What Do Salmon and Injection Drug Users Have in Common?

Laura L. E. Cowen
University of Victoria, Victoria, BC

Wendell O. Challenger, and Carl J. Schwarz
Simon Fraser University, Burnaby, BC

Many populations consist of elusive members that can make these populations difficult to study using standard sampling methods. These populations (e.g., salmon, large and small mammals, birds, injection drug users, sex workers) are impossible to census and most “regular” sampling techniques produce biased estimates (estimates that are, on average, too large or too small) of demographic processes (e.g., birth, death, immigration, and emigration) and underestimate the size of the population when detectability (elusiveness) is ignored. Capture-recapture has evolved to deal with this situation and highlights the pivotal role statistics can play in aiding general scientific understanding, of which many Canadian researchers are at the forefront. Capture-recapture studies are used to estimate the population size, determine if the population is growing, determine the rate of population change, estimate the rate of survival, determine if individuals move from one location to another, and/or determine the rate of movement between locations.

17.1 Methodology Background

The fundamental problem associated with elusive populations is that individuals are less than 100% detectable, which reduces our ability to fully enumerate members of the population or to fully resolve individual fates. For example, if we are interested in the number of injection drug users, we may attempt to enumerate the population at some point in time by a census of known locations with a large number of users. However, estimates based on direct counts will consistently underestimate the true population size because injec-
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tion drug users face social stigma and lack trust in health researchers, often making them elusive to surveys.

To gain an accurate estimate of the total number injection drug users we need to inflate the number we observe by a factor proportional to the rate that individuals were missed. If we had an estimate of the detection rate \( p \), an estimator of the population size \( N \) at a single point in time would be

\[
\hat{N} = n / \hat{p},
\]

where \( n \) is the number of injection drug users we did observe and \( \hat{p} \) is the estimate of the detection rate (the circumflex above \( p \) and \( N \) indicates these are estimates of the true detection rate \( p \) and the true population size \( N \) respectively). An estimated detection rate of \( \hat{p} = .1 \) would indicate we only observed 10% of the population during enumeration, therefore we can expect the true number of users would be roughly 10 times our observed count.

Estimates of demographic processes such as births, deaths, initiation (an individual begins injection drug use), cessation (an individual ends injection drug use), immigrations (a user that moved to a new city), and emigrations (a user moving from a city) will also have to be similarly adjusted. This can be of critical importance because accurate estimates of demographic processes are required to define policy for at-risk human populations or to manage wildlife populations.

At the heart of capture-recapture methodology is the explicit handling of imperfect detection. This is done through the application of “marks” (unique identifiers, typically referred to as “tags”) and sampling protocols that attempt to recapture a subset of marked individuals. The use of uniquely marked individuals allows previously captured individuals to be identified in subsequent sampling occasions, which in turn allows for the proportion of missed individuals to be estimated. The exact method of how detection rates are estimated depends on the sampling protocol and modeling assumptions, but all capture-recapture models share this simple premise. Today, a wealth of tag types (Figure 17.1) and sampling protocols exist, supplemented by an equally rich set of modeling frameworks and associated software available to practitioners. In this exposition, we will only be scratching the surface of the type of research done, but we hope to demonstrate the real-world applicability of capture-recapture type studies.

### 17.2 Closed Population Models and Two-Sample Experiments

The simplest study design that allows for the estimation of the detection rate and of the population size is a two-sample experiment. Two samples are obtained from the population. Individuals captured on the first occasion are
marked and returned to the population. The second sample of the population again captures individuals, but now the sample contains a mixture of previously marked individuals and individuals captured for the first time. There are three potential fates of individuals after the first sample time (Figure 17.2): they are alive and are captured, they are alive and not captured, or they are dead.

Of all the possible fates, individuals that are alive and in the study area provide information about detection efficiency. In some circumstances, it is possible to choose the sampling occasions so that the assumption of population closure holds (closure implies that negligible births, deaths, immigration, or emigration events have occurred). Under closure, individuals identified in the first sample, but not the second, can be assumed to have been missed (Figure 17.2). Thus, under closure, the proportion of “recaptures” (observing the same individual again) provides a direct estimate of the detection rate $p$, thereby allowing for estimation of $N$ via (17.1).

If $n_1$ represents the total individuals in the first sample and $n_2$ the total number caught in the second sample (with $m_2$ representing the number caught in both samples, or the number of marked-individuals captured at occasion 2) we can estimate the true population size $N$. Assuming that all individuals are equally catchable at each sampling occasion, the proportion recaptured on
FIGURE 17.2: Possible fates in a two-sample study. Individuals captured and marked at the first time point may be alive and captured, alive and not captured or dead at the second sampling point. When sampling is done close in time, it can be assumed that no deaths occurred, removing death as a possible outcome (greyscale). Observed data for an individual is a “1” if captured and a “0” if not captured.

the second occasion should on average be the same as the proportion initially marked. In other words, \[ \frac{n_1}{N} = \frac{m_2}{n_2}, \]
which can be rearranged to give
\[ \hat{N} = \frac{n_1 n_2}{m_2}. \] (17.2)

For example, Xu et al. (2013) had \( n_1 = 254 \) injection drug users in the first sample, \( n_2 = 250 \) in the second, and \( m_2 = 19 \) in both. Thus \( \hat{N} = 254 \times 250/19 = 3342 \) individuals. Using our earlier form (17.1), we would substitute \( m_2/n_1 \) for \( \hat{p} \). While an estimate of \( N \) is our primary interest, estimating \( p \) is also important, despite often being referred to as a “nuisance” parameter. By accounting for detection, we are able to derive an estimate of \( N \), which we would not be able to do with a simple count. While we have taken the first steps of accounting for detection, we must also be careful that \( p \) is an appropriate description of the detection process and that we did not make any mistakes reading tags, nor that individuals lose their tags between sampling occasions.
The described estimator is termed a Lincoln–Petersen type estimator and was originally developed to estimate the population of France in 1783 (Laplace, 1786). Today it is one of the most widely used two-sample capture-recapture estimators by wildlife ecologists and epidemiologists. Despite the simple study design, much of the current work involves relaxing or dealing with violations to various modeling assumptions. For example, the assumption that all individuals are equally catchable is often violated, which is referred to as heterogeneity in catchability. Normally, there is not sufficient information to detect or to adjust for heterogeneity in the simple two-sample experiment; however, for both injection drug users and migrating salmon, we can make use of additional information to understand and to adjust for heterogeneity. Chapter 18 by Louis-Paul Rivest and Sophie Baillargeon takes a detailed look at heterogeneity.

17.2.1 Victoria’s Injection Drug Users

Xu et al. (2013) first “captured” individuals in Victoria, British Columbia, in 2003 through a national cross-sectional survey designed to track changes in the prevalence of HIV and hepatitis C. Participants were recruited in Victoria through AIDS Vancouver Island’s needle exchange program and at shelter services run by the Victoria Cool Aid society. Posters, flyers, word of mouth, and contact with Vancouver Island Health Authority staff were other methods used for recruitment. Individuals were associated with a unique identifier — a combination of birth date and initials. A second survey was completed in 2005 and individuals whose identifiers matched those from the first sample were considered to be “recaptured.” A standard Lincoln–Petersen approach resulted in estimates that were much higher than the accepted population size estimate of Stajduhar et al. (2004) obtained from the client load of AIDS Vancouver Island’s needle exchange program.

Xu et al. (2013) also looked at two other methods to account for heterogeneity in capture probability by incorporating covariates (information from other variables) using methods of Huggins (1989); and by using (hidden) mixture models (Pledger, 2000) that assume the existence of groups of individuals with different catchabilities (but does not rely on additional covariate information). In the Huggins model, capture probabilities varied by the sex of an individual and whether or not an individual had been captured before, through the use of the function

\[
\log \left( \frac{p_{ij}}{1 - p_{ij}} \right) = \beta_0 + \beta_1 \text{sex}_i + \beta_2 z_{ij},
\]

where \( p_{ij} \) is the capture probability for individual \( i \) on occasion \( j \), and \( z_{ij} \) is equal to one if individual \( i \) was captured before occasion \( j \) and zero otherwise. As the sex of unobserved individuals is unknown, one can consider only individuals captured at least once.
In Pledger’s model, we assume that individuals belong to groups with different capture probabilities, but group membership is latent (or unobservable). Capture probabilities are allowed to vary by time, behavior and/or group. Here capture probability $p_{jab}$ is the probability of capture for an individual $i$ at occasion $j$ who has behavior type $b$ in group $a$. It is modeled as

$$\log\left(\frac{p_{jba}}{1-p_{jab}}\right) = \mu + \tau_j + \beta_b + \eta_a + (\tau \beta)_j + (\tau \eta)_j + (\beta \eta)_ba + (\tau \beta \eta)_jba,$$

where $b$ equals one if individual $i$ was not caught before occasion $j$ and two otherwise, $\tau_j$ is the effect of time, $\beta_b$ is the effect of behavior, and $\eta_a$ is the effect of group $a$. Parameters are typically estimated using maximum likelihood methods.

Ultimately the three estimates from the different models were very similar (with confidence intervals of between 2246 and 5078 injection drug users) and all three differed drastically from the accepted population size estimate of 1500–2000 individuals (Stajduhar et al., 2004). The Vancouver Island Health Authority will use these new estimates to secure resources and plan harm reduction programs such as fixed-site needle exchanges to meet the health care needs of the injection drug user population. In turn, implementation of these services will help control the transmission of HIV and hepatitis C, which will benefit the population at large.

### 17.2.2 Rotary Screw Traps and the Time Stratified Petersen Estimator

Rotary screw traps have long been used as a method to sample salmonoid smolts during outward migration (Figure 17.3). These devices capture an unknown proportion of the migrating smolts as they move downstream. In one study design, fish are captured at an up-river trap, marked, and released. Some of the marked fish are recaptured at a second trap downstream giving an estimate of the capture efficiency (Schwarz and Dempson, 1994). For example, if 100 smolts are marked at the upstream trap and only 10 are recaptured at the downstream trap, then the downstream trap is estimated to have a 10% capture efficiency. Creative approaches using a single trap can also be constructed by capturing, then moving captured smolts upstream and releasing them, which allows for recaptures to occur at the single trap as the smolts resume their downstream migration; see, e.g., Macdonald and Smith (1980).

This outward migration occurs over long periods of time (i.e., weeks to months) necessitating multiple periods of time when smolts are captured, tagged, and released. The efficiency of the trap can vary dramatically across the study as water levels and other environmental variables (e.g., water temperature) change. This results in a violation of the assumption of homogenous catchability. Consequently, the simple approach of pooling all releases and recoveries over the entire duration of the study and using a simple Lincoln–
FIGURE 17.3: Rotary screw traps have long been used by biologists to capture juvenile salmonoids migrating downstream in medium- and large-sized streams. Image Credit: FISHBIO.

Petersen estimator (17.2) to estimate population size could result in a biased estimate (Arnason et al., 1996).

Temporal stratification (breaking up the study into sub-studies or groups over time) has been the standard approach used to deal with changing catchability. Strata (an individual sub-study or group) are constructed such that roughly uniform catchability can be expected (e.g., weekly strata), separate population size estimates are then derived for each stratum, and then estimates from each stratum are combined to derive an overall population size estimate. The stratified-Petersen estimator has a long history in terrestrial surveys (Schaefer, 1951; Chapman and Junge, 1956; Darroch, 1961), but suffered from the constraint that the number of release and recovery strata needed to be equal. Arnason et al. (1996) developed user-friendly software to implement this estimator that is still in use today and Plante et al. (1998) relaxed this constraint of equal strata.

This method has been used, for example, to study the problem of “five million missing salmon” that occurred in the Fraser River watershed in 1991. A discrepancy occurred between the estimate of the number of adult fish allowed to escape the fishery and the numbers adult spawners observed on the spawning ground. This discrepancy was thought to be due to a statistical artefact of naively applying the simple pooled-Petersen estimator when catchability differed for each stratum. Schwarz and Taylor (1998) applied a stratified-Petersen estimator to account for the heterogeneity in catchability, and indeed showed that the missing fish were just a statistical artefact due to not incorporating variable catchability into the estimator.

While the stratified-Petersen proved to be an important advancement for Canadian fishery science, it was not without limitations. Heterogeneity in both catchability and degree of mixing can be extreme, requiring large numbers of
strata to adequately deal with the changes in heterogeneity. A large number of strata often results in poor precision for the estimate of sample size due to small stratum sample sizes combined with a large number of model parameters that must be estimated. In doing so an unfortunate trade-off between bias and precision is created.

One way of avoiding this trade-off is to add additional structure to the models that can reduce the effective number of parameters used to describe the problem (e.g., adjacent strata should have similar parameter values). One approach used information about smolt travel times to provide information about catchability (Schwarz and Dempson, 1994); another approach used environmental factors to model recapture probabilities (Plante et al., 1998). A more modern approach (Bonner and Schwarz, 2011) assumed the number of smolts passing the traps over time can be expected to occur in a smooth and predictable manner (e.g., increasing over time to a peak, followed by a decrease) and used splines to model this process. They also used Bayesian methods to share information from neighboring strata about the capture rates in a particular stratum.

Furthermore the use of smooth functions (splines) has additional advantages such as the ability to provide abundance estimates for strata that may be missing due to crew illness, high water flows, or other causes. The approach of Bonner and Schwarz (2011) also removes the need to make arbitrary decisions when defining strata, as the model is self-selecting so that with poor data, more extensive sharing of information among strata takes place, while with rich data, very little sharing of information among strata takes place. A user-friendly \texttt{R} package (BTSPAS) was also developed (Bonner and Schwarz, 2012) and is in use extensively on the west coast of North America.

17.2.3 Extending the Closed Population Models

The two-sample experiment can be generalized with additional sampling occasions and by allowing for known subgroups (e.g., sex) in the population. The catchability of individuals can now vary over time, because of behavior, or because of intrinsic heterogeneity. For example, small rodents may become “trap-happy” (they like the bait) or “trap-shy” (they dislike being handled) after being captured, thus subsequent capture probabilities may be affected. Trap stations may be dispersed over a geographical grid and because of home range limitations, animals captured in the northwest section of a trapping grid cannot be captured in the southeast portion of a trapping grid. Larger animals may be more visible than smaller animals and more difficult to recapture. While the closure assumption is still paramount, the additional information in larger experiments allows for quite complex modeling to take place to deal with a variety of these other complications.
17.3 Open Populations

In most populations of interest, some amount of birth, death, immigration or emigration is likely occurring between sampling occasions and these populations are considered “open.” In the case of Cassin’s Auklets on Triangle Island, British Columbia, Bertram et al. (2000) studied annual survival rates between 1994 and 1997. With a multi-year open population study there are a number of possible fates that must be considered (Figure 17.4). Because survival rate (rather than population size) was of primary interest, Bertram et al. (2000) used the Cormack–Jolly–Seber (CJS) model (Cormack, 1964; Jolly, 1965; Seber, 1965) and considered both age of the bird and capture (netting) location in their model, thus controlling for some amount of capture heterogeneity.

The data obtained in these studies are typically a sequence of digits (termed a capture history) that provide a concise summary of whether or not an individual was encountered during the course of the study. A “1” indicates an individual was observed, and a “0” indicates the individual was unobserved. For example, the capture history \( \{1010\} \) indicates a four sample experiment, where the individual was observed (alive) on the first and third sample times. The zero observed at time 2 indicates that the individual was not detected, but is known to be alive due to the subsequent detection. The...
missed detection may have resulted from the individual not being present in the study area during sampling (due to temporary emigration) or the result of individual detectability being less than 100% (i.e., the individual was not captured). The missed detection provides information on the detection rate at sample time 2, assuming emigration did not happen. The final zero at sample time 4 is less informative — now a third possibility (death) must be considered, in addition to imperfect detection or emigration as the other possibilities (Figure 17.5).

The key to the analysis of such a capture-recapture dataset is to construct a probability for each possible capture history. For example, a probability expression for the history \{1010\} takes the form

\[ \phi_1 (1 - p_2) \phi_2 p_3 \{1 - \phi_3 + \phi_3 (1 - p_4)\}, \]

where \( \phi_t \) represents the probability of surviving between times \( t \) and \( t + 1 \), and \( p_t \) is the probability of capture at time \( t \). Notice that after the third sample time, the last term in the expression represents the probability of death, \( 1 - \phi_3 \), or survival but no detection on the last occasion, \( \{\phi_3 (1 - p_4)\} \). These probability statements are produced for each individual under study and are combined to create a model whereby survival can be estimated (using maximum likelihood methods for example). Biological hypotheses can be investigated by looking at several plausible models. For example, Bertram et al. (2000) studied models where capture rates varied over time, or netting location, or both.

For more complicated studies, the “digits” in the capture-history can be generalized to record other information, such as the breeding state and location of the individual (e.g., “Ab” could indicate the individual was observed breeding (b) on site A).

If population size is of interest, then the Jolly–Seber model (Jolly, 1965; Seber, 1965) is typically employed where entrance to the population must also be modeled. Schwarz and Seber (1999) provide a thorough review of this model.

17.3.1 Novel Applications — Pacific Ocean Shelf Tracking

Open-population models are arguably the most popular approach and can be applied to a diverse array of situations. While much of our discussion of capture-recapture has focused on physical captures, many studies relax this constraint by using a variety of methods to “capture” individuals. For example, once a tag is applied (requiring capture), subsequent recaptures can consist of non-invasive approaches such as resightings (e.g., reading bird bands from a distance) or recoveries (e.g., through hunting or fishery harvest). Furthermore, physical capture can be avoided in some circumstances by relying on naturally occurring markings (e.g., whale fluke patterns), camera traps, or DNA sampling (e.g., using hair or feces) to sample individuals. Other unique implementations can be creative constructions of what constitutes a “capture
FIGURE 17.5: Fate diagram and corresponding capture history probability expression for the capture history \( \{1010\} \) under an open population scenario. The expression is conditioned on first capture (the probability of observing a “1” is 1), with survival \((\phi)\) and capture \((p)\) probability parameters used to describe the possible states. Living individuals may be captured with probability \(p\), or missed with probability \(1 - p\), while deceased are missed (“0”) with probability 1.

\[
P(1010) = \phi_1 (1 - p_2) \phi_2 p_3 \{1 - \phi_3 + \phi_3 (1 - p_4)\}
\]

The use of electronic tagging in the study of migrating marine animals, such as salmon, is a good example of this type of approach. Traditional non-electronic tags have been used to tag fish or other marine organisms; however, these provide only crude estimates of animal movements and often require intensive sampling to recover a small proportion of tags, resulting in low precision estimates of model parameters. Electronic tags now exist that are small enough to implant into juvenile salmon (Figure 17.1d), providing rich datasets from a much smaller sample size. These tags carry a power source allowing them to actively transmit information for extended periods of time. Transmissions are in the form of a coded signal, which contain a unique identifier, allowing individuals to be identified as they come within proximity of specialized passive receivers. Acoustic tags transmit sound waves, which can be detected across salt and freshwater; while radio tags may only be detected in freshwater due to saltwater signal attenuation.

Similar to the rotary screw trap studies, capture histories can be constructed by setting up multiple listening lines of receivers along known migration routes (Figure 17.6). Migration pathways of many anadromous fish species, such as Pacific salmon, are well known and occur in a directed manner. As such, tagged fish can be expected to transverse the listening lines in a predictable manner, creating well defined capture histories, with intervals
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FIGURE 17.6: The POST project deployed acoustic listening lines along the continental shelf and along several major rivers, spanning from California to Alaska. This allowed acoustically tagged salmon, such as Fraser River sockeye, to be tracked during parts of the oceanic and river phases of migration. Reproduced from Jackson (2011).

A large-scale research program that employed this type of approach was the Pacific Ocean Shelf Tracking (POST) program. A field program of the decade-long Census of Marine Life, from 2003 through to 2012, the POST program deployed a series of acoustic listening lines along the continental shelf, and in select rivers of the West Coast of North America. The POST array spans nearly 3,000 km from Alaska, through British Columbia, to California and can track migrating salmon through the river and along the ocean shelf. While the receiver lines can detect a variety of species — 18 species as of 2011 (Jackson, 2011) — much of the published work has focused on Steelhead trout and Pacific salmon such as chinook and sockeye; see, e.g., Crossin et al. (2007),
Welch et al. (2003), and Welch et al. (2009). Studies combining the POST array, as well as radio tagging studies restricted to the Fraser River, have been instrumental in furthering our understanding of some factors impacting Pacific salmon. An example of this has been the insights gained into the mortality problem that has recently emerged for late-run Fraser River sockeye.

Fraser River sockeye are divided into roughly four management groups based on the timing of their spawning migrations. Late-run sockeye typically enter the Fraser River last, at the end of summer, after spending a period of time (historically six weeks) holding, off the mouth of the Fraser River. Sometime around 1995 this holding period was drastically reduced and stocks within this timing group began experiencing severe spawning mortality problems somewhere within the Fraser River (Cooke et al., 2004). For some late-run stocks the mortality was as high as 90% (Hinch et al., 2012). The changes in river migration timing were also unprecedented, with holding periods reduced by three weeks and even eliminated in some years. Due to the sampling techniques used (abundance estimates at river entry and at the spawning grounds), the exact timing and location of the in-river mortality was not known.

Driven by concern over these events, and the inability of more standard sampling approaches to provide the necessary information, a series of large-scale capture-recapture telemetry experiments using both acoustic (POST) and radio technologies were carried out. POST listening lines were used to allow researchers to track the movement and timing of individually tagged sockeye from as far away as the Gulf of Alaska to just off the spawning ground; see, e.g., Crossin et al. (2009). Due to the sequential nature of the migration route, studies could use standard capture-recapture approaches to analyze the data.

This finer scaled approach allowed for much clearer understanding of the major mortality mechanisms. Using sockeye radio-tagged in the ocean it was found that the date of river entry strongly predicted subsequent in-river survival (English et al., 2005). After removing fishery-related mortality it was also found that this mortality followed a smooth function related to date of entry, with earlier entrants exhibiting the highest levels of in-river mortality. Sockeye that displayed little to no ocean holding prior to entering the river had virtually no prospects of arriving on the spawning grounds. Temperature exposure (and subsequent freshwater disease expression) was thought to be driving this mortality. This suspicion was confirmed by the discovery that fish held in warm water incurred much higher mortality levels during the subsequent river migration than fish held in cool water (Crossin et al., 2008). The mechanism was also further established in follow-up observational studies; see, e.g., Mathes et al. (2010). Interestingly, some of the early entrants that do survive to the spawning ground appear to hold in the coolest portions of their natal lakes after migrating up the river (Mathes et al., 2010; Hinch et al., 2012).

Furthermore, by combining telemetry with physiological sampling at the time of capture, studies have shown that sockeye may already be compromised
prior to river entry (Cooke et al., 2006; Miller et al., 2011) and that early-entry behavior may be triggered by the physiological and energetic status of the fish (Cooke et al., 2006). All of these scientific insights relied on being able to track individual movements and subsequent survival. None of this would be possible without capture-recapture methodology.

### 17.4 Additional Complications

As we have seen, complications to standard mark-recapture studies typically arise when assumptions of the models are violated. We discussed some possible sources of heterogeneity affecting capture probabilities, but there are many other sources of heterogeneity that can be incorporated. Capture rates might vary with individual characteristics that differ each sample time such as body mass or wing length. Bonner and Schwarz (2006) showed how this information can be incorporated for meadow voles whose body mass was measured on each sampling occasion. The difficulty here is that when a vole was not captured, the value of body mass for that sample time was missing.

Similarly, individuals in different locations or breeding states might have different catchabilities. In this context, capture-recapture can also be used to determine patterns of migration through the use of a multistate model (Arnason, 1972, 1973; Schwarz et al., 1993). Cowen et al. (2009) incorporated the location of an individual into a multistate model to estimate the fishery exploitation rates of yellowtail flounder on the Grand Bank of Newfoundland.

Another important capture-recapture assumption is that individuals behave independently of one another. This is often violated in waterfowl that form pair-bonds and share fates. Challenger (2010) considered the problem in a Harlequin duck population in Hinton, Alberta, and was able to estimate the degree to which one individual was associated with its pair in terms of survival and catchability.

Finally, tag loss is assumed to be negligible in standard capture-recapture studies. When individuals are double-tagged, tag loss can be estimated and accounted for in the models; see Cowen and Schwarz (2006), Cowen et al. (2009) and Xu et al. (2014). Cowen and Schwarz (2006) studied walleye in Mille Lacs, Minnesota, that had been double-tagged and found tag loss rates changed over time, which in turn affected population size estimates from standard methods. Tag loss in radio-telemetry studies comes in the form of battery failure. Cowen and Schwarz (2005) studied chinook smolts traveling down the Columbia River, WA and were able to account for battery failure by incorporating information about battery lifetimes into the model, thus producing more accurate survival estimates for the smolts.
17.5 Concluding Remarks

Capture-recapture experiments continue to provide new problems for Canadian researchers. This is particularly true with the arrival of new technologies for monitoring animals that promise to provide information about animal locations and interactions in real time. With these new technologies, methodological research will be shifting from problems with a sparsity of data to an overabundance of data, often collected on very fine time (daily) and large spatial (over continents) scales, or collected from different sources (e.g., radio collars; DNA) that will have to be integrated together. These data will require development of models with many thousands of parameters, all of which are highly interrelated.

Capture-recapture methodological development has quickly been integrated into mainstream ecological fields. A short illustrative list of the application of capture-recapture methods to Canadian wildlife populations is: Cassin’s and Rhinoceros Auklet survival (Bertram et al., 2000), humpback whales abundance (Smith et al., 1999), Black Brant site fidelity Reed et al. (1998), Norway rat eradication (Drever, 1997), population change in Ancient Murrelets (Gaston and Descamps, 2011), and grizzly bear abundance (Mowat and Strobeck, 2000).

About the Authors

Laura L. E. Cowen is an associate professor of statistics at the University of Victoria. She received an MMath from the University of Waterloo and a PhD in statistics from Simon Fraser University. She is a statistical ecologist with a primary research focus in capture-recapture methodology. Her earlier background in biological science has led to collaborations with seabird ecologists, fisheries scientists, microbiologists, anthropologists, and ophthalmologists.

Wendell O. Challenger was formerly a biologist before focusing on statistics for his PhD. Now a statistical ecologist, his primary research interests are on capture-recapture methodology with an emphasis on accommodating implementation issues associated with field studies. He has recently completed a postdoctoral fellowship working on the acoustic tracking of salmon.

Carl J. Schwarz is a professor of statistics at Simon Fraser University. He graduated from the University of Manitoba in 1985 and joined SFU in 1994. He specializes in statistical methods for ecology, notably capture-recapture and multi-list techniques for estimating abundance, survival, movement and
other demographic parameters of wildlife populations. He is a former editor of the *Journal of Agricultural, Biological, and Environmental Statistics*.

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