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Selection and Application of a Mark-and-Recapture Technique for Estimating Pink Salmon Escapements

by

J. M. Maselko, A. C. Wertheimer, and J. F. Thedinga

U.S. DEPARTMENT OF COMMERCE

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Alaska Fisheries Science Center
7600 Sand Point Way N.E.
Seattle, WA 98115
www.afsc.noaa.gov

U.S. DEPARTMENT OF COMMERCE

Donald L. Evans, Secretary

National Oceanic and Atmospheric Administration

Vice Admiral Conrad C. Lautenbacher, Jr., U.S. Navy (ret.), Under Secretary and Administrator

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ABSTRACT

As part of a larger study to estimate straying rates of pink salmon (*Oncorhynchus gorbuscha*), escapements of pink salmon were estimated for eight streams in lower Chatham Strait, southeastern Alaska. Prior to stream sampling, computer simulations were used to compare stratified Schaefer and Petersen population estimators. The Petersen estimator was chosen for superior performance and used in conjunction with an efficient sampling design to calculate escapement for the eight streams. Live fish entering each stream were tagged with two opercular tags to account for tag loss, and streams were surveyed for tagged carcasses. Streams were sampled at least twice per week after fish were tagged. Petersen escapement estimates varied from 8,609 fish at William Creek to 79,070 fish at Deep Cove Creek, and all estimates had low coefficients of variation (≤ 0.11) and narrow confidence intervals. Some of the tagged fish were observed later in streams other than where they were tagged. Estimates of these “probing” fish varied from 0 to 11.7% of the estimated escapements. We used the estimates of probing to adjust the escapement estimates and variances.

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INTRODUCTION

Fishery managers and researchers working with salmon (*Oncorhynchus* spp.) often require estimates of escapements. Methods for estimating escapements include weirs, foot and aerial surveys, and mark-recapture experiments. The choice of method is often constrained by limited resources. As part of a research project to examine straying of pink salmon (*O. gorbuscha*) (Wertheimer et al. 1999, Thedinga et al. 1999), we needed escapement estimates for a number of streams. We also needed to examine all available salmon carcasses in the streams to determine the number of fish marked as fry that spawned in the streams. Weirs to enumerate and examine live fish or mark-recapture techniques would have been suitable; however, weirs are expensive to build and operate, and we wanted to examine post-spawning fish. Hence, we chose to tag live fish captured in a stream and recover their carcasses after spawning.

Mark-recapture methods to estimate fish populations are based on either an open- or a closed-population model. In a closed model, a fixed population size during sampling is assumed. An open model allows for the population size to change during sampling. The open-population model most often used is the Jolly-Seber model (Parker 1968, Sykes and Botsford 1986, Schwarz et al. 1993), whereas the Petersen and Schaefer models are commonly used for closed populations (Schwarz et al. 1993). The Schaefer model is commonly used in populations not meeting all the assumptions under the Petersen model (Law 1994, Boydston 1994).

In a 1995 pilot study, a carcass mark-recapture sampling design was used to estimate pink salmon escapement into Lovers Cove Creek (Wertheimer et al. 1997). The Jolly-Seber model (Parker 1968, Sykes and Botsford 1986) was used to estimate escapement. However,

during floods, many carcasses were flushed out of the stream sampling area, causing the loss of whole time strata from which no recoveries were made and which resulted in a biased estimate of escapement (Parker 1968).

To compensate for the dynamic nature and frequent flooding of the streams, we decided to tag live fish entering a stream and recover the marks later from carcasses after spawning. We assumed the tagged fish would remain within the stream and would disperse throughout the spawning area before dying. The Jolly-Seber estimator was no longer appropriate because our design precluded multiple recaptures; marking and sampling were not concurrent. Sykes and Botsford (1986) point out that in carcass-tagging, fresh carcasses are sampled more easily than decayed ones, resulting in undercounting older, more decayed tagged carcasses. Marking live fish addresses the problems associated with carcass tagging and stream flooding, provided that the tagged fish mix with the escapement and flooding does not remove them.

Pink salmon escapement may be regarded as a closed population for which all fish can be examined as they enter a stream and again later as the entire spawning area is sampled for marks. When marking and recovery sampling take place throughout the run and the spawning area, respectively, all fish pass through the marking area and become carcasses in the recovery sampling area. Using surveys at fixed intervals over the course of recovery sampling, equal probability of recapturing all fish can be assumed. A fixed number of fish escape into a stream system, and when the run has finished, this number will not change unless immigration or emigration occur. In a mark-and-recapture study to estimate escapement of coho salmon (*O. kisutch*), Schwartz et al. (1993) showed that the Petersen

closed-population model gives acceptable results similar to results from open-population models when a constant proportion of carcasses is sampled (as expected with our recovery surveys), or a constant proportion of the population is marked (unlikely with our tagging schedule).

We therefore decided to use a closed population estimator. Prior to beginning field sampling, we generated population estimates for simulated, hypothetical, pink salmon spawning escapements to compare performance of the Schaefer model population temporally (stratified) to that of the Petersen model population (unstratified). We simulated three different levels of marking intensity to determine numbers of fish to mark and used both models to estimate known simulated escapements.

METHODS

Simulation Model

Simulation Methods

A Monte Carlo model was used to simulate a large number of mark-and-recapture experiments on a hypothetical pink salmon escapement of 30,003 fish, which was the average expected escapement of the streams to be sampled. All the simulated fish entered the stream, spawned, and died within 45 days. Live fish entry pattern was normal and occurred only during the first 30 days. Carcasses were recovered until day 45. The escapement was divided into two temporal distributions: live fish available for marking (marking distribution) and carcasses by day after first entry (Fig. 1). The marking distribution equaled the live fish in the stream minus the live fish that were already marked. When plotted by day, after first entry, the available live fish produce the marking distribution. The distribution of the entry

timing was based on long-term averages of spawner returns to Sashin Creek in southeastern Alaska (Heard 1991). Daily fish deaths were generated by assuming that the live fish had a 0.8 probability of dying 8 days after they had entered the stream (Heard 1991, Sharr and Bue 1993). Subsequent mortality was also 0.8 of the leftover fish per day after the initial 8 days. The carcasses available for sampling from which recoveries were made equaled the sum of all daily mortalities minus previously recovered carcasses (Fig. 1).

A fixed number of fish were marked from the marking distribution during each of five events, 4 days apart. The first marking event began when fish first entered the stream. The last marking event was on day 31 of the run, when most fish were in the stream and effort shifted to recovery of carcasses. To determine the sensitivity of the population estimates to marking effort, three marking levels were examined: 100, 200, and 300 fish per event.

“Recoveries” were made from the carcass distribution. The random number of recovered carcasses at a sampling event equaled the product of a uniform (0, 0.5) random number and the number of available carcasses. The random number of recovered marked carcasses equaled the product of a uniform (0, 1) random number, the marked proportion of fish in the stream, and the number of carcasses recovered. This recovery model was intended to simulate a range of possibilities expected under varying environmental conditions -- from floods that could flush most carcasses out (resulting in few recoveries) to droughts (resulting in high carcass retention and recoveries; Fig. 2). Recovery sampling did not take place until after the second marking event, when tagged fish began to die and enter the carcass distribution. Sampling continued every 4 days until day 44.

Two mark-and-recapture population estimators, Schaefer (Pooled Petersen) and Petersen (Seber 1982), were used. The Schaefer estimator stratifies the population by time, generating an estimate for each marking event. The Schaefer estimate for population size, N_s , is

$$\hat{N}_s = \sum_{i=1}^t \sum_{j=1}^u \frac{n_j m_i c_{ij}}{c_i c_j},$$

where m_i = number of fish marked at event i , c_{ij} = number of carcasses recovered at event j that were marked at event i , c_i = total number of carcasses recovered that were marked at event i , c_j = total number of carcasses recovered at event j , n_j = total number of carcasses examined at event j , t = total number of marking events, and u = total number of recovery events.

Our purpose for modeling was to decide whether mark-and-recapture sampling should be stratified throughout the escapement or treated as a single mark and recapture. Therefore, the simple Petersen and the Schaefer estimators were compared to examine the appropriateness of time stratification. To apply the Petersen estimator, the sequence of marking and recapture events was considered as a single experiment. The number of marks are summed for all marking events, and the number of carcasses and recaptures are summed for all recapture events. The Petersen estimate for population size, N_p , is

$$\hat{N}_p = \frac{\sum_{i=1}^t m_i \sum_{j=1}^u n_j}{\sum_{i=1}^t \sum_{j=1}^u c_{ij}}.$$

Both Schaefer and Petersen estimates were computed for each of 1,000 mark-and-recapture simulations generated for each of the three levels of marking intensity. Monte Carlo means and variances were computed for each marking level.

Simulation Results

As expected, precision of the escapement estimate was positively related to the marking effort and the proportion of marked carcasses recovered (Robson and Regier 1964). Standard errors of both the Schaefer and Petersen estimators were reduced with increase in the number of fish marked at a marking event (m_i) and the proportion of marked fish recovered (Table 1; Fig. 3). Bias, or average error, decreased with number of fish marked (Table 1) but was always negligible.

The Schaefer escapement estimator produced more outliers than the Petersen estimator (Fig. 4). Errors in estimation were especially large when no recoveries ($c_{.i} = 0$) were made during a recovery event j of tagged fish released during a marking event i . The standard deviations of the Schaefer estimates were almost twice those of the Petersen estimates (Table 1). When no tagged fish were recovered from a release event ($c_i = 0$), the escapement calculation was based on the remaining marking events as we assumed that all the carcasses from that stratum were flushed out of the stream. Overall, the Petersen

estimator was unaffected by whole strata losses because the total proportion of marked to unmarked carcasses remained unchanged.

The standard deviation of the Petersen population estimates was similarly affected by marking and sampling intensity. The standard deviation increased almost threefold when m_i decreased from 300 to 100 marks per marking event at all tag-recovery proportions. The standard deviation increased only 50% when m_i was decreased from 300 to 200 marks. The proportion of tagged fish recovered had an even greater effect on the error estimates (Fig. 4). Under actual field conditions of this study, tag recoveries are expected to range from 10% to 30%.

Based on this simulation, the Petersen model was selected to estimate pink salmon escapement because it produced more consistent and precise estimates. Although both estimators showed less than 0.1% bias, the Petersen model biased high and the Schaefer model biased low, with the overall bias smaller for the Petersen model (Table 1). In the field, however, we observed increased bias due to tag loss and fish leaving the streams. To account for that bias, we reduced the original number of tagged fish to account for tag loss, and subtracted estimated numbers of fish leaving the stream from escapement estimates. Escapement estimates were computed with Bailey's modified Petersen estimator.¹ Precision of estimates was determined by a combination of a parametric bootstrap method and the delta method.

¹Murphy, M. L., J. F. Thedinga, and J. J. Pella. 1994. Bootstrap confidence intervals for trap-efficiency estimates of migrating fish. Unpublished manuscript, Auke Bay Laboratory, 11305 Glacier Hwy., Juneau, Alaska, 99801-8626.

Field Application

Field Methods

The study streams consisted of eight of the most productive pink salmon spawning streams in lower Chatham Strait within a 35-km radius of the Little Port Walter research hatchery (LPW) on Baranof Island, southeast Alaska (Fig. 5). The study was based out of LPW as it was part of a larger study effort to estimate straying rates of pink salmon released from the LPW hatchery. Stream selection was based on aerial survey counts by personnel of the Alaska Department of Fish and Game (ADF&G).²

Based on the simulation and available resources, the target tagging effort was set at 300 pink salmon per each of five marking events in each stream. Live fish were tagged above the mean high water in the first pool with adequate numbers of fish. Fish were seined with a beach seine or a pole seine, then tagged with a Ketchum No. 1 operculum tag on each operculum. The tags, aluminum “staples” commonly used in the poultry industry to tag the wings of chicks, were numbered with a 5-digit code, allowing stream and time of tagging to be determined from recaptured carcasses. The tags were inconspicuous so that samplers (or predators and scavengers) were not attracted to marked fish. Fish were handled carefully and released immediately after they were tagged to minimize the possibility of stress-induced straying (Thrower 1988).

Recovery consisted of hiking the streams and examining each observed carcass for a tag on either operculum. Each carcass was counted as tagged or untagged and chopped in half to avoid resampling. For each tagged carcass, both (if present) tag numbers were

²Scott Johnson, ADF&G, Douglas, Alaska; pers. commun. July 1996.

recorded to estimate tag-loss rates. Numbers of marking and recovery events were equal; both were usually done on the same day.

Streams were sampled from 1 September to 10 October, which effectively encompassed the spawning period. Three crews of three or four people each sampled the streams. In six streams, fish were tagged and carcasses were recovered twice per week. The two main streams nearest LPW, Lovers Cove and Borodino Creeks, were sampled more intensely to maximize recoveries of coded-wire tags from the associated straying studies (Wertheimer et al. 1999, Thedinga et al. 1999). These two streams were sampled four times weekly; in addition, carcass weirs were constructed across the outlets of these streams to increase carcass recoveries. The weirs were checked daily until they were destroyed by floods in early October.

In addition to the 8 streams sampled systematically, 28 streams and one hatchery (Armstrong-Keta, Inc. (AKI)) within 50 km of LPW were also sampled for tagged fish. We sampled the total return at the LPW hatchery and at the weir on Sashin Creek; the other streams were sampled opportunistically, with no attempt to estimate the proportion of the population sampled.

Estimation

The escapement to each stream was estimated using Bailey's adjustment of the Petersen estimator, which corrects for statistical bias of the uncorrected Petersen formula (Seber 1982):

$$\hat{N}_b = \frac{\sum_{i=1}^t m_i \left(1 + \sum_{j=1}^u n_j \right)}{1 + \left(\sum_{i=1}^t \sum_{j=1}^u c_{ij} \right)},$$

with a variance of

$$\text{Var}(\hat{N}_b) = \frac{\left(\sum_{i=1}^t m_i \right)^2 \left(1 + \sum_{j=1}^u n_j \right) \left(\sum_{j=1}^u n_j - \sum_{i=1}^t \sum_{j=1}^u c_{ij} \right)}{\left(1 + \sum_{i=1}^t \sum_{j=1}^u c_{ij} \right)^2 \left(2 + \sum_{i=1}^t \sum_{j=1}^u c_{ij} \right)}.$$

Because we tagged both opercula, we were able to estimate the number of carcasses recovered that were missing both tags assuming that the losses were independent. Let the probability of losing one tag be denoted by p , and let the numbers of carcasses recovered with no tags, a single tag, and with both tags present be denoted by m_0 , m_1 , and m_2 , respectively. First, an estimate of p is obtained from the observed m_1 and m_2 . The probability that a fish lost both tags is p^2 if the losses are independent events, and so the probability the fish lost either one or none of the tags is $1-p^2$. If attention is restricted to recovered carcasses with one or two tags present, these counts are binomially distributed with parameter, $N = m_1+m_2$, and

respective probabilities, $2p(1-p)/(1-p^2)$ and $(1-p)^2/(1-p^2)$. The corresponding maximum likelihood estimate of p is

$$\hat{p} = \frac{\frac{m_1}{2}}{\frac{m_1}{2} + m_2}.$$

If the number of fish losing both tags, m_0 , were known, an estimate of p would equal the fraction of total tags lost, or

$$\tilde{p} = \frac{2m_0 + m_1}{2(m_0 + m_1 + m_2)} = \frac{m_0 + \frac{m_1}{2}}{(m_0 + m_1 + m_2)}.$$

Setting the two estimates of p equal and solving for m_0 produces the estimate for carcasses missing both tags as

$$\hat{m}_0 = \frac{m_1^2}{4m_2}.$$

Additional uncertainty was introduced by tag loss and by *probing* -- fish entering the stream but subsequently leaving to spawn elsewhere. To account for this, escapement and variance were then estimated with a parametric bootstrap procedure. This estimation

procedure provides a bootstrap point estimate and bootstrap variance for the population at tagging time, including fish that die in the stream (either after spawning or as pre-spawning mortality due to factors such as predation and stranding) and probing fish. The average estimated escapement and variance of escapement estimate from 1,000 simulations were used as point estimates. Probing was evident in a particular stream, A, by the recovery in stream A of fish tagged in another stream, B, (immigration of probing fish) and by the recovery in stream B of fish tagged in stream A (emigration of probing fish).

Immigration and emigration of tagged fish were accounted for differently. Tagged carcasses that originated in other streams were simply counted as unmarked fish for estimating escapement to the stream where they ultimately spawned. Emigration of tagged fish was more difficult to estimate than immigration. We estimated the number of fish emigrating from stream A into stream B by using tag recoveries from stream B, and by expanding the sampling effort in stream B, using the following variables: R_{ab} = observed number of fish tagged in stream A, and later recovered in stream B, T_a = number of fish tagged in stream A, T_b = number of fish tagged in stream B, R_b = observed number of fish tagged in stream B, and later recovered in stream B, C_a = number of carcasses examined in stream A, C_b = number of carcasses examined in stream B, N_a = unknown escapement to source stream A, N_b = unknown escapement to target stream B, N_{ab} = unknown number of probers from stream A that went into stream B, and T_{ab} = unknown number of fish tagged in stream A that went into stream B.

Our two assumptions were that

$$\frac{T_{ab}}{T_a} = \frac{N_{ab}}{N_a}, \text{ and} \quad (1)$$

$$\frac{T_{ab}}{R_{ab}} = \frac{T_b}{R_b}. \quad (2)$$

Assumption (2) ignores emigrants from stream B, and provided their fraction is small, the assumption should provide a reasonable approximation for estimating T_{ab} below. Therefore, the estimated number of fish leaving stream A and arriving in stream B from Assumption(1) was

$$\hat{N}_{ab} = \frac{\hat{T}_{ab}}{T_a} \hat{N}_a,$$

where the estimated number of fish tagged in stream A that went into stream B from Assumption (2) was

$$\hat{T}_{ab} = R_{ab} \frac{T_b}{R_b},$$

and the estimated escapement to stream A was \hat{N}_a . After substitution, we obtained the estimated number of probers from stream A that went into stream B as

$$\hat{N}_{ab} = \frac{R_{ab} T_b}{R_b T_a} \hat{N}_a.$$

To calculate the variance estimator for the above term, we assumed that the number of tagged fish captured was best described by a hypergeometric distribution, so that

$$\text{Var}(x) = \frac{kpq(\hat{N} - k)}{(\hat{N} - 1)},$$

where \hat{N} is the estimated population size, k is the number of carcasses sampled, x is the number of marked carcasses, $p = x/k$ (marked fraction observed in sample), and $q = 1 - p$.

$\text{Var}(R_{ab})$ and $\text{Var}(R_b)$ were calculated as

$$\text{Var}(R_{ab}) = \frac{C_b \left(\frac{R_{ab}}{C_b} \right) \left(1 - \frac{R_{ab}}{C_b} \right) (\hat{N}_b - C_b)}{(\hat{N}_b - 1)} = \frac{R_{ab} \left(1 - \frac{R_{ab}}{C_b} \right) (\hat{N}_b - C_b)}{(\hat{N}_b - 1)}, \text{ and}$$

$$\text{Var}(R_b) = \frac{C_b \left(\frac{R_b}{C_b} \right) \left(1 - \frac{R_b}{C_b} \right) (\hat{N}_b - C_b)}{(\hat{N}_b - 1)} = \frac{R_b \left(1 - \frac{R_b}{C_b} \right) (\hat{N}_b - C_b)}{(\hat{N}_b - 1)}.$$

We then used the delta method to estimate the variance of the probing population estimate,

\hat{N}_{ab} :

$$Var(\hat{N}_{ab}) = Var\left(\hat{N}_a \frac{R_{ab}T_b}{R_bT_a}\right)$$

substitution and simplification gave

$$Var(\hat{N}_{ab}) = \left(\frac{R_{ab}T_b}{R_bT_a}\right)^2 Var(\hat{N}_a) + \left(\frac{\hat{N}_a T_b}{T_a}\right)^2 \left(\frac{Var(R_{ab})}{R_b^2} + \frac{R_{ab}^2 Var(R_b)}{R_b^4}\right)$$

For streams where probing fish were recovered but the sampling fraction was either 100% (e.g., Sashin Creek and AKI Hatchery) or unknown, probing estimates assumed

$$\hat{T}_{ab} = R_{ab},$$

so that

$$\hat{N}_{ab} = \frac{R_{ab}}{T_a} \hat{N}_a;$$

the estimate of \hat{N}_{ab} is biased low for streams with unknown sampling fraction. Variance of these estimates depends on the variance of \hat{N}_a and R_{ab} ,

$$Var(\hat{N}_{ab}) = \left(\frac{R_{ab}}{T_a}\right)^2 Var(\hat{N}_a) + \left(\frac{\hat{N}_a}{T_a}\right)^2 Var(R_{ab}).$$

To determine the spawning escapement in stream A, the population in stream A at tagging time (\hat{N}_a) was adjusted by subtracting the estimated number of probing emigrants,

$$\sum_{i=1}^n \hat{N}_{ab_i},$$

recovered in all n streams to which fish tagged in stream A emigrated. Variance estimators were originally summed for all $Var(\hat{N}_{ab_i})$ and added to $Var(\hat{N}_a)$ to compute the variance estimate for the estimated spawning escapement (Maselko et al. 1999). However, because

\hat{N}_a and \hat{N}_{ab_i} are not independent, we used the delta method to obtain the combined variance of $\left(\hat{N}_a - \sum_{i=1}^n \hat{N}_{ab_i}\right)$.

Because $\hat{N}_{ab} = \hat{N}_a \sum_{i=1}^n \frac{R_{ab_i} T_{b_i}}{R_{b_i} T_a}$ we obtain by the delta method:

$$Var\left[\hat{N}_a - \sum_{i=1}^n \hat{N}_{ab_i}\right] = \left(1 - \sum_{i=1}^n \frac{R_{ab_i} T_{b_i}}{R_{b_i} T_a}\right) Var(\hat{N}_a) + (\hat{N}_a^2 + Var(\hat{N}_a)) \left(\frac{1}{T_a^2} \sum_{i=1}^n \left(T_{b_i}^2 \left(Var(R_{ab_i}) + \left(\frac{R_{ab_i}}{R_{b_i}^2}\right) Var(R_{b_i})\right)\right)\right)$$

RESULTS

In the eight streams combined, a total of 12,859 live pink salmon (range was 553–2,978 for individual streams) were tagged, and 62,784 carcasses were examined for marks (range was 1,302 - 21,803 for individual streams) (Table 2). Number of fish tagged varied between streams due to sampling effort, run size, and physical configuration of the streams. The most fish were tagged at Borodino and Lovers Cove Creeks, where fish were sampled and tagged four times per week. For the other streams, the total number of fish tagged biweekly was roughly proportional to the escapement magnitude, except that fewer fish were tagged in Pile Driver Creek (estimated escapement about 50,000) than in Parry Creek (estimated escapement about 18,000). Because Parry Creek had limited amounts of upstream spawning habitat and a single deep holding pool just upstream of tidewater, our sampling gear caught more live pink salmon there than in Pile Driver Creek. The number of fish tagged in a stream on a particular date varied from 50 to 350, depending on availability. The number of fish tagged during a particular tagging event occasionally exceeded the 300-fish target, to allow tagging crews to complete tagging a seine haul.

Although fish were tagged in lower stream reaches in pools near mean high tide, tagged carcasses were found throughout the stream systems from the intertidal zone to the upper reaches of spawning habitat, supporting our assumption of random dispersion of tagged fish throughout the spawning population. The number of carcasses recovered in a stream varied from about 20 to 4,000 per day. Variability in recoveries (e.g., Fig. 6) was due to an interaction of run timing and stream conditions, which affected both the longevity of spawning

fish and the probability of recovery. Stream flows in the sampling area fluctuate widely due to high and irregular precipitation (NOAA 1996). The high variability in carcass recoveries was consistent with the widely varying probabilities of carcass recovery on any particular day that were used in the simulation (Fig. 2).

Double-tagging provided the opportunity to measure tag loss. The “chick” tag proved to be reasonably reliable. Estimated loss of both tags averaged 1.4% in all streams combined (range 0.4-4.7%; Table 2); variation was due primarily to differences between tagging crews (crew means were 0.5%, 0.8%, and 2.6%).

After adjusting the number of tags released in each stream for tag loss, we estimated the escapement, or the number of pink salmon entering the stream (population at time of tagging) and the adjusted escapement (number of fish that entered and remained to spawn, adjusted for probers leaving the stream). The number of fish entering the streams (unadjusted escapement) ranged from 8,609 in Williams Creek to 79,070 in Deep Cove Creek (Table 2). The precision of the escapement estimates, as represented by the coefficients of variation, ranged from 0.024 to 0.110.

We recovered 139 tagged fish in streams other than those in which they were tagged (Table 3). Although tagged fish were observed as far as 51 km from the tagging site, probing was most frequent between neighboring streams: 97% of tagged probers were recovered in the nearest systematically sampled stream (Fig. 7) to where they were tagged.

Minimum estimates of the number of fish probing each stream ranged from 0 to 1,868 fish (Table 4). The coefficient of variation of these estimates tended to be large due to the small sample sizes on which they were based. Probing fish may not have been detected in

streams where we sampled opportunistically, and we could not adjust for the sampling fraction in these streams because their population size was unknown.

Where we quantified escapement, probers averaged 2.4% of the fish entering the stream (Table 4). Probers made up a small proportion (< 3%) of the escapements (Fig. 8) except in Borodino Creek (11.7%).

The sexes differed in probing (Table 3). After adjusting for different sex recoveries, the rate of male probers (6.3%) was twice that of female probers (2.9%; $P = 0.0001$, chi-square test; Table 3). This difference was weighted heavily by the large number and the sex distribution of fish probing Borodino Creek, where 82% of the probers were recovered with three times as many males as females (29.8% vs. 10.8%; $P < 0.0001$). Frequency of probing in the other streams was much lower for both sexes; males remained the more frequent probers (1.3% vs. 0.9%), but the difference was much less and not statistically significant ($P > 0.5$).

The physical characteristics of streams and possibly the magnitude of the pink salmon escapement affected probing. The streams with the highest probing rates, Borodino and Parry Creeks, were both lake-fed systems with large stream discharges, limited intertidal spawning habitat, and little upstream spawning habitat due to barrier falls (Borodino Creek) and steep gradient (Parry Creek). The nearest systematically sampled neighbors to each stream, Lovers Cove Creek near Borodino Creek and Deep Cove Creek near Parry Creek, had the greatest escapements. These streams had much more extensive spawning habitat, escapements more than four times as great, and substantially lower probing rates than their nearest neighbor (Table 4). Probing frequency differed significantly between Borodino and Lovers Cove

Creeks ($P < 0.001$, chi-square); sample size was too small to test for statistical significance between Parry and Deep Cove Creeks.

The estimated spawning escapements, adjusted for probing fish, ranged from 8,440 to 79,070 fish (Table 4). The precision of the estimates (CV) averaged 6%, ranging from 2% to 11%. These CVs were consistent with those previously reported by Maselko et al. (1999) even though some of the variances are lower because we accounted for covariance in the estimates of \hat{N}_a and \hat{N}_{ab} , rather than simply summing the variances. For all streams except Borodino Creek, the computational change caused small (0-5%) changes in the variance estimates. Because of the relatively large number of probers at Borodino Creek, the change in computation method reduced the estimate of variance by 28%, from 454,036 to 354,265, reducing the CV for the population estimate from 4.2% to 3.7%. The high uncertainty of the probing estimates thus did not greatly increase the CV of the spawning escapement estimates because of the relatively low percentage of the initial escapement estimates that were composed of probing fish. Numbers of tags recovered were more important in determining the precision of the estimates; the two streams with the lowest number of tag recoveries, Deep Cove and William Creeks, had the highest CV and relatively widest 95% confidence intervals (Table 4).

Percentage of carcasses recovered varied greatly among streams. The highest rates were in Borodino and Lovers Cove Creeks. These streams had carcass weirs and were sampled more frequently than the other streams. For the other six streams, percentage of carcasses recovered varied with stream gradient. In Joyce Creek, which had a low gradient,

we recovered 23% of the tagged fish, whereas in Deep Cove Creek, which had the steepest gradient, we recovered 8% of the tagged fish (Table 2).

DISCUSSION

The bias-corrected Petersen estimator had a number of advantages for estimating pink salmon escapement. Not only was this estimator cost-effective, it also provided precise escapement estimates with well-defined confidence intervals. Live-marking with carcass-recapture can be adapted readily to the Petersen closed-population model, especially when precautions are taken to account for emigrants and tag loss. This design is especially relevant when carcasses must be sampled for tags. In Schwarz et al. (1993), the closed-population, single-sample, Petersen estimator gave population estimates for coho salmon similar to our pink salmon estimates, as did stratified open-population estimates based on live-marking and live recoveries.

The dynamic, unpredictable nature of carcass recoveries in some pink salmon streams makes stratification difficult. Although Parker (1968) did not think flushing of pink salmon carcasses was a problem in a British Columbia stream, he did not estimate the rate of carcass retention. Wertheimer et al. (1997) observed all fish of certain entry dates were flushed from streams, thus violating the assumption of equal catchability of carcasses. We also observed such flushing events during our field study, in particular for Deep Cove Creek, where carcass recovery rates were less than 10%. The Petersen estimator is less affected by these flushing events than either the open-population Jolly-Seber estimator that Wertheimer et al. (1997) used in their study, or the stratified, closed-population Schaefer model. We observed tagged fish migrating from the tagging stream to another stream to spawn, which violated this closed-

population assumption. However, we were able to estimate the magnitude of this probing and adjust our escapement estimates accordingly. The estimates of probing caused only marginal increases in the variance for spawning escapements; however, the probing estimates themselves were broad. To estimate probing more precisely, intensive tagging and recovery efforts would be required because relatively few fish probe.

Although salmon straying has been the subject of numerous studies (Blair 1968, Boyd 1964, Mortensen et al. 1999, Quinn 1984, Tallman and Healey 1994, Thedinga et al. 1999, Wertheimer et al. 1999), probing has been poorly documented (Thrower 1988, Berman and Quinn 1991) and had not been estimated previously. For seven of our eight streams, probing rates were low -- less than 3% of the number of fish entering the stream. However, for Borodino Creek the rate was more than 10%. Such high rates emphasize the need to understand the degree of probing in pink salmon streams, especially where escapements are enumerated by one-way weirs, which retain probers.

We could not determine the natal origin of the fish that we marked in the streams. Therefore, we could not determine whether 1) fish enter their natal stream, and upon finding unfavorable conditions (e.g., flow rates and access, density of spawners, predation pressure), leave for another stream; or 2) fish probe other streams in search of favorable conditions before they settle on their natal stream, or 3) both types of behavior occur. We noted that streams with large discharges but limited spawning habitat had a much higher proportion of probers than their near neighbors that had substantially greater spawning areas but lower flow rates and larger spawning escapements, suggesting that the high flow rates attracted fish. Such behavior could be highly adaptive for colonizing new habitats and for avoiding catastrophic

flow conditions in natal streams, such as low-oxygen events (Murphy 1985). Due to their 2-year life cycle, pink salmon lack an age structure to buffer against unfavorable stream conditions when they return to spawn; probing that leads to straying might compensate for unforeseen environmental events that would otherwise result in extinction (Quinn 1984, Ricker 1972, Thedinga et al. 1999).

Male pink salmon probed at a higher rate than females did. Competition among males on spawning grounds may induce some to leave a stream. Males may also not home so precisely as females, which could lead to more searching of non-natal streams. More studies are needed to discern the driving force behind probing of male versus female pink salmon. Hard and Heard (1999) found that male chinook salmon were more likely to stray than females. However, Thedinga et al. (1999) did not find any differences in straying rates between male and female pink salmon.

Thrower (1988) found that pink salmon tagged at one stream were more likely to leave and spawn in another stream if fish were tagged off a stream mouth rather than in a stream itself. Thrower attributed this movement to stress, speculating that less-mature fish holding in saltwater were more stressed by capture and tagging. Alternatively, a fish in a school off the stream mouth may be more likely to have originated from another stream than a fish that has entered the stream. Based on Thrower's (1988) observations, we felt that tagging in the stream instead of the stream mouth was important to minimize the tagging of strays and the emigration of tagged fish. Because substantial intertidal spawning occurred in almost all our streams, tagging pools were chosen in the stream, but within the reaches of the upper intertidal

zone. In the field, tagged carcasses were found throughout the intertidal zone as well as upstream, confirming that the intertidal spawners were included.

If tagging does induce emigration, the capture-recapture experiments become biased. We had no way to determine whether tagging stress induced emigration. However, we did observe highly variable rates of probing between pairs of streams, even though the fish were handled and tagged in the same manner in each stream, indicating that factors other than tagging were the primary determinants of the probing.

Aerial surveys are most commonly used to estimate or index pink salmon escapements (Dangel and Jones 1988, Bue et al. 1998). Unless factors such as observer efficiency and fish visibility are accounted for, aerial surveys can be highly biased (Dangel and Jones 1988, Jones 1995). Alaska Department of Fish and Game's peak aerial escapement counts varied from more than 100% of our estimated escapement (Lovers Cove Creek) to 5% (Joyce Creek; Fig. 10). The proportion of the escapement observed was highest for streams with predominately intertidal spawning, where foliage did not obscure the fish, and pre-spawning fish held in the estuary rather than in stream pools. A substantially smaller proportion of the escapement was observed in streams where pink salmon held and spawned in upstream areas obscured by dense riparian vegetation. Aerial counts are typically expanded to total escapement using the counts, frequency of counts, the estimated stream life, and the estimate of observer efficiency (Bue et al. 1998, Hilborn et al. 1999). Our data indicate that observer efficiency for pink salmon varies strongly with stream type.

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Table 1.--Statistics: average, average error, and standard deviation from 1,000 simulations of escapement estimation for a hypothetical pink salmon population of 30,003 fish. Petersen and Schaefer population estimators were used. Tagging level is the maximum number of live fish tagged per time period.

Tagging level	Average \hat{N}	Average error (30,003 - \hat{N})	Standard Deviation
		Petersen	
100	30,018	-15	111.75
200	30,006	-3	58.29
300	30,007	-4	39.31
		Schaefer	
100	29,987	+16	165.11
200	29,993	+10	91.10
300	30,000	+3	67.53

Table 2.--Number of live pink salmon marked with opercular tags, number of carcasses examined with and without tags, the estimated proportion of fish that lost both tags, and the Petersen escapement estimate with coefficient of variation (CV), by stream.

Stream	Live fish tagged	Carcasses Examined			Both tags lost (%)	Petersen estimates	
		Unmarked	Double mark	Single mark		Escapement	CV
Deep Cove	1,709	6,240	114	19	0.7	79,070	0.086
Parry	1,423	2,476	158	18	0.6	19,819	0.074
Joyce	1,693	14,268	323	70	1.0	60,761	0.044
Pile Driver	1,186	7,812	136	41	1.7	51,174	0.072
Wolf	1,152	2,136	130	73	4.7	11,494	0.068
William	553	1,225	65	12	1.3	8,609	0.110
Borodino	2,165	4,111	478	76	0.5	15,951	0.041
Lovers Cove	2,978	21,671	993	139	0.4	56,733	0.024
Total	12,859	59,939	2,397	448	1.4	303,611	0.028

Table 3.--Number of adult pink salmon tagged and number of fish that probed.*

Stream	Tagged		Probers	
	Males	Females	Males	Females
Deep Cove	969	736	0	0
Parry	1,104	317	2	1
Joyce	997	694	2	0
Pile Driver	779	396	1	0
Wolf	735	407	2	0
William	287	264	1	2
Borodino	1,425	740	84	30
Lovers Cove	1,716	1,262	8	6
Total*	8,012	4,816	100	39

*Note the total tagged numbers differ from those in Table 2 due to adjustment for tag loss in Table 2 and occasional missing sex information.

Table 4.--Estimated numbers and associated coefficients of variation (CV) of pink salmon emigrating from streams, their percentage of entrants (probing rate), estimated spawning escapements adjusted for probing fish that left a stream to spawn in another stream, and associated 95% confidence intervals (CI) for spawning escapements for eight streams in southeastern Alaska, 1997.

Stream	Estimated*		Probing rate (%)	Adjusted		
	Emigra- tion	CV		Escapement	Variance	95% CI
Deep Cove	0		0	79,070	46,752,180	(65,668 – 92,472)
Parry	524	0.564	2.6	19,295	2,256,772	(16,351 – 22,239)
Joyce	2		< 0.1	60,759	7,265,669	(55,476 – 66,042)
Pile Driver	307	0.929	0.6	50,867	13,552,968	(43,651 – 58,082)
Wolf	119	0.660	1.0	11,375	617,364	(9,835 – 12,915)
William	169	0.643	2.0	8,440	913,285	(6,567 – 10,313)
Borodino	1,868	0.088	11.7	14,083	454,036	(12,763 – 15,404)
Lovers Cove	945	0.236	1.7	55,788	1,863,314	(53,113 – 58,464)
Total	3,933			299,677	73,675,889	(263,424 – 335,931)

*Includes tags found in streams where escapement was not estimated.

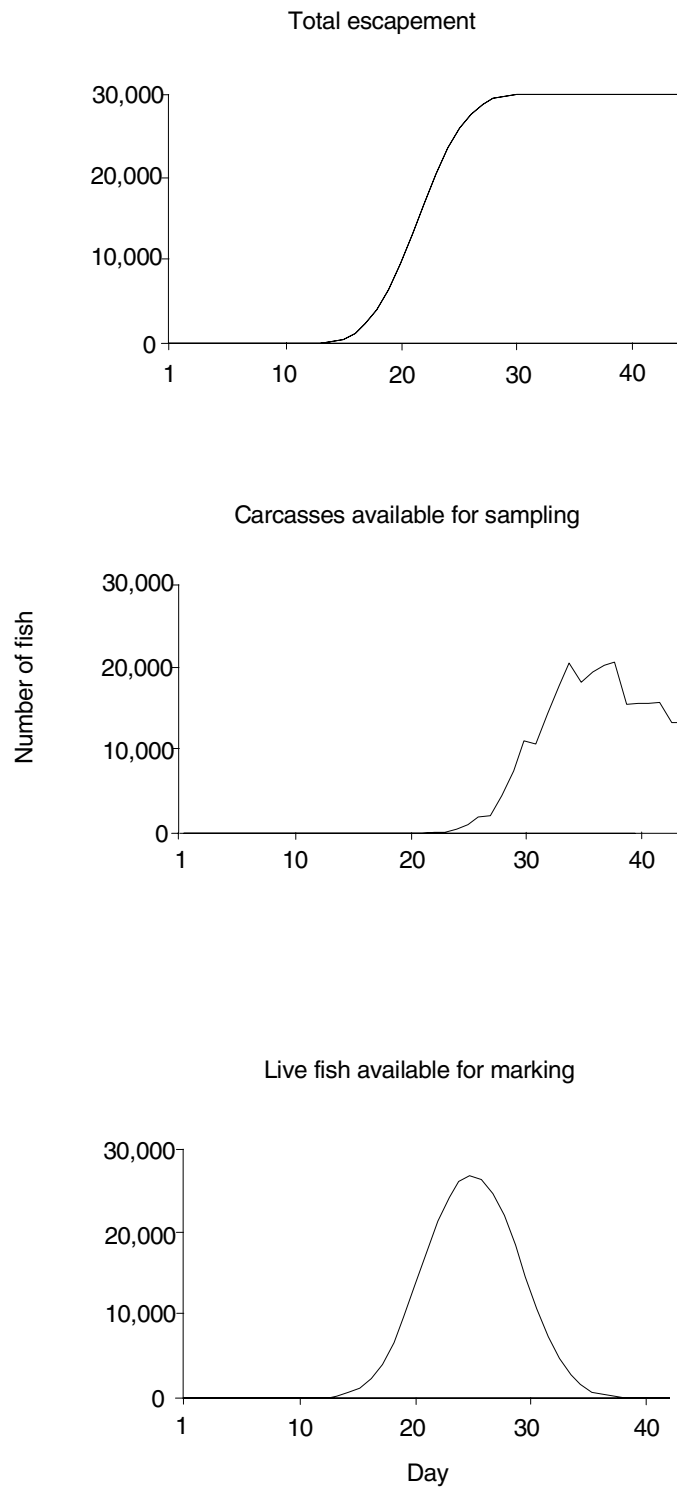


Figure 1.--The sampling design was applied to a hypothetical pink salmon escapement. Fish available for marking (marking distribution) and recovery are plotted against day after first entry.

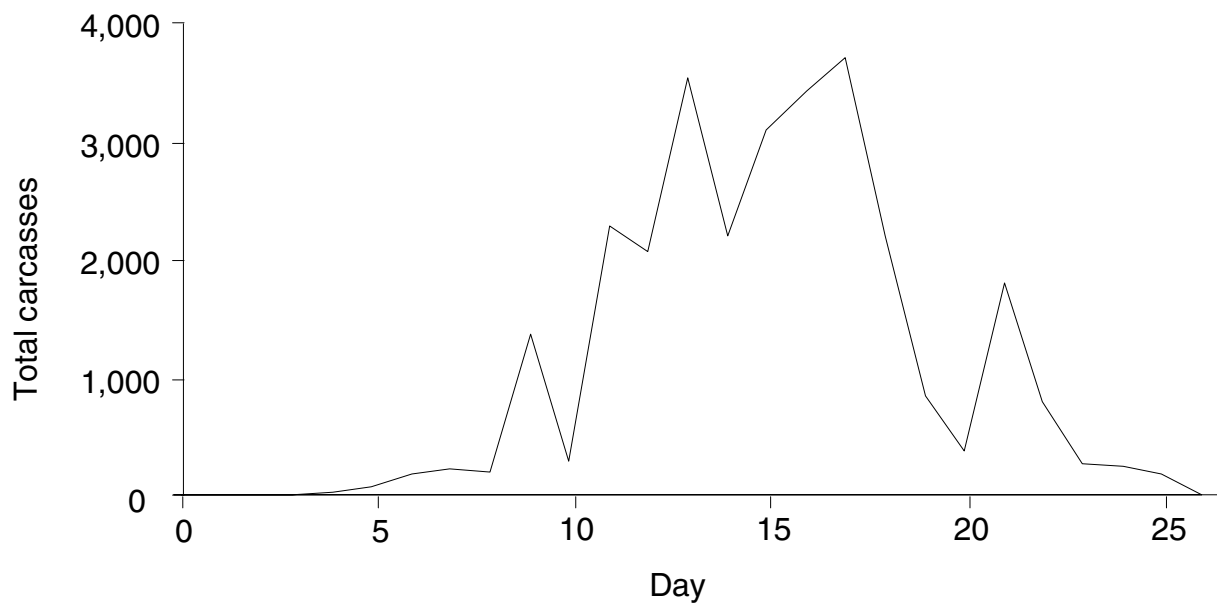


Figure 2.--A typical history of all carcass recoveries used to calculate escapement estimates for comparing the Schaefer and Petersen estimators. The probability of recovering a carcass was assigned at random; therefore, this graph changed with each of the 1,000 mark-recapture simulations.

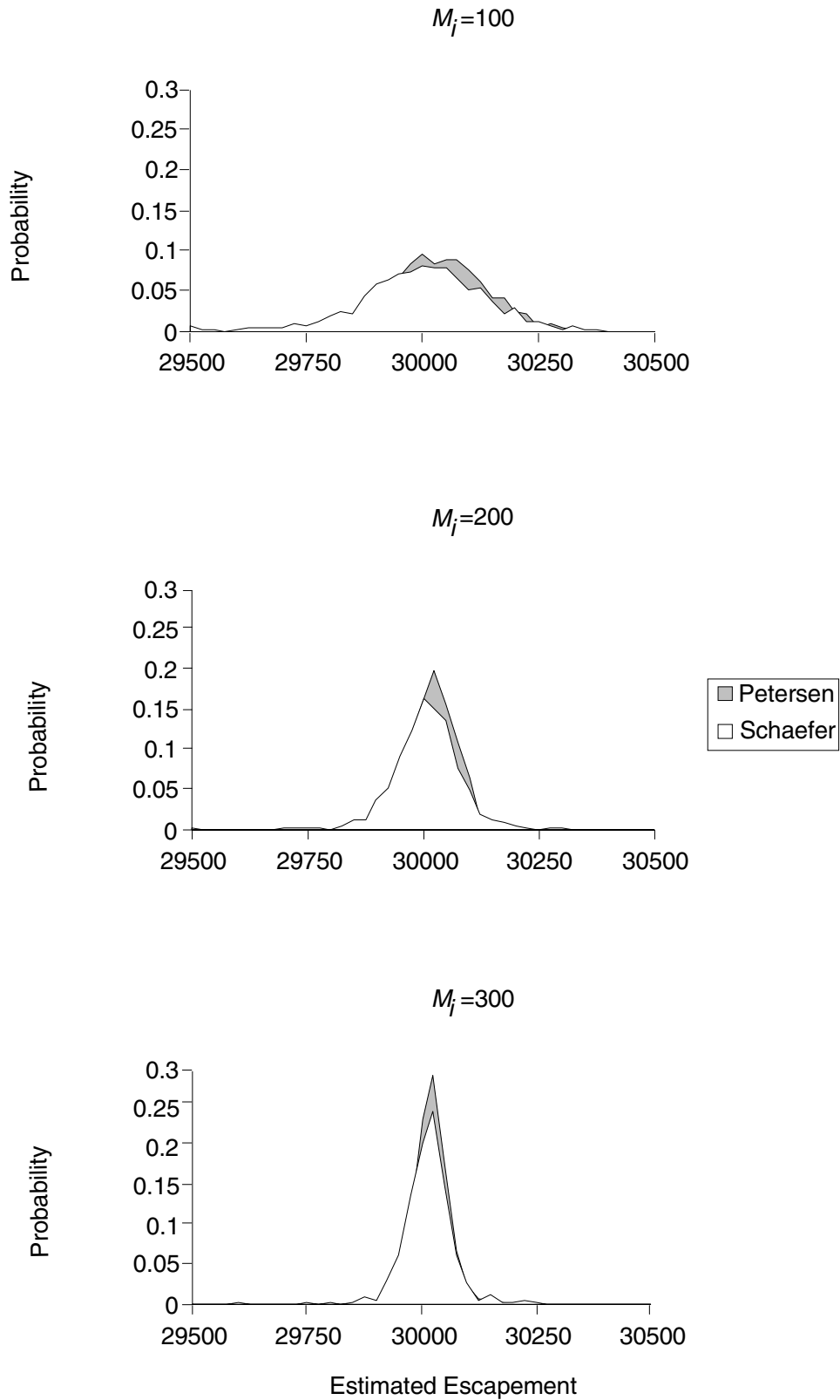


Figure 3.--Monte Carlo distributions of the estimated population sizes for the Petersen and Schaefer estimators based on 1,000 iterations. M_i is the number of live fish tagged at each of the five marking events.

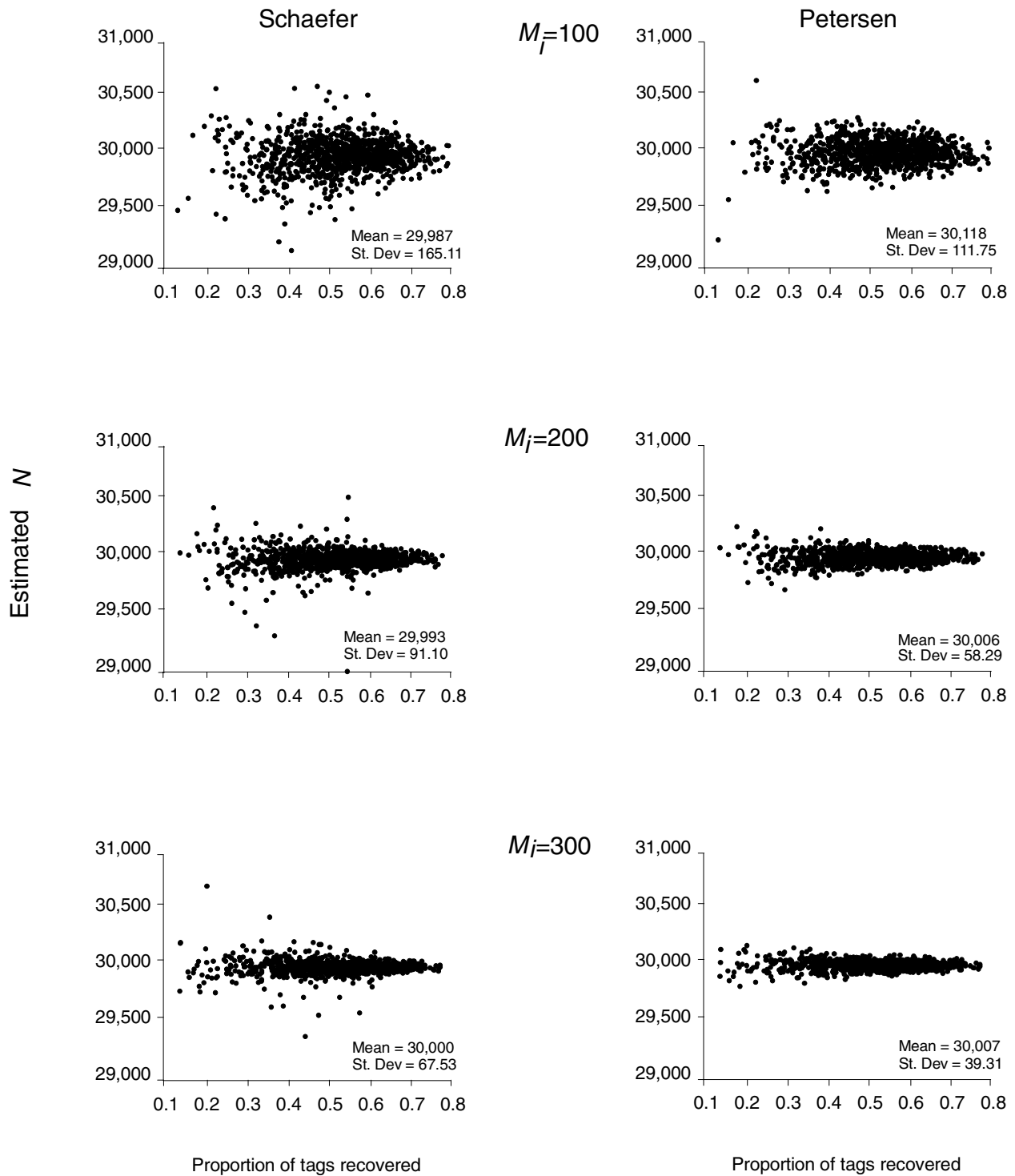


Figure 4.--Results of 1,000 iterations of the Petersen and Schaefer models where M_i is the number of live fish tagged at each tagging event. The escapement size N is 30,003 fish.

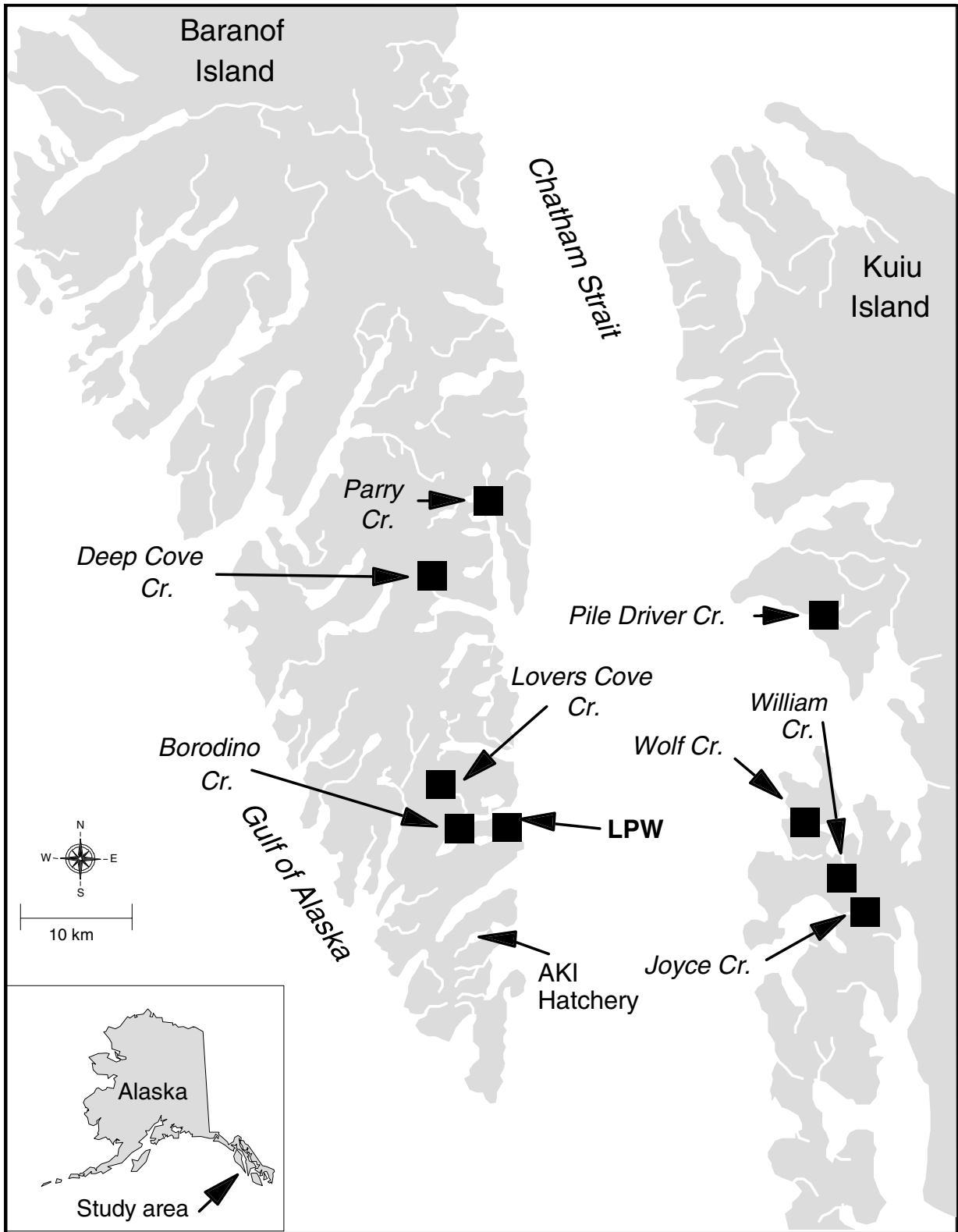


Figure 5.--Map of study streams sampled within a 35-km radius of the Little Port Walter research hatchery.

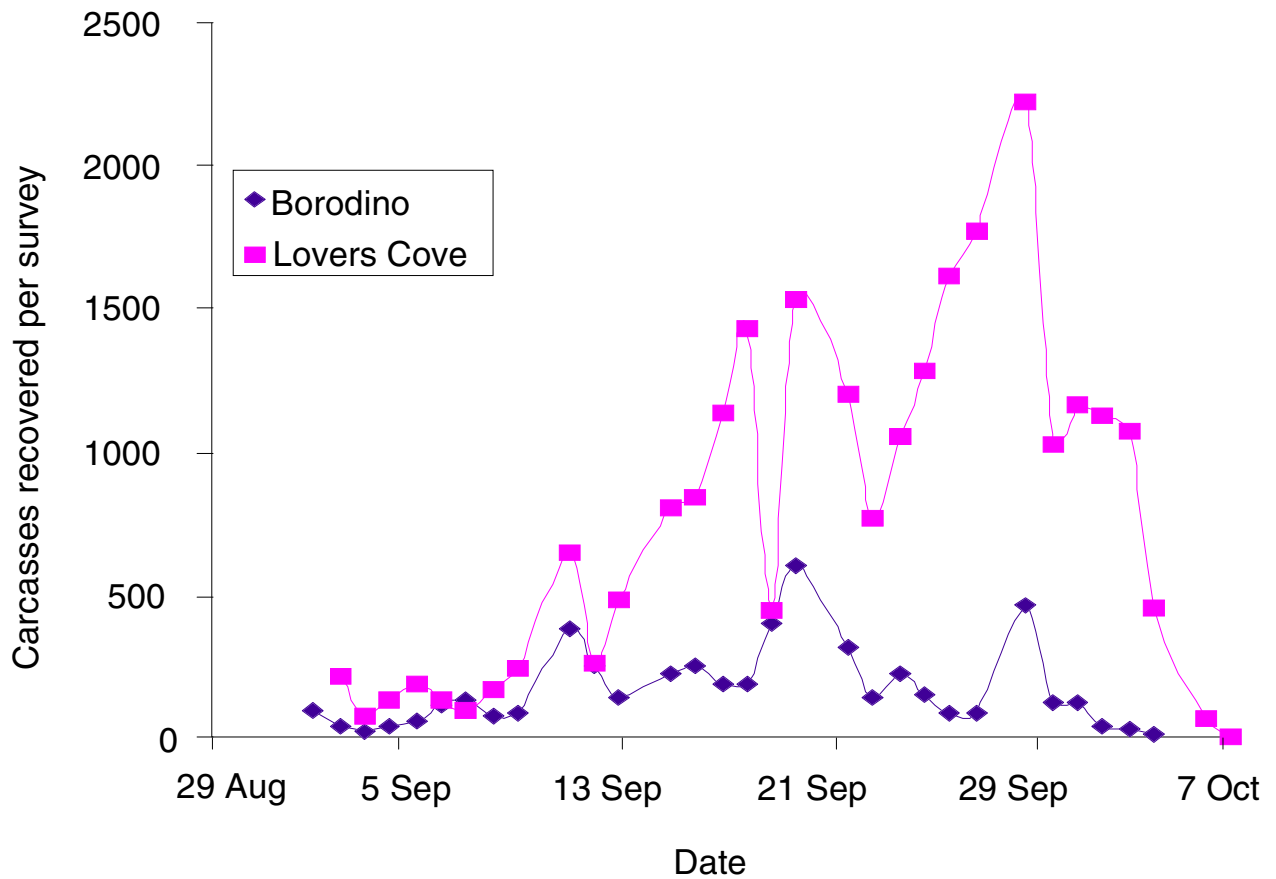


Figure 6.--Carcass recoveries at Borodino Creek and Lovers Cove Creek in 1997. Due to their close proximity to the Little Port Walter research station, carcasses were sampled in these streams 4–6 times per week.

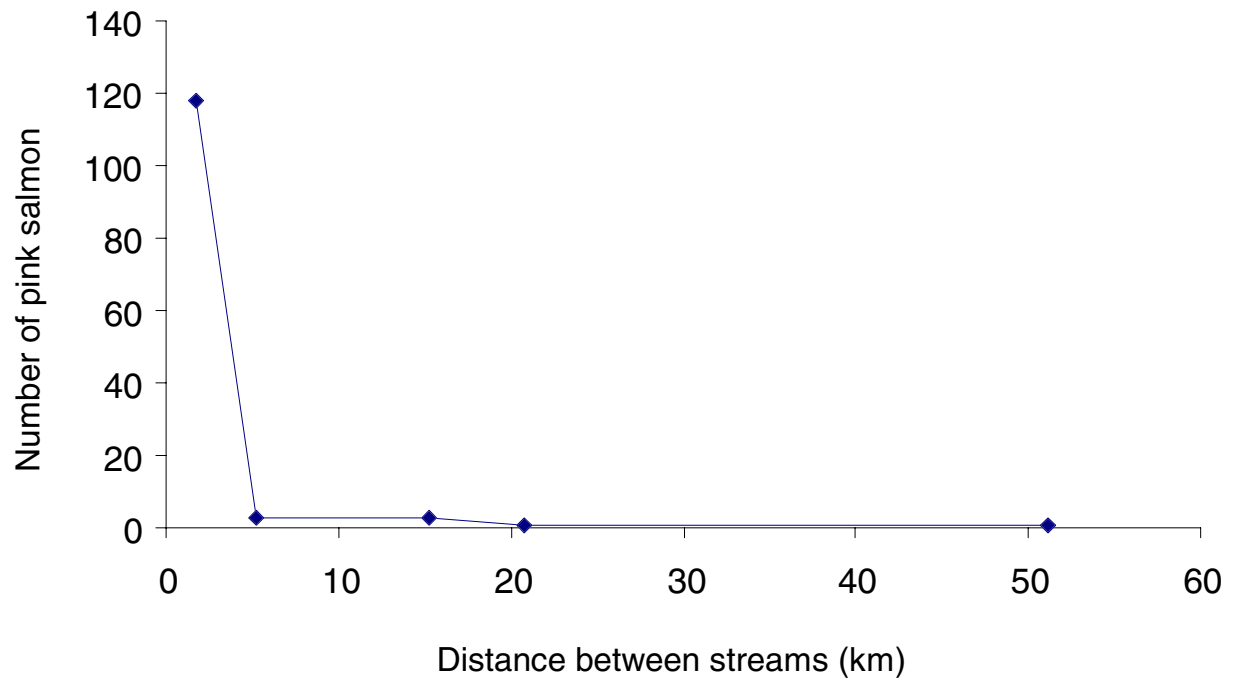


Figure 7.--The relationship between the distance pink salmon probed and observed number of fish that probed.

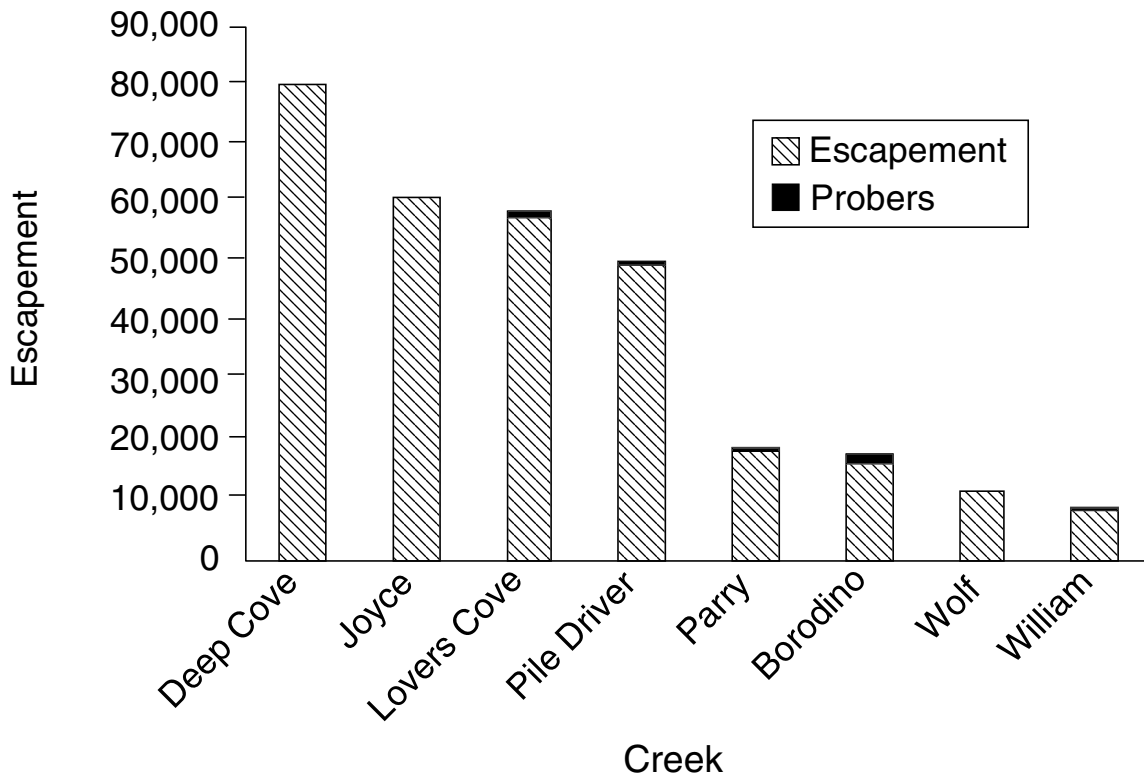


Figure 8.--Estimated escapements of pink salmon in eight study streams in southeastern Alaska, adjusted for the expanded number of probers.

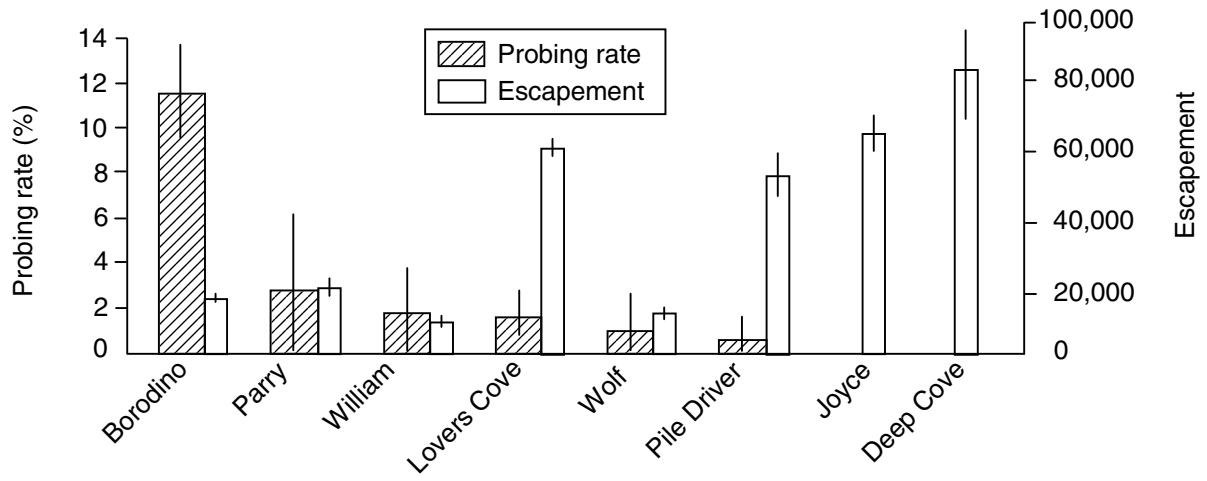


Figure 9.--Probing rate and escapement of pink salmon into the eight study streams in southeastern Alaska.

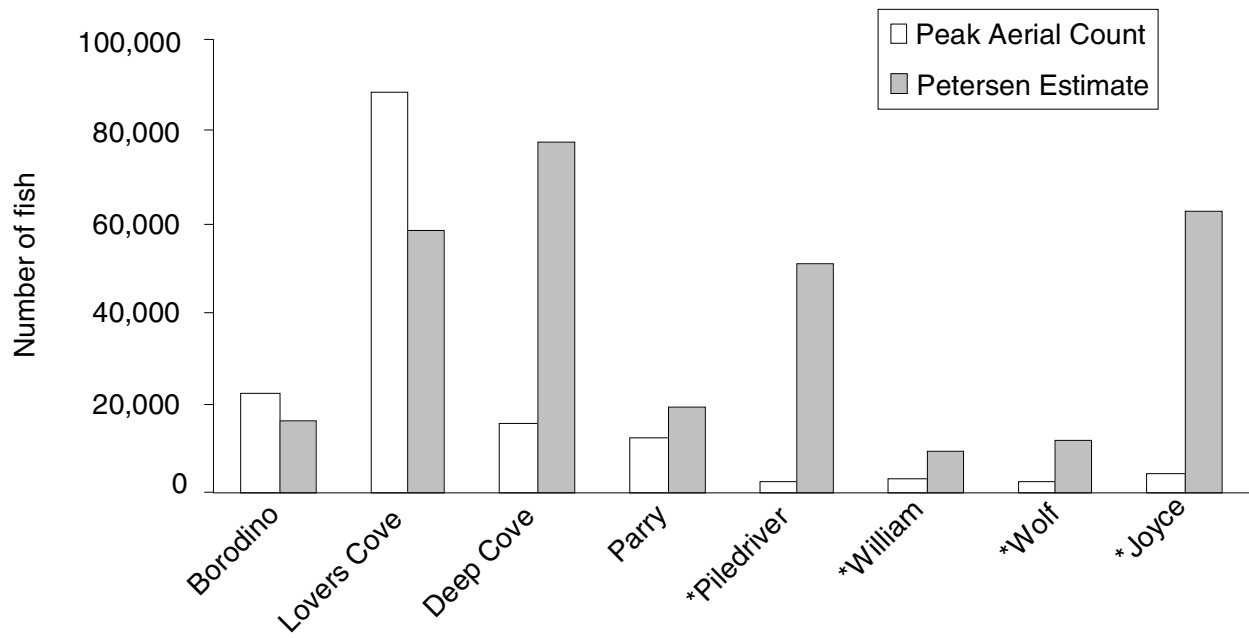


Figure 10.--Comparison between peak aerial counts and Petersen estimates of pink salmon. Peak escapement counts were based on aerial surveys for all streams except Joyce Creek, which was based on foot surveys. All streams were surveyed by Alaska Department of Fish and Game, August 1997. Kuiu Island streams are denoted by an asterisk.

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