The second group of fish had tags that were larger (with a longer battery life) and were implanted later. The second group was released May 16 into Sweltzer Creek.

### 10.2.2 Smolt tagging

At Tenderfoot Creek Hatchery, 199 coho smolts were tagged, split among UVB-exposed and UVB-shaded treatment groups in the two exposure duration treatments. Body size frequency distributions of these four groups are shown in Fig. 10.4a. Average body sizes were slightly smaller in the 9-month UVB-exposed tagging group than in the other three tagging groups (Table 10.1). Tagged fish from all groups represented the upper end of the size distribution of fish in each tank at the end of the experimental treatments (Fig. 10.4a). VEMCO V7-2L coded acoustic tags with a 30–90 s random delay between transmissions were used for all fish, with tags measuring 7 × 20 mm. Resulting tag length to body length ratios ranged from 13.6–16.0%, in line with recommendations by Lacroix et al. (2004). Tag implantation methods are described in Appendix A.

At Inch Creek Hatchery, 319 Cultus Lake sockeye smolts were tagged, split among UVB-exposed and UVB-shaded treatment groups in each of the two release groups. Body size
frequency distributions of the four groups are shown in Fig. 10.4b. Fish that were not tagged were not measured (like in Fig. 10.4a), but all fish sampled were well above the minimum threshold size of 140 mm for V9 tags so lengths of tagged fish were likely representative of fish in the experimental tanks at the end of the treatment period. With three extra weeks to grow, body sizes were larger in the second release group, but within each release period average body length was similar between UVB treatments (Table 10.1). VEMCO V9-6L acoustic tags, measuring 9 x 20 mm, were used for smolts in the first release, while V9-1L tags, measuring 9 x 24 mm, were used for smolts in the second release. Resulting tag to body length ratios ranged from 10.8–12.5% for the first release and 11.1–14.1% for the second release. All tags had a 30–90 s random delay between tag emissions.

10.2.3 Study sites and stationary acoustic arrays

Cultus Lake (1.50 m annual precipitation; 179 d per year with ≥0.2 mm precipitation) drains into Sweltzer Creek, then the Vedder River, the Sumas River, and finally the Fraser River before reaching Georgia Strait (Fig. 10.5a). Cultus Lake sockeye were released into Sweltzer Creek. They passed up to four receiver stations in the Fraser River (14 receivers deployed in seven sub-stations) ranging from Mission to below Annacis Island (Fig. 10.5a). Tenderfoot Creek (2.37 m annual precipitation; 193 d per year with ≥0.2 mm precipitation) drains into the Cheakamus River, then into the Squamish River before reaching Howe Sound (Fig. 10.5b). Howe Sound drains into Georgia Strait about 40 km south of the river mouth. Fish were released into Tenderfoot Lake, the acclimation pond upstream of Tenderfoot Creek. Nine freshwater stations of single or paired receivers were deployed to detect Tenderfoot Creek coho during the outmigration: one station in Tenderfoot Creek, two stations in the Cheakamus River, four stations in the Squamish River, and one in Squamish Harbour (Fig. 10.5b). These lower river and estuary stations permit the partitioning of survivorship into freshwater and inshore components.

Deployment methods for ocean lines of acoustic receivers are described in Appendix A. Receiver lines used for this study included those in Howe Sound (two lines for Tenderfoot Creek coho, HS_{inner} and HS_{outer}), the northern Strait of Georgia (NSOG), Queen Charlotte Strait (QCS), and Juan de Fuca Strait (JDF) (Fig. 1.4). Exit routes to the Pacific Ocean from Georgia Strait include Johnstone Strait and Queen Charlotte Strait to the north, and Juan de Fuca Strait to the south (Fig. 1.4). Ocean receivers and Fraser River receivers were in place throughout the summer, past expected tag battery life. Cheakamus and Squamish River receivers were in place.
until either mid-June or mid-August, well beyond the typical migration period of coho smolts observed in years 2003–2006.

10.2.4 Operating mobile hydrophone on boat

Mobile sampling aided in quantifying the potential for differential mortality between the UVB-exposed and UVB-shaded Tenderfoot coho during their migration through Howe Sound. Tagged coho smolts were actively tracked from a boat after they left the Squamish River and entered Howe Sound, using a VEMCO VR-28 acoustic receiver with a towed, directional hydrophone. Sampling periods occurred towards the end of the smolt migration through Howe Sound (late May to early June, 9 d) and again several weeks after the migration (late July to early August, 9 d), with the aim to identify locations where tags had stopped moving and were presumably laying on the seabed. Although the fates of fish carrying these stationary tags are unknown, we assume these locations represent approximate locations of mortality. Assuming a horizontal detection radius of 300m, about 75% of the area of Howe Sound in the first trip and 85% in the second trip was covered by mobile sampling (Fig. 10.6a, b). Actual detection widths were likely narrower than 300 m, however (Chapter 5), so the effective area covered was possibly <50%. Grid survey methods are described in Chapter 5 and Appendix A.

10.2.5 Data analyses

During their migration out of Georgia Strait, tagged sockeye smolts passed up to six detection points: four stations in the Fraser River (Fig. 10.5a) and one or two lines of ocean receivers covering the southern and northern exit routes from Georgia Strait (Fig. 1.4). Tagged coho smolts passed up to 12 detection points: seven stations in freshwater, one station in Squamish Harbour (Fig. 10.5b), two stationary lines of receivers in Howe Sound, and one or two lines of receivers after leaving Howe Sound (Fig. 1.4). In previous years, however, Tenderfoot Creek coho were rarely detected after leaving Howe Sound and entering Georgia Strait (Chapter 7). Due to the possibility of summer residency in the Strait, we limited survival inferences to the migration through Howe Sound (including the portion of the lower sound sampled by mobile tracking). We aggregated detections at the NSOG, QCS, and JDF stations to represent detection anywhere after entry into Georgia Strait.

It was necessary to estimate detection probabilities ($p$) at each receiver station to estimate the extent of migration of tagged fish. We concurrently estimated survival probabilities ($\phi$) in each segment of the migration of Cultus Lake sockeye using models based on the Cormack-
Jolly-Seber recaptures-only mark-recapture model (CJS). The final segment $\phi$ leading to QCS or JDF is confounded with $p$ at the final station (QCS/JDF) for Cultus Lake sockeye. We estimated an overall $p$ for the NSOG line ($p_{\text{NSOG}}$, 90.4% for V9 tags in 2007) and assumed this value for the QCS/JDF lines, correcting for slight differences in line geometry ($p_{\text{QCS}}$, 92.4%; $p_{\text{JDF}}$, 91.8%). The estimate of $p_{\text{NSOG}}$ came from a regression model incorporating POST tags crossing the NSOG station in years 2004–2007 and allowing year-specific and tag type-specific variation in $p$ (Appendix A). The predictions of $p_{\text{QCS}}$ and $p_{\text{JDF}}$ were made from the same regression model, adjusting for coverage values specific to QCS and JDF in 2007 (Appendix A). After assuming fixed values for the final stage $p$, we used the 7-digit detection histories for Cultus Lake sockeye in a CJS model implemented with Program MARK (White and Burnham 1999) through RMark (Laake and Rexstad, 2007). See Appendix A for model details and assumptions.

Multiple data sources were used for estimating survival of Tenderfoot Creek coho, including both mark-recapture data from stationary receiver lines and tag-recovery data from mobile tracking identifications of approximate mortality locations of coho smolts in Howe Sound between lines of stationary receivers. The Burnham joint live-recaptures and dead-recoveries model (Burnham 1993) incorporates both types of data. In addition to survival probabilities ($S$) in each segment of the migration and $p$ at each detection station, the model involves other parameters representing detection efficiency ($r$) of motionless tags on the seabed of Howe Sound and ‘fidelity’ parameters ($F$) allowing for migration among mutually exclusive sampling areas (which is not relevant in this spatial case). The resulting detection history of each fish was comprised of 24 digits, with 12 representing detection or not at stationary lines and 12 representing tag recovery periods (i.e., locating tags in fish that died) between stationary lines. All $F$ values were fixed at 1, and all $r$ values other than those corresponding to the three segments in Howe Sound (river mouth to HS$_{\text{inner}}$, HS$_{\text{inner}}$ to HS$_{\text{outer}}$, and after HS$_{\text{outer}}$) were fixed at 0. Fixing a value of $p$ for the final (aggregated) station was not necessary for the Tenderfoot Creek coho data because inferences were limited to Howe Sound. The product of segment-specific survival estimates, either $\hat{\phi}$ or $\hat{S}$, becomes the cumulative survivorship decline along migration routes.

We used model goodness-of-fit diagnostics in Program RELEASE (Burnham et al. 1987) and Program MARK to assess the fit of a reasonably general mark-recapture model to detection data. The general model for Cultus Lake sockeye involved full independence among migration segments (Seg), releases (Release) and UVB treatments (Treat) in terms of $\phi$ and $p$, i.e., $[\phi(\text{Seg} \times \text{Release} \times \text{Treat}), p(\text{Station} \times \text{Release} \times \text{Treat})]$. The model for Tenderfoot Creek coho
involved full independence among UVB treatments and exposure duration (Duration), common \( p \) at each station among these groups, and common \( r \) among groups in each Howe Sound segment, i.e., \( \{S(Seg\times Treat\times Duration), p(Station), r(Seg), F(=1)\} \). For both datasets, the goodness-of-fit of the model to detection data was adequate (based on 1000 Monte Carlo parametric bootstrap simulations; \( p = 0.207 \) for the Cultus Lake sockeye dataset and \( p = 0.065 \) for the Tenderfoot Creek coho dataset). This was confirmed for the Cultus Lake CJS model through a Program RELEASE overall \( \chi^2 \) goodness-of-fit test (\( \chi^2 = 39.4 \), d.f. = 37, \( p = 0.36 \)). An overdispersion parameter, \( \hat{c} \) (Burnham et al. 1987), was estimated using the deviance bootstrap simulation method in Program MARK. The estimated values were \( \hat{c} = 1.074 \) for the Cultus Lake sockeye dataset and \( \hat{c} = 1.132 \) for the Tenderfoot Creek coho dataset. These values of \( \hat{c} \) were used to adjust AIC values for comparing candidate models (Lebreton et al. 1992), and also for expanding confidence limits on parameter estimates (Burnham et al. 1987).

The overall hypothesis of differing survival among UVB treatment groups during the smolt migration was addressed by directly comparing candidate models, some of which included this factor. Under this umbrella hypothesis, candidate models were treated as competing hypotheses on a more detailed level, each providing specific predictions about how survival or detection probabilities may differ among UVB treatment groups and either release periods (Cultus Lake sockeye) or exposure duration of UVB treatments (Tenderfoot Creek coho). Models were compared using Akaike’s Information Criterion (i.e., AIC; Burnham and Anderson 2002) on the basis of their goodness-of-fit to the data and the number of parameters in the model required to achieve that fit. For both datasets, sub-models for \( p \) (\([p]\)) were compared while assuming a general sub-model for survival (\([\phi]\)), and the best \([p]\) was then held constant for comparing \([\phi]\).

**Cultus Lake sockeye models**

In the Fraser River, water level (or discharge) has a strong influence on \( p \) at river stations (Chapters 3, 9). Higher river levels and faster flows, typically later in the migration season, generally result in decreased \( p \) due to greater background noise or smolts spending less time within detection range of a given receiver as they travel downstream. Since the two Cultus Lake sockeye groups were released nearly 3 weeks apart, \( p \) were treated as independent among releases periods in most candidate models for \( p \). Some models assumed an additive effect of ‘Release’ that was consistent across all stations, others assumed full independence among stations and releases (i.e., with a Station:Release interaction), while others assumed full
independence among releases at Fraser River stations but common estimates among releases at ocean stations. In one highly-constrained model, \( p \) was modelled as common among the two releases at each station. Finally, to allow for the possibility that \( p \) could differ among UVB treatment groups (due to behavioural effects like differences in swimming speeds or depths travelled), some \([p]\) allowed for either an additive effect of UVB treatment that was consistent across all stations or a fully-independent effect of UVB treatment at each station. In total, eight \([p]\) were considered while holding constant a general \([\phi]\):

1. \( \phi(Seg \times Release \times Treat), p(Station \times Release \times Treat) \)  
   fully-independent \( p \) estimates among release periods and UVB treatments at each station

2. \( \phi(Seg \times Release \times Treat), p(Station \times Release) \)  
   fully-independent \( p \) estimates among release periods at each station

3. \( \phi(Seg \times Release \times Treat), p(Station \times Release + Treat) \)  
   fully-independent \( p \) estimates among release periods at each station, with an additive effect of UVB treatment across all stations

4. \( \phi(Seg \times Release \times Treat), p(Station_{fw} \times Release + Station_{sw} + Treat) \)  
   fully-independent \( p \) estimates among release periods at each Fraser River station, but common \( p \) estimates at ocean stations

5. \( \phi(Seg \times Release \times Treat), p(Station_{fw} \times Release + Station_{sw} + Treat) \)  
   fully-independent \( p \) estimates among release periods at each Fraser River station, but common \( p \) estimates at ocean stations, with an additive effect of UVB treatment across all stations

6. \( \phi(Seg \times Release \times Treat), p(Station + Release) \)  
   additive effect of release period on \( p \) across all stations

7. \( \phi(Seg \times Release \times Treat), p(Station + Release + Treat) \)  
   additive effects of release period and UVB treatment on \( p \) across all stations

8. \( \phi(Seg \times Release \times Treat), p(Station) \)  
   fully-pooled \( p \) estimates among release periods and UVB treatments at each station

The best \([p]\) in terms of AIC scores was selected and then held constant while comparing \([\phi]\).

Candidate models for \( \phi \) involved possible effects of UVB treatment, release period, and body size. Some \([\phi]\) incorporated release period and/or UVB treatment as additive effects on \( \phi \), whereas one model assumed full independence among these factors and migration segments. In two models, the potential effect of UVB treatment was assumed to occur only after ocean entry in the case that survival consequences of UVB exposure were related to saltwater tolerance. Two models incorporated body size as an additive covariate. In total, 10 models were considered:
1. $\phi(\text{Seg}), p(\text{Station} \times \text{Release})$ fully-pooled $\phi$ estimates among UVB treatments and release periods in each segment

2. $\phi(\text{Seg+FL}), p(\text{Station} \times \text{Release})$ fully-pooled $\phi$ estimates among UVB treatments and release periods in each segment, with fork length as an additive individual covariate

3. $\phi(\text{Seg+Release}), p(\text{Station} \times \text{Release})$ $\phi$ estimates pooled among UVB treatments, with an additive effect of release period

4. $\phi(\text{Seg+Treat}), p(\text{Station} \times \text{Release})$ $\phi$ estimates pooled among release periods, with an additive effect of UVB treatment

5. $\phi(\text{Seg+Treat}_{sw}), p(\text{Station} \times \text{Release})$ $\phi$ estimates pooled among release periods, with an additive effect of UVB treatment in ocean segments only (pooled in freshwater segments)

6. $\phi(\text{Seg+Release+Treat}), p(\text{Station} \times \text{Release})$ additive effects of both release period and UVB treatment

7. $\phi(\text{Seg+Release+Treat}_{sw}), p(\text{Station} \times \text{Release})$ additive effect of release period, and additive effect of UVB treatment in ocean segments only (pooled in freshwater segments)

8. $\phi(\text{Seg+Release+Treat}), p(\text{Station} \times \text{Release})$ additive effects of both release period and UVB treatment, with an interaction between release period and UVB treatment on $\phi$

9. $\phi(\text{Seg+Release+Treat+FL}), p(\text{Station} \times \text{Release})$ additive effects of both release period and UVB treatment, with an interaction between release period and UVB treatment on $\phi$, and with fork length as an additive individual covariate

10. $\phi(\text{Seg+Release+Treat}), p(\text{Station} \times \text{Release})$ fully-independent $\phi$ estimates among release periods and UVB treatments in each segment

Candidate models were compared on the basis of AIC scores.

After comparing the above [$\phi$], we suspected that the best model in terms of AIC scores may have over-fit the data. This was the general model; the other nine models in the above comparison were much more constrained. It was not necessarily true that detection data supported independent effects of both release period and UVB treatment in each segment, since none of the above models considered only one of these as a multiplicative effect with segment. We conducted a further, post-hoc comparison of [$\phi$] to gauge whether reductions from the general model would result in more parsimonious [$\phi$]. Since models in this post-hoc comparison were not a part of the initial model set prior to analyses, we note the results from this further comparison should be treated as preliminary (Anderson et al. 2001, Burnham and Anderson 2002). Four additional [$\phi$] were considered:
1. $\phi(\text{Seg} \times \text{Release} \times \text{Treat}),$ $p(\text{Station} \times \text{Release})$ fully-independent $\phi$ estimates among release periods and UVB treatments in each segment; best $p$ from previous step

2. $\phi(\text{Seg} \times \text{Release}),$ $p(\text{Station} \times \text{Release})$ fully-independent $\phi$ estimates among release periods in each segment

3. $\phi(\text{Seg} \times \text{Release} + \text{Treat}),$ $p(\text{Station} \times \text{Release})$ fully-independent $\phi$ estimates among release periods in each segment, with an additive effect of UVB treatment

4. $\phi(\text{Seg} \times \text{Treat}),$ $p(\text{Station} \times \text{Release})$ fully-independent $\phi$ estimates among UVB treatments in each segment

5. $\phi(\text{Seg} \times \text{Treat} + \text{Release}),$ $p(\text{Station} \times \text{Release})$ fully-independent $\phi$ estimates among UVB treatments in each segment, with an additive effect of release period

Models were compared on the basis of AIC scores.

**Tenderfoot Creek coho models**

Coho smolts from all four treatment groups were released at the same time, so neither effects of UVB treatment nor exposure duration on $p$ were expected. This possibility was still allowed for in some candidate models, with UVB treatment and/or exposure duration modelled as additive effects on $p$ across stations. Two models assumed fully-independent effects of ‘Treat’ and ‘Duration’ on $p$ at each station. An index of tag strength was assessed while activating the 199 V7 tags used for coho, prior to implanting tags into smolts (Chapter 6). In some models, this index was treated as an additive individual covariate on $p$, while in other models, it was absent (these two $p$ had similar support in the data in an earlier analysis; Table 6.1). The tag strength index was not considered in models for Cultus Lake sockeye since only fish in the first release had a strength index measured. In total, the following 10 $p$ were considered while assuming a general $[\phi], [S(\text{Seg} \times \text{Treat} \times \text{Duration})],$ a segment-independent but group-pooled sub-model for mobile detection efficiency in Howe Sound segments, $r(\text{Seg})$, and fidelity parameters fixed to 1:

1. $S(\text{Seg} \times \text{Treat} \times \text{Duration}),$ $p(\text{Station} \times \text{Treat} \times \text{Duration}),$ $r(\text{Seg}), F(=1)$ fully-independent $p$ estimates among UVB treatments and exposure durations in each segment

2. $S(\text{Seg} \times \text{Treat} \times \text{Duration}),$ $p(\text{Station} + \text{Treat}),$ $r(\text{Seg}), F(=1)$ additive effect of UVB treatment on $p$ across all stations

3. $S(\text{Seg} \times \text{Treat} \times \text{Duration}),$ $p(\text{Station} + \text{Duration}),$ $r(\text{Seg}), F(=1)$ additive effect of exposure duration on $p$ across all stations
The best \( p \) in terms of AIC scores was carried forward to the comparison of \( \phi \).

In terms of survival \( S \), instead of different release periods, UVB treatments were crossed with different exposure durations. Otherwise, the same 10 \( \phi \) for Tenderfoot Creek coho were considered as for Cultus Lake sockeye:

1. \( S \) (Seg),
   \( p \) (Station+Treat+Duration),
   \( r \) (Seg), \( F(=1) \)
   fully-pooled \( S \) estimates among UVB treatments and exposure durations in each segment

2. \( S \) (Seg+FL),
   \( p \) (Station+Treat+Duration),
   \( r \) (Seg), \( F(=1) \)
   fully-pooled \( S \) estimates among UVB treatments and exposure durations in each segment, with fork length as an additive individual covariate

3. \( S \) (Seg+Duration),
   \( p \) (Station+Treat+Duration),
   \( r \) (Seg), \( F(=1) \)
   \( S \) estimates pooled among UVB treatments, with an additive effect of exposure duration

4. \( S \) (Seg+Treat),
   \( p \) (Station+Treat+Duration),
   \( r \) (Seg), \( F(=1) \)
   \( S \) estimates pooled among exposure durations, with an additive effect of UVB treatment

5. \( S \) (Seg+Treat\text{\_}ocean),
   \( S \) estimates pooled among exposure durations, with an additive effect of exposure duration
To guard against the possibility that the best \([p]\) from the previous step (involving additive effects of UVB treatment and exposure duration) was over-fitting the data, these 10 candidate models for survival were later compared assuming a more constrained \([p], [p_{\text{Station}}]\).

### 10.3 Results

**10.3.1 General migration patterns**

Cultus Lake sockeye smolts generally migrated downstream rapidly, reaching the mouth of the Fraser River on average 2.5–4.4 d after release. Fish from the second release period took slightly longer to travel through Sweltzer Creek, the Vedder River and Sumas River, but after arriving in the Fraser River, travel times in the remaining river segments were similar among release periods (Fig. 10.7a). Smolts continued to migrate rapidly through Georgia Strait. There was little difference among UVB treatments in travel speeds for either release period in either freshwater or ocean segments of the migration (Fig. 10.7a). There were slight differences among release groups in the migration direction taken after ocean entry: in the first release, 24 fish were detected on QCS and 0 on JDF, while in the second release group, 44 fish were detected on QCS and 6 on JDF. There also appeared to be slight differences among release groups in the proportion of fish that residualized in Cultus Lake: in the first release group, 1 of 119 tagged fish...
(UVB-shaded) was detected in Cultus Lake on a stationary array operated by Fisheries and Oceans Canada, while in the second group, 12 of 200 tagged fish (8 of which were UVB-shaded) were detected in the lake. This proportion of fish residualizing varied significantly by release group (since a 2x2x2 $\chi^2$ goodness-of-fit test showed no interactions, $\chi^2 = 0.491$, 1 d.f. $p = 0.484$, a Fisher exact test was used with UVB treatments pooled, $p = 0.036$), but not by UVB treatment (Fisher exact test with release groups pooled, $p = 0.167$). It is unclear whether fish actually residualized in the lake or were eaten by predators after release and were subsequently detected in the lake.

Tagged coho salmon smolts also migrated downstream after release at Tenderfoot Creek Hatchery. On average, smolts took 2.7–4.1 d to arrive in the Squamish River estuary, ranging from 1.4–11.1 d. There was little difference among treatment groups in downstream travel time (Fig. 10.7b). One smolt from the 9-month UV-exposed group was detected in the Cheakamus River upstream of the confluence with Tenderfoot Creek. It was detected >1000 times between May 12–May 25 but was not detected on any other station. This smolt could have either residualized in freshwater (reverting to parr), delayed its migration at least several weeks, or been consumed by a predator and transported past the receiver. Otherwise, coho smolts spent little time in the rivers or estuary. After ocean entry, most smolts continued to migrate rapidly out of Howe Sound. Two smolts (from the 9-month UVB-shaded group) spent considerable time in Howe Sound, not crossing HS$_{outer}$ until 37.6 or 71.5 d after release and contributing to the high variance in average travel time for this group (Fig. 10.7b). Excluding these two fish, average travel times from release to HS$_{outer}$ was 6.5 d, similar to other treatment groups. Of the smolts that were detected on the HS$_{outer}$ line, 78% took the eastern route around Gambier Island, and this proportion did not differ much among treatment groups. Only nine fish were detected at NSOG and one at QCS, with all four treatment groups represented in these 10 fish.

### 10.3.2 UVB exposure effects on coho growth

For two months following the transfer of fish from the hatchery rearing channel to experimental tanks in July 2006, fish had similar average weights (and lengths) among UVB treatments (Fig. 10.8). By mid-January 2007, however, when fish were weighed again the average body mass of the UVB-shaded group was greater than that of the UVB-exposed group. In February, lengths of individual fish were measured from random samples of each group, and a clear difference was observed between treatments (Fig. 10.8). This difference was maintained
among UVB treatment groups for the remainder of spring 2007 until smolts were tagged and released.

Neither of the UVB treatment groups is a true control group with respect to the Tenderfoot Creek Hatchery production stock. Both treatment groups were reared in smaller, shallower tanks of a lighter colour than the channel where the production stock reared. Fish from both treatment groups were smaller on average than fish from the production stock during most of the rearing period (Fig. 10.8). Fish from the production stock were similar in average weight to those from both treatment groups shortly after the experiment was re-started in July 2006, but through the remainder of the summer and fall they grew faster relative to fish from both treatment groups. This margin of difference decreased between the production stock and the 9-month UVB-shaded group during winter and spring 2007. By the time the 1-month exposure experiment was initiated and then by the time of tagging, all treatment groups had similar average body lengths to those of the production stock with the exception of the 9-month UVB exposed group, which had considerably shorter body lengths (Fig. 10.8).

10.3.3 Howe Sound mobile tracking results

In 2007, 12 motionless coho tags were located in Howe Sound, which we assumed to be approximate locations of mortality (Fig. 10.6c). Similar patterns of random scattering of mortality locations were observed as in previous years (Fig. 7.11). All four treatment groups were represented in these mortality locations, although the proportion of mortalities detected for the 9-month UVB-exposed group (6 tags out of 34 fish tagged = 17%) was considerably higher than the proportions observed for the other three groups (2–6%). Although suggestive of lower survival after ocean entry in the 9-month UVB-exposed group, a proper comparison of survival among groups requires considering detection data on stationary lines as well.

10.3.4 Survival comparison of UVB-exposed and UVB-shaded groups

Mark-recapture model estimates of survival to successive receiver stations along the migration routes of Cultus Lake sockeye and Tenderfoot Creek coho indicate periods of fairly high mortality in both populations, but little difference among UVB treatment groups. This is observed by initially fitting general, very flexible models to detection data allowing for the best possible fit (at the potential expense of poor precision and over-fitting). These general models for both populations involve fully-independent survival and detection probabilities for each of the four treatment groups in each segment (or station) of the migration, i.e., \( \phi(\text{Seg} \times \text{Release} \times \text{Treat}) \),
\( p(\text{Station}\times\text{Release}\times\text{Treat}) \) for Cultus Lake sockeye (Fig. 10.9a) and \([S(\text{Seg}\times\text{Treat}\times\text{Duration}), p(\text{Station}\times\text{Treat}\times\text{Duration}), r(\text{Seg}_{HS}), F(=1)] \) for Tenderfoot Creek coho (Fig. 10.9b).

In Cultus Lake sockeye, initial survivorship estimates from the general model differed among release periods but not among UVB treatment groups. Fish from the second release group suffered higher mortality between release and the first Fraser River station (at Mission) than fish from the first group (Fig. 10.9a). A small part of this initial decline can be explained by the higher proportion of tagged fish from the second release being detected in Cultus Lake (either residualizing or having been carried into the lake by a predator), which is interpreted as ‘apparent mortality’ in this mark-recapture analysis. The first release group had relatively high survival in the first segment after release, but lower survival after ocean entry in the segment from the Fraser River mouth to NSOG. By the end of the inshore migration, estimated survivorship was similar for both release groups, with no difference among UVB treatment groups (Fig. 10.9a).

In Tenderfoot Creek coho, high mortality (>20%) was observed immediately after release in all four treatment groups (Fig. 10.9b). This is likely attributable to predation in Tenderfoot Lake following the smolt release before smolts started actively migrating (smolts took 1.6–2.2 d on average to travel from the hatchery to the first detection station in Tenderfoot Creek, a distance <400 m). Relatively high mortality continued throughout the downstream migration to the first of the Squamish River stations, Sqm_4 (Fig. 10.5b), as well as in the first segment after ocean entry from Sqm_H to the inner Howe Sound line (Fig. 10.9b). At the end of the downstream migration there was little difference among groups in survivorship given the uncertainty of survivorship estimates. Similarly, there was little difference among treatment groups by the time fish crossed the HS_{outer} line (especially assuming more parsimonious models, see below). We now turn to comparisons of candidate models to evaluate whether other models provide more parsimonious fits to detection data than the general models.

**Cultus Lake sockeye**

Detection probabilities of fish at receiver stations varied among release periods (Table 10.2). The top five candidate models all involved an interaction between ‘Release’ and ‘Station’, whereas the two models with only an additive effect of ‘Release’ across all stations or the one model with no effect of ‘Release’ had essentially no support from the data within the model set. Models with full independence among ‘Release’ and river stations only (with pooled \( \hat{p} \) among releases at ocean stations) fit the data just as well as similar models with full independence among ‘Release’ and all stations (as seen in the similar log-likelihoods), but required an extra
parameter to be estimated so had higher QAICc values ($\Delta$QAICc $\geq$ 2.2; Table 10.2). Once ‘Release’ was accounted for, there was very little support for an additive effect of UVB treatment on $p$ ($\Delta$QAICc = 1.6) and essentially no support for a model further incorporating an interaction between ‘Treat’ and ‘Station’ ($\Delta$QAICc = 13.4). We carry the best $[p]$ from this comparison, $[p(\text{Station} \times \text{Release})]$, forward for comparing candidate models for $\phi$. This model seems reasonable as $p$ at river stations are expected to differ among groups since they were released 3 weeks apart, during which time Fraser River water levels rose (Fig. 3.4).

In the initial model set considered, the greatest support by far was found in the general $[\phi]$ (Table 10.3), with interaction effects of ‘Release’ and ‘Treat’ with each segment of the migration on $\phi$. All other models involved only additive effects of ‘Release’, ‘Treat’, fork length (‘FL’) or combinations thereof across segments. The AIC preference for the general model could be a result of only one of the interactions with ‘Seg’ being important, not necessarily both ‘Release’ and ‘Treat’. After noting this result (Table 10.3), additional $[\phi]$ were considered that involved only one of these interactions. Models with an interaction between ‘Seg’ and ‘Release’ had great support relative to models with a ‘Treat’ interaction instead or the general model with both interactions as well as a three-way interaction (Table 10.4). This appears to be driven by the second release group having lower survival in the first segment after release but higher survival in the 5th segment after release, from the Fraser River mouth to NSOG (Fig. 10.9a). Once the multiplicative model with ‘Release’ was accounted for, there was very little effect of UVB treatment as an additive effect on survival ($\Delta$QAICc = 1.8 with a difference of only 1 parameter; Table 10.4).

**Tenderfoot Creek coho**

Although all four treatment groups were released at the same time (Table 10.1) and travel speeds were similar among them (Fig. 10.7), the comparison of $[p]$ showed that UVB treatment and exposure duration both had a slight effect on $p$ (Table 10.5). The model with an additive effect of ‘Treat’ and ‘Duration’ on $p$ was better in terms of AIC scores than models involving only one or neither of these factors (Table 10.5). Of these two factors, ‘Duration’ had a slightly stronger effect on $p$ ($\Delta$QAICc = 1.4 compared with 0.4 following single-factor removals; Table 10.5). Selection as the best model could reflect behavioural differences among fish in the 9-month vs. 1-month exposure durations or UVB treatments, or else could simply be a case of over-fitting detection data. The fully-independent model with interactions of ‘Treat’ and ‘Duration’ with ‘Station’ on $p$ had much less support than the more constrained models. Models
involving the index of tag strength (Chapter 6) as an additive individual covariate were weakly supported ($\Delta QAIC_c = 1.3$ based on comparison with the best [$p$], and $\Delta QAIC_c = 2.1$ based on comparison with the more constrained [$p$(Station)], in both cases with a difference of only one parameter; Table 10.5). We carried forward the best [$p$], [$p$(Station+Treat+Duration)], for comparing [$\phi$], but in the case that this best [$p$] over-fit detection data, we also compared the same [$\phi$] assuming a more constrained [$p$], [$p$(Station)], where fish from all four treatment groups shared the same $\hat{p}$ at each station.

Assuming the AIC-best model for $p$, survivorship estimates are shown in Fig. 10.9c. Similar to Fig. 10.9b, the general sub-model is assumed for $S$, but [$p$] in Fig. 10.9c is much more parsimonious (Table 10.5) than that in Fig. 10.9b. This shows more clearly the lack of survival differences among treatment groups. The best-supported [$\phi$] was the most constrained, in which $\hat{S}$ were pooled among all four treatment groups in each segment of the migration, [$S$(Seg)]. Models with only one extra parameter, an additive effect of either ‘Duration’, ‘Treat’, or ‘FL’, gave very little improvement in terms of goodness-of-fit, so essentially have no support ($\Delta QAIC_c = 1.9–2.1$; Table 10.6). Models that allowed for a survival difference between UVB treatments only in ocean segments provided little improvement to the goodness-of-fit. Models with interactions of ‘Treat’ and ‘Duration’ on $S$, as well as the general [$S$(Seg$\times$Treat$\times$Duration)] had essentially no support (Table 10.6).

Similar results for [$\phi$] comparisons were observed when the [$p$] assumed was the more constrained [$p$(Station)] rather than the AIC-best [$p$(Station+Treat+Duration)]. The ranking of models was slightly different (not shown), but the most constrained sub-model [$S$(Seg)] was still best, and had little improvement in the goodness-of-fit by incorporating one extra parameter as an additive covariate (‘Duration’, ‘Treat’, or ‘FL’; $\Delta QAIC_c = 1.6–2.1$). The conclusion of no observed effects of ‘Duration’, ‘Treat’, or ‘FL’ on $S$ thus appears to be robust to choice of models assumed for $p$.

### 10.3.5 Detection probabilities

Detection probability estimates assuming the most parsimonious model for each dataset are shown in Fig. 10.10. For Cultus Lake sockeye, the later release period was associated with lower $\hat{p}$ at 3 of 4 stations in the Fraser River under model [$\phi$(Seg$\times$Release), $p$(Station$\times$Release)]. This was especially true for the first station; this large discrepancy between releases at Fra_1 was likely the dominating factor behind the strong support for a Station:Release interaction on $p$. 
Estimates of $p$ also differed among releases at the NSOG station (Fig. 10.10), but this was partly just a result of differences in northerly movement proportions (24/24 for 1st release and 38/44 for 2nd release; these are fish detected at QCS/fish detected at both outer lines), being confounded with the actual probability of detection at NSOG.

For Tenderfoot Creek coho, there was considerable variation in $p$ among stations, with high $\hat{p}$ at receivers in Tenderfoot Creek, the Cheakamus River (Chk_2 and Chk_3), the Squamish River (Sqm_6 and Sqm_7), and the outer Howe Sound line (Fig. 10.10). High $p$ in the lower Squamish River in particular allowed for precise partitioning between downstream and inshore mortality components. Additive treatment group effects on $p$ in the AIC-best $[p]$ resulted in higher $\hat{p}$ for UVB-exposed fish than for UVB-shaded fish, and higher $\hat{p}$ for the 1-month duration group than for the 9-month duration group. It is unclear whether there is biological basis for this difference as a result of behavioural effects, or whether the result was simply due to over-fitting of sparse data. The within-station variation among treatment groups was small compared to the among-station variation in $p$. Again, these differences in $\hat{p}$ among treatment groups neither mask nor artificially create survivorship effects, since under a model where $\hat{p}$ is instead common across treatment groups, estimated survivorship is also similar among treatment groups. For both populations, $\hat{p}$ and precision in estimates seem to be reasonably high enough overall that inferences of survival should be reasonable in terms of bias and precision, respectively.

10.4 Discussion

Thinning of the atmospheric ozone layer has increased levels of UV-B radiation reaching the ground at temperate latitudes over the past several decades. This has resulted in deleterious effects on several taxa at sub-cellular, cellular, tissue, and organismal levels of organization (reviewed by Zagarese and Williamson 2001, Häder et al. 2007) as well as in functions of ecosystems like primary and secondary productivity (Bothwell et al. 1994, Kelly et al. 2003). While Walters and Ward (1998) proposed that UVB may be a factor responsible for declining marine survival in salmon populations that rear in shallow streams, this hypothesis remained untested for nearly 10 years.

UVB may potentially have damaging effects on DNA repair and enzyme production mechanisms during the shallow stream- or hatchery-rearing phase of juvenile salmon, but the consequences of this exposure may not be realized until ocean entry (Walters and Ward 1998). This hypothesis is not mutually exclusive with others commonly suggested to explain declines in
marine survival of salmonids, such as shifts in the abundance or distribution of predators; physiological impairment from UVB damage is likely to make smolts more vulnerable to predation. UVB exposure effects on survival in the laboratory are typically dose-dependent. Some DNA damage resulting from UVB radiation can be repaired at low doses, but at higher doses damage is irreparable and mortality ensues (Mitchell et al. 2009). The timing and intensity of UVB exposure during freshwater rearing may therefore be important determinants of mortality consequences.

Stunted growth was observed in the 9-month UVB-exposed treatment group compared with the UVB-shaded group of Tenderfoot Creek coho (also compared with the hatchery production stock by the end of the exposure period, at the time of smoltification; Fig. 10.8). This difference between treatment groups cannot be explained by size-dependent differential mortality in hatchery tanks, as few fish from any treatment died while rearing. Since treatment groups of fish were otherwise treated similarly, it appears that UVB radiation from sunlight caused reduced growth. This difference was established by January 2007, and was maintained until smoltification. There was little overhead sunlight during fall 2006 and winter, so the critical exposure period that led to the difference was likely the remainder of the 2006 summer after July 20 (when the experiment was re-started). To note, both shaded and exposed groups initially displayed reduced growth relative to the production stock, but by the time of smoltification average body length of the UVB-shaded group had caught up to that of the production stock (Fig. 10.8). The production stock was also exposed to sunlight and hence UVB, but fish were reared at a much higher density than in the experimental tanks, and could seek shade refuge not from overhead structures, but from each other. Fish commonly aggregated in dense formations in the rearing channel, so fish at the bottom of schools would be exposed to reduced UVB. The greater depth of the rearing channel (~1 m) compared with the experimental tanks (~45 cm) may have also contributed to the difference in growth between the production stock and UVB-exposed treatment group as a result of differences in UVB attenuation.

Other studies have found effects of UVB exposure on growth of juvenile salmonids. In Atlantic salmon, treatment with sunlight-enhanced UVB levels resulted in stunted growth and reduced immune function (plasma immunoglobulin concentration, IgM) compared with natural sunlight and UVB-shaded treatments (Jokinen et al. 2008). There was no difference in growth or IgM among natural sunlight and UVB-shaded treatments, which could have resulted from a shorter exposure duration (52 d in July-August 2001), a cloudier-than-average year in which the experiment was conducted (Jokinen et al. 2008), or the shallower angle of incident sunlight at the
more northerly latitude (60.9°N, Institute of Marine Research, Norway) compared with the experiment at Tenderfoot Creek Hatchery. Growth effects could result from UVB exposure causing increased oxygen consumption and swimming activity (in a laboratory study with rainbow trout; Alemanni et al. 2003), or increased DNA-repair metabolic activity (specifically, nucleotide excision repair is an energetically expensive process used by rainbow trout in response to UVB exposure; Olson and Mitchell 2006).

The apparent effect of UVB exposure on growth of Tenderfoot Creek coho did not later lead to survival differences during the smolt migration downstream and through Howe Sound. With or without accounting for the smaller average body size of the 9-month UVB-exposed group (Table 10.1) by using fork length as a covariate, no overall difference in survival was observed among treatment groups (Table 10.6). Upon arrival at the outer Howe Sound line, all four groups had similar survivorship (Fig. 10.9c). It is not possible to make survival inferences beyond Howe Sound since Tenderfoot coho may reside in Georgia Strait through summer months where they may go undetected (Chapter 7). It is justified to make survival inferences to the area covered by mobile sampling, however, which did extend beyond HS\textsubscript{outer} (Fig. 10.6). The steeper decrease in survivorship for the 9-month UVB-exposed group from HS\textsubscript{outer} to ocean lines (Fig. 10.9c) is largely a result of observing three mortality locations of fish in this group after they crossed HS\textsubscript{outer} (other groups had 0 or 1 mortality locations; Fig. 10.6c). There is thus some indication of higher mortality in the 9-month UVB exposed group after crossing HS\textsubscript{outer}, but the possibility of summer residency in the Strait prevents a further assessment of the spatial mortality patterns.

There was slight evidence that UVB shading resulted in two different types of behavioural effects. First, the best-supported \( p \) in the Tenderfoot Creek coho dataset involved additive effects of UVB treatment (and exposure duration) on \( p \), with higher \( \hat{p} \) for UVB-exposed fish (Fig. 10.10). Travel speeds were similar among treatments at least during the downstream migration (Fig. 10.7b), but if UVB exposure led to differences in depth or proximity to river banks while migrating, such fine scale habitat selection could have led to differences in \( p \) among treatment groups. Alternatively, the observed effect in terms of AIC scores (Table 10.5) may be spurious, resulting from over-fitting the model to sparse data where a more constrained model, \([p(\text{Station})]\), may actually be more appropriate. Second, there appeared to be a weak (and non-significant) effect of UVB shading on the proportion of Cultus Lake sockeye moving upstream into Cultus Lake (either in fish residualizing or having been eaten by a predator). Fish from the second release were detected in Cultus Lake more frequently (6%) than fish from the first release.
(<1%), but after this stronger effect is accounted for, UVB-shaded fish were detected slightly more often than UVB-exposed fish in Cultus Lake (1.7% vs. 0% in first release; 8% vs. 4% in second release). Other studies have found behavioural differences in juvenile salmonids as a result of UVB exposure (Kelly and Bothwell 2002, Holty and Bothwell 2008), though we found no other studies that found depth or residualization effects.

From a salmon conservation viewpoint it is a great relief that differences in survival were not observed between UVB-exposed and UVB-shaded fish in either population. Still, there are several reasons why a true difference, if it exists, may not have been detected:

1) there is uncertainty in the critical exposure period. The experiment at Tenderfoot Creek was re-started in mid-July 2006. If UVB exposure during late spring to mid-July has survival consequences, these would have been missed in the experiment. Other studies have shown that the egg-to-alevin stage is particularly susceptible to mortality from UVB exposure (Bell and Hoar 1950, Flamarique and Harrower 1999), but other critical exposure periods could exist.

2) There is uncertainty in latency between exposure and the ensuing period of mortality. Survival was only monitored through Howe Sound for Tenderfoot Creek coho and through Georgia Strait for Cultus Lake sockeye. Since the physiological mechanisms are not entirely clear, it is possible that UVB exposure effects may not be realized until several months after ocean entry.

3) The two experiments were not conducted in particularly sunny areas, for logistical reasons. Effects of UVB exposure may be more severe in sunnier areas such as the east coast of Vancouver Island, the southern interior of B.C. including the Thompson River watershed, or interior streams of Washington and Oregon.

4) There may be confounding physiological effects of UVB shading. In some species, low doses of UVB radiation may actually be beneficial by stimulating pigmentation development (Adachi et al. 2005; M. Bothwell, pers. comm.). The complete removal of UVB wavelengths by the plastic film (Fig. 10.3) may have actually been slightly deleterious.

5) These experiments were conducted using available tanks at the two hatcheries, and such tanks may not be reflective of UVB exposure faced by the production stocks or by wild stocks. At Tenderfoot Creek Hatchery, the experimental tanks were narrower and shallower than the channel where the production stock reared, and fish were at a lower density. UVB levels reaching the fish would have been stronger in these experimental tanks when the sun was overhead (due to the shallower depth and to fish not able to place themselves beneath
thousands of other fish in the rearing channel), but less during other hours of the day when tank walls would shade sunlight under both treatments. Similarly, at Inch Creek Hatchery, the large circular tanks were about 1 m tall and 3 m in diameter, so unless the sun was directly overhead, some shaded refuges would exist in tanks under both treatments. Since salmonids can see in the UV-A range and likely at least to some extent in the UVB range of wavelengths (e.g., rainbow trout, Browman et al. 1994), they could have sometimes avoided exposure in the UVB-exposed treatment (Kelly and Bothwell 2002).

Given these remaining uncertainties and the potential consequences for salmon population viability that may arise if an effect of UVB exposure does exist, it would seem premature to disregard outright the hypothesis of metabolic impairment from UVB exposure. Further experiments could be conducted at hatcheries, without great increase in cost or effort above current operations. Larger rearing channels could be shaded from above with a UVB filter to avoid the possible effects of shading from tank walls in narrow experimental tanks. Shading materials could be in place from the moment that fish are transferred from indoor incubation facilities to outdoor rearing ponds. Survival could be assessed over different time scales using a combination of methods. Acoustic tags could again be used to monitor the first few hundred kilometres of the smolt migration, but more importantly, coded wire tags (CWT) could be used to monitor the full smolt-to-adult period. CWT returns from fisheries and spawning salmon could be used to estimate survival over this period for each treatment group. At several hatcheries CWT programs are already in use, so the extra marking and recapture costs would be trivial for setting up shading experiments and allocating differently-coded CWTs among treatment groups. This would ideally be tested in sunny areas where the water in rearing channels is shallow and/or low in dissolved organic material (which causes rapid attenuation in UVB levels with increasing depth; Kirk 1994). If any differences are observed among treatment groups under this approach of full-rearing exposure and full-smolt-to-adult survival assessment, then subsequent experiments could seek to identify on finer time scales when the critical periods of UVB exposure and ensuing mortality occur.
Table 10.1. Release groups of Tenderfoot Creek coho salmon and Cultus Lake sockeye salmon smolts tagged in 2007 under UVB-exposed and UVB-shaded treatments and different exposure times or release times. FL denotes fork length.

<table>
<thead>
<tr>
<th>Population</th>
<th>Exposure duration or release time</th>
<th>Treatment</th>
<th>Release date</th>
<th>Start of shading</th>
<th>Mean FL (mm) [SD]</th>
<th>Range FL (mm)</th>
<th>Number released</th>
</tr>
</thead>
<tbody>
<tr>
<td>Tenderfoot Creek coho</td>
<td>9-month exposure duration</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>UVB-exposed</td>
<td>10 May</td>
<td>20 July 2006</td>
<td>129.1 [2.9]</td>
<td>125–137</td>
<td>34</td>
<td></td>
</tr>
<tr>
<td></td>
<td>UVB-shaded</td>
<td>10 May</td>
<td>20 July 2006</td>
<td>131.9 [5.3]</td>
<td>125–146</td>
<td>55</td>
<td></td>
</tr>
<tr>
<td></td>
<td>1-month exposure duration</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>UVB-exposed</td>
<td>10 May</td>
<td>3 April 2007</td>
<td>133.4 [6.1]</td>
<td>126–147</td>
<td>56</td>
<td></td>
</tr>
<tr>
<td></td>
<td>UVB-shaded</td>
<td>10 May</td>
<td>3 April 2007</td>
<td>133.2 [5.7]</td>
<td>125–147</td>
<td>54</td>
<td></td>
</tr>
<tr>
<td>Cultus Lake sockeye</td>
<td>1st release, smaller V9-6L tag</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>UVB-exposed</td>
<td>26 April</td>
<td>22 June 2006</td>
<td>171.5 [6.0]</td>
<td>160–184</td>
<td>61</td>
<td></td>
</tr>
<tr>
<td></td>
<td>UVB-shaded</td>
<td>26 April</td>
<td>22 June 2006</td>
<td>171.3 [5.9]</td>
<td>160–185</td>
<td>58</td>
<td></td>
</tr>
<tr>
<td></td>
<td>2nd release, larger V9-1L tag</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>UVB-exposed</td>
<td>16 May</td>
<td>22 June 2006</td>
<td>189.4 [8.2]</td>
<td>172–208</td>
<td>100</td>
<td></td>
</tr>
<tr>
<td></td>
<td>UVB-shaded</td>
<td>16 May</td>
<td>22 June 2006</td>
<td>188.1 [8.3]</td>
<td>170–217</td>
<td>100</td>
<td></td>
</tr>
</tbody>
</table>

* The shading experiment was initially set up on 7 June 2006, but had to be re-started 6 weeks later following a collapse of the partition separating UVB-exposed and UVB-shaded fish.
Table 10.2. Model selection results for detection probability ($p$) sub-models for Cultus Lake sockeye experiment. $^a$

<table>
<thead>
<tr>
<th>Sub-model</th>
<th>$k$</th>
<th>$-2\cdot\ln(L)$</th>
<th>QAICc</th>
<th>ΔQAICc</th>
</tr>
</thead>
<tbody>
<tr>
<td>$p$(Station$\times$Release)</td>
<td>34</td>
<td>1875.4</td>
<td>1817.0</td>
<td>0.0</td>
</tr>
<tr>
<td>$p$(Station$\times$Release+Treat)</td>
<td>35</td>
<td>1874.8</td>
<td>1818.5</td>
<td>1.6</td>
</tr>
<tr>
<td>$p$(Station$<em>{fw}$$\times$Release+Station$</em>{sw}$)</td>
<td>35</td>
<td>1875.4</td>
<td>1819.1</td>
<td>2.2</td>
</tr>
<tr>
<td>$p$(Station$<em>{fw}$$\times$Release+Station$</em>{sw}$+Treat)</td>
<td>36</td>
<td>1875.2</td>
<td>1821.1</td>
<td>4.2</td>
</tr>
<tr>
<td>$p$(Station$\times$Release$\times$Treat)</td>
<td>44</td>
<td>1866.3</td>
<td>1830.4</td>
<td>13.4</td>
</tr>
<tr>
<td>$p$(Station+Release)</td>
<td>30</td>
<td>1960.8</td>
<td>1887.8</td>
<td>70.9</td>
</tr>
<tr>
<td>$p$(Station+Release+Treat)</td>
<td>31</td>
<td>1960.0</td>
<td>1889.3</td>
<td>72.3</td>
</tr>
<tr>
<td>$p$(Station)</td>
<td>29</td>
<td>2003.3</td>
<td>1925.3</td>
<td>108.3</td>
</tr>
</tbody>
</table>

$^a$ Quantities shown are number of parameters ($k$), log-likelihoods, and QAIC$_c$ values (adjusted for small sample sizes and extra-binomial variation with $\hat{c} = 1.074$). Sub-models for $p$ are compared while the fully segment and treatment group-varying CJS [$\phi$] is held constant, [$\phi$(Seg$\times$Release$\times$Treat)]. The final station $p$ is fixed for all treatment groups and models at the 2007-specific prediction (0.923) for V9 tags. Station$_{fw}$ = station in river; Station$_{sw}$ = station in ocean; Seg = segment; Release = release period; Treat = UVB treatment.
Table 10.3. Model selection results for survival ($\phi$) sub-models for Cultus Lake sockeye experiment. $^a$

<table>
<thead>
<tr>
<th>Model</th>
<th>$k$</th>
<th>$-2\cdot\ln(L)$</th>
<th>QAICc</th>
<th>(\Delta\text{QAICc})</th>
</tr>
</thead>
<tbody>
<tr>
<td>$\phi$(Seg\times Release\times Treat)</td>
<td>34</td>
<td>1875.4</td>
<td>1817.0</td>
<td>0.0</td>
</tr>
<tr>
<td>$\phi$(Seg)</td>
<td>16</td>
<td>1940.8</td>
<td>1839.7</td>
<td>22.7</td>
</tr>
<tr>
<td>$\phi$(Seg+Treat)</td>
<td>17</td>
<td>1940.4</td>
<td>1841.4</td>
<td>24.5</td>
</tr>
<tr>
<td>$\phi$(Seg+FL)</td>
<td>17</td>
<td>1940.5</td>
<td>1841.5</td>
<td>24.5</td>
</tr>
<tr>
<td>$\phi$(Seg+Release)</td>
<td>17</td>
<td>1940.6</td>
<td>1841.6</td>
<td>24.7</td>
</tr>
<tr>
<td>$\phi$(Seg+Release+Treat)</td>
<td>18</td>
<td>1940.3</td>
<td>1843.4</td>
<td>26.4</td>
</tr>
<tr>
<td>$\phi$(Seg+Treat$_{sw}$)</td>
<td>18</td>
<td>1940.7</td>
<td>1843.7</td>
<td>26.8</td>
</tr>
<tr>
<td>$\phi$(Seg+Release\times Treat)</td>
<td>19</td>
<td>1940.3</td>
<td>1845.5</td>
<td>28.5</td>
</tr>
<tr>
<td>$\phi$(Seg+Release+Treat$_{sw}$)</td>
<td>19</td>
<td>1940.5</td>
<td>1845.7</td>
<td>28.8</td>
</tr>
<tr>
<td>$\phi$(Seg+Release\times Treat+FL)</td>
<td>20</td>
<td>1940.1</td>
<td>1847.4</td>
<td>30.4</td>
</tr>
</tbody>
</table>

$^a$ Quantities shown are number of parameters ($k$), log-likelihoods, and QAIC$_c$ values (adjusted for small sample sizes and extra-binomial variation with $\hat{c} = 1.074$). Sub-models for $\phi$ are compared while $[p]$ is held constant at $[p(\text{Station}\times\text{Release})]$. The final station $p$ is fixed for all treatment groups and models at the 2007-specific prediction (0.923) for V9 tags. Seg = segment; Release = release period; Treat = UVB treatment; Treat$_{sw}$ = UVB treatment effect only in ocean segments; FL = fork length.

Table 10.4. Post-hoc model selection results for survival ($\phi$) sub-models reduced from the general model, for Cultus Lake sockeye experiment. $^a$

<table>
<thead>
<tr>
<th>Model</th>
<th>$k$</th>
<th>$-2\cdot\ln(L)$</th>
<th>QAICc</th>
<th>(\Delta\text{QAICc})</th>
</tr>
</thead>
<tbody>
<tr>
<td>$\phi$(Seg\times Release)</td>
<td>22</td>
<td>1879.1</td>
<td>1794.8</td>
<td>0.0</td>
</tr>
<tr>
<td>$\phi$(Seg\times Release+Treat)</td>
<td>23</td>
<td>1878.7</td>
<td>1796.6</td>
<td>1.8</td>
</tr>
<tr>
<td>$\phi$(Seg\times Release\times Treat)</td>
<td>34</td>
<td>1875.4</td>
<td>1817.0</td>
<td>22.1</td>
</tr>
<tr>
<td>$\phi$(Seg\times Treat)</td>
<td>22</td>
<td>1938.8</td>
<td>1850.4</td>
<td>55.5</td>
</tr>
<tr>
<td>$\phi$(Seg\times Treat+Release)</td>
<td>23</td>
<td>1938.7</td>
<td>1852.4</td>
<td>57.6</td>
</tr>
</tbody>
</table>

$^a$ This analysis was not based on candidate models established before data analyses began, but was conducted after the initial model comparison for $[\phi]$. Quantities shown are number of parameters ($k$), log-likelihoods, and QAIC$_c$ values (adjusted for small sample sizes and extra-binomial variation with $\hat{c} = 1.074$). Sub-models for $\phi$ are compared while $[p]$ is held constant at $[p(\text{Station}\times\text{Release})]$. The final station $p$ is fixed for all treatment groups and models at the 2007-specific prediction (0.923) for V9 tags. Seg = segment; Release = release period; Treat = UVB treatment.
<table>
<thead>
<tr>
<th>Sub-model</th>
<th>$k$</th>
<th>$-2\ln(L)$</th>
<th>QAICc</th>
<th>ΔQAICc</th>
</tr>
</thead>
<tbody>
<tr>
<td>$p$(Station+Treat+Duration)</td>
<td>65</td>
<td>1672.0</td>
<td>1616.0</td>
<td>0.0</td>
</tr>
<tr>
<td>$p$(Station+Duration)</td>
<td>64</td>
<td>1675.0</td>
<td>1616.4</td>
<td>0.4</td>
</tr>
<tr>
<td>$p$(Station+Treat+Duration+Strength)</td>
<td>66</td>
<td>1670.9</td>
<td>1617.3</td>
<td>1.3</td>
</tr>
<tr>
<td>$p$(Station+Treat)</td>
<td>64</td>
<td>1676.2</td>
<td>1617.4</td>
<td>1.4</td>
</tr>
<tr>
<td>$p$(Station)</td>
<td>63</td>
<td>1680.7</td>
<td>1619.2</td>
<td>3.2</td>
</tr>
<tr>
<td>$p$(Station+Duration+Strength)</td>
<td>65</td>
<td>1675.9</td>
<td>1619.5</td>
<td>3.5</td>
</tr>
<tr>
<td>$p$(Station+Treat+Strength)</td>
<td>65</td>
<td>1676.2</td>
<td>1619.7</td>
<td>3.7</td>
</tr>
<tr>
<td>$p$(Station+Strength)</td>
<td>64</td>
<td>1680.6</td>
<td>1621.3</td>
<td>5.3</td>
</tr>
<tr>
<td>$p$(Station×Treat×Duration)</td>
<td>96</td>
<td>1641.4</td>
<td>1662.1</td>
<td>46.1</td>
</tr>
<tr>
<td>$p$(Station×Treat×Duration+Strength)</td>
<td>97</td>
<td>1642.2</td>
<td>1665.3</td>
<td>49.3</td>
</tr>
</tbody>
</table>

$^a$ Quantities shown are number of parameters ($k$), log-likelihoods, and QAIC$\_c$ values (adjusted for small sample sizes and extra-binomial variation with $\hat{c} = 1.132$). Sub-models for $p$ are compared while the fully segment and treatment group-varying Burnham sub-model for $S$ is held constant, $[S(Seg\timesTreat\timesDuration)]$. Other sub-models are also held constant: mobile tracking detection efficiency in Howe Sound segments, $r(Seg_{HS})$, and fidelity, $F(Station)$, which is fixed to 1. Seg = segment; Treat = UVB treatment; Duration = 9 or 1 month exposure of treatment.
Table 10.6. Model selection results for survival ($S$) sub-models for Tenderfoot Creek coho experiment. $^a$

<table>
<thead>
<tr>
<th>Sub-model</th>
<th>$k$</th>
<th>$-2\cdot\ln(L)$</th>
<th>QAICc</th>
<th>ΔQAICc</th>
</tr>
</thead>
<tbody>
<tr>
<td>$S$(Seg)</td>
<td>29</td>
<td>1690.1</td>
<td>1552.8</td>
<td>0.0</td>
</tr>
<tr>
<td>$S$(Seg+Duration)</td>
<td>30</td>
<td>1689.9</td>
<td>1554.7</td>
<td>1.9</td>
</tr>
<tr>
<td>$S$(Seg+Treat)</td>
<td>30</td>
<td>1690.1</td>
<td>1554.9</td>
<td>2.1</td>
</tr>
<tr>
<td>$S$(Seg+FL)</td>
<td>30</td>
<td>1690.1</td>
<td>1554.9</td>
<td>2.1</td>
</tr>
<tr>
<td>$S$(Seg+Treat$_{sw}$+Duration)</td>
<td>31</td>
<td>1689.9</td>
<td>1556.9</td>
<td>4.1</td>
</tr>
<tr>
<td>$S$(Seg+Treat$_{sw}$×Duration)</td>
<td>32</td>
<td>1689.7</td>
<td>1558.8</td>
<td>6.0</td>
</tr>
<tr>
<td>$S$(Seg+Treat×Duration)</td>
<td>32</td>
<td>1689.9</td>
<td>1559.0</td>
<td>6.2</td>
</tr>
<tr>
<td>$S$(Seg+Treat×Duration+FL)</td>
<td>33</td>
<td>1689.9</td>
<td>1561.1</td>
<td>8.3</td>
</tr>
<tr>
<td>$S$(Seg×Treat×Duration)</td>
<td>65</td>
<td>1672.0</td>
<td>1616.0</td>
<td>63.2</td>
</tr>
</tbody>
</table>

$^a$ Quantities shown are number of parameters ($k$), log-likelihoods, and QAIC$_c$ values (adjusted for small sample sizes and extra-binomial variation with $\hat{\phi} = 1.132$). Sub-models for $S$ are compared while the best $[p]$ is held constant, $[p(\text{Station+Treat+Duration})]$. Other sub-models are also held constant: mobile tracking detection efficiency in Howe Sound segments, $r(\text{Seg}_{HS})$, and fidelity, $F(\text{Station})$, which is fixed to 1. Seg = segment; Treat = UVB treatment; Duration = 9 or 1 month exposure of treatment.
Figure 10.1. Average annual ozone levels from 1957–2001 (a) and ultraviolet-B radiation during summer (May-Aug.; b) and winter (Nov.-Feb.; c) from 1979–1999 at Canadian latitudes. Ozone data are from the Meteorological Service of Canada, measured over stations at Toronto, Ontario (43°47'N); Edmonton, Alberta (53°33'N); Resolute, Northwest Territories (74°43'N); Churchill, Manitoba (58°45'N); and Goose Bay, Labrador (53°19'N). Ozone measurements include tropospheric (ground-level; about 10% of total column ozone) as well as stratospheric ozone (about 90%). UV-B data are seasonal averages of monthly mean erythemal-action spectrum-weighted UV-B exposure measurements (Tarasick et al. 2003).
Figure 10.2. Smolt-to-adult survival for coho salmon populations released from the Tenderfoot Creek Hatchery and returning in years 1985–2002 (a), and total returns of Cultus Lake sockeye from 1953–2007. Marine survival in (a) are likely underestimated for coho populations other than Tenderfoot Creek due to incomplete escapement monitoring. Data provided by Fisheries and Oceans staff at Tenderfoot Creek Hatchery, calculated from coded wire tag recoveries. Sockeye returns are separated by cycle line of the 4-year abundance cycle, with data provided by S. Grant, Fisheries and Oceans Canada.
Figure 10.3. Percent transmittance of radiation (200–700 nm) through the Dupont-Teijin Melinex® 943 plastic film used in the shading experiments. Transmittance spectra are shown for a new film and two samples taken directly from the hatchery tank shade covers following the end of the experiment, one after 1 month of exposure from April-May 2007 and the other after 9 months of exposure from July 2006–May 2007. Scans were conducted with a spectrophotometer blanked against air at 1 nm intervals, courtesy of M. Bothwell (Environment Canada).
Figure 10.4. Fork length distributions of the four treatment groups of Tenderfoot Creek coho salmon smolts (a) and the four treatment groups of Cultus Lake sockeye smolts (b). White bars (for coho only) show the lengths of fish \( (n = \text{approximately } 300 \text{ for 9-month exposures and } 200 \text{ for 1-month exposures}) \) in each tank at the end of the experiment at time of tagging. Black bars show the subset of these fish that were tagged (in (b), only fish that were tagged were measured). Note that x-axes differ between (a) and (b).
Figure 10.5. Locations of river receiver stations encountered during the 2007 migration of Cultus Lake sockeye (a) and Tenderfoot Creek coho (b). Release sites are shown by yellow X’s. Red circles indicate locations of in-river acoustic receiver stations, and are labelled. Red lines indicate the two outer Howe Sound receiver lines (a, HS_{outer}) and the inner Howe Sound line (b, HS_{inner}).
Figure 10.6. Sampling tracks in Howe Sound during first (a) and second (b) mobile tracking trips in 2007, and locations within Howe Sound where 2007 coho tags stopped moving (c). Spacing between parallel tracks (in blue) was approximately 500 m. Approximate mortality locations in (c) are shown by treatment group (9-month UVB-shaded, 9; 9-month UVB-exposed, 9; 1-month UVB-shaded, 1; 1-month UVB-exposed, 1). Red lines show stationary receiver lines in Howe Sound.
Figure 10.7. Average travel time past successive detection stations during the smolt migration for Cultus Lake sockeye (a) and Tenderfoot Creek coho (b). Data are separated by UVB treatment groups, and points show cumulative travel time estimates since release plotted against cumulative distance travelled. Error bars show 1 S.E. Note the x-axes in (a) and (b) are at different scales.
Figure 10.8. Average body size of coho treatment groups during rearing at Tenderfoot Creek Hatchery. Some average lengths (those with 95% confidence limits) were based on measurements of 50 individuals in each group, while others (those without error bars) were based on total mass of several fish weighed together, with average mass then converted to length. UVB-shaded and UVB-exposed groups were reared in small tanks. Also shown is average fork length (FL) over time of the production stock, which reared in a larger, deeper hatchery channel.
Figure 10.9. Survivorship curves for Cultus Lake sockeye salmon from release to the Queen Charlotte Strait or Juan de Fuca line (a) and Tenderfoot Creek coho salmon from release to the northern Strait of Georgia line (b and c, next page). Survivorship estimates are shown for each treatment group, plotted against the cumulative distance from release site to the detection station. The CJS model presented for sockeye involves fully-independent survival and detection probabilities for each treatment group in each segment or at each station, i.e., model \([\phi(Seg \times Release \times Treat), p(Station \times Release \times Treat)]\). The Burnham model presented in (b) for coho involves fully-independent survival and detection probabilities for each treatment group in each segment or at each station, mobile tracking detection efficiencies in each Howe Sound segment that are pooled across treatment groups, and fidelity parameters fixed at 1, i.e., model \([S(Seg \times Treat \times Duration), p(Station \times Treat \times Duration), r(Seg_{HS}), F(=1)]\). The Burnham model presented in (c) differs from (b) in that detection probabilities are station-specific but \(p\) is constrained with an additive difference among treatment groups that is consistent across stations, i.e., model \([S(Seg \times Treat \times Duration), p(Station + Treat + Duration), r(Seg_{HS}), F(=1)]\). Error bars show 1 s.e.
Figure 10.9 cont.
Figure 10.10. Detection probability estimates at successive stations for Cultus Lake sockeye (a) and Tenderfoot Creek coho (b) in 2007. For sockeye, independent $\hat{p}$ are assumed for the two release groups at each station, but UVB treatments within each release group share the same $p$, i.e., model $[\phi(Seg \times Release), \pi(Station \times Release)]$. For coho, the four treatment groups are constrained by additive differences of UVB treatment and exposure duration on $p$ across all stations, i.e., model $[\phi(Seg), \pi(Station + Treat + Duration), \tau(Seg_{HS}), \psi(=1)]$. Error bars show 95% confidence limits, estimated with profile likelihoods.
10.5 References


Jokinen, I.E., Markkula, E.S., Salo, H.M., Kuhn, P., Nikoskelainen, S., Arts, M.T., and Browman, H.I. 2008. Exposure to increased ambient ultraviolet B radiation has negative effects on growth, condition and immune function of juvenile Atlantic salmon (Salmo salar). Photochem. Photobiol. 84: 1265-1271.


11 General discussion

I used acoustic telemetry methods to monitor the movements of outmigrating salmon smolts, and used mark-recapture methods to estimate survival from tag detection data at receiver stations deployed along migration routes. I combined data from multiple populations and years into the same analysis framework so as to compensate for small sample sizes in some release groups and provide greater generality in estimating the effects of various factors on survival.

Estimation of detection probabilities was critical for making survival inferences, and various ways of estimating $p$ were the focus of Chapters 2–6. In Chapter 3, I showed how multiple groups can be combined in the same analysis even if their migration routes overlap only partially, how environmental covariates for $p$ or survival may be useful only when multiple groups are considered, and how increasing the spacing between receivers on a line does not necessarily result in a proportional decrease of $p$ for the entire line. In Chapter 4, I presented a new method for estimating $p$ using only local information at a detection station, based on patterns of detected and undetected tag transmissions as tagged fish crossed a station. The method was only reliable as a predictor of mark-recapture $p$ under larger sample sizes, so it cannot be used for smaller tagging studies. In Chapter 5, I described different ways of estimating $p$ for mobile tracking transect surveys, where tags may be particularly difficult to locate. A trade-off between $p_{\text{mobile}}$ per unit area and area swept was identified, which was largely due to boat speed during transects. In Chapter 6, I tested the assumption that individual tags of a particular type were homogeneous in terms of $p$ by measuring indices of acoustic strength prior to tagging fish. A weak effect of tag strength on $p$ was identified, suggesting that some of the overall variation in $p$ might be accounted for with simple measurements of tags prior to tagging fish.

Remaining chapters used these methods of estimating $p$ to quantify mortality patterns during the smolt migration. In Chapter 7, I described basic migration patterns during the downstream and inshore migration. Average travel speeds through Georgia Strait were found to be independent of body size. Steelhead and sockeye smolts moved rapidly, and most fish took the northern exit route through Queen Charlotte Strait. Coho and Chinook smolts were slower, and were rarely detected after ocean entry, which limited the interpretation of their inshore survival estimates. In Chapter 8, I showed that large survival differences between wild and hatchery-reared steelhead were primarily established immediately after release, during the downstream migration. A new method for estimating residualization rates of tagged fish...
suggested slightly higher residualization of hatchery fish, although estimates were based on small sample sizes. In Chapter 9, I found considerable variation in survival during the downstream and inshore migration among years, species, and watersheds, and showed that much of this variation was related to differences in body size and migration distance (or travel time) of smolts. Size-selective mortality within release groups occurred during the inshore migration but not the downstream migration, while size-related survival differences among groups occurred primarily during the downstream migration. In general, average travel time appeared to be a more reliable predictor of mortality than minimum migration distance. Finally, in Chapter 10, I addressed the hypothesis that solar ultraviolet radiation during freshwater rearing leads to increased mortality during the smolt migration, after ocean entry. I found evidence of stunted growth in UV-exposed fish compared to UV-shaded fish in a coho population, but in coho as well as a sockeye population I found no consistent difference between treatment groups in survival during the smolt migration.

11.1 Partitioning mortality during smolt-to-adult life

Mortality during the downstream migration (which would typically be considered a part of ‘marine mortality’) was higher on a per-distance or per-time basis than during the migration through Georgia Strait. Downstream mortality was not size-selective within release groups, but was among groups and also likely involved at least some degree of tag-related mortality. Mortality of hatchery-reared fish was generally higher than that of wild fish in the first river segment after release. Another period of high mortality appeared to occur after ocean entry, where within release groups, larger fish had higher survival than smaller fish. Considering the long migration distances and times remaining during smolt-to-adult life, along with estimates of total marine survival from smolt-to-adult ratios and other tagging methods (e.g., coded-wire tags), mortality rates ($M_d$ or $M_{TT}$) are necessarily much lower later in ocean life.

An ongoing study since 1997 involving pelagic surface trawls in Georgia Strait during early to mid-July and early September to mid-October (Beamish et al. 2000, 2008) provides another means of partitioning marine survival. Abundances of hatchery coho post-smolts in the Strait were estimated using trawl surveys (Fig. 11.1a), and from known numbers of hatchery releases, survival from release-to-July and release-to-September were estimated (Fig. 11.1b). Accounting for estimated escapement to these hatcheries (since fishing mortality is negligible; Fig. 1.3), total smolt-to-adult survival was estimated, which permits the component of overwinter
survival to also be estimated (Beamish et al. 2008). Estimated survival from release-to-July was variable among years due to high variation in July abundance estimates, but percent survival from release-to-September was on average similar to overwinter survival.\(^{17}\) Accounting for the different durations of these periods, calculated \(M\) for release-to-September was approximately twice that of overwinter \(M\) (Fig. 11.1b; mean dates of hatchery releases were from May 10–21). Further partitioning this early ocean period, \(M\) from release-to-July was much higher, suggesting that mortality per day was much higher before July surveys than between July and September.

Echoing the critique of Pearcy and McKinnell (2007), we still do not have a detailed temporal life table for any Pacific salmon species. Looking across the above and other studies of salmon survival, however, we can identify general patterns of how mortality changes during the salmon life cycle. Partitioning smolt-to-adult survival among shorter periods allows for assessments of how \(M\) might change over this longer period. Figure 11.2 shows a summary of time-based instantaneous mortality rates, \(M\), from several different studies where authors were able to estimate some portion of smolt-to-adult survival. These estimates are plotted against the duration over which they were assessed. Estimates for coho are separated from those of other species for clarity, but both parts of the figure generally show high \(M\) shortly after release or migration downstream, followed by a sharp decrease in \(M\) during the first few weeks or months of ocean life. For the remainder of ocean life, typically much longer than the inshore portion addressed for smolts under POST, \(M\) is evidently much lower, about 0.6% d\(^{-1}\).

Across these studies, \(\bar{M}\) ranged widely in the first 2–3 weeks after release, from roughly 6.5–18% d\(^{-1}\). Many of these are likely overestimated for two main reasons: (1) as discussed in Chapter 9, any components of mortality that might have to do with specific events (like saltwater entry) rather than simply elapsed time will have the ‘time-independent’ mortality component averaged over a shorter period of time. (2) Survival is likely underestimated. For POST-derived estimates, tagging-related mortality could lead to overestimating \(M\) (Chapter 9). For Georgia Strait coho pelagic surface trawl estimates, an assumption of 100% catchability (Beamish et al. 2008) and the possibility of emigration out of the Strait and offshore before July both lead to underestimating at-sea smolt abundances in the Strait and thus underestimating survival, as noted by the authors. Magnitudes of \(M\) and patterns of decline appear to be more stable after these first

\(^{17}\) The relationship between release-to-September survival and overwinter survival oscillated over time as a result of the 2-year abundance cycle of pink salmon, with coho survival from release-to-September lower in even years when the abundance of juvenile pink salmon was higher (Beamish et al. 2008).
few weeks despite tremendous variation in latitude, decade, species, and methodology of survival estimation among studies.

11.2 Hypotheses for variation in smolt-to-adult survival

Key results from this thesis that can be used to address the main hypotheses for variation in smolt-to-adult survival and declines in survival since the 1970s include: (1) high mortality occurred during the downstream migration, with some component that was independent of minimum distance travelled; (2) an additional distance-independent component of mortality occurred during the inshore migration, probably soon after ocean entry; (3) mortality was not size-selective within release groups during the downstream migration, but selected against smaller fish during the inshore migration and this selection likely continued in the remaining portion of ocean life given smolt-to-adult size-selection results from other studies.

‘Growth rate’ hypotheses predict that slow growth after ocean entry increases the duration of the period that fish are vulnerable to high levels of predation risk, thus leading to increased overall mortality. Slow growth may be the result of either poor ocean conditions (Fisher and Pearcy 1988) or high densities of juvenile salmon or competing species (Peterman 1978, Walters et al. 1978), both of which result in low food availability for individual fish. Hatchery releases of salmon have increased since the early 1970s in many regions including Georgia Strait and Puget Sound (Simpson et al. 2001, Beamish et al. 2008), so even though abundances of many wild populations are low, density-dependent competition after ocean entry could still be important. In years of poor ocean conditions (such as those currently, compared with previous decades), size-selective mortality may be stronger (it may be non-selective in years of good conditions; Holtby et al. 1990). I did find evidence of size-selective mortality after ocean entry, but the duration of our study each year was short enough that early ocean growth per se did not likely contribute substantially to variation in mortality. My results are thus not very informative in terms of support for or against growth rate hypotheses.

Size-selective mortality after ocean entry, as well as distance-independent components of mortality during the downstream (especially for hatchery fish) and inshore migration, are consistent with ‘predation intensity’ hypotheses. Predation rates on migrating juvenile salmon have been found to be high in many studies, several of them within Georgia Strait. Aggregations of predators targeting smolts soon after freshwater release or ocean entry may account for the distance-independent components of mortality during the downstream and inshore migration,
respectively. Abundances of harbour seals in the Strait increased by nearly a factor of 10 between the early 1970s to early 1990s (Olesiuk 1999), and are likely at least partly responsible for the smolt-to-adult survival declines over this period.

Results here are consistent with the critical size and period hypothesis (Beamish and Mahnken 2001). There was a period of high mortality early in ‘marine’ life (which was actually largely during the downstream migration), and this was likely caused by intense predation, whether size-dependent or not. Survival estimates for the inshore migration were not reliable for coho and Chinook due to possible confounding with summer residency in the Strait, but survival of steelhead and sockeye were not so low that considerable mortality later in ocean life was unlikely. Overwinter mortality also appears to be considerable; the per-day overwinter $M$ for coho may be low, but the cumulative effect over a period of 12–16 months results in high percent mortality for the period. The finding that size-biased directional selection was weaker during the migration through Georgia Strait than has been observed after smolt-to-adult life for Keogh River steelhead (Fig. 9.16) suggests that the later mortality is also size-dependent, consistent with the critical size and period hypothesis. Sampling in winter months would permit further partitioning of specifically when during the 12-month overwinter period this second phase of high mortality occurs.

Other hypotheses for mortality during the smolt migration (like pollution, disease, and nutrient deficits after freshwater rearing) do not necessarily predict acute mortality events shortly after release or ocean entry. It is unknown whether the effect of these agents may change under the physiologically demanding time of smoltification and saltwater exposure, however, so they cannot be ruled out as possible explanations for the observed periods of high mortality. Whatever may be the ultimate causes of variation in mortality, predation is likely the principle proximal agent of high and variable mortality (Pearcy 1992, Mesa et al. 1994).

Survival estimates during years of the POST study (2004–2008) and the pelagic surface trawl study (1997–current) both show interannual variation, although these recent periods are short compared with the decades over which smolt-to-adult survival declined (Figs. 1.1, 1.2). They are literally a single snapshot on the time scale of ocean regime changes (Hare and Francis 1995). In a different regime period (before the late 1970s) when smolt-to-adult survival was much higher, $M$ during the early migration was likely considerably lower. There is not enough contrast in survival among years during these recent shorter periods to fully assess what factor(s) caused the much higher variation in survival over the longer term or were responsible for the survival declines. If the current ocean regime shifts in future years, continuing these studies
would provide greater contrast for evaluating important factors affecting survival among years as well as how these factors may act in different portions of smolt-to-adult life.

11.3 Recommendations for future work

This work has provided some indication of where and when important periods of mortality occur, and some of the factors responsible for variation in survival. Several information gaps remain, however, which could be addressed with further work.

- If absolute estimates of downstream or inshore mortality are desired, then effort should be put into quantifying tag-related effects on survival of freely-migrating fish. The cumulative impact of tag shedding, battery failure, effects of the surgery, and effects of an implanted tag on swimming ability of a migrating fish are not trivial. These effects can be assessed using double-tagging experiments or weirs to quantify survival of fish with acoustic tags versus those with much smaller tags assumed to have negligible effects on survival (Chapter 9).

- If comparisons of survival among treatment groups are instead desired, relative estimates of mortality may be acceptable under the assumption that tagging-related factors affect treatment groups equally. There is great potential for the POST array to be used in experiments or direct comparisons for hypothesis testing (Crossin et al. 2008, Rechisky et al. 2009; Chapters 8, 10). There is currently much interest in the possible role of disease (Arkoosh et al. 2004, Jacobson et al. 2008) and pollution (Barry et al. 2000, Heintz et al. 2000, Coghlan and Ringler 2005) on salmon survival. Exposure trials with pathogens or pollutants could be conducted in hatchery tanks, and survival of tagged fish could be compared among treatment groups.

- Additional sampling could be done at the time of surgeries to relate the fate of individual fish during the migration to their physiological or genomic characteristics. Variation in survival or migration speeds of returning adult sockeye has been attributed to factors such as differential gene expression, disease, river temperature, and hormone levels (reviewed in Cooke et al. 2008). Similar attempts for tagged smolts may be illuminating; some of the unexplained variation in survival normally attributed to stochasticity, either among years or among individuals in the same year, may be the result of physiological or genetic differences that have previously gone unnoticed.

Greater efforts should be made to integrate approaches for studying salmon survival among regions and assessment technologies. Recent efforts for integrating (mainly) pelagic trawl data from the continental shelf and high seas among regions from Alaska to California (Grimes
et al. 2007) have resulted in a broader understanding of the distributions, movements, feeding patterns, and growth of juvenile salmon. Similar efforts are underway to compare salmon survival from acoustic tracking studies across large river systems in western North America (Fraser, Columbia, Sacramento Rivers). Additional efforts could integrate acoustic tagging studies, inshore pelagic trawl sampling studies (Beamish et al. 2008), outer coast pelagic trawl sampling, and smolt-to-adult survival estimates from coded-wire tags, PIT tags, or rivers with weirs for enumerating smolts and adults. Together, these could further our understanding of how $M$ varies during ocean life, and what factors account for this variation.
Figure 11.1. Summary of coho abundances (a), percentage survival (b), and instantaneous mortality ($M$; c) from Georgia Strait hatcheries during 1997–2006 years of ocean entry. Smolt releases are from eight major hatcheries, and abundances in July and September were estimated with pelagic trawl surveys conducted by Fisheries and Oceans Canada. All data for (a) and (b) were tabulated in Beamish et al. (2000, 2008). Estimates for (c) were calculated from survival estimates in (b), median release dates, and median trawl survey dates in July and September of each year. Overwinter $M$ assumes a return date of October 1 the year following ocean entry. Note the log scale for (a).
Figure 11.2. Instantaneous mortality rates ($M$) of juvenile salmon during different portions of smolt-to-adult life. Time-based $M$ (roughly equivalent to daily % mortality) are plotted against the period over which $M$ was estimated. Estimates are separated by species: in (a) coho – blue; and in (b) sockeye/kokanee – red; steelhead – green; Chinook – black; chum – purple; and pink – pink. Estimates of $M$ were taken from or calculated from data in: POST data – Chapter 9 (Table 9.5); coho pelagic trawls – in Georgia Strait (Beamish et al. 2008, showing only year 2004 estimates of release-to-Sept. and overwinter $M$ for clarity), and the Oregon coast (Pearcy 1992); coho predictions of $M$ based on weight (Mathews and Buckley 1976); chum from Little Port Walter, Alaska (Wertheimer and Thrower 2007); and pink from Bella Coola, central B.C. (Parker 1968).
Figure 11.2 cont.
11.4 References


Appendix A  General methods

A.1 Study sites

The hydrology of southern British Columbia is diverse. Steep coastal mountains generate a steep gradient for many streams, creeks and rivers. Estuaries range from small areas with abrupt transitions between freshwater and saltwater to vast areas of brackish water. Several fjords line the coast of B.C., and inshore straits have oceanographic conditions that are often different to those on the outer coast.

Salmon smolt populations tagged under POST were mainly selected for ecological interest, conservation concern, and logistic factors (i.e., large enough body sizes for tags, and wild smolt capture operations already in place). Tagged smolt populations also happened to be distributed across a wide range of river conditions in terms of watershed size/discharge and productivity (Table A.1). The Thompson River watershed was one focal region, with tributaries of moderate productivity and relatively low relief before draining into the Thompson River and then the middle Fraser River. The lower Fraser River has a lower gradient and is wide, silty, and sees considerable industrial and navigational activity. Other coastal watersheds such as the Squamish and Seymour Rivers vary in size and productivity, but generally have a steep gradient. In contrast, most watersheds studied on the east coast of Vancouver Island have a lower gradient; these are also variable in terms of size and productivity (Table A.1). Most of these watersheds are driven by snowmelt and glacial runoff, with flows generally peaking in late June.

Most of the watersheds in Table A.1 drain into Georgia Strait (Fig. 1.4) with the exception of the Keogh and Nimpkish Rivers from northeastern Vancouver Island (which drain into Queen Charlotte Strait) and the Stamp River from the west coast of Vancouver Island. The Fraser River drains directly into Georgia Strait and has considerable influence on the oceanography and productivity of the strait (Thompson 1981). There are numerous inlets on both the B.C. mainland side and east coast Vancouver Island side of Georgia Strait. Howe Sound is one of these, a coastal fjord 25 km north of the Fraser River mouth. Surface currents are driven largely by winds (especially in Squamish Harbour, the upper part of Howe Sound; Buckley and Pond 1976), as they are in Georgia Strait.

Exit routes to the open Pacific Ocean from the inshore Georgia Strait include Johnstone Strait and Queen Charlotte Strait to the north, and Juan de Fuca Strait to the south (Fig. 1.4). Tidal currents are relatively strong in these exit straits (Thompson 1981). The southern outer
coast of B.C. is part of the California Current system, where current and wind-driven upwelling results in highly productive waters.

### A.2 Study populations and smolt release groups

Four species of Pacific salmon were tagged and released in southern B.C. under the POST Project over six years, from 2003–2008. Coho salmon (*Oncorhynchus kisutch*) and steelhead trout (*O. mykiss*, the anadromous form of rainbow trout, often considered a salmon) were widely represented in study populations throughout the Fraser River watershed, the B.C. south mainland coast north of the Fraser River mouth, and the east coast of Vancouver Island (Fig. 1.4). Stream-type Chinook salmon (*O. tshawytscha*) populations were tagged in the Thompson River watershed in 2005–2006 as well as in the Nimpkish River on northern Vancouver Island in 2006. Sockeye salmon (*O. nerka*) from Cultus Lake in the lower Fraser River basin were tagged (as well as a small number of sockeye from the Alouette River in 2005, also in the lower Fraser River basin). Populations of sockeye and genetically-distinct kokanee salmon (also *O. nerka*, as kokanee are closely related to sockeye but often found in landlocked lakes) from Sakinaw Lake (which is not landlocked) were also released.

Study populations consist of a group of smolts of a particular species from a particular watershed of origin with a particular provenance—either wild or hatchery-reared. Different smolt years typically consist of distinct cohorts of a population (e.g., fish that are 1.5 or 2.5 years old at smoltification), but in some populations ages of smolts may be mixed. Most study populations were tagged in 2004–2006, the main years of the POST Project demonstration phase (Tables A.2 and A.3). These years contribute the majority of the data for the overall analyses of migration patterns (Chapter 7) and survival (Chapter 9). A small pilot study was conducted in 2003 with Tenderfoot Creek Hatchery coho, with the study area limited to the Cheakamus and Squamish Rivers and Howe Sound. In 2007, an experiment to test the hypothesis of reduced survival as a result of ultraviolet-B radiation from sunlight was conducted using fish from Tenderfoot Creek Hatchery (coho) and Inch Creek Hatchery (Cultus Lake sockeye) (Chapter 10). Hatchery-reared steelhead from the Cheakamus and Seymour Rivers were also tagged in 2007. A direct comparison of survival and residualization rates between wild and hatchery-reared steelhead smolts from the Cheakamus River was made in 2008 (Chapter 8).

To provide generality in the influence of various factors on survival, populations were analyzed jointly in an overall framework for the years 2004–2007 (Chapter 9). A total of 44 populations (combinations of species, watershed of origin, provenance, and smolt year) were
considered for this analysis (Table A.2, with the two Cheakamus River steelhead groups from 2007 that were reared at different hatcheries considered together and the two Cultus Lake sockeye groups from 2007 that had different tag types and release dates considered together), distributed among the middle Fraser River watershed (13 populations), the lower Fraser River watershed (4), the south mainland coast north of the Fraser River mouth (12), and the east coast of Vancouver Island (15). In many cases two or more different tag types were distributed among fish from a given population. Some populations had various experimental treatments applied (Table A.2), but for the analysis in Chapter 9 these treatments were pooled together for each population. Other populations were tagged under POST, but were not included in this overall analysis of survival (Table A.3). Three of these populations excluded were Cheakamus River steelhead in 2008; these were analyzed separately for a more controlled comparison of wild and hatchery-reared survival. Reasons for excluding the remaining 11 populations include small sample sizes, freshwater residency of the population, different acoustic output or average pulse interval of tags, fall releases, suspected poor physical condition, and absence of receiver stations with which to detect migrating smolts (Table A.3).

The timing of migration was variable among smolt populations, even within the relatively narrow latitudinal range of southern B.C. Most smolts were released in May, but dates ranged from 15 April–1 July. Smolts were usually released at dusk to reduce the efficiency of visual predators immediately after release. Tagged hatchery-reared smolts were released with the remainder of the production stock when possible, but occasionally had to be held after the release of production stock fish for tagging and post-tagging recovery. Wild smolts were generally caught in rotary screw traps, weirs, or side channel traps during their downstream migration, and were held in river traps (in some cases for several weeks) until sufficient numbers were available for tagging and until tagging crews arrived. This often resulted in several release periods of a given wild population (e.g., 67 Englishman River steelhead smolts were tagged and released over 10 periods in 2004; Table A.2). Wild fish were generally held for 2 d after tagging to monitor for signs of tag extrusion or altered swimming behaviour; hatchery-reared fish were often tagged several days or weeks before they were released.

Body sizes of tagged smolts varied considerably. Minimum size threshold guidelines were adopted to reduce the possibility of tag-related effects, and this meant the technology was only suitable for stream (or lake) rearing species that overwinter at least once in freshwater. Species not studied include pink salmon, chum salmon, and ocean-type Chinook salmon that migrate to the ocean in the first year after emergence. Smolts tagged with VEMCO V9 tags were
generally >140 mm fork length (FL), and those tagged with smaller V7 tags were generally >125 mm FL. Fork length of all tagged smolts in Table A.2 ranged from 112–251 mm. The average FL of tagged smolts ranged from 117–213 mm among these 44 release groups (Table A.2).

A.3 Detailed field methods

Recent developments in acoustic tagging technology have yielded individually-coded tags small enough to be surgically implanted into juvenile salmonids. By deploying a series of acoustic receivers in rivers and coastal areas, the migration routes and rates of individual fish can be quantified and survival rates of populations crossing receiver stations can be estimated. These methods have been evaluated for several salmon smolt populations in British Columbia under the Pacific Ocean Shelf Tracking Project (POST, see www.post-coml.org). Tagging of salmon smolts and deployment of ocean receivers and most river receivers in B.C. was done by Kintama Research Corp., the company contracted by POST.

A.3.1 Tag and receiver characteristics

A variety of VEMCO tag types and programming were used for salmon smolts, depending on fish size, repetition rate of pulse trains, and ‘sleep’ periods. All tags were individually-coded and transmitted pulse trains at 69 KHz, with either 7 or 8 pulses in a pulse train. Most tags used were either V7-2L (20 mm x 7 mm diameter, 1.6 g in air, 136 dB re 1 µPa at 1 m) or V9-6L (21 x 9 mm, 2.9 g, 142 dB) models. For some Cultus Lake sockeye and Sakinaw Lake sockeye or kokanee smolts, two other tag types were also used, which permitted a longer battery life: V9-1L (24 x 9 mm; 3.6 g, 142 dB) and V9-2L (29 x 9 mm; 4.7 g, 142 dB) models (Table A.2). These tags had a ‘sleep’ period programmed into them, so after several weeks or months of transmitting during the smolt migration, they stopped and then re-started two years later during the adult return migration. One population was tagged with high-power tags (V9-1H, 24 x 9 mm, 3.6 g, 147 dB), but was not included in the overall survival analysis because of the expected effect on detection probabilities (Table A.3). Most tags were programmed with a 30–90 s random time interval between successive transmissions of pulse trains (average 60 s).

Variation in body size of tagged smolts (Tables A.2 and A.3) led directly to variation in tag length to body length ratios (TBL; Fig. A.1). Very few (3.1%) TBL ratios of fish tagged with V9-6L tags were above a recommended threshold value of 16% for salmon smolts (Lacroix et al. 2004), but 19.2% of fish tagged with V7-2L tags were above this 16% TBL threshold (Fig. A.1). These ratios only consider tag length, however. V7 and V9 tags differed by only 1 mm length, but the 2 mm difference in diameter resulted in considerably greater mass of V9 tags. Tag type
was accounted for in estimated detection probabilities (due to the differing acoustic output) as well as in the possibility of impacts on survival (due to differing tag sizes). All the 758 sockeye and kokanee smolts tagged with V9-1L tags and 23.9% of the 188 sockeye smolts tagged with V9-2L tags were below the recommended 16% TBL threshold. Tag mass to body mass ratios are likely a better metric for assessing tag effects on performance and survival (Perry et al. In review), but to minimize the time spent on the surgery table tagged fish were rarely weighed.

Tag battery life is an important concern in tagging studies. Battery life depends on both tag type and transmission delay intervals, with longer intervals generally prolonging tag life. Variation in strength among individual batteries results in a wide possible range in the expected life of tags. VEMCO typically quotes expected tag duration estimates based on the lower end of this range. A laboratory monitoring experiment was conducted by Kintama Research Corp. in 2008 and 2009 to verify the proportion of V7-2L tags that transmitted at least past their expected duration estimates. This consisted of using a VEMCO VR-60 receiver with hydrophone tip and tag both placed in water about three times per week to check whether tag signals were detected. If a tag was not immediately heard and decoded, it was left with the hydrophone in a water-filled container for 20–60 min to monitor whether the tag transmitted. In 2008, 17 tags with 45 sec. average delay intervals (group A in Fig. A.2) and two tags with 60 sec. intervals (group B; these were recovered from Columbia River smolts that died in a hatchery tank post-tagging) were monitored. Most of these tags (17/19, 89%) transmitted well past their expected durations (Fig. A.2). Seven tags transmitted until the end of the monitoring experiment (~300 d), five transmitted past the expected battery duration but stopped abruptly sometime before 300 d, and five transmitted past the expected battery duration but instead of stopping abruptly, transmitted occasionally with periods of no transmissions interspersed. Of the two tags that stopped transmitting prior to the expected battery duration, one transmitted until 17 d after activation and the other had stopped transmitting sometime between tag activation and incorporation into the monitoring experiment 51 d after activation. This is not a result of tags not activating initially: prior to tagging fish, all tags are verified to transmit properly, so these tags stopped prematurely. They were returned to VEMCO and were not transmitting on arrival. Following tag dissection, batteries were still fully charged and the cause of failure was not determined. This tag failure rate of 11% is particularly worrisome given that survival estimates assume no tag failure. A second experiment is currently underway in 2009, using 10 tags with a 60 sec. average interval (group C, one of which was recovered from a dead Columbia River smolt) and 13 tags with a 90 sec. interval (group D, three of which were recovered from dead Columbia River smolts). Most tags
transmitted until past their expected duration estimates, but one stopped prematurely sometime between 81–85 d after activation (Fig. A.2). This tag was returned to VEMCO and was dead on arrival. Another two tags are still transmitting, but have not yet reached their expected duration date. With both years combined, an estimated 7.5% of tags stopped prematurely, which generally results in underestimating survival although bias corrections have been developed (Townsend et al. 2006).

Apart from this laboratory monitoring, it appeared that a few tags in the field were still transmitting signals >1 year after activation, well past their expected expiry date. Five V9 tags used in Keogh River steelhead or coho happened to remain situated near the river mouth receiver in 2004 (likely following either tag extrusion or smolt death), and four of these were still transmitting regularly in April-May 2005. The fifth, curiously, was not detected in 2005 but was subsequently detected at the river mouth station regularly in March-Aug. 2006. Either slight year-to-year variation in deployment position of the receiver made the tag not detectable in 2005 but detected in 2006, or the tag had ceased to transmit during all or a portion of 2005, after which it began transmitting (similar to some patterns in Fig. A.2, group A). One V9 tag used in a Cheakamus River steelhead in 2005 was detected in Howe Sound with a mobile sampling program in Aug. 2006. This tag was transmitting (and detected) in the same location throughout May 2005, but it is unclear if it transmitted continuously over the following 15 months or stopped for some time and started transmitting again.

Narrow-band acoustic receivers (resonant at 69 kHz) were used to detect VEMCO tags. VEMCO VR-2 receivers (which must be retrieved to download data) were used at ocean and river stations in 2004–2005. Beginning in 2006, VEMCO VR-3 receivers (which are downloaded using an underwater modem from a boat at the surface) were used at most ocean stations.

**A.3.2 Fish tagging**

Acoustic tags were surgically implanted into smolts following standard protocols (Moore et al. 1990, Welch et al. 2007). Smolts were sedated with 1 ppm metomidate HCl (Aquacalm™) for a minimum of 10 min, then 3–4 min prior to surgery they were brought under full anaesthesia using 70 ppm tricaine methanesulphonate (MS-222) mixed with a 140 ppm NaHCO3 buffer. Gills were continuously irrigated during surgery with a purpose-built surgical table with recirculating water containing 50 ppm MS-222 (100 ppm NaHCO3) flowing into the mouth. A tag was inserted into the abdominal cavity through a mid-ventral line incision, which was closed using 1–3 polydioxanone monofilament sutures. Fish were then transferred to a recovery tank.
Water baths were continually monitored for temperature and dissolved oxygen (DO). All water baths were changed as needed to maintain DO between 8–11 ppm and to maintain water temperatures within 2°C of ambient river or hatchery tank water. Air bubblers and a mucous-protectant (Vidalife™) were used in all water baths. Animal care protocols were reviewed and approved annually by institutional animal care committees prior to all field work (permits were obtained by Kintama Research Corp.).

Tagged smolts were generally held for ≥2 d after surgery (up to several weeks for smolts tagged at hatcheries) to assess direct tagging-related mortality, tag extrusions, and monitor for signs of impaired swimming behaviour. Of the smolts tagged from the populations listed in Table A.2 as well as Cheakamus River steelhead in 2008, 1.3% died prior to release, likely as a direct result of tagging. Nearly half of these mortalities (25 of 54) were from a single population, Sakinaw Lake kokanee in 2005. Multiple and extended drugging may have contributed to the high number of tagging-related mortalities in this population: fish were seined from the lake using a boat, put in a bucket with a high dose of Aquacalm, then transferred to freshwater where they were hand netted and placed in new sedation baths prior to tagging. A lack of recovery time and immediate exposure to saltwater may have also contributed: after surgeries were finished, tagged fish were transferred to a holding cage the mouth of the lake (an estuary) where they were released the following day. The dead fish were discovered this next day. Excluding this population, tagging-related mortality was observed in 0.7% of tagged smolts. In all years and populations, only a single tag was extruded prior to releasing fish, from a hatchery-reared Cheakamus River steelhead smolt in 2008.

A.3.3 Receiver deployments

Acoustic receivers were deployed in successive locations along migration routes of salmon smolts to detect tagged fish during their migration out of freshwater and through Georgia Strait. In the inshore waters of southern B.C., receivers were arranged in lines across the northern Strait of Georgia (NSOG), Juan de Fuca Strait (JDF), Queen Charlotte Strait (QCS), and two latitudes in Howe Sound (HS_{inner}, HS_{outer}) in 2004–2008 study years (Figure 1.4). Other inshore ocean stations were occasionally used in some years, deployed either under POST or under related studies: off the Fraser River mouth in 2006, across Burrard inlet in 2006–2008, near Campbell River and Discovery Passage in 2006 (operated by C. Chittenden, U.B.C.), near Sakinaw Lake in 2007 (operated by L. Godbout, Fisheries & Oceans Canada), off Point Atkinson in 2005–2006 (operated by J. Marlieve, Vancouver Aquarium), and in several locations...
throughout Puget Sound, Washington, in 2004–2008 (operated by various agencies). Receivers were also deployed on the outer coast, extending from near shore towards the continental shelf break (ca. 200 m depth). One receiver line was off the west coast of Vancouver Island at either Brooks Peninsula (2004–2005) or Lippy Point (2006–2008). One line was deployed off southeast Alaska (2004–2008), while other lines were deployed off the coast of Washington at Cape Elizabeth (2004–2005) or Willipa Bay (2006–2008). These outer coast lines differ from the ‘sealed off’ inshore strait lines in that (in addition to crossing a line undetected), fish may swim around the outside of a line.

Receivers were deployed near most river mouths from which smolts emigrated (Figure 1.4). Additionally, I deployed several receiver stations (4–12) in the Cheakamus and Squamish Rivers in 2003–2008 for studies involving Tenderfoot Creek coho and Cheakamus River steelhead. In the lower Fraser River, rather than right at the river mouth, 2–4 receiver stations (comprising a total of 4–14 receivers) were deployed by POST over ~65 km ranging from Mission (furthest upstream) to Deas Island, between Richmond and Delta.

Most receivers from ocean lines were recovered with the exception of the JDF line in 2004, when 10/30 receivers were lost to trawling activity (Fig. A.3a). At the three larger ocean stations of multiple receivers, units were generally spaced 750–850 m apart, while spacing was generally 600–700 m at Howe Sound stations (Fig. A.3b). This was predicted to provide sufficient overlap in detection radii of receivers (generally about 450 m in calm waters) that most tagged smolts are expected to transmit at least a few signals while crossing the line (Welch et al. 2003). This required 22–30 receiver units to span the distance across NSOG, QCS and JDF. After 2004, average depth of receivers was similar among ocean stations (Fig. A.3c). Using floats, receivers were raised from the seabed where they were anchored, to a depth usually within 150 m of the surface. In rivers, acoustic receivers were generally installed as single or paired units, with receiver pairs deployed from opposite sides of the river when possible. A variety of receiver deployment methods were used in rivers, attempting to let VR-2 receivers remain vertically-oriented to achieve the greatest possible horizontal radial detection distance. Receivers in rivers and coastal areas were generally left in place several weeks or months until after tag batteries had likely expired. Beginning in 2006, ocean stations were operable year-round.

A.3.4 Mobile tracking

Transect samples were conducted by boat, towing a directional hydrophone, to quantify movement and mortality patterns on a finer spatial scale than the stationary POST ocean lines.
allowed. Mobile sampling trips were conducted in Howe Sound once or twice per summer in 2003–2007, and once in Georgia Strait in July–August 2005. Most of the sampling effort was devoted to running parallel transects to find as many tags as possible, rather than following individual fish once they had been located to gain detailed behavioural observations. As not all fish were detected on the stationary Howe Sound lines, the mobile sampling program aided in quantifying the proportion of salmon smolts that died during their migration through the fjord (assuming that locations where tags stop moving represent approximate locations of mortality). This was especially important for the 2007 study that compared survival of solar ultraviolet radiation treatment groups (Chapter 10). Further methodological details are described in Chapter 5. Basic migration patterns and approximate locations of mortality are presented in Chapter 7. Animal care protocols for tracking tagged fish by boat are listed in Appendix E.

A.4 Data analyses

A.4.1 Filtering of likely false detections

Occasionally, detections logged on acoustic receivers are false positives rather than legitimate detections. False detections for VEMCO tags most commonly occur when the pulse trains of two tags within detection range of a receiver ‘collide’, i.e., overlap in time. When pulse overlaps occur, usually no detections are logged since the timing between pulses is what codes for tag identifications, and the receiver does not distinguish between pulses of different tags. More rarely when pulse overlaps occur, the particular timing and combination of pulses from the two tags may falsely code for a novel tag identification, and this is logged on the receiver. False detections can also occur if only one or even no other tags are near the receiver around the time of the false detection as a result of echoes or background noise. The probability of any particular logged detection being false lies on a continuum from 0–1. If a detection is considered false and rejected, there is a chance that it was actually legitimate. If a detection is considered legitimate, it could have actually been a false positive. It is often recommended that single detections of a tag code at a station be rejected as likely false (e.g., www.vemco.com/education/faqs.php). This may be reasonable for studies with high site fidelity and many detections expected over time at a station. For migrating fish, however, tags are often not expected to be detected more than one or a few times as they pass a station, especially in rivers where movements are assisted by currents. In the 2004–2006 POST dataset, 16% of all crossing events thought to be legitimate involved only a single detection (Chapter 4). Outright rejection of single detections without detailed inspection would lead to biased survival and detection probabilities in mark-recapture models.
Two independent false detection screens were conducted and compared in an attempt to identify which of the ~1 million detections of B.C. POST salmon smolts in 2004–2007 were likely false. My method generally followed a decision tree (Fig. A.4) based on the plausibility of tag detections along migration routes and the amount of ‘traffic’, or other tags present around the time of the suspect detection at the receiver in question. For every B.C. salmon smolt tagged under POST, I constructed a temporal sequence of detections at all receiver stations (where stations may contain multiple receivers). I summarized these within stations (over a period where the fish was continually detected at only a single station) in order to allow rapid visual assessment of the spatio-temporal succession of detections. I conducted the scan for all detections, not just single detections, which also permitted evaluation of whether irregular detection sequences may have been the result of detecting duplicate tag codes (non-unique tag codes were issued by VEMCO to researchers in B.C. and the U.S. Pacific Northwest, usually in different years but occasionally in the same year by mistake). For each tag, if either of the following were observed, I conducted a traffic test: (1) the spatial detection sequence was questionable; (2) there was only a single detection at a station within a period 60 min before or 60 min after the suspect detection, and the time of that single detection was outside the 95% confidence limits of travel times of other fish in the population to the station in question. Otherwise, the detection(s) was considered legitimate. A traffic test consisted of inspecting the VEMCO receiver file containing the suspect detection(s) in the period 10 min before to 10 min after the suspect detection. If one or more other tag codes was detected within that period, the suspect detection was considered likely false.

A second false detection screen was carried out by Aswea Porter (Kintama Research Corp.) for tag codes corresponding to populations listed in Table A.2. Detections were identified as likely false if the following criteria were all observed: (1) a tag code was detected only once at a station within a period 30 min before or 30 min after the suspect detection; (2) there were ≥1 other tag codes detected on the same receiver around the time of the suspect detection; and (3) the suspect detection did not have supporting detections from other time periods or stations. Supporting detections are defined as a chronological sequence of detections from the release date along typical migration paths for each population.

Simple rules like these above for identifying suspect detections are attractive in the name of simplicity, but occasionally these were bent (more often in my screen, which was more subjective by nature, less often in AP’s screen). Detection situations (i.e., migration routes, timing, number of detections, other tags present in the area, temporal spacing of detections, etc.)
are quite variable, and some cases required detailed consideration beyond these guidelines which do not cover all situations appropriately. In most cases, the lists of suspect detections under these two approaches were similar, and the detections identified as such under both methods were considered false. Whenever the two approaches differed, the suspect detections were examined more closely for evidence supporting or not the likely presence of the tag in that location at that time. If only one other tag was present around the time of the suspect detection at the same receiver, VEMCO provided information about the similarity of the pulse trains of the two tag codes in attempts to distinguish whether a tag ID was decoded incorrectly. We eventually reached consensus for all suspect detections on whether to consider them false or legitimate.

In both approaches, only the detections whose ID codes matched up with B.C. salmon smolts tagged under POST were screened. The total number of detections each year at all POST stations for the B.C. salmon smolt populations listed in Table A.2 varied from 83,741 to 365,148. The number of likely false detections identified ranged from 43–343, and the resulting proportion of false detections ranged from 0.0002–0.0022. Although these represented a small proportion of all detections, many of these would have affected survival estimates if they had been considered legitimate, so it was important to screen out detections that were likely false. There are many more false detections that were logged on POST receivers whose ID codes did not correspond with B.C. salmon smolts tagged under POST; these were not inspected. After eliminating detections that were likely false, I used these filtered data to estimate survival and detection probabilities, travel times and speeds, and migration routes of tagged smolts.

A.4.2 Travel time summaries

Segment distances were measured with mapping software as shortest-route in-water distances between receiver stations. These were added for measures of cumulative distance from release to successive stations. Cumulative travel times were measured as the time from release until the first detection of a tag at a station, and were averaged across fish within each population. Occasionally, the average travel time to a station \( i \) was greater than the average travel time to a station \( i+1 \) that was later along the migration route. This was simply a result of a different subset of fish being detected at adjacent stations. To present a continually increasing sequence of cumulative travel times, whichever station \( i \) or \( i+1 \) had the greater number of fish detected, that cumulative travel time was applied to the other. Thus, travel times for each segment derived from differences between cumulative travel times to adjacent stations.
occasionally had a travel time of 0 d between stations $i$ and $i+1$. 95% confidence limits of cumulative travel times were calculated for each population in each year.

**A.4.3 Mark-recapture methods**

*General model construction and optimization routines*

Receiver stations (consisting of a single or multiple acoustic receivers) in either rivers or coastal areas do not provide a perfect probability of detection. It is necessary to estimate detection probabilities ($p$) in order to estimate the extent of migration of tagged fish, determined by their survival probabilities ($\phi$). These parameters $p$ and $\phi$ are generally estimated simultaneously with maximum likelihood procedures. The Cormack-Jolly-Seber model (CJS; Cormack 1964, Jolly 1965, Seber 1965) involves uniquely-specified $p$ at each station and $\phi$ in each segment of the migration (between receiver stations) for each release group in the analysis. Variations on the classic CJS model may involve use of covariates to constrain some model parameters to be shared across release groups, detection stations, or migration segments. The maximum likelihood estimators are asymptotically unbiased, normally distributed, and of minimum variance (Burnham et al. 1987, Lebreton et al. 1992). To optimize the likelihood function, Program MARK (White and Burnham 1999) uses the Newton-Raphson method (with the VA09AD algorithm from Harwell library). To estimate the variance-covariance matrix of parameter estimates, MARK uses central difference approximations to the 2nd partial derivatives of the likelihood function.

Program MARK calculates the number of identifiable parameters (i.e., the maximum number of estimable linear combinations of the parameters) in a model applied to a dataset. It uses a numerical approach based on singular-value decomposition (the DSVDC algorithm, Dongarra et al. 1979) to compute the effective rank of the Hessian matrix (i.e., the 2nd derivatives of the likelihood function). This calculated number of independent, estimable parameters is sometimes less than the number of $\phi$ and $p$ parameters actually in a model (it is constantly recommended to double-check the number of parameters estimated by MARK; White and Burnham 1999). The ability of MARK to count the number of parameters correctly is impaired when design matrices are used instead of parameter index matrices, especially in sparse data sets (Laake and Rexstad 2009). Since design matrices were used almost exclusively for the ability to implement additive models applied to interrelated datasets, a more conservative approach was taken: I assumed that all $\phi$ and $p$ model parameters were estimable rather than adopting the
counts by MARK. This is the same philosophy taken by RMark (Laake and Rexstad 2009) in implementation of mark-recapture models, and avoids selecting overly complex models in which the number of parameters is improperly counted (biased low).

Survival and detection probability models can involve various types of covariates, or ‘factors’ potentially affecting survival, built in directly (Lebreton et al. 1992). This is statistically preferable to looking for effects of these factors on estimated parameters from general CJS models (i.e., running statistics on statistics), as it appropriately accounts for the error structure in covariate models. Covariates may apply to all individuals of a group (e.g., experimental treatments, hatchery- or wild-rearing history, river level at the mean arrival time of the group at a receiver station), or may apply to individual fish (e.g., body size, or release date for populations that were released over several days). Interactions between covariates and segments or stations, or interactions among covariates can also be modelled. Such models under this approach can be expressed in the framework of generalized linear models (McCullagh and Nelder 1989), where variation in survival or detection probabilities is attributed to various combinations of ‘effects’, or explanatory variables. Typically, these effects are modelled as some function, e.g., \( \phi = f(\beta_0 + \beta_1 \cdot \text{BS}, \beta_2 \cdot \text{TS}) \). The function \( f \) links the model parameter \( \phi \) to linear coefficients \( \beta_0, \beta_1, \) and \( \beta_2 \), and is often called a ‘link function’. A common link function in mark-recapture modelling is the logit-link, based on \( \logit(x) = \ln \left( \frac{x}{1-x} \right) \), with \( x \) ranging from 0–1 (use of this link ensures that back-transformed model parameters will be constrained as \( 0 \leq \phi, p \leq 1 \)).

As an example, consider a situation where: (1) body length (BL, across a continuous range) affects the probability of smolt survival during some segment of the migration, with larger fish enjoying a survival advantage over smaller fish, and (2) acoustic tag size (TS, two different sizes, V7 and V9) may also affect survival, with fish of a given BL tagged with a small tag potentially having a survival advantage over fish of the same BL tagged with a larger tag. Further, a TS effect may interact with the BL effect on \( \phi \). Consider three possible models:

1. A model with a common TS effect, \( \logit(\phi) = (\beta_0 + \beta_1 \cdot \text{BL}) \), would have no difference between V7 and V9-tagged fish in the relationship between BL and \( \phi \), either on the logit scale (Fig. A.5a) or when back-transformed to the probability scale (Fig. A.5b). (A linear relationship in logit-space is a logistic curve in probability-space.) This can also be termed a ‘pooled’ model, where the effect of BL on \( \phi \) is pooled across tag sizes. Here, \( \beta_0 \) represents an overall intercept (for both tag types) and \( \beta_1 \) represents the slope of \( \logit(\phi) \) vs. BL.
2. A model with an additive TS effect, logit(\(\phi\)) = (\(\beta_0 + \beta_1 \cdot BL + \beta_2 \cdot TS\)), would have a consistent difference in \(\phi\) on the logit scale between tag sizes. This *difference* in logit-space would be constant across other parameters like BL; in this example, \(\phi\) of fish with a V9 tag is consistently lower than \(\phi\) of a same-sized fish with a V7 tag (Fig. A.5c). This is also termed ‘parallelism’ (Lebreton et al. 1992). Additive models do not appear parallel when back-transformed to the probability scale (Fig. A.5d). Here, \(\beta_0\) represents an overall intercept for V7 tags, \(\beta_2\) represents the difference in intercepts between V9 and V7 tags, and TS is a ‘dummy’ variable equal to 0 for V7 tags and 1 for V9 tags.

3. A model with an interaction effect between BL and TS on \(\phi\), expressed as either logit(\(\phi\)) = (\(\beta_0 + \beta_1 \cdot BL \times \beta_{2,3} \cdot TS\)) or logit(\(\phi\)) = (\(\beta_0 + \beta_1 \cdot BL + \beta_2 \cdot TS + \beta_3 \cdot TS \cdot BL\)), would have independent relationships between BL and \(\phi\) for fish tagged with V7 and with V9 tags. This results in separate slopes in logit space (Fig. A.5e) for the two tag sizes, and may result in considerably different relationships when back-transformed (Fig. A.5f). Such models are also termed ‘multiplicative’ or ‘fully-independent’. Here, \(\beta_1\) represents the slope for V7 tags and \(\beta_3\) represents the difference in slopes between V9 and V7 tags. For V7 tags, TS = 0 and the equation simplifies to logit(\(\phi\)) = (\(\beta_0 + \beta_1 \cdot BL\)), with \(\beta_0\) and \(\beta_1\) still representing the intercept and slope for V7 tags, respectively.

These possible types of effects are considered throughout this thesis, involving several possible explanatory variables for \(\phi\) or \(p\). Typically, several different models are hypothesized, and data-based model selection procedures are used to identify a suitable one (see below).

**CJS model assumptions**

Typical assumptions of open-population mark-recapture models are reviewed in detail elsewhere (Burnham et al. 1987, Pollock et al. 1990, Lebreton et al. 1992, Hightower et al. 2001, Skalski et al. 2001). 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 \(\phi\) and \(p\)
- probabilities of \(\phi\) in each segment and \(p\) at each station are homogenous among individuals within the groups specified in the model structure (although use of individual covariates like body size can relax this assumption since variation in \(\phi\) or \(p\) among individuals is accounted for explicitly)
- 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.

In spatial migration forms of tag-detection studies, it is also important to assume:
- 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 receiver stations—they either die during the migration or continually migrate past receiver lines. 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 stations.

In general, survival estimators are fairly robust to the partial failure of assumptions (compared to population size, for example; Pollock et al. 1990, Lebreton et al. 1992, Skalski et al. 1998, Zabel et al. 2005).

**Evaluating goodness-of-fit and overdispersion**

Mark-recapture models assume only binomial variation, but recapture data are frequently over-dispersed (Anderson et al. 1994). Overdispersion (or extra-binomial variation, extra-multinomial variation) can result from non-independence among individuals in probabilities of surviving or being captured (typically positive covariation among individuals) or from heterogeneity in \( \phi \) or \( p \). In animal trapping studies, variation among individuals in behaviour can lead to heterogeneity in both survival and detection probabilities. In spatial-migration studies, however, behaviour may play a comparatively minor role in affecting detection probabilities, which are expected to be primarily determined by characteristics of tags and acoustic receivers. Whether or not detection probabilities are independent and heterogeneous in spatial-migration studies, overdispersion is still a likely result due to non-independence in survival probabilities among individuals. Although parameter estimates often remain unbiased in the face of overdispersed data, variances of model parameters are underestimated (McCullagh and Nelder 1989, Anderson et al. 1994).

Goodness-of-fit diagnostic tools were used for assessing the fit of a global CJS model to a detection dataset. Program RELEASE uses a series of contingency tables for \( \phi \) in each segment and \( p \) at each station to test the assumption that \( \phi \) and \( p \) are equal among tagged animals (Burnham et al. 1987). Parametric bootstrap methods are used to verify whether the deviance of
a general model fit to detection data falls within a range of expected deviances from the same model fit to simulated datasets where model assumptions are not violated (White and Burnham 1999). It is generally more difficult or not possible to assess the goodness-of-fit of models containing group or individual covariates (White 2002). Goodness-of-fit assessments generally require large sample sizes, especially for RELEASE. The contingency table approach of RELEASE also requires at least 3 detection stations to test model assumptions; some populations only passed up to 2–3 stations. Focus instead tends to be put on estimating the degree of overdispersion in detection data: “Although much of the goodness-of-fit literature concerns testing the hypothesis of lack of fit, I instead view the problem as estimation of c” (White 2002).

To avoid underestimating the variance of parameter estimates when data are overdispersed (as well as to correct model selection criteria, described in the following section), the level of overdispersion can be quantified and then used to adjust variance estimates (Burnham et al. 1987). There are three methods typically used to estimate the variance inflation factor, $c$, all with their own strengths and weaknesses (White and Burnham 1999). Estimates from Program RELEASE involve pooling across contingency tables and calculating the ratio of the overall goodness-of-fit to the model degrees of freedom, $\hat{c} = \chi^2 / df$ (Burnham et al. 1987). Parametric bootstrap methods involve calculating either the ratio of observed deviance (of the global model fit to the detection dataset) to the mean of simulated deviances (of the global model fit to simulated datasets under the assumption of no violations of model assumptions), or else the ratio of observed $\chi^2 / df$ to the mean of simulated $\chi^2 / df$ (White and Burnham 1999). The median $\hat{c}$ approach uses a logistic regression to find the expected value of $c$ where 50% of simulated $\hat{c}$ estimates fall above and 50% fall below the observed $\chi^2 / df$ (White and Burnham 1999). With any of these methods, if the model fits the data, the expected $\hat{c}$ is 1. Large $\hat{c}$ values (generally >3) can result either from overdispersion or from a structurally inappropriate model. Values of $\hat{c}$ estimated for datasets presented in Chapters 6 and 8–10 were all relatively small (<1.5), possibly because the behavioural aspect of ‘catchability’ was removed for detection probabilities. These $\hat{c}$ values were used for two purposes: they multiplied variances and covariances of parameter estimates (leading to inflated standard errors in the face of overdispersion), and they were used in formal model comparisons to correct each calculated information criterion for extra-binomial variation (see below).

**Predicting detection probability at terminal stations**
The final segment $\phi$ is confounded with $p$ at the terminal station in classic CJS models because there is no more distant location at which the ratio of detected to undetected tags can be assessed. There is no reliable detection information after the outer QCS and JDF stations with which to tease apart these confounded parameters, unless a value is assumed for one or the other. Because of limited detection stations in the ocean and the importance of the final segment (in some cases, the only ocean segment) to inferences of early ocean survival (Chapters 8–10), I assumed a fixed value for $p_{\text{final}}$ in order to estimate $\phi_{\text{final}}$. This assumption carries the risk of mis-estimating $\phi_{\text{final}}$ if the fixed value of $p_{\text{final}}$ is incorrect. Determining values of $p_{\text{final}}$ to assume as fixed values involved two main steps: (1) accurately estimating $p$ on other ocean lines; and (2) using these values to predict $p$ for the terminal ocean lines, adjusting for slight differences in line geometry. Because of the risk involved with this approach, I evaluated the sensitivity of early ocean survival estimates to values assumed for $p_{\text{final}}$.

(a) Isolated detection probability analysis at NSOG and HS stations: To estimate $p$ at inner ocean stations (NSOG, HS$_{\text{inner}}$, HS$_{\text{outer}}$) as accurately as possible, I constructed a shortened detection history of tags with digits for release, the station(s) of interest, and detection at all later stations combined. To estimate $p_{\text{NSOG}}$, populations that originated south of NSOG and migrated north were included in a 3-digit dataset (detections at JDF were not paired with QCS in this case, to avoid confounding $p_{\text{NSOG}}$ with the probability of southward movement after entering Georgia Strait; Chapter 3.4). To estimate $p_{\text{HS}_{\text{inner}}}$ and $p_{\text{HS}_{\text{outer}}}$, populations that originated from the Squamish River watershed were included in a 4-digit dataset. These shortened detection history versions reduced the dependence of $\hat{p}$ and uncertainty in $\hat{p}$ on parameters from other segments and detection stations. For each of these datasets, several candidate models for $p$ were considered while the $\phi$ model assumed full independence between segments and groups (including tag type) to be as flexible as possible, i.e., $\phi_{\text{Segment} \times (\text{Group}/\text{TagType})}$. All models for $p$ assumed full independence between station and year. The best $p$ model overall in terms of 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 A.4). 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 stations (like 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 30–90 s were included in the analysis since the delay between transmissions should affect $p$ in theory.

The sample size of V7 tags detected at and after NSOG was insufficient to estimate $p_{V7,NSOG}$, even when all years were pooled (this is why the effect of tag type was less important at NSOG in Table A.4). I assumed that the relative difference in $p$ between V7 and V9 tags (i.e., the intercept difference between parallel slopes in logit space) assessed at HS stations from the other dataset also held for the NSOG station. A simple regression between $\hat{p}_{V7,HS,year}$ and $\hat{p}_{V9,HS,year}$ was performed in logit space. The regression slope and intercept parameters were used to infer reasonable values of $\text{logit}(\hat{p}_{V7,NSOG,year})$ from $\text{logit}(\hat{p}_{V9,NSOG,year})$, after which values were back-transformed to the probability scale. Isolated $\hat{p}$ for these receiver stations, tag types, and years are shown in Fig. A.6a.

(b) Predicting detection probability at QCS and JDF stations: At terminal detection stations, $p_{QCS}$ and $p_{JDF}$ are not estimable with mark-recapture methods, but I assume they are similar to $\hat{p}_{NSOG}$. These three receiver lines experience similar oceanographic conditions and are deployed at similar depths, so I expect a similar probability of detecting a tag as it crosses the station. Nevertheless, these receiver lines do differ slightly in terms of geometry, or the average spacing between receivers and the proportion of receivers successfully recovered, so I accounted for these differences in making predictions of $p_{QCS}$ and $p_{JDF}$.

Using $\hat{p}_{NSOG}$, $\hat{p}_{HS,in}$, and $\hat{p}_{HS,out}$ for each of the two tag types derived from the isolated $p$ analysis, I used multiple regression to model $\hat{p}$ as a function of one or more line geometry covariates. These covariates included mean horizontal spacing between receivers on a line, mean deployment depth, the proportion of receivers recovered and successfully downloaded, and the proportion of coverage on a line under an assumed value of receiver detection range (e.g., if a detection range of 400 m is assumed for all receivers on a line, what fraction of the one-dimensional receiver line is covered by the radius of at least one receiver?; Chapter 3.6). Detection ranges of 300, 350, 400, 450, 500, and 550 m were considered for these ‘proportion of coverage’ covariates, with longer assumed detection ranges (e.g., 450–550 m) implying greater coverage on the line, and shorter assumed detection ranges (e.g., 300–350 m) implying a lower proportion of coverage across the entire line (Figure 3.7). 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, I
also considered a main effect for receiver station, hypothesizing that possible differences in local noise conditions among inner ocean stations could result in overall differences in \( p \).

For each tag type and year, \( \hat{p}_{NSOG}, \hat{p}_{HS, in}, \) and \( \hat{p}_{HS, out} \) were logit-transformed for the regression. The candidate regression models were ranked in terms of AIC and adjusted \( r^2 \) values. 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 \( r^2 = 0.28 \) for V9 tags and 0.23 for V7 tags when regressed separately). A similar model containing an additive ‘station’ effect had less support in the data (\( \Delta \text{AIC} = 2.9 \)), but did admit more uncertainty in the predictions. To be more conservative, I assumed this model, \( \hat{p} \sim \text{TagType} + \text{station} + \text{cover}_{400} \), for predicting \( p_{QCS} \) and \( p_{JDF} \) even though the station effect was weak. This simply suggests that after accounting for variation in \( \hat{p} \) due to \text{cover}_{400}, there was little further explanatory power in a geographical effect, which strengthens the assertion that \( p_{QCS} \) and \( p_{JDF} \) can be reasonably predicted from \( \hat{p} \) at stations in other geographic areas. The \text{cover}_{400} effect allowed for \( p_{QCS} \) and \( p_{JDF} \) predictions to be specific to those terminal stations by using their specific \text{cover}_{400} covariate values in the regression relationship established for the other stations. The station effect value for NSOG was assumed for QCS and JDF, i.e., \( \hat{p}_{QCS} \sim \text{TagType} + \text{stationNSOG} + \text{cover}_{400,QCS} \). Values of logit(\( \hat{p}_{QCS} \)) and logit(\( \hat{p}_{JDF} \)) were generated for each year and tag type since line geometry varied slightly 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: (1) the maximum of yearly \( \hat{SE}(\hat{p}_{NSOG}) \) using the reduced-digit CJS model (i.e., uncertainty in \( \hat{p} \) due to binomial probabilities at limited sample sizes and uncertainty in survival, assumed to be similar among NSOG, QCS, and JDF stations); and (2) uncertainty in \( p_{QCS} \) and \( p_{JDF} \) predictions associated with the regression against \text{cover}_{400} (i.e., uncertainty in \( \hat{p} \) due to differences in line geometry among lines and years). The 95% confidence limits for the first component were estimated with profile likelihoods in logit space, using Program MARK (White and Burnham 1999). The largest of the resulting variances over the four years (range, 0.153–0.194 in logit space) was used to be conservative. For the second (and usually smaller) component, \( \hat{SE}(\hat{p}_{QCS}) \) and \( \hat{SE}(\hat{p}_{JDF}) \) 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 at QCS and JDF were pooled in the final digit of the detection history to represent exit from the Georgia Strait system, so a combined prediction of \( p, \hat{p}_{QCS/JDF} \), is required for these outer lines. 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 stations (the number of tags detected at a station divided by \( \hat{p} \) for that station, year, and tag type). The same approach was used for combined estimates of upper and lower 95% confidence limits of \( \hat{p}_{QCS/JDF} \). Predictions of \( p \) for both terminal stations as well as their combined estimate are shown in Fig. A.6b.

To quantify the uncertainty in early ocean \( \hat{\phi} \) associated with assuming a fixed value for \( p_{QCS/JDF} \), the uncertainty of this final \( \hat{p} \) was taken into account. Mark-recapture models were fit to detection data for both Fraser and non-Fraser datasets (Chapter 9), but rather than assuming only \( \hat{p}_{QCS/JDF} \), the approximate 95% confidence limits of \( \hat{p}_{QCS/JDF} \) were also assumed as fixed values. Fixing \( \hat{p}_{\text{final}} \) to the upper 95% CL results in a lower \( \hat{\phi}_{\text{final}} \), and fixing \( \hat{p}_{\text{final}} \) to the lower 95% CL 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 (downstream+inshore) survival estimate. This error is additional to the mark-recapture error estimated with fixed values of \( \hat{p}_{QCS/JDF} \) at the final stations; both types of error are presented in Chapter 9.

A.4.4 Model selection methods

“…in our view, the starting point for all analyses in the new statistics is the formulation of a set of models representing multiple competing hypotheses about the way ecological systems work.”

\&

“…the foundation of the new statistics in ecology is built from the ability of ecologists to represent testable ideas as mathematical models.”

(Hobbs and Hilborn 2006)

Model selection criteria can be used as an objective means of assessing how complex a model data support. Information-theoretic approaches are based on quantifying the information lost when a model is used to approximate the ‘truth’, i.e., a real-world phenomenon with an unknown number of sources of variation. This amount of information loss between a model approximation and ‘truth’ is known as the Kullback-Leibler distance (Kullback and Leibler 1951). The expected value of the relative K-L distance, known as Akaike’s Information Criterion (AIC), can be estimated without explicitly knowing ‘truth’ (Akaike 1973):
The first term, \(2 \times \text{the negative log-likelihood}\), represents the model deviance, or a measure of lack of fit to data. \(L\) is the likelihood of the model given the data at the maximum likelihood estimates of model parameters, \(\hat{\theta}\). \(k\) is the number of parameters in the model. This linkage of information theory and likelihood theory provides a means to evaluate the strength of evidence in the data for competing candidate models. AIC is lower under lower negative log-likelihoods (better fits of the model to data) or lower \(k\). Models with lower values of AIC are considered more parsimonious: they are preferred in a balance of goodness-of-fit and the number of parameters required to achieve that fit.

This approach seeks to find a data-supported balance between possibilities of over-fitting an overly complex model to data (at the expense of precision of parameter estimates and the risk of spurious results) and under-fitting (at the risk of failing to capture real sources of variation in the data). AIC can be modified to correct for small sample sizes:

\[
(A.2) \quad \text{AIC}_c = \text{AIC} + \frac{2k(k+1)}{n-k-1},
\]

where \(n\) is the effective sample size of the data. In mark-recapture analyses, \(n\) is generally obtained by summing the releases over all time periods (Burnham et al. 1994, Williams et al. 2002: 432), or in the spatial migration case, summing the number of tags detected at a station over all stations. This \(\text{AIC}_c\) correction downweights complex models when sample sizes are small, leading to simpler models being selected; this tends to hold in mark-recapture models over a wide range of parameter values, \(n\), and recapture occasions (Burnham et al. 1994). As \(n\) increases (\(\text{AIC}_c \rightarrow \text{AIC}\) as \(n \rightarrow \infty\)), more complex models may be selected if justified by variation in the data. The criterion can also be modified to correct for overdispersion (or extra-binomial variation) in count data (Lebreton et al. 1992) using a quasi-likelihood approach:

\[
(A.3) \quad \text{QAIC}_c = \frac{-2 \ln \left( L(\hat{\theta}|\text{data}) \right)}{c} + 2k + \frac{2k(k+1)}{n-k-1},
\]

where \(c\) is a variance inflation factor. As detection data become increasingly overdispersed, \(c\) and therefore QAICc increases. The likelihood term becomes smaller and the term for the number of
parameters begins to dominate. As a result, overdispersion in the data tends to favour less complex models when $c$ is accounted for. When multiple models are considered, $c$ is typically estimated for the largest, or most general of them, and applied to all models in the model set.

In the last decade, the use of AIC in ecology has been popularized by Burnham and Anderson (2002). Proponents of the approach (and other likelihood-based approaches of data analysis) claim that ecology is under a paradigm shift away from null hypothesis testing towards a competition among multiple alternative hypotheses, arbitrated by data (Burnham and Anderson 2002, Johnson and Omland 2004, Hobbs and Hilborn 2006). Critics of the approach object to its use for a variety of reasons, mainly because AIC-selected models do not necessarily represent the best model in terms of ecological reality (Guthery et al. 2005) or appropriate ensuing policy options, and also because AIC tends to select an overly-parameterized model (Kass and Raftery 1995, Link and Barker 2006) compared with other model selection criteria like Bayesian Information Criterion (BIC; Schwarz 1978), Deviance Information Criterion (DIC; Spiegelhalter et al. 2002), or likelihood ratio tests. In models where overdispersion is not accounted for, AIC-best models may indeed be over-parameterized if data are overdispersed (Anderson et al. 1994). Mark-recapture models, however, may be better-suited for model selection comparisons using AIC since $c$ can generally be estimated easily, and QAIC can be used instead of AIC. Extensive simulation testing with open-population CJS models has shown that QAIC performs well in the face of overdispersed data. QAICc has a good balance between under-fitting and over-fitting recapture data across a wide range of simulated values of $c$, $\phi$, $p$, $n$, and number of recapture occasions, even when models are fit to large, interrelated datasets (Anderson et al. 1994, Richards 2008). In simulation studies fitting CJS mark-recapture models to simulated (not overdispersed) data, AICc approaches to model selection outperformed likelihood ratio tests by consistently selecting models with a smaller residual sum of squares between estimated and ‘true’ model parameter values (Burnham et al. 1995). In other simulation studies, estimation models that incorporated individual heterogeneity in survival or detection probabilities generated unbiased estimates $\hat{\phi}$ and $\hat{p}$ whether or not simulated datasets involved heterogeneity (Zabel et al. 2005).

Multiple candidate models representing hypotheses about sources of variation in survival and detection probabilities are compared on the basis of calculated QAICc values. Comparison of a small, carefully-considered set of candidate models is preferred to all-possible-subset approaches or other forms of data dredging (Burnham and Anderson 2002). Typically there are umbrella hypotheses represented by models (e.g., body size contributes to variation in survival),
and within these there are sub-hypotheses about the form of the relationship (e.g., the effect of body size on survival is additive across all species and detection stations, or there is an interaction of body size and tag size on survival). Since there are often several umbrella hypotheses for survival probabilities (e.g., effects of body size, release date, rearing history, experimental treatment, and distance of migration segments) and others for detection probabilities (e.g., effects of tag size, river flow), this can lead to model sets containing hundreds of models if the above combinations of effects are considered. This clearly violates recommendations for a small set of carefully-hypothesized models (even if the umbrella hypotheses and sub-hypotheses were carefully considered) and also a large set of models may not be supported by tag sample sizes. An alternative is to use a sequential approach of model comparisons (e.g., Lebreton et al. 1992, Zabel and Achord 2004, Keeler et al. 2007). For example, detection probability sub-models can be first be compared assuming a general sub-model for survival. Next, the QAICc-selected sub-model for \( p \) can be held constant to compare candidate sub-models for survival. I employed this strategy throughout Chapters 8–10, using multiple sequential steps for survival probability sub-models in order to maintain a small number of models compared overall. I did not employ model averaging (Burnham and Anderson 2002) in this thesis, so the potential for underestimating model selection uncertainty in each sequential set of models compared is a relatively minor issue.

QAICc values are determined objectively, but interpretation of a set of compared models does carry with it some degree of subjectivity. Several ‘rules-of-thumb’ have been developed through experience (Burnham and Anderson 2002) to help guide model selection procedures. Within a model set, QAICc values for models \( i \) are re-scaled as differences to the lowest value in the model set, permitting comparisons of \( \Delta \text{QAICc} (= \text{QAICc}_i - \text{QAICc}_{\text{min}}) \). Models with \( \Delta \text{QAICc} \) within 0–2 of the best model have substantial support and should be considered when making inferences. Models with \( \Delta \text{QAICc} \) within about 4–7 of the best model have some degree of support in the data, and models with \( \Delta \text{QAICc} > 10 \) have essentially no support within the model set and are likely either over-fit (too many unjustifiable parameters) or under-fit (poor goodness-of-fit). One important exception is that if two nested models differ by a single parameter and the larger model has QAICc \( \approx 2 \) higher than the simpler model, there is essentially no support for the larger model (it does not much improve goodness-of-fit, and the ‘penalty’ for the extra parameter is the expected difference of \( \approx 2 \)). Aside from AIC scores, to evaluate alternative models, coefficients and parameter estimates are routinely inspected to make sure that confounding between parameters or covariates is not strong, which could lead to spurious results.
Table A.1. Watersheds in which salmon smolts were tagged and released under POST in 2003–2008 studies. Data are drawn from Ahrens (2004), the Water Survey of Canada (Environment Canada), and the B.C. Watersheds Database.

<table>
<thead>
<tr>
<th>Region</th>
<th>Tagging watershed</th>
<th>Stream order</th>
<th>Drainage area (km²)</th>
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<th>Anadromous length (km) a</th>
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a Anadromous length includes the portion accessible to anadromous fish, including tributaries and excluding waters upstream of barriers like waterfalls.

b Cultus Lake drains into Sweltzer Creek, which drains into the Vedder River.
Table A.2. Southern British Columbia salmon smolt populations tagged under POST from 2003–2007 and included in the multi-stock survival analysis in Chapter 9. Species abbreviations: Chnk, Chinook; Kok, kokanee; Sock, sockeye; Sth, steelhead. Rearing history abbreviations: H, hatchery-reared; W, wild-caught without an adipose fin clipped so presumed wild; UN, unknown provenance since wild-caught but with unclipped hatchery fish released upstream. \( n \) = number of smolts tagged and released. FL = fork length, in mm. Release times are Pacific daylight savings times. FW dist = distance from release point to river mouth (or lowest in-river receiver). Letters in the last column correspond to release locations on the map in Fig. 1.4.

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<th>Watershed</th>
<th>Species</th>
<th>H/W</th>
<th>Year</th>
<th>( n )</th>
<th>Mean FL ± SD (Range)</th>
<th>Release date(s) (( n ))</th>
<th>Tag type(s) (( n ))</th>
<th>FW dist (km)</th>
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<td>Chnk</td>
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<td>V7-2L</td>
<td>407.1</td>
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<th>Release date(s) (n)</th>
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</tr>
<tr>
<td>Sakinaw Lake</td>
<td>Sock</td>
<td>H</td>
<td>2006</td>
<td>62</td>
<td>213.4 ± 11.5 (170 – 239)</td>
<td>Jun 02 21:15</td>
<td>V9–1L (50), V9–6L (12)</td>
<td>NA</td>
<td>Ocean release</td>
<td>N</td>
</tr>
<tr>
<td>Seymour River</td>
<td>Sth</td>
<td>H</td>
<td>2007</td>
<td>60</td>
<td>185.9 ± 12.6 (160 – 224)</td>
<td>Apr 27 15:15 (20), May 08 14:50 (20), May 15 12:00 (20)</td>
<td>V9–6L</td>
<td>1.2</td>
<td>Summer run (30), Winter run (30)</td>
<td>J</td>
</tr>
</tbody>
</table>

East coast Vancouver Island

<p>| Cowichan River  | Sth     | H   | 2006 | 50  | 177.8 ± 13.8 (156 – 200) | May 09 15:10      | V9–6L             | 1.6          | O            |
| Englishman River| Sth     | W   | 2005 | 43  | 159.4 ± 14.8 (133 – 196) | May 13 21:00 (11), May 18 21:30 (12), May 19 19:00 (14), May 23 11:30 (6) | V9–6L             | 2.3          | P            |
| Englishman River| Sth     | W   | 2006 | 50  | 168.7 ± 12.5 (149 – 206) | May 03 17:00 (8), May 04 21:00 (6), May 05 21:00 (16), May 07 21:00 (20) | V9–6L             | 1.6          | P            |</p>
<table>
<thead>
<tr>
<th>Watershed</th>
<th>Species</th>
<th>H/W</th>
<th>Year</th>
<th>n</th>
<th>Mean FL ± SD (Range)</th>
<th>Release date(s) (n)</th>
<th>Tag type(s) (n)</th>
<th>FW dist (km)</th>
<th>Treatment(s)</th>
<th>Letter on map</th>
</tr>
</thead>
<tbody>
<tr>
<td>Keogh River</td>
<td>Coho</td>
<td>W</td>
<td>2004</td>
<td>107</td>
<td>154.6 ± 6.8 (139 – 173)</td>
<td>May 27 09:30 (37), May 27 22:00 (40), May 28 22:00 (30)</td>
<td>V9-6L</td>
<td>0.8</td>
<td></td>
<td>T</td>
</tr>
<tr>
<td>Keogh River</td>
<td>Coho</td>
<td>W</td>
<td>2005</td>
<td>49</td>
<td>157.5 ± 10.5 (143 – 183)</td>
<td>May 01 19:30</td>
<td>V9-6L</td>
<td>0.8</td>
<td></td>
<td>T</td>
</tr>
<tr>
<td>Keogh River</td>
<td>Coho</td>
<td>W</td>
<td>2006</td>
<td>50</td>
<td>152.4 ± 18.6 (140 – 240)</td>
<td>May 07 19:30 (20), May 10 21:00 (30)</td>
<td>V9-6L</td>
<td>0.8</td>
<td></td>
<td>T</td>
</tr>
<tr>
<td>Keogh River</td>
<td>Sth</td>
<td>H</td>
<td>2004</td>
<td>92</td>
<td>188 ± 18.4 (150 – 231)</td>
<td>May 17 16:00 (50), May 19 11:00 (42)</td>
<td>V9-6L</td>
<td>0.8</td>
<td></td>
<td>T</td>
</tr>
<tr>
<td>Keogh River</td>
<td>Sth</td>
<td>H</td>
<td>2005</td>
<td>50</td>
<td>204 ± 14.7 (163 – 247)</td>
<td>May 25 16:00</td>
<td>V9-6L</td>
<td>0.8</td>
<td></td>
<td>T</td>
</tr>
<tr>
<td>Keogh River</td>
<td>Sth</td>
<td>W</td>
<td>2004</td>
<td>78</td>
<td>174.6 ± 20 (147 – 250)</td>
<td>May 27 09:30 (25), May 27 22:00 (8), May 28 22:00 (13), May 29 22:00 (9), Jun 04 22:00 (23)</td>
<td>V9-6L</td>
<td>0.8</td>
<td></td>
<td>T</td>
</tr>
<tr>
<td>Keogh River</td>
<td>Sth</td>
<td>W</td>
<td>2006</td>
<td>50</td>
<td>184 ± 17.1 (159 – 232)</td>
<td>May 31 19:30</td>
<td>V9-6L</td>
<td>0.8</td>
<td></td>
<td>T</td>
</tr>
<tr>
<td>Nimpkish River</td>
<td>Chnk</td>
<td>UN</td>
<td>2006</td>
<td>50</td>
<td>139 ± 9.6 (126 – 171)</td>
<td>May 08 19:00</td>
<td>V7-2L</td>
<td>8.3</td>
<td></td>
<td>R</td>
</tr>
<tr>
<td>Nimpkish River</td>
<td>Coho</td>
<td>H</td>
<td>2004</td>
<td>99</td>
<td>140.6 ± 4.2 (125 – 151)</td>
<td>Apr 28 18:00 (2), Jun 14 15:30 (97)</td>
<td>V9-6L</td>
<td>61.7</td>
<td></td>
<td>S</td>
</tr>
<tr>
<td>Nimpkish River</td>
<td>Coho</td>
<td>H</td>
<td>2005</td>
<td>57</td>
<td>130.9 ± 7 (122 – 149)</td>
<td>Jun 17 16:00</td>
<td>V7-2L (49), V9-6L (8)</td>
<td>62.8</td>
<td></td>
<td>S</td>
</tr>
<tr>
<td>Nimpkish River</td>
<td>Coho</td>
<td>W</td>
<td>2006</td>
<td>50</td>
<td>145.9 ± 4.8 (140 – 165)</td>
<td>May 11 16:20</td>
<td>V9-6L</td>
<td>62.8</td>
<td></td>
<td>S</td>
</tr>
</tbody>
</table>
Table A.3. Southern British Columbia salmon smolt populations tagged under POST from 2003–2008 but not included in the multi-stock survival analysis in Chapter 9. See Table A.2 for symbols.

<table>
<thead>
<tr>
<th>Watershed</th>
<th>Species</th>
<th>H/W</th>
<th>Year</th>
<th>n</th>
<th>Mean FL ± SD (Range)</th>
<th>Release date(s) (n)</th>
<th>Tag type(s) (n)</th>
<th>Treatment(s)</th>
<th>Letter on map</th>
<th>Reason for excluding</th>
</tr>
</thead>
<tbody>
<tr>
<td>Middle Fraser River</td>
<td>Coldwater River</td>
<td>Chnk UN</td>
<td>2004</td>
<td>2</td>
<td>137.5 ± 7.8 (132 – 143)</td>
<td>May 07 20:00</td>
<td>V9-6L</td>
<td>B</td>
<td>Small n</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Coldwater River</td>
<td>Chnk W</td>
<td>2004</td>
<td>2</td>
<td>135 ± 9.9 (128 – 142)</td>
<td>May 15 20:00</td>
<td>V9-6L</td>
<td>B</td>
<td>Small n</td>
<td></td>
</tr>
<tr>
<td>Lower Fraser River</td>
<td>Alouette River</td>
<td>Sock W</td>
<td>2005</td>
<td>19</td>
<td>129.4 ± 5.4 (122 – 142)</td>
<td>Aug 09 21:30</td>
<td>V7-2L</td>
<td>H</td>
<td>Small n and late release</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Coquitlam Lake</td>
<td>Coho H</td>
<td>2005</td>
<td>117</td>
<td>127.9 ± 6 (120 – 150)</td>
<td>Apr 15 10:22 (24), Apr 22 08:30 (24), Apr 29 08:30 (24), May 06 09:30 (30), May 13 09:22 (15)</td>
<td>V7-2L</td>
<td>I</td>
<td>Non-migrant a</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Cultus Lake</td>
<td>Sock H</td>
<td>2005</td>
<td>90</td>
<td>184.8 ± 9.6 (164 – 212)</td>
<td>May 31 19:30 (14), Jun 06 19:30 (76)</td>
<td>V9–1L (25), V9–2L (61), V9–6L (4)</td>
<td>G</td>
<td>Suspected poor physical condition b</td>
<td></td>
</tr>
<tr>
<td>South coast</td>
<td>Cheakamus River</td>
<td>Sth H</td>
<td>2008</td>
<td>58</td>
<td>185.1 ± 12.7 (155 – 206)</td>
<td>May 08 11:17 (40), May 22 09:37 (18)</td>
<td>V9-6L</td>
<td>FVTH c</td>
<td>K, M</td>
<td>Intervals 20–60 s, only population in 2008</td>
</tr>
<tr>
<td></td>
<td>Cheakamus River</td>
<td>Sth H</td>
<td>2008</td>
<td>40</td>
<td>176.7 ± 8.7 (158 – 192)</td>
<td>May 05 16:00</td>
<td>V9-6L</td>
<td>TCH d</td>
<td>L</td>
<td>Intervals 20–60 s, only population in 2008</td>
</tr>
<tr>
<td></td>
<td>Cheakamus River</td>
<td>Sth W</td>
<td>2008</td>
<td>100</td>
<td>177.9 ± 11.9 (149 – 209)</td>
<td>May 06 19:30 (72), May 12 20:30 (28)</td>
<td>V9-6L</td>
<td>M</td>
<td>Intervals 20–60 s (81) and 20–40 (19), only population in 2008</td>
<td></td>
</tr>
<tr>
<td>Watershed</td>
<td>Species</td>
<td>H/W</td>
<td>Year</td>
<td>n</td>
<td>Mean FL ± SD</td>
<td>Release date(s)</td>
<td>Tag type(s)</td>
<td>Treatment(s)</td>
<td>Letter on map</td>
<td>Reason for excluding</td>
</tr>
<tr>
<td>------------------------</td>
<td>---------</td>
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<td>-------------</td>
<td>--------------</td>
<td>--------------</td>
<td>---------------------------------------------</td>
</tr>
<tr>
<td>Tenderfoot Creek</td>
<td>Coho</td>
<td>H</td>
<td>2003</td>
<td>15</td>
<td>142 ± 14.7</td>
<td>May 19 16:00</td>
<td>V9-6L</td>
<td></td>
<td>L</td>
<td>Intervals 10–30 s, only population in 2003, no sampling beyond Howe Sound</td>
</tr>
<tr>
<td>Sakinaw Lake</td>
<td>Kok</td>
<td>W</td>
<td>2005</td>
<td>24</td>
<td>224.8 ± 7.7</td>
<td>Nov 11 16:15 (6),</td>
<td>V9-6L</td>
<td></td>
<td>N</td>
<td>Late release</td>
</tr>
<tr>
<td>Seymour River</td>
<td>Sth</td>
<td>H</td>
<td>2006</td>
<td>50</td>
<td>207.4 ± 16.2</td>
<td>May 09 21:45 (25),</td>
<td>V9–1H</td>
<td>Summer/day (13), Summer/night (13), Winter/day (12), Winter/night (12)</td>
<td>J</td>
<td>High acoustic power tags</td>
</tr>
<tr>
<td>East coast Vancouver Island</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Big Qualicum River</td>
<td>Coho</td>
<td>H</td>
<td>2004</td>
<td>96</td>
<td>137.8 ± 6.4</td>
<td>May 26 13:30</td>
<td>V9-6L</td>
<td></td>
<td>Q</td>
<td>Suspected poor physical condition</td>
</tr>
<tr>
<td>Nimpkish River</td>
<td>Sth</td>
<td>H</td>
<td>2004</td>
<td>1</td>
<td>138 ± 0</td>
<td>Apr 28 18:00</td>
<td>V9-6L</td>
<td></td>
<td>S</td>
<td>Rather a small n</td>
</tr>
<tr>
<td>West coast Vancouver Island</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Stamp River</td>
<td>Coho</td>
<td>H</td>
<td>2005</td>
<td>100</td>
<td>146.7 ± 5</td>
<td>May 23 17:00</td>
<td>V9-6L</td>
<td></td>
<td>U</td>
<td>Outer coast, no river receivers or reliable ocean stations</td>
</tr>
</tbody>
</table>

a This population did not emigrate from Coquitlam Reservoir, likely a result of B.C. Hydro operations limiting fish passage.
b Smolts from these two release groups were the sole survivors of an overnight power outage at the hatchery, and were suspected to have suffered severe oxygen deprivation. The third group, not affected by the power outage, was included in the analysis.

c Reared at Fraser Valley Trout Hatchery, released in Cheakamus River at upstream location (n = 40) and downstream location (n = 18).
d Reared and released at Tenderfoot Creek Hatchery.
e Released in four experimental groups, with crossed combinations of summer run or winter run steelhead, and daytime release or night-time release.
f Fish from this hatchery population suffered from signs of disease: scoliosis, saddle back, and fungus. This hatchery also had a known history of bacterial kidney disease.
Table A.4. Comparison of detection probability sub-models for isolated estimation of \( p \) at Howe Sound and northern Strait of Georgia stations.

<table>
<thead>
<tr>
<th>Detection probability model(^a)</th>
<th>( k )</th>
<th>(-2 \cdot \ln(L))</th>
<th>AICc</th>
<th>( \Delta \text{AICc} )</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Howe Sound dataset</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>( p_{\text{Station} \times \text{Year} + \text{TagType}} )</td>
<td>43</td>
<td>1645.4</td>
<td>1734.7</td>
<td>0.0</td>
</tr>
<tr>
<td>( p_{\text{Station} \times \text{Year}} )</td>
<td>42</td>
<td>1657.1</td>
<td>1744.3</td>
<td>9.6</td>
</tr>
<tr>
<td>( p_{\text{Station} \times (\text{Year:Species:Population} + \text{TagType})} )</td>
<td>58</td>
<td>1636.7</td>
<td>1758.8</td>
<td>24.1</td>
</tr>
<tr>
<td>( p_{\text{Station} \times (\text{Group:TagType})} )</td>
<td>60</td>
<td>1632.8</td>
<td>1759.4</td>
<td>24.7</td>
</tr>
<tr>
<td>( p_{\text{Station} \times (\text{Year:Species:Population})} )</td>
<td>57</td>
<td>1644.8</td>
<td>1764.8</td>
<td>30.1</td>
</tr>
<tr>
<td><strong>NSOG dataset</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>( p_{\text{Station} \times \text{Year}} )</td>
<td>104</td>
<td>3434.6</td>
<td>3648.3</td>
<td>0.0</td>
</tr>
<tr>
<td>( p_{\text{Station} \times \text{Year} + \text{TagType}} )</td>
<td>105</td>
<td>3434.4</td>
<td>3650.2</td>
<td>1.9</td>
</tr>
<tr>
<td>( p_{\text{Station} \times (\text{Year:Species:Population} + \text{TagType})} )</td>
<td>181</td>
<td>3404.1</td>
<td>3783.5</td>
<td>135.3</td>
</tr>
<tr>
<td>( p_{\text{Station} \times (\text{Year:Species:Population})} )</td>
<td>180</td>
<td>3407.1</td>
<td>3784.3</td>
<td>136.0</td>
</tr>
<tr>
<td>( p_{\text{Station} \times (\text{Group:TagType})} )</td>
<td>192</td>
<td>3404.1</td>
<td>3807.8</td>
<td>159.5</td>
</tr>
</tbody>
</table>

\(^a\) The survival probability sub-model assumed was \( \phi_{\text{Segment} \times (\text{Group:TagType})} \).
Figure A.1. Frequency distributions of body lengths of tagged B.C. salmon smolts. Data are shown combining populations listed in Tables A.2 and A.3, and separated by tag type. The lower x-axis shows fork lengths and the upper x-axis shows the corresponding tag length to body length ratios for V7 tags (20 x 7 mm) and V9 tags (21 x 9 mm). Red dashed lines show the tag-to-body length ratio of 16% recommended by Lacroix et al. (2004).
Figure A.2. Tag battery duration monitoring experiment conducted with VEMCO V7-2L tags. Each horizontal series represents one tag, with circle outlines showing the days where it was monitored. Circles are filled on the days when the tag was detected: red, if the tag was always detected on monitoring days prior to the expected tag battery life (blue dashed lines), and black, if the tag was not detected on at least one monitoring day prior to expected battery life. Tag groups are: (A) average 45 s delay intervals, monitored in 2008; (B) average 60 s intervals, monitored in 2008; (C) average 60 s intervals, monitored in 2009 (ongoing); and (D) average 90 s intervals, monitored in 2009 (ongoing). Three tags were returned to VEMCO after failure, but the cause was not determined. Raw data were provided by Kintama Research Corp.
Figure A.3. Characteristics of five ocean receiver stations deployed in 2004–2007. (a) Proportion of deployed receivers that were recovered and successfully downloaded. (b) Average horizontal spacing between adjacent recovered receivers. (c) Average depth below surface of recovered receivers.
Figure A.4. Decision tree used for scanning for false detections of B.C. tagged salmon smolts. SUSPECT SEQUENCE: the suspect detection(s) breaks the spatio-temporal migration sequence of that fish, i.e., the detection is ‘out of order’ along the migration. SINGLE: there was only a single detection of the suspect code at the station in question within 60 min before or after the detection. SUSPECT TIME: the time from fish release to the suspect detection(s) at the station in question is outside the 95% confidence limits of travel times for the rest of the population. HIGH TRAFFIC: there were $\geq 1$ other tag codes detected on the receiver in question within 10 min before or after the detection.
Figure A.5. Three hypothetical models in which survival varies with fish body length, and in which there is also either a common (a,b), an additive (c,d), or a multiplicative (e,f) effect of tag size on survival. Estimates of survival are shown both in logit-space (a, c, e) and probability space (b, d, f).
Figure A.6. Detection probability estimates (a) and predictions (b) at ocean receiver stations for two tag types. Estimates in (a) are from isolated analyses with reduced detection history digits, and 95% confidence limit error bars are from profile likelihoods with standard mark-recapture statistics. Predictions in (b) are made based on the estimates in (a) and adjusted for variation in line geometry among years and stations in a regression model. Approximate 95% c.l. error bars in (b) combine mark-recapture uncertainty and regression uncertainty associated with the prediction.
A.5 References


Appendix B  Pseudocode for constructing a sequence of detections and missed emissions

This appendix relates to Chapter 4. Consider the following detections of two tags at a receiver station, arranged in chronological order:

- tag 555, 25-05-2004, 16:49:02
- tag 555, 25-05-2004, 16:50:54
- tag 555, 25-05-2004, 16:51:38
- tag 555, 25-05-2004, 16:56:17
- tag 2222, 25-05-2004, 17:30:12

The goal is to construct the most likely sequence of ‘1’s and ‘0’s representing detections and missed transmissions of tag 555 during this time period.

______________________________

Define variables:

- \( r \)  
  average repeat rate, or time between the start of successive transmissions (62 s)
- \( cut \)  
  threshold for parsing detection data into separate crossing sequences (60 min)
- \( i \)  
  row index, start with 1

1) Read in tag code, and (date+time), from row \( i \) of detection times and assign this detection a corresponding ‘1’ in a crossing sequence

2) If tag code\(_{i+1}\) on row \( i+1 \) is the same, calculate \( \Delta \text{time} = (\text{date+time})_{i+1} - (\text{date+time})_i \)
   If tag code\(_{i+1}\) on row \( i+1 \) is not the same, end sequence.

3) If \( \Delta \text{time} < cut \), construct a hypothetical sequence of transmission times beginning with \( (\text{date+time})_i \) and incrementing by \( r \)

4) Find the closest match between \( (\text{date+time})_{i+1} \) and all possible times in the hypothetical transmission sequence, and assign a ‘1’ in the crossing sequence corresponding to this best-matched time in the transmission sequence

5) Reset this best-matched time in the transmission sequence to \( (\text{date+time})_{i+1} \)

6) Assign a ‘0’ in the crossing sequence corresponding to all hypothetical transmission times between \( (\text{date+time})_i \) and \( (\text{date+time})_{i+1} \)

7) Increase \( i \) by 1 and go to #1

______________________________
**Results:**

<table>
<thead>
<tr>
<th>Detection time</th>
<th>Hypothetical transmission time</th>
<th>Crossing sequence</th>
</tr>
</thead>
</table>

Boldfaced hypothetical transmission times are those that were reset to the actual detection time after the process of finding a closest match. We can calculate $n$ as the number of detections of a tag crossing a station during a crossing event, and $m$ as the sequence length of the crossing event including both detections and missed transmissions. By definition $n \leq m$, and in this case, $n = 5$ and $m = 9$. For stations with multiple receivers, the detections from all receivers at the station would first be sorted in chronological order, all but one simultaneous detections on multiple receivers would be excluded, and the same procedure would then be followed. Finally, a large number of ‘0’s (e.g., 50–100) would be added to either end of the crossing sequence for numerical estimation purposes.
Appendix C  Alternate \( p_{\text{ping}} \) attenuation model descriptions and comparison

Four \( p_{\text{ping}} \) attenuation models are described below, which relate to Chapter 4. These models, along with \( [M_{\text{logit}} p_{\text{ping}}] \), are then compared using information-theoretic methods. General forms of the five models fit to an example crossing sequence are shown in Fig. 4.1.

C.1 Alternate model descriptions

(i) \( M_{\text{lin}} p_{\text{ping}} \)

This is a three-parameter model \( (p_{\text{max}}, x_c, b) \) that predicts a linear increase in \( p_{\text{ping}} \) from the early portion of \( X \) towards the centre point, \( x_c \):

\[
\begin{align*}
\text{C.1} & \quad p_{\text{ping},i} = p_{\text{max}} \left( \begin{cases} 
1 + b(X_i - x_c) & \text{if } X_i < x_c \\
1 - b(X_i - x_c) & \text{if } X_i > x_c 
\end{cases} \right).
\end{align*}
\]

At \( x_c \), \( p_{\text{ping}} = p_{\text{max}} \). A linear decrease is symmetrical about \( x_c \), with \( p_{\text{ping}} \) decreasing towards the later portion of \( X \). The slope of the increase in \( p_{\text{ping}} \) is \( b \) (and \( -b \) for the decrease in \( p_{\text{ping}} \)). Higher \( b \) implies a more rapid increase towards \( p_{\text{max}} \) and decrease away from \( p_{\text{max}} \). Typically, \( x_c \) occurs near the middle of \( X \), \( X_{m/2} \), although asymmetrical patterns of detections and missed signals can draw \( x_c \) to one side or another of \( X_{m/2} \). Constraints were placed on the parameters for numerical estimation purposes: \( 0.001 < p_{\text{max}} < 1 \); \( 0.01 < b < 200 \); \( X_1 < x_c < X_m \), where \( X_1 \) and \( X_m \) are the first and last values in \( X \) respectively. Additionally, \( p_{\text{ping},i} \) was constrained to be \( \epsilon \in (1.0 \times 10^{-9}, 0.999999999) \), which prevented negative values of predicted \( p_{\text{ping}} \) outside of \( X \) but within the range of the 50 ‘0’s to either side of \( X \).

(ii) \( M_{\text{norm}} p_{\text{ping}} \)

This is a three-parameter model \( (p_{\text{max}}, \mu, \sigma) \) that predicts a bell-shaped increase in \( p_{\text{ping}} \) from the early part of \( X \) towards \( \mu \) (the centre point, \( \mu \), is equivalent to \( x_c \) in the linear model, but typical notation for the normal probability distribution is used here):

\[
\begin{align*}
\text{C.2} & \quad p_{\text{ping},i} = p_{\text{max}} \left( \frac{1}{\sigma \sqrt{2\pi}} e^{-\frac{(X_i-\mu)^2}{2\sigma^2}} \right).
\end{align*}
\]

At \( \mu \), \( p_{\text{ping}} = p_{\text{max}} \). As \( X_i \) increases, the rate of increase in \( p_{\text{ping}} \) towards \( p_{\text{max}} \) at \( \mu \) or decrease in \( p_{\text{ping}} \) away from \( \mu \) is determined by the standard deviation of the normal curve, \( \sigma \). Similar to the
logistic model, lower values of $\sigma$ imply a more rapid change in $p_{\text{ping}}$ with change in $X_i$.
Constraints were placed on the parameters: $0.001 < p_{\text{max}} < 1$; $0.1 < \sigma$; $X_1 < \mu < X_m$. The normal probability density at $X_i$ was standardized by dividing this quantity by the normal density at $\mu$ so that the maximum standardized density of the curve was 1 before multiplication with $p_{\text{max}}$.

(iii) $M_{ai} p_{\text{ping}}$
This is a four-parameter model ($p_{\text{max}}$, $x_c$, $\alpha$, $\beta$) that predicts a decrease in $p_{\text{ping}}$ with increasing tag-to-receiver distance according to physical properties of underwater attenuation and spreading of acoustic intensity. I assume that $p_{\text{ping}}$ is proportional to intensity, so $p_{\text{ping}}$ decreases exponentially from $p_{\text{max}}$ toward zero as the absolute distance from $X_i$ to $x_c$ increases:

$$p_{\text{ping},i} = p_{\text{max}} \begin{cases} \frac{e^{-\frac{2\cdot\alpha\cdot(X_i-x_c)}{20\cdot\log_{10}(\epsilon)}}}{(-X_i-x_c)\beta} & \text{if } X_i < x_c \\ \frac{e^{-\frac{-2\cdot\alpha\cdot(X_i-x_c)}{20\cdot\log_{10}(\epsilon)}}}{(X_i-x_c)\beta} & \text{if } X_i > x_c \end{cases}.$$  

The attenuation coefficient, $\alpha$, and exponent, $\beta$, together control the steepness of attenuation with increasing distance. Typical measurements of $\alpha$ are, for 69 kHz transmissions in seawater, 0.015–0.025 dB·m$^{-1}$ (Leighton 1998). Although attenuation in pure water is less, the effect of suspended sediments and microbubbles can drastically increase attenuation, so overall attenuation may be higher in rivers that contain turbulent flow (Richards et al. 1996). Attenuation in seawater due to microbubbles under windy or surf conditions has been measured at about 4–5 dB·m$^{-1}$ (Leighton et al. 2004, Richards and Leighton 2003). The exponent $\beta$ determines the geometrical attenuation of the wavefront through the water due to spreading: $\beta = 2$ implies spherical spreading and $\beta = 1$ implies cylindrical spreading, which may be more appropriate for riverine attenuation. Despite the lack of theory to support it, to better fit the data I also chose to consider cases where $\beta$ ranges as low as 0.01 to reduce the importance of the geometrical spreading effect (at $\beta = 0$, intensity decreases with distance are solely due to absorptive attenuation). The form of Eq. C.3 is slightly different than typically presented for intensity attenuation since it involves $\alpha$ in units of dB·m$^{-1}$ rather than Nepers·m$^{-1}$, so requires the conversion (dB·m$^{-1}$) = 20·$\log_{10}e$ (Np·m$^{-1}$). Parameters were constrained to: $0.001 < p_{\text{max}} < 1$;
0.01 < \alpha < 4 \text{ dB} \cdot \text{m}^{-1}; 0.01 < \beta < 2; X_1 < x_c < X_m. (Note that a constraint of 1 \leq \beta \leq 2 would have resulted in an even poorer fit relative to model \([M_{\logit p_{\text{ping}}}]\). Additionally, the term in outer brackets was constrained to be \in (1.0 \times 10^{-9}, 0.999999999) prior to multiplication with \(p_{\text{max}}\).}

(iv) \(M_{\text{ai-thr}} p_{\text{ping}}\)

This is a five-parameter model \((p_{\text{max}}, x_c, \alpha, \beta, I_{\text{max}})\) that is similar to model (iii), but also includes a parameter, \(I_{\text{max}}\), that allows a threshold effect:

\[
(C.4) \quad p_{\text{ping},i} = p_{\text{max}} \begin{cases} 
\frac{I_{\text{max}} e^{(\frac{2 \alpha \cdot (X_1-x_c)}{20 \cdot \log_{10}(e)})}}{-(X_1-x_c)^{\beta}} & \text{if } X_1 < x_c \\
\frac{I_{\text{max}} e^{(\frac{-2 \cdot \alpha \cdot (X_1-x_c)}{20 \cdot \log_{10}(e)})}}{(X_1-x_c)^{\beta}} & \text{if } X_1 > x_c
\end{cases}
\]

Instead of assuming \(p_{\text{ping}}\) is directly proportional to intensity across all tag-to-receiver distances, in this model I assume a uniform \(p_{\text{ping}}\) out to some distance threshold to either side of \(x_c\), beyond which \(p_{\text{ping}}\) decreases at a similar rate as in model (iii). There is no physical interpretation of \(I_{\text{max}}\), but it extends \(p_{\text{max}}\) out to this threshold distance. Parameters were constrained for numerical estimation purposes: 0.001 < \(p_{\text{max}}\) < 1; 0.01 < \alpha < 4 \text{ dB} \cdot \text{m}^{-1}; 0.01 < \beta < 2; 1 \leq I_{\text{max}}; and X_1 < x_c < X_m. Additionally, the term in outer brackets was constrained to be \in (1.0 \times 10^{-9}, 0.999999999) prior to multiplication with \(p_{\text{max}}\), which is what generated the threshold (i.e., the threshold occurred whenever the term in brackets was $>1$ before it was constrained to ~1, and this threshold then had a value of \(p_{\text{max}}\) after multiplication).

C.2 Comparison of \(p_{\text{ping}}\) models

Model \([M_{\logit p_{\text{ping}}}]\) was the most parsimonious in terms of AIC scores (Table C.1). The total number of parameters and total likelihood represent sums over all 4 153 crossing sequences (crossing sequences were treated separately when fitting each model so that eventually a corresponding \(\hat{N}\) could be associated with each crossing event, hence the large AIC and \(\Delta\text{AIC}\) values). Models \([M_{\text{norm}} p_{\text{ping}}]\), \([M_{\text{lin}} p_{\text{ping}}]\), and \([M_{\text{ai-thr}} p_{\text{ping}}]\) had relatively similar levels of support compared to the large difference between \([M_{\logit p_{\text{ping}}}]\) and these three models (\(\Delta\text{AIC} = 21\ 054–23\ 281\)). Alternative parameter counts involving the number of unique sequences rather
than total sequences change these values and ranking somewhat ($\Delta AIC = 18 567$ for $[M_\text{ai-thr} p_{\text{ping}}]$), $25 768$ for $[M_\text{norm} p_{\text{ping}}]$, and $27 868$ for $[M_\text{lin} p_{\text{ping}}]$), but AIC of $[M_\text{logit} p_{\text{ping}}]$ is still much lower than these. Model $[M_\text{ai} p_{\text{ping}}]$ had the least support among these models.

The number of total parameters estimated varies with sample size, since a set of parameters are estimated for each sequence or unique sequence. To compare models on a per-sequence basis rather than over all sequences, the average AIC can be calculated as $\text{AIC}/4153$, which helps to remove this dependence. The average $\Delta AIC$ values for these models are: $[M_\text{logit} p_{\text{ping}}]$, 0; $[M_\text{norm} p_{\text{ping}}]$, 5.1; $[M_\text{lin} p_{\text{ping}}]$, 5.4; $[M_\text{ai-thr} p_{\text{ping}}]$, 5.6; and $[M_\text{ai} p_{\text{ping}}]$, 11.7. This ranked pattern of average $\Delta AIC$ values generally held across sequences of different length, or different number of detections (Fig. C.1; longer sequences are expected to have higher AIC values since they involve more terms in the log-likelihood summation). For shorter sequences ($n = 3\text{-}10$), $[M_\text{logit} p_{\text{ping}}]$ had a lower average AIC than other models, and was similar to $[M_\text{norm} p_{\text{ping}}]$ and $[M_\text{lin} p_{\text{ping}}]$ at $n = 2$ (Fig. C.1a). For longer sequences ($n \geq 11$), $[M_\text{logit} p_{\text{ping}}]$ performed increasingly better than the other models as $n$ increased (Fig. C.1b). This ranked pattern also held when crossing sequences were separated by habitat, with $[M_\text{logit} p_{\text{ping}}]$ having a lower AIC than all other models in all habitats (not shown; the smallest habitat-specific average $\Delta AIC$ was 3.5, for $[M_\text{norm} p_{\text{ping}}]$ fit to Fraser River crossing sequences).

Table C.1. Information-theoretic comparison of $p_{\text{ping}}$ models fit independently to 4 153 crossing sequences (765 sequences of $n = m = 1$ are excluded), with number of parameters ($k$), log-likelihood, and AIC values given.

<table>
<thead>
<tr>
<th>Model</th>
<th>$k$ per sequence</th>
<th>Total $k^*$</th>
<th>Total $\ln(L)$</th>
<th>AIC</th>
<th>$\Delta AIC$</th>
</tr>
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<tbody>
<tr>
<td>$M_\text{logit} p_{\text{ping}}$</td>
<td>4</td>
<td>16 612</td>
<td>–65 814</td>
<td>164 853</td>
<td>0</td>
</tr>
<tr>
<td>$M_\text{norm} p_{\text{ping}}$</td>
<td>3</td>
<td>12 459</td>
<td>–80 494</td>
<td>185 907</td>
<td>21 054</td>
</tr>
<tr>
<td>$M_\text{lin} p_{\text{ping}}$</td>
<td>3</td>
<td>12 459</td>
<td>–81 159</td>
<td>187 237</td>
<td>22 384</td>
</tr>
<tr>
<td>$M_\text{ai-thr} p_{\text{ping}}$</td>
<td>5</td>
<td>20 765</td>
<td>–73 302</td>
<td>188 134</td>
<td>23 281</td>
</tr>
<tr>
<td>$M_\text{ai} p_{\text{ping}}$</td>
<td>4</td>
<td>16 612</td>
<td>–90 160</td>
<td>213 543</td>
<td>48 690</td>
</tr>
</tbody>
</table>

* Total parameters are counted as $k$ per sequence x 4 135 sequences. Alternative counts of $k$ per sequence x number of unique sequences change AIC scores of all models, but that of $[M_\text{logit} p_{\text{ping}}]$ is still lowest.
Figure C.1. Average ΔAIC values of $p_{\text{ping}}$ attenuation models fit to 4153 crossing sequences, separated by number of detections in sequence: (a) $n$, 2–10; (b) $n$, 11–90+.

C.3 References


Appendix D  Additional peer-reviewed thesis-related publications

For the following publications, I was either involved as a co-author but was not the senior author, or I chose not to include the manuscript as a thesis chapter.

D.1 Published papers


D.2 Papers in review

Chittenden, C.M., Melnychuk, M.C., Welch, D.W., and McKinley, R.S. Evidence for poor freshwater survival of endangered Thompson River coho salmon smolts during the Fraser River out-migration.

Welch, D.W., Jackson, G.D., Melnychuk, M.C., Rechisky, E., Porter, A., Neaga, L., and O’Dor, R. Applications of the Pacific Ocean Shelf Tracking System (POST): A permanent continental-scale acoustic tracking array for marine management, conservation and ocean observing.

D.3 Non-peer-reviewed book chapters submitted

ANIMAL CARE CERTIFICATE

Application Number: A06-0305
Investigator or Course Director: Carl J. Walters
Department: Fisheries
Animals:

Salmon 200

Start Date: May 1, 2007 Approval Date: June 26, 2006

Funding Sources:

<table>
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<th>Funding Agency</th>
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<tr>
<td>British Columbia Pacific Salmon Forum</td>
<td>Early marine survival assessment of Coho salmon in Southern BC</td>
</tr>
<tr>
<td>Canadian National Railway</td>
<td>Assessment of Juvenile Survival of Hatchery-reared Coho Salmon during the Downstream Migration in the Cheakamus and Squamish Rivers and Early Ocean Life</td>
</tr>
<tr>
<td>Pacific Salmon Foundation</td>
<td>Mobile acoustic tracking of juvenile salmon - PSF</td>
</tr>
<tr>
<td>FishAmerica Foundation</td>
<td>Mobile acoustic tracking of juvenile salmon - FishAmerica</td>
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</table>

Unfunded title: Mobile acoustic tracking of juvenile salmon

The Animal Care Committee has examined and approved the use of animals for the above experimental project.

This certificate is valid for one year from the above start or approval date (whichever is later) provided there is no change in the experimental procedures. Annual renewal is required by the CCAC and some granting agencies.

A copy of this certificate must be displayed in your animal facility.