THE DESIGN AND ANALYSIS OF SALMONID TAGGING STUDIES IN THE COLUMBIA BASIN

VOLUME XXIII

Effects of Array Configuration on Statistical Independence of Replicated Telemetry Arrays used in Smolt Survival Studies

Prepared by:
Russell W. Perry and John R. Skalski
School of Aquatic and Fishery Sciences
University of Washington
1325 Fourth Avenue, Suite 1820
Seattle, WA 98101-2509

Prepared for:
U.S. Department of Energy
Bonneville Power Administration
Division of Fish and Wildlife
P.O. Box 3621
Portland, OR 97208-3621

Project No. 198910700
Contract No. 00025091

August 2008

The Design and Analysis of Salmonid Tagging Studies in the Columbia Basin

Other Publications in this Series

Volume I: Skalski, J. R., J. A. Perez-Comas, R. L. Townsend, and J. Lady. 1998. Assessment of temporal trends in daily survival estimates of spring chinook, 1994-1996. Technical report submitted to BPA, Project 89-107-00, Contract DE-BI79-90BP02341. 24 pp. plus appendix.

Volume II: Newman, K. 1998. Estimating salmonid survival with combined PIT-CWT tagging. Technical report (DOE/BP-35885-11) to BPA, Project 91-051-00, Contract 87-BI-35885.

Volume III: Newman, K. 1998. Experiment designs and statistical models to estimate the effect of transportation on survival of Columbia River system salmonids. Technical report (DOE/BP-35885-11a) to BPA, Project 91-051-00, Contract 87-BI-35885.

Volume IV: Perez-Comas, J. A., and J. R. Skalski. Submitted. Preliminary assessment of the effects of pulsed flows on smolt migratory behavior. Technical report to BPA, Project 89-107-00, Contract DE-BI79-90BP02341.

Volume V: Perez-Comas, J. A., and J. R. Skalski. Submitted. Analysis of in-river growth for PIT-tagged spring chinook smolt. Technical report to BPA, Project 89-107-00, Contract DE-BI79-90BP02341.

Volume VI: Skalski, J. R., J. A. Perez-Comas, P. Westhagen, and S. G. Smith. 1998. Assessment of season-wild survival of Snake River yearling chinook salmon, 1994-1996. Technical report to BPA, Project 89-107-00, Contract DE-BI79-90BP02341. 23 pp. plus appendix.

Volume VII: Lowther, A. B., and J. R. Skalski. 1998. Monte-Carlo comparison of confidence interval procedures for estimating survival in a release-recapture study, with applications to Snake River salmonids. Technical report (DOE/BP-02341-5) to BPA, Project 89-107-00, Contract 90-BI-02341.

Volume VIII: Lowther, A. B., and J. R. Skalski. 1998. Improved survival and residualization estimates for fall chinook using release-recapture methods. Technical report (DOE/BP-02341-6) to BPA, Project 89-107-00, Contract 90-BI-02341.

Volume IX: Townsend, R. L., and J. R. Skalski. Submitted. A comparison of statistical methods of estimating treatment-control ratios (transportation benefit ratios), based on spring chinook salmon on the Columbia River, 1986-1988. Technical report to BPA, Project 91-051-00, Contract 87-BI-35885.

Volume X: Westhagen, P., and J. R. Skalski. 1998. Instructional guide to using program CaptHist to create SURPH files for survival analysis using PTAGIS data files. Technical report (DOE/BP-02341-4) to BPA, Project 89-107-00, Contract 90-BI-02341.

Volume XI: Skalski, J. R., R. L. Townsend, A. E. Giorgi, and J. R. Stevenson. Submitted. Recommendations on the design and analysis of radiotelemetry studies of salmonid smolts to estimate survival and passage efficiencies. Technical report to BPA, Project 89-107-00, Contract DE-BI79-90BP02341. 33 pp.

Volume XII: Ryding, K. E., and J. R. Skalski. 1999. A multinomial model for estimating ocean survival from salmonid coded wire-tag data. Technical report (DOE/BP-91572-3) to BPA, Project 91-051-00, Contract 96-BI-91572.

Volume XIII: Perez-Comas, J. A., and J. R. Skalski. 2000. Appraisal of system-wide survival estimation of Snake River yearling chinook salmon using PIT-tags recovered from Caspian tern and double-crested cormorant breeding colonies on Rice Island. Technical report to BPA, Project No. 8910700, Contract DE-BI79-90BP02341.

Volume XIV: Perez-Comas, J. A., and J. R. Skalski. 2000. Appraisal of the relationship between tag detection efficiency at Bonneville Dam and the precision in estuarine and marine survival estimates of returning pit-tagged chinook salmon. Technical report to BPA, Project No. 8910700, Contract DE-BI79-90BP02341.

Volume XV: Perez-Comas, J. A., and J. R. Skalski. 2000. Appraisal of the relationship between tag detection efficiency at Bonneville Dam and the precision in-river survival estimates of returning PIT-tagged chinook salmon. Technical report to BPA, Project No. 8910700, Contract DE-BI79-90BP02341.

Volume XVI: Skalski, J. R., and J. A. Perez-Comas. 2000. Alternative designs for future adult PIT-tag detection studies. Technical report to BPA, Project No. 8910700, Contract DEBI79-90BP02341.

Volume XVII: Burgess, C. A., and J. R. Skalski. 2001. Effects of ocean covariates and release timing on first ocean-year survival of fall Chinook salmon from Oregon and Washington coastal hatcheries. Technical report to BPA, Project No. 199105100, Contract 1996BI91572.

Volume XVIII: Burgess, C. A., T. J. Miller, and J. R. Skalski. 2003. Precision and accuracy of the transportation-to-inriver (T/I) ratio estimator of survival benefits to juvenile salmonids transported around the Columbia River Basin dams. Technical report to BPA, Project No. 19910500, Contract 00013690.

Volume XIX: Buchanan, R. A., and J. R. Skalski. 2006. Analysis of fall Chinook salmon PIT-tag data: Estimating transportation effects. Technical report to BPA, Project No. 198910700, Contract 00012494.

Volume XX: J. R. Skalski. 2006. Evaluation and recommendations on alternative hydroacoustic array deployments for the mouth of the Columbia River to provide estimates of salmonid smolt survival and movements. Technical report to BPA, Project No. 198910700, Contract 00012494.

Volume XXI: J. R. Skalski and J. Griswold. 2006. A summary of methods for conducting salmonid fry mark-recapture studies for estimating survival in tributaries. Technical report to BPA, Project No. 198910700, Contract 00012494.

Volume XXII: R. W. Perry and J. R. Skalski. 2008. Evaluating wetland restoration projects in the Columbia River Estuary using hydroacoustic telemetry arrays to estimate movement, survival, and residence times of juvenile salmonids. Technical report to BPA, Project No. 198910700, Contract 00012494.

Other Publications Related to this Series

Other related publications, reports and papers available through the professional literature or from the Bonneville Power Administration (BPA) Public Information Center - CKPS-1, P.O. Box 3621, Portland, OR 97208.

Hedgepeth, J. B., G. E. Johnson, J. R. Skalski, and J. Burczynski. 2002. Active fish sonar (AFTS) for assessing fish behavior. Acta Acoustic United with Acustica 88:739-742.

Skalski, J. R., R. Townsend, J. Lady, A. E. Giorgi, and J. R. Stevenson. 2002. Estimating route-specific passage and survival probabilities at a hydroelectric project from smolt radiotelemetry studies. Canadian Journal of Fisheries and Aquatic Sciences 59: 1385-139.

Skalski, J. R., J. Lady, R. Townsend, A. E. Giorgi, J. R. Stevenson, C. M. Peven, and R. D. McDonald. 2001. Estimating inriver survival of migrating salmonid smolts using radiotelemetry. Canadian Journal of Fisheries and Aquatic Sciences 58:1987-1997.

Lowther, A. B., and J. R. Skalski. 1998. A multinomial likelihood model for estimating survival probabilities and overwintering for fall chinook salmon using release-recapture methods. Journal of Agricultural, Biological, and Environmental Statistics 3: 223- 236.

Skalski, J. R. 1998. Estimating season-wide survival rates of outmigrating salmon smolt in the Snake River, Washington. Canadian Journal of Fisheries and Aquatic Sciences 55: 761-769.

Skalski, J. R., and J. A. Perez-Comas. 1998. Using PIT-tag recapture probabilities to estimate project-wide fish efficiency and spill effectiveness at Lower Granite Dam. School of Fisheries, University of Washington. Report prepared for U.S. Army Corps of Engineers, Contract No. DACW68-96-C0018, Walla Walla District, 201 North Third Street, Walla Walla, WA 99362-9265, 67 pp.

Skalski, J. R., and J. A. Perez-Comas. 1998. Using steelhead and chinook salmon PIT-tag recapture probabilities to estimate FGE and SE at Lower Granite Dam. School of Fisheries, University of Washington. Report prepared for U.S. Army Corps of Engineers, Contract No. DACW68-96-C0018, Walla Walla District, 201 North Third Street, Walla Walla, WA 99362-9265, 44 pp.

Skalski, J. R., S. G. Smith, R. N. Iwamoto, J. G. Williams, and A. Hoffmann. 1998. Use of PIT-tags to estimate survival of migrating juvenile salmonids in the Snake and Columbia Rivers. Canadian Journal of Fisheries and Aquatic Sciences 55:1484-1493.

Newman, K. 1997. Bayesian averaging of generalized linear models for passive integrated tag recoveries from salmonids in the Snake River. North American Journal of Fisheries Management 17: 362-377.

Mathur, D., P. G. Heisey, E. T. Euston, and J. R. Skalski. 1996. Turbine passage survival estimates for chinook salmon smolt (*Oncorhynchus tshawytscha*) at a large dam on the Columbia River. Canadian Journal of Fisheries and Aquatic Sciences 53:542-549.

Skalski, J. R. 1996. Regression of abundance estimates from mark-recapture surveys against environmental variables. Canadian Journal of Fisheries and Aquatic Sciences 53: 196-204.

Skalski, J. R., R. L. Townsend, R. F. Donnelly, and R. W. Hilborn. 1996. The relationship between survival of Columbia River fall chinook salmon and inriver environmental factors: Analysis of historic data for juvenile and adult salmonid production. Final report, Phase II. Technical Report (DOE/BP-35885-10) to BPA, Project 91-051-00, Contract 90-BI-02341.

Smith, S. G., J. R. Skalski, J. R., J. W. Schlechte, A. Hoffmann, and V. Cassen. 1996. Introduction to SURPH.1 analysis of release-recapture data for survival studies. Technical report DOE/BP-02341-3) to BPA, Project 89-107-00, Contract 90-BI-02341.

Newman, K. 1995. Adult salmonid PIT-tag returns to Columbia River's Lower Granite Dam. Technical report (DOE/BP-35885-5) to BPA, Project 91-051-00, Contract 87-BI-35885.

Smith, S. G., J. R. Skalski, J. R., J. W. Schlechte, A. Hoffmann, and V. Cassen. 1994. SURPH.1 Manual: Statistical survival analysis of fish and wildlife tagging studies. Technical report (DOE/BP-02341-2) to BPA, Project 89-107-00, Contract 90-BI-02341.

Dauble, D. D., J. R. Skalski, A. Hoffmann, and A. E. Giorgi. 1993. Evaluation and application of statistical methods for estimating smolt survival. Technical report (DOE/BP-62611-1) to BPA, Project 86-118-00, Contract 90-AI-62611; Project 89-107-00, Contract 90-BI-02341; and Project 91-051-00, Contract 87-BI-35885.

Skalski, J. R., A. Hoffmann, and S. G. Smith. 1993. Development of survival relationships using concomitant variables measured from individual smolt implanted with PIT-tags. Annual report 1990-1991 (DOE/BP-02341-1) to BPA, Project 89-107-00, Contract 90-BI-02341.

Skalski, J. R., and A. E. Giorgi. 1993. Juvenile passage program: A plan for estimating smolt travel time and survival in the Snake and Columbia rivers. Technical report (DOE/BP-35885-3) to BPA, Project 91-051-00, Contract 87-BI-35885.

Smith, S. G., J. R. Skalski, and A. E. Giorgi. 1993. Statistical evaluation of travel time estimation based on data from freeze-branded chinook salmon on the Snake River, 1982-1990. Technical report (DOE/BP-35885-4) to BPA, Project 91-051-00, Contract 87-BI-35885.

Giorgi, A. E. 1990. Mortality of yearling chinook salmon prior to arrival at Lower Granite Dam on the Snake River. Technical report (DOE/BP-16570-1) to BPA, Project 91-051-00, Contract 87-BI-35885.

Preface

Project 1989-107-00 was initiated to develop the statistical theory, methods, and statistical software to design and analyze PIT-tag survival studies. This project developed the initial study designs for the NOAA Fisheries/University of Washington (UW) Snake River survival studies of 1993−present. This project continues to respond to the changing needs of the scientific community in the Pacific Northwest as they face new challenges to extract life-history data from an increasing variety of fish-tagging studies. The project's mission is to help assure tagging studies are designed and analyzed from the onset to extract the best available information using state-of-the-art statistical methods. In so doing, investigators can focus on the management implications of their findings without being distracted by concerns of whether the study's design and analyses are correct.

All studies in the current series, the Design and Analysis of Tagging Studies in the Columbia Basin, were conducted to help maximize the amount of information that can be obtained from fish tagging studies for the purposes of monitoring fish survival and related demographic parameters throughout its life cycle. Volume XXIII of this series investigates the statistical independence of replicated telemetry arrays used to estimate survival from release-recapture study designs. It is critical to ensure independence of replicated telemetry arrays *before* conducting a field study because lack of independence will cause bias in parameter estimates.

Abstract

Mark-recapture studies in the Columbia basin often use closely spaced replicated telemetry arrays to estimate the probability of detecting transmitters. Using this approach, detection probabilities are estimated with the Lincoln-Petersen single mark-recapture model. The primary assumption of this model is that telemetry arrays are statistically independent, but often it is unclear how to assess the independence of telemetry arrays. In this report, we define and assess statistical independence of four different array configurations where each configuration consists of a different pair of detection zones. We found that the minimum criterion for ensuring independence among telemetry arrays is to implement one array with a detection zone that encompasses the entire fish passage zone through a volume of water (we assumed the fish passage zone consisted of the entire water column). Given this criterion is satisfied, the replicate arrays will be independent even when the second array does not completely encompass the entire water column. Arrays were not independent under scenarios where neither array encompassed the entire water column. Lack of independence introduced bias into estimates of detection probabilities, and the bias was either positive or negative depending on the nature of the array configuration. We found that the magnitude of bias may be substantial under realistic array configurations and show how bias in detection probabilities can introduce bias into biological parameters such as survival probabilities. When lack of independence between arrays has occurred in a field study, it is difficult to remove the bias or even estimate its magnitude. Thus, *prior to* conducting a study it is critical to design replicate arrays to achieve independence and to map detection zones to ensure independence.

Executive Summary

Mark-recapture studies in the Columbia basin often use closely spaced replicated telemetry arrays to estimate the probability of detecting transmitters. Using this approach, detection probabilities are estimated with the Lincoln-Petersen single mark-recapture model. The primary assumption of this model is that telemetry arrays are statistically independent, but often it is unclear how to assess the independence of telemetry arrays. In this report, we define and assess statistical independence of four different array configurations where each configuration consists of a different pair of detection zones. We found that the minimum criterion for ensuring independence among telemetry arrays is to implement one array with a detection zone that encompasses the entire fish passage zone through a volume of water (we assumed the fish passage zone consisted of the entire water column). Given this criterion is satisfied, the arrays will be independent even when the second array does not completely encompass the entire water column. Arrays were not independent under scenarios where neither array encompassed the entire water column. Lack of independence introduced bias into estimates of detection probabilities, and the bias was either positive or negative depending on the nature of the array configuration. We found that the magnitude of bias may be substantial under realistic array configurations and show how bias in detection probabilities can introduce bias into biological parameters such as survival probabilities. When lack of independence between arrays has occurred in a field study, it is difficult to remove the bias or even estimate its magnitude. Thus, *prior to* conducting a study it is critical to design replicate arrays to achieve independence and to map detection zones to ensure independence.

Table of Contents

Table of Figures

Table of Tables

Acknowledgements

Funding for this work came from the Pacific Northwest region's electrical ratepayers through the Columbia River Fish and Wildlife Program administered by the Bonneville Power Administration through Project No. 1989-107-00.

1.0 Introduction

Detection probabilities of telemetry arrays are integral parameters of mark-recapture models, allowing separation of the sampling process from the survival process. All mark-recapture models assume that individual telemetry arrays are independent from one another. Failure of this assumption could lead to bias in detection probabilities, which in turn will introduce bias into the biological parameters of interest. Therefore, it is critical to understand how lack of independence may be introduced into a mark-recapture study and to design array configurations that ensure independence among arrays.

For CJS-type models (Cormack-Jolly-Seber), telemetry arrays are often separated by tens of kilometers, but are still subject to the assumption of independence. For example, if fish do not mix throughout the water column and individuals remain vertically or horizontally stratified as they move through the series of telemetry arrays, then incomplete coverage of the water column by telemetry arrays could introduce lack of independence among the arrays. Detection probabilities are also estimated using closely spaced (< 2 km) replicate telemetry arrays. This approach uses the Lincoln-Petersen single mark-recapture model to estimate detection probabilities, and this model is typically incorporated as an auxiliary likelihood into a CJS-type model. For example, use of this auxiliary likelihood is requisite in the route-specific survival model in order to estimate route-specific detection probabilities at a hydroelectric project. Since fish are more likely to remain at constant depth or distance from shore as they migrate through closely spaced replicate arrays, ensuring independence between replicate arrays is critical to avoid bias in parameter estimates.

It is often unclear just what “independence” means (e.g. physical independence of electrical components versus statistical independence) and how lack of independence may introduce bias into estimates of detection probabilities. To better understand the direction and magnitude of bias due to non-independent telemetry arrays, we investigated how the spatial configuration of telemetry arrays affects their statistical independence. Our goals were to (1) clearly define statistical independence of telemetry arrays, (2) describe by example how array configuration may introduce lack of independence between arrays, (3) quantify detection probabilities for both independent and dependent arrays, and (4) model the magnitude of bias introduced when the assumption of independence is violated.

To assess independence, we examined detection probabilities estimated from closely spaced replicate arrays with the Lincoln-Petersen model because fish are less likely to mix over the short distance between the replicate arrays. However, our findings also extend to widely spaced arrays commonly used in CJS-type models. This analysis has practical application as researchers are often confronted with technical and logistical difficulties that limit the range of alternative array configurations. Further, once lack of independence in introduced and the study conducted, there is little recourse for removing the bias or even estimating its magnitude. Careful design *a priori* is therefore critical to ensure the assumption of independence is satisfied. Our hope is that this report assists researchers during the design phase of a study and aids in implementation of telemetry arrays that fulfill the assumption of independence.

2.0 Assessing Independence of Telemetry Arrays

To assess independence of replicate telemetry arrays, we used four possible scenarios of array configurations and subjected these scenarios to formal tests of statistical independence. First the scenarios are described and formal tests of independence defined. Next, to understand how independence or lack thereof affects estimates of detection probability, we calculate the true detection probability under each scenario and also the biased estimate of detection probability that results from applying the Lincoln-Petersen model to data from non-independent arrays. Last, for each scenario where arrays are not independent, we examine the magnitude of bias over a range of array configurations.

2.1 Defining the Scenarios: Four Array Configurations

We investigated four scenarios, each having a different spatial configuration of detection zones, to understand how array configuration affects statistical independence of the arrays (Fig. 2.1). Detection zones are defined as the area within which a transmitter has a non-zero probability of detection, and beyond which there is zero probability of detection. Specifically, we examined detection zones for each array where

1) both detection zones encompassed the entire water column,

2) one detection zone covered the entire water column, but the other array had a detection "gap" where fish in the upper 30% of the water column had a zero probability of being detected,

3) both arrays had a detection gap, but one gap occurred at the surface and the other occurred at the bottom, and

4) both arrays had a detection gap at the surface.

These scenarios consider only the vertical dimension, but the configurations in Fig. 2.1 may also be envisioned as a plan view of a river channel where detection gaps occur at either the left or right river banks. Thus, the analysis applies to the spatial configuration of telemetry arrays as viewed from any spatial dimension.

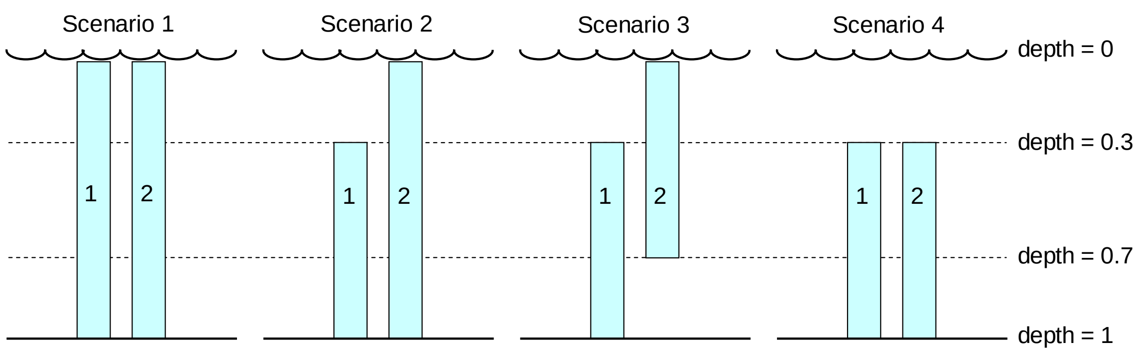

Figure 2.1. Vertical detection zones of two replicated arrays under four scenarios.

We made a number of assumptions to simplify interpretation and modeling of the four scenarios. First, by restricting attention to only the vertical (z) dimension of water column, we assumed that the detection zone completely encompassed the x, y, and t dimensions. We also assumed the probability of detection was distributed uniformly within each detection zone, and outside of the detection zone of each array the probability of detection was zero. Third, we considered relative depth from 0 (surface) to 1 (bottom) and assumed fish to be uniformly distributed from surface to bottom. This assumption greatly simplifies defining the probability of a fish passing through the detection zone. For example, if the detection zone encompasses 70% of water column and fish are uniformly distributed, then there is a 70% probability of a fish passing through the detection zone. Last, we assumed fish remained at a constant depth when passing through both arrays.

2.2 Testing for Statistical Independence

Informally, two events are statistically independent if the occurrence of one event does not affect the probability of occurrence the other event. Since detection zones do not encompass the entire water column under Scenarios 2, 3, and 4, we have four events to consider:

Event A_1 – a fish passes through the detection zone of array 1.

Event A_2 – a fish passes through the detection zone of array 2.

Event D_1 – a fish is detected by array 1.

Event D_2 – a fish is detected by array 2.

However, to test whether the arrays are independent, we need only consider events A_1 and A_2. A formal test of statistical independence of these events is

$$\Pr(A_1 \cap A_2) = \Pr(A_1)\Pr(A_2) \tag{1}$$

where $\Pr(A_1 \cap A_2)$ is the probability of a fish passing through the detection zone of both arrays and $\Pr(A_1)$ and $\Pr(A_2)$ is the probability of passing through the detection zone of each array. Thus, if $\Pr(A_1 \cap A_2) \neq \Pr(A_1)\Pr(A_2)$, then the telemetry arrays are not independent. Given known detection zones and event probabilities, we can subject each scenario to these formal definitions to determine the independence of the arrays.

For scenario 1, we should expect the arrays to be independent since both detection arrays encompass the entire water column. Thus, the probability of fish passing through either detection zone is 1 ($\Pr(A_1) = \Pr(A_2) = 1$). Since the overlap of the two detection zones encompasses the entire water column, $\Pr(A_1 \cap A_2) = 1$. Clearly, $\Pr(A_1 \cap A_2) = \Pr(A_1)\Pr(A_2)$, and independence is satisfied under Scenario 1.

For scenario 2, the first detection zone covers 70% of the water column and the second detection zone covers the entire water column, so $\Pr(A_1) = 0.7$ and $\Pr(A_2) = 1$. From examining Figure 2.1, we can see that the vertical overlap of the two detection zones encompasses 70% of the water column and thus $\Pr(A_1 \cap A_2) = 0.7$. Again we find $\Pr(A_1 \cap A_2) = \Pr(A_1)Pr(A_2)$ and independence is satisfied under Scenario 2.

Under scenario 3, each detection zone covers 70% of the water column so the probability of a fish passing through the detection zone of each array is 0.7 (i.e., $\Pr(A_1) = \Pr(A_2) = 0.7$). The overlap of the two detection zones encompasses 40% of the water column and thus $\Pr(A_1 \cap A_2) = 0.4$. However, note that $\Pr(A_1)\Pr(A_2) = 0.49$ and thus $\Pr(A_1 \cap A_2) \neq \Pr(A_1)\Pr(A_2)$. We therefore conclude that the arrays are *not* independent under Scenario 3.

Scenario 4 is similar to scenario 3 in that the probability of fish passing through each array is 0.7, but now the detection zones of both arrays encompass the same area of the water column, and any fish passing through the upper 30% of the water column will not be detected. The overlap of detection zones encompasses 70% of the water column, so $\Pr(A_1 \cap A_2) = 0.7$. Again we find $\Pr(A_1)\Pr(A_2) = 0.49$, and $\Pr(A_1 \cap A_2) \neq \Pr(A_1)\Pr(A_2)$. We find that the arrays are *not* independent under Scenario 4.

2.3 Quantifying Bias Induced by Lack of Independence

Having established independence of arrays in each scenario, the next step is to understand how the lack of independence introduces bias into estimates of detection probabilities. To quantify bias, we first define equations for the true detection probability of arrays in each scenario discussed above. These equations define the true model under which frequencies of detection histories will be generated. Next, likelihood models are described to estimate detection probabilities from telemetry data. Given an estimation model (i.e., the Lincoln-Petersen model) and the true model under which detection data is generated, we then examine the magnitude of bias introduced by applying a model that assumes independence to data from arrays that are not independent.

2.3.1. The True Probability of Detection

Because detection zones in each scenario cover different fractions of the water column, the overall detection probability of each array is a weighted average of the detection probabilities inside and outside the detection zone with weights equal to the fraction of fish passing inside and outside of the detection zone. Thus, the unconditional probability of detection for telemetry array 1 can be defined in context of the events described above:

$$\begin{aligned} P_1 &= \Pr(A_1)\Pr(D_1|A_1) + \Pr(A_1^c)\Pr(D_1|A_1^c) \\ &= \Pr(A_1)\Pr(D_1|A_1) \end{aligned} \tag{2}$$

Returning to our definition of the four possible events, D_1 is the event that a fish is detected by array 1, and thus $\Pr(D_1|A_1)$ is the probability of being detected by array 1 given that a fish passes through the detection zone of array 1. Event A_1^c is the complement of A_1, which is the event that a fish *does not* pass through the detection zone of array 1. Since the detection probability is zero outside of the detection zone, $\Pr(D_1|A_1^c) = 0$ and the equation simplifies. The detection probability for array 2 (P_2) is defined similarly.

The probability of being detected by both arrays is:

$$P_{12} = \Pr(A_1 \cap A_2)\Pr(D_1|A_1)\Pr(D_2|A_2) \tag{3}$$

Note that this equation holds for all four scenarios regardless of whether the arrays are independent. The primary parameter of interest in mark-recapture models is the overall detection probability (P), which is the probability of being detected by either array 1 or array 2:

$$P = P_1 + P_2 - P_{12} \tag{4}$$

2.3.2. The Estimate of *P* from Telemetry Data

In a field study, the goal is to estimate P from the observed counts of fish detected by only the first array (detection history "10"), detected by only the second array (detection history "01"), and detected by both arrays (detection history "11"). Without assuming independence between the arrays, the probability of occurrence of each detection history is shown in Table 2.1. Thus, the model in Table 2.1 applies to all four scenarios and represents the true model under which detection histories will be generated. However, a problem arises when attempting to estimate the parameters of this model from telemetry data. The model contains three unique parameters (P_1, P_2, and P_{12}) but there are only two minimum sufficient statistics, and therefore only two unique parameters can be estimated from the data. However, if we assume the arrays are independent, then $P_{12} = P_1P_2$ (recall the definition of independence in Eq. 1), and the likelihood model in Table 2.1 reduces to the Lincoln-Petersen model (Table 2.2). Note there are only two unique parameters in the Lincoln-Petersen model and both are estimable. This analysis shows how the assumption of independent arrays becomes embodied in the Lincoln-Petersen model.

The maximum likelihood estimators for the Lincoln-Petersen model are

$$\hat{P}_1 = \frac{n_{11}}{n_{01} + n_{11}} \tag{5}$$

$$\hat{P}_2 = \frac{n_{11}}{n_{10} + n_{11}} \tag{6}$$

where n_{11} is the number of fish detected by both arrays, n_{01} is the number of fish detected by the second but not the first array, and n_{10} is the number of fish detected by the first but not the second array. The overall probability of detection (P) is estimated as in Eq. 4, where $P_{12} = P_1P_2$ because independence is assumed:

$$\hat{P} = \hat{P}_1 + \hat{P}_2 - \hat{P}_1\hat{P}_2 \tag{7}$$

$$= \frac{n_{11}\left(n_{10} + n_{01} + n_{11}\right)}{\left(n_{01} + n_{11}\right)\left(n_{10} + n_{11}\right)}$$

Table 2.1. Probability of occurrence for each detection history when independence between arrays is not assumed.

Detection history	Probability of occurrence
11	$P_{12}/(P_1 + P_2 - P_{12})$
10	$(P_1 - P_{12})/(P_1 + P_2 - P_{12})$
01	$(P_2 - P_{12})/(P_1 + P_2 - P_{12})$

Table 2.2. Probability of occurrence for each detection history of the Lincoln-Petersen model, which assumes independence between telemetry arrays.

Detection history	Probability of occurrence
11	$P_1P_2/(P_1 + P_2 - P_1P_2)$
10	$P_1(1 - P_2)/ (P_1 + P_2 - P_1P_2)$
01	$P_2(1 - P_1)/ (P_1 + P_2 - P_1P_2)$

2.3.3. The Biased Probability of Detection

Given the scenarios described above, we can calculate the bias that arises from applying the Lincoln-Petersen model to data from non-independent telemetry arrays. The (possibly) biased estimates are calculated by substituting the probability of occurrence of each detection history in Table 2.1, which does not assume independence, into the Lincoln-Petersen estimators (Eq. 5 and 6), which do assume independence. Here, the detection history probabilities in Table 2.1 are used as the expected *relative* counts of the detection histories in the Lincoln-Petersen estimators. Using this approach, the equations for the detection probabilities reduce to:

$$\tilde{P}_1 = \frac{P_{12}}{P_2} \tag{8}$$

$$\tilde{P}_2 = \frac{P_{12}}{P_1} \tag{9}$$

where $\tilde{P}_1$ and $\tilde{P}_2$ represent the biased detection probabilities that will result when applying the Lincoln-Petersen model to non-independent arrays. Note that re-arrangement of Eq. 8 and 9 yields $P_1P_2 = P_{12}$ (the definition of statistical independence in Eq. 1) explicitly showing how independence is couched in the Lincoln-Petersen estimators.

The true (unbiased) detection probabilities are calculated using Eq. 4–6 with the known event probabilities of each scenario. The right-hand side of Eq. 8 and 9 is calculated using Eq. 4 and 5, and $\tilde{P}$ is calculated with Eq. 7 substituting $\tilde{P}_i$ for $\hat{P}_i$. Bias is calculated as the Lincoln-Petersen estimates ($\tilde{P}_1$, $\tilde{P}_2$, and $\tilde{P}$) minus the true values (P_1, P_2, and P). Thus, we should expect bias to be zero under scenarios 1 and 2, but non-zero under scenarios 3 and 4. For all scenarios we used a value of 0.6 for the probability of detection within each detection zone (i.e., $\Pr(D_1|\, A_1) = \Pr(D_2|\, A_2) = 0.6$; Table 2.3).

Table 2.3. Input parameter values based on the scenarios defined in Fig. 2.1 for calculating true and Lincoln-Petersen estimates of detection probabilities.

	Scenario 1	Scenario 2	Scenario 3	Scenario 4
Arrays Independent?	Yes	Yes	No	No
$\Pr(A_1)$	1.000	0.700	0.700	0.700
$\Pr(A_2)$	1.000	1.000	0.700	0.700
$\Pr(A_1 \cap A_2)$	1.000	0.700	0.400	0.700
$\Pr(D_1|\, A_1) = \Pr(D_2|\, A_2)$	0.600	0.600	0.600	0.600

As expected, the Lincoln-Petersen model produced unbiased estimates under Scenarios 1 and 2 when the arrays are independent but produced biased estimates under Scenarios 3 and 4 when arrays are not independent (Table 2.4). The Lincoln-Petersen estimator produces negatively biased detection probabilities under Scenario 3, but positively biased detection probabilities under Scenario 4. Furthermore, the magnitude of bias in P is quite substantial under both scenarios, highlighting the sensitivity of the Lincoln-Petersen model to violations in the assumption of independence.

Next, we extended these results to a range of detection zones for scenarios 3 and 4 to understand the magnitude of bias as a function of the size of the detection gap (Fig. 2.2). Under Scenario 3, as the detection gap increases, the Lincoln-Petersen estimate of P declines more quickly than the true value of P, causing negative bias. Negative bias in the Lincoln-Petersen estimate is less than 5 percentage points when the size of the detection gap of each array is less than 20% of the water column. However, bias increases at an accelerating rate as the detection gap increases above 20%. Under Scenario 4, the Lincoln-Petersen estimate remains constant but the true value of P declines, causing positive bias in the Lincoln-Petersen estimate. Under scenario 4, positive bias is less than 5 percentage points when the size of the detection gap is less than 5% of the water column, but increases linearly with the size of the detection gap.

Table 2.4. True values of detection probabilities compared to those estimated under the Lincoln-Petersen model for the scenarios defined in Fig. 2.1 and input parameters given in Table 2.3.

Parameter	True value	Lincoln-Petersen estimate	Bias
	Scenario 1		
P_1	0.600	0.600	0.000
P_2	0.600	0.600	0.000
P	0.840	0.840	0.000
	Scenario 2		
P_1	0.420	0.420	0.000
P_2	0.600	0.600	0.000
P	0.768	0.768	0.000
	Scenario 3		
P_1	0.420	0.343	-0.077
P_2	0.420	0.343	-0.077
P	0.696	0.568	-0.128
	Scenario 4		
P_1	0.420	0.600	0.180
P_2	0.420	0.600	0.180
P	0.588	0.840	0.252

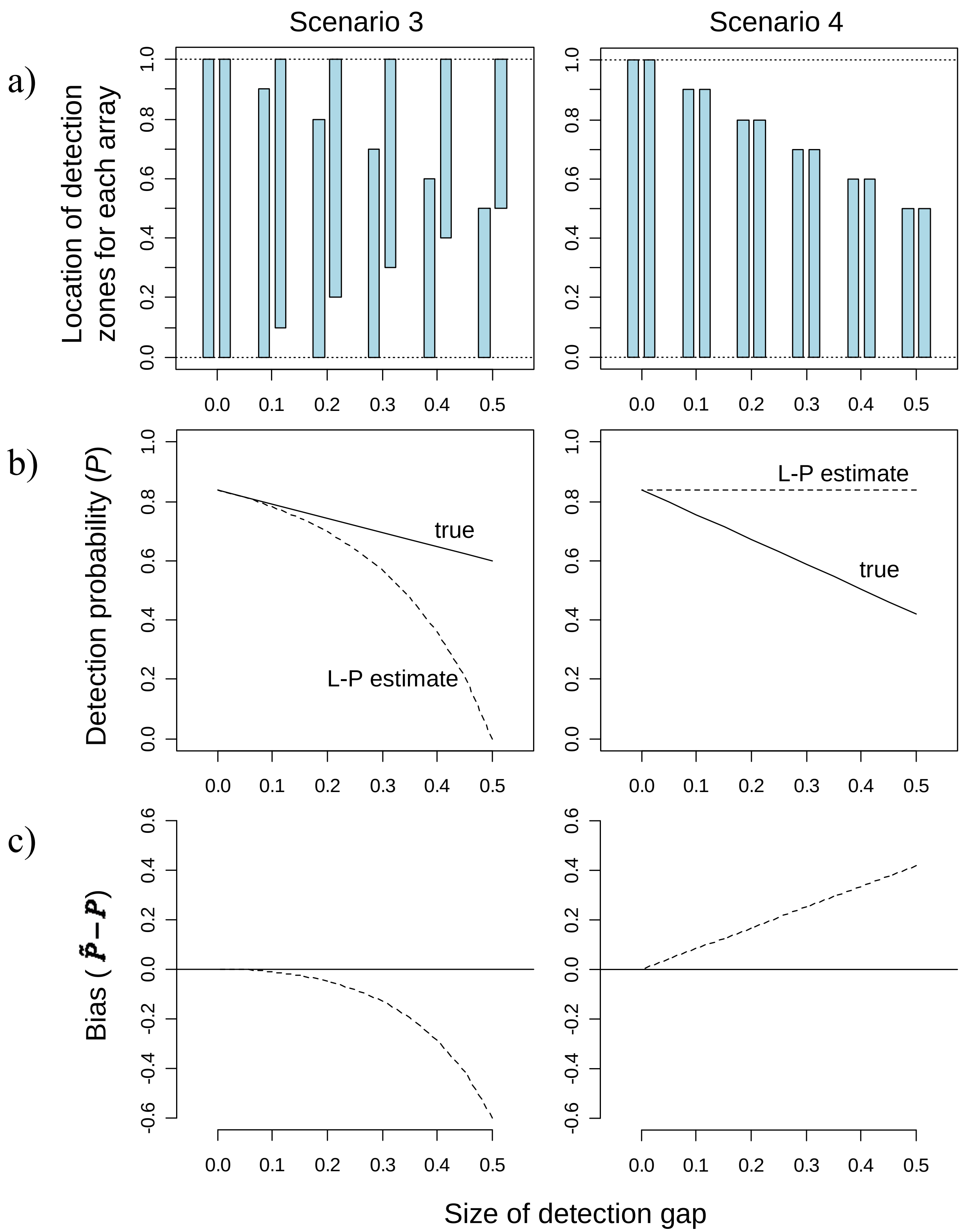

Figure 2.2. Location of detection zones (a), true and Lincoln-Petersen (L-P) estimates of *P* (b), and bias in Lincoln-Petersen estimates (c) under Scenarios 3 and 4 (left and right column) as a function of the size of the detection gap of each telemetry array.

3.0 Discussion and Recommendations

Our analysis raises a number of important considerations for researchers implementing replicated telemetry arrays. Most importantly, to ensure independence between replicated telemetry arrays, the minimum design criterion is one telemetry array where the detection zone encompasses the entire fish passage zone through a volume of water. If this design criterion is satisfied, then the assumption of independence will be fulfilled even when the detection zone of the second array does not completely encompass the water column. However, as shown under Scenarios 3 and 4, when neither detection zone fully encompasses the water column, the assumption of independence will be violated and the consequence will be bias in the detection probabilities.

The direction of bias for non-independent arrays will depend on the nature of the array configuration. If both arrays combined cover the entire water column (as in Scenario 3) then detection probabilities will be negatively biased. In this case, negative bias occurs because the ratio of the number of fish detected by both arrays to the total number of fish detected is less than expected under the assumption of independence. In contrast, detection probabilities will be positively biased when both arrays cover the same fraction of the water column but a detection gap exists where fish are never detected (as in Scenario 4). Here, positive bias results because ratio of the number of fish detected by both arrays to the total number of fish detected is greater than expected under independence.

The magnitude of bias differed under each scenario, with the Lincoln-Petersen model being most sensitive to violations of independence under Scenario 4. For example, due to the non-linear trend in bias under Scenario 3, bias remains relatively low (<5%) even if the detection gap of each array is 20% of the water column (Fig. 2.2). In contrast, under Scenario 4 the bias is roughly 15% when the detection gap is 20% of the water column. Although some scenarios are relatively robust to the violation of independence, we recommend researchers strive to achieve independence between the arrays because estimating the magnitude of bias from field data is often extremely difficult, if not impossible. Furthermore, since bias in detection probabilities will introduce bias into the biological parameters, the necessary course of action is to design for independence.

Although we have shown how different array configurations may introduce bias into detection probabilities, ultimately, interest lies in understanding how bias in P affects estimates of the biological parameters. Consider a replicated array that is implemented at the last telemetry station in a single-release mark-recapture study (i.e., a CJS model). In a CJS model, only the joint probability (λ) of surviving the last reach (S) and being detected at the last array (P) can be estimated from the data. However, if we use the Lincoln-Petersen model to estimate P at the last array, then S can be calculated as $S = \lambda/P$. Thus, when P is negatively biased S will be positively biased, and when P is positively biased S will be negatively biased. Now suppose that the true survival is 0.8. Based on Scenarios 3 and 4 shown in Fig. 2.1 and Table 2.4, our estimate of S would be 0.98 and 0.56 and the bias is 0.18 and -0.24 respectively for scenario 3 and 4. As this example shows, it is critical to achieve independence between telemetry arrays as the magnitude of bias in biological parameters may be substantial.

To simplify our analysis, we assumed fish were uniformly distributed throughout the water column, but a non-uniform spatial distribution could either magnify or reduce the bias introduced by non-independent arrays. For example, under scenario 4 with a detection gap at the surface where fish are not detected (Fig. 2.1), we would expect the vertical distribution of juvenile salmonids to be concentrated near the surface. This vertical distribution decreases the probability of fish passing through the detection zone (relative to a uniform distribution), which would consequently increase the magnitude of positive bias compared to our findings. In contrast, radio-telemetry arrays consisting of aerial antennas are often used to monitor movements of juvenile salmonids, but are unable to detect fish deeper than about 10 m. For this example, the surface concentration of juvenile salmonids increases the probability of passing through the detection zone relative to a uniform vertical distribution. Thus, the magnitude of bias would be less than expected under a uniform vertical distribution. These examples show that the magnitude of bias will depend strongly on the interaction between the spatial distribution of fish and spatial coverage of the replicated telemetry arrays. This interaction causes great difficulty in accurately quantifying bias introduced by non-independent arrays in a field study and stresses the importance of implementing independent telemetry arrays.

Our findings also apply to widely spaced telemetry arrays used in CJS-type models to estimate survival over an entire study area. Here the key process affecting the magnitude of bias is the mixing of individuals across space and time. For example, even if juvenile salmonids are concentrated near the surface, variation in the depth of individuals across space and time will ensure that telemetry arrays “draw” a random sample from the population at any given array, regardless of the detection zone of individual arrays. Thus, mixing of individuals over space as they migrate through the study area ensures independence among the telemetry arrays in CJS-type study designs. However, fish may not fully mix across space and time due to individual variation in habitat preferences. For instance, some individuals could prefer shallow depths whereas others always remain deep as they migrate through the study area. In the case of aerial radio-telemetry arrays, individual variation in depth preference would lead to positive bias (similar to scenario 4) if some individuals preferred to migrate at depths greater than 10 m. A similar scenario could occur in PIT-tag studies if some fish consistently pass hydroelectric projects through fish passage facilities (where PIT-tag detectors are located), whereas other individuals prefer to pass through unmonitored passage routes such as turbines or spillways. Again, the bias here is of the nature described in scenario 4. The best solution to lack of mixing in CJS-type study designs is to ensure that the detection zones of all arrays fully encompass the spatial distributions of the fish. This array configuration leads to a random sample of the population and ensures independent detection probabilities across the arrays.

This report outlines scenarios under which the assumption of independence of telemetry arrays is fulfilled or violated, and assesses the consequences of non-independence between arrays. Our findings can be used to help design independent arrays prior to a field study. However, it is also important for investigators to verify the spatial extent of the detection zones once the arrays are deployed and before the study is conducted. Only then can researchers be sure that telemetry arrays are independent and ensure that detection probabilities and biological parameters are estimated without bias.