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ARTICLE

Application of the Genetic Mark–Recapture Technique for Run Size Estimation of Yukon River Chinook Salmon

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Abstract

We present an application of the genetic mark–recapture technique to estimate salmon run size in a large river. Application of this technique requires modifications to estimation methodology. Under a typical Lincoln–Petersen mark–recapture estimation of salmon run size ($N = M/p$), individual fish are captured and marked (M) in the lower river and are recaptured (m) at escapement (E: the number of fish reached spawning ground) monitoring sites selected upriver where the proportion of marked individuals ($p = m/E$) is estimated. In this genetic mark–recapture technique, the marked individuals are not captured and recaptured, but rather the naturally distinctive genetic (marked) population is captured and recaptured. Genetically, the lower river population is a mixture of multiple genetic stocks, whereas the upriver escapement population consists of a single genetic stock. Hence, the mark–recapture experiment ($N = M/p_m$) is reversed. The proportion of "marked" genetic stock (p_m) is estimated in the lower river, and size of the "marked" stock in the lower river (M) is estimated by summing its upriver escapement (E_m) and harvest (C_m) between the lower and upper portions of river ($M = E_m + C_m$). The harvest is calculated as a product of total upriver harvest (C) and the proportion of the "marked" stock (p_{cm}) in the harvest ($C_m = C \cdot p_{cm}$). Further, when the proportion of multiple genetic stocks (p_k) is identified, stock-specific run size ($N_k = N \cdot p_k$), escapement ($E_k = N_k - C_k$, where $C_k = C \cdot p_{ck}$), and exploitation rate ($Ex_k = C_k / N_k$) can also be estimated, which provides substantially more information than does the conventional approach. We illustrate an application of this technique for estimating run size of Chinook Salmon *Oncorhynchus tshawytscha* in the Yukon River, Alaska.

The advancement of DNA genetic identification of stocks and individuals has enabled the use of genetic markers for mark–recapture abundance estimation (e.g., Mills et al. 2000; Lukacs and Burnham 2005; Petit and Valiere 2006). The fundamental form of the capture–recapture estimator of abundance is

$$\hat{N} = \frac{M}{\hat{p}}, \tag{1}$$

where M is the number of marked unique individuals and p is the probability that the marked individuals are encountered at least once again (i.e., recapture probability) (Seber 1982; Pollock et al. 1990; Lukacs and Burnham 2005). The underlining fundamental assumption of mark–recapture is unbiased mark–recapture probabilities, or that marked individuals are representative of a population and that both marked and unmarked individuals have equal capture probability. To assure these assumptions, it is important to eliminate the effects of marking, such as increased mortality due to capturing, handling, and marking of individuals, loss of marks, or behavioral changes of marked individuals (Seber 1982; Pollock et al. 1990; Kendall 1999; Underwood et al. 2004). In the genetic mark–recapture

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technique, marked individuals (M) are replaced with genetically identifiable individuals or a genotype, and p is their proportion at subsequent sampling events (Lukacs and Burnham 2005). The major advantage of genetic mark–recapture is the elimination of the loss of marks and marking effects, especially when the collection of genetic samples is done unobtrusively and noninvasively (e.g., scales, fin clips). One disadvantage is the misidentification of genetically "marked" and "unmarked" individuals, such as from "shadow effects," in which two individuals have identical genotypes (Mills et al. 2000), and "genotyping error," in which an individual's genotype is concluded to be from several individuals (Macbeth et al. 2011). However, that disadvantage will be greatly reduced through the advancement of DNA analyses technology. Thus far, the majority of the applications of genetic mark–recapture technique has been for estimating the size of small and rare (mostly mammal) populations (Mills et al. 2000; Lukacs and Burnham 2005; Petit and Valiere 2006). We are not aware of any application of this technique for the estimation of a large population, such as a salmon run size.

METHODS

Application of the genetic mark–recapture technique for the estimation of salmon run size.—Before presenting an approach, two issues should be clarified: (1) the approach is not strictly a "mark–recapture" in a sense that the same "marked" individuals are captured and recaptured, but rather the same "marked" genetic population is captured and recaptured, and (2) the mark–recapture experiment is reversed in that the marked population is captured at a second sampling event. In a typical mark–recapture approach for estimating salmon run size in large rivers, a closed form, single, capture–recapture Lincoln–Petersen model is used (Seber 1982; Pollock et al. 1990; Kendall 1999; Bromaghin et al. 2010). In this method, the first capturing and marking of fish (M) occurs at the lower main stem of the river, and the second capturing occurs at several upriver escapement (i.e., the number of fish moved to spawning grounds) monitoring tributaries, where escapement (E_1, E_2, E_3) and the number of marked fish (m_1, m_2, m_3) are counted and the proportion of marked individuals ($p_i = m_i/E_i$) at each tributary is estimated (Figure 1A). Meeting a condition that the marked proportions are the same across recovery sites ($p_1 \approx p_2 \approx p_3$), the overall marked proportion ($p = \sum m_i/\sum E_i$) is calculated, and run size ($N = M/p$) is estimated (Spencer et al. 2009; Stuby 2007; Pawluk et al. 2006a, 2006b; Bromaghin et al. 2010).

Genetically, fish in the lower river's main stem are a mixture of multiple genetic stocks, whereas fish at an upriver spawning tributary are of a single genetic stock. Thus, in genetic mark–recapture the above protocol is reversed. The proportion of "marked" genetic stock is estimated ($p = p_m$) at the lower river main stem, and the abundance (e.g., escapement) of the "marked" genetic stock ($M = E_m$) is estimated at the upriver tributary (Figure 1B). Then, $N = E_m/p_m$ is an unbiased estimate of salmon run size at the second event, providing that there is no fishery between the two sampling events or that all genetic stocks are harvested at equal rate. Those assumptions, however, are often violated. When fisheries occur throughout the river drainage, the upriver stocks are more heavily harvested than lower river stocks (Criddle 1996; Criddle and Streletski 2000). The above violation can be corrected if harvests of the target genetic stock between the first and the second events (C_m) are available. These can be estimated by multiplying the total harvest (C) with the proportion of target genetic stock in the harvest ($p_{c,m}$), $C_m = C \cdot p_{c,m}$ (Figure 1B). By adding the harvests with upriver abundance, the abundance of "marked" genetic stock at the first sampling event is estimated as $N_m = E_m + C_m$. Then, $N = N_m/p_m$ is an unbiased estimate of salmon run abundance at the first sampling event (Figure 1B); i.e.,

$$\hat{N} = \frac{\hat{N}_m}{\hat{p}_m} = \frac{\hat{E}_m + \hat{C}_m}{\hat{p}_m} = \frac{\hat{E}_m + \hat{C} \cdot \hat{p}_{c,m}}{\hat{p}_m}. \quad (2)$$

In many cases, the genetic stock identification technique can estimate the proportion of multiple stocks (p_k). In those cases, the genetic mark–recapture technique can simultaneously estimate genetic stock-specific run size (N_k), escapement (E_k), and exploitation rate (Ex_k) as follows (Figure 1B):

$$\hat{N}_k = \hat{N} \cdot \hat{p}_k, \quad (3)$$

$$\hat{E}_k = \hat{N}_k - \hat{C}_k, \text{ and} \quad (4)$$

$$\hat{E}x_k = \hat{C}_k/\hat{N}_k. \quad (5)$$

Here, we present an application of the genetic mark–recapture technique for estimating the run size of Chinook Salmon *Oncorhynchus tshawytscha* in the Yukon River upriver of Pilot Station, Alaska, during 2005–2011, using Canada stock as the genetic marker stock (Figure 2). Prior to 2005, the Canada stock of Chinook Salmon was distinguished using scale pattern analyses (JTC 2013) and its passage to the U.S.–Canada border (E_m). Canada stock harvests in the United States (C_m) have been estimated since the 1980s (JTC 2013). Passage and genetic stock composition of Chinook Salmon in the lower river (p_m) has been monitored at the Pilot Station sonar program (Figure 2) since 2005 (Carroll et al. 2007; Carroll and McIntosh 2008). Further, Chinook Salmon radiotelemetry mark–recapture experiments were conducted during the 2002–2004 run periods at Russian Mission, about 100 river miles (160 river kilometers) upriver from Pilot Station (Spencer et al. 2009). Chinook Salmon fishery harvests between the two locations are about 2,000 fish and no major spawning tributaries exist (Figure 1). Thus, though it is not direct, a comparison of the two estimates provides insights about the accuracy of the genetic mark–recapture technique.

Data source and genetic sampling.—Passage of Canada Chinook Salmon at the U.S.–Canada border was estimated at Eagle,

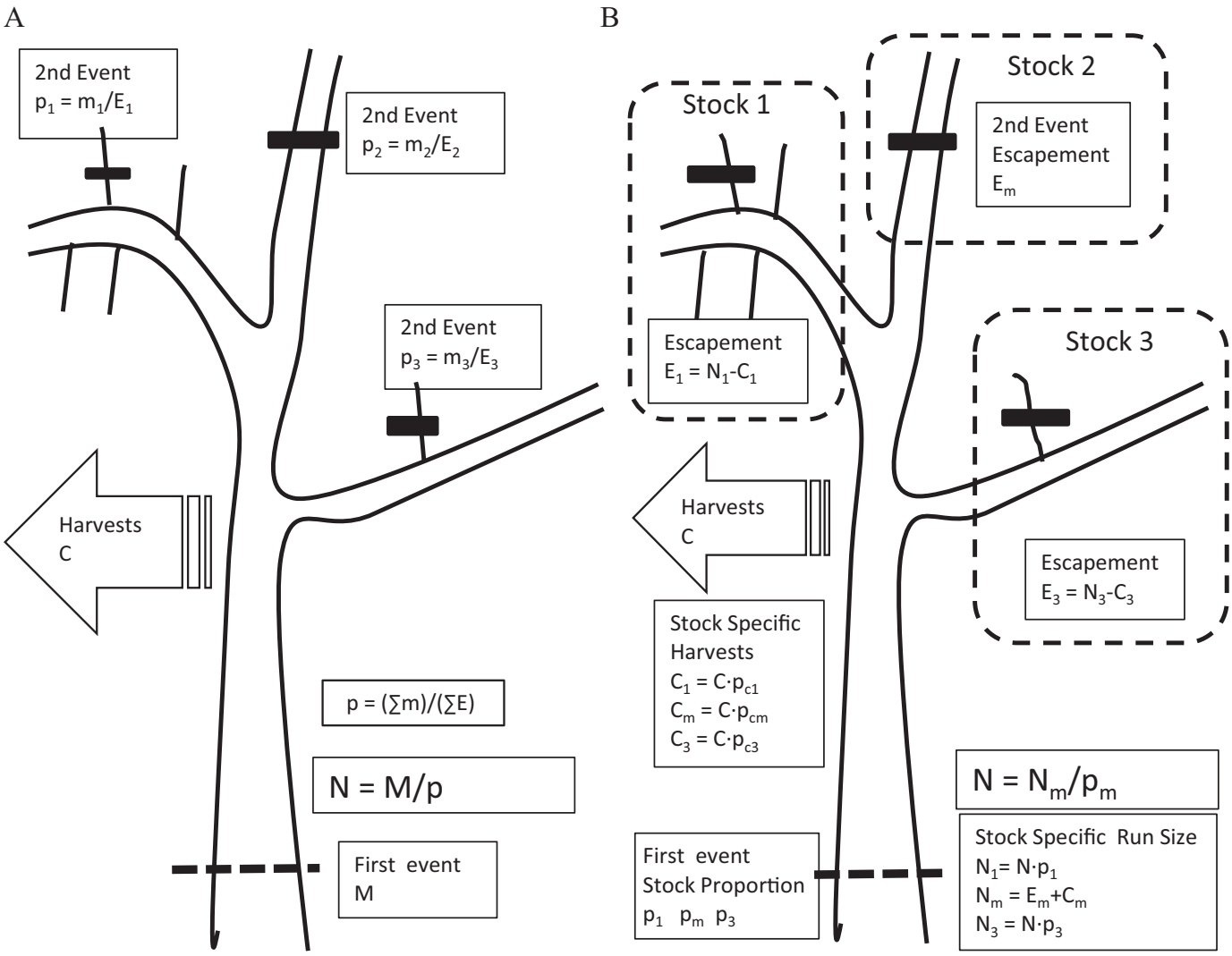

FIGURE 1. Comparison of application of typical (**A**) mark–recapture and (**B**) genetic mark–recapture experiments for estimation of salmon run size in a large river. In panel A: M = the number of marked fish released, E = escapement counts at each tributary, m = the number of marked fish recaptured at each tributary, p = proportion of marked fish, and C = harvests. In panel B: dashed line around squares indicates the boundary of each stock. Stock 2 is a "marked" genetic stock. p = stock proportion at main stem, p_c = stock proportion of harvest, E = escapement of stock.

Alaska, using hydro-acoustics (sonar) (see Dunbar and Crane 2007; Crane and Dunbar 2009a, 2009b, 2011). Generally, the CV (100·SD/mean) of the Eagle sonar estimate passage was less than 5% (see Table 2). Run size and timing of all salmon and nonsalmon species in the lower river are estimated at the Pilot Station sonar project, in which daily run size of all fish counted by sonar is apportioned by daily test-fishery sampling that consists of gill nets of five mesh sizes (2.75, 4.00, 5.25, 6.5, 7.5, and 8.5 in). The test fishery is conducted twice daily across the river (both banks and offshore) from which the proportion of all fish species including Chinook Salmon is estimated by a combination of net selectivity of each species and CPUE. By multiplying daily run size with the proportion of each fish species, run size of each species is estimated (see Carroll et al. 2007; Carroll and McIntosh 2008).

Subsistence fishery harvests of Chinook Salmon between Pilot Station and Eagle are estimated by annual postseason harvest surveys (see Busher et al. 2007; Jallen and Hamazaki 2011). Commercial catch harvests are obtained from a fish ticket database by fishery district (Figure 2) and by fishery opening period (i.e., the commercial fishery is usually closed, but can be opened for a few days at the discretion of its manager). Because Pilot Station is located on an upriver section of fishery district 2 (Figure 2) and commercial harvest data were available only at the district level, we assumed that 20% of the district 2 harvests occurred upriver from Pilot Station.

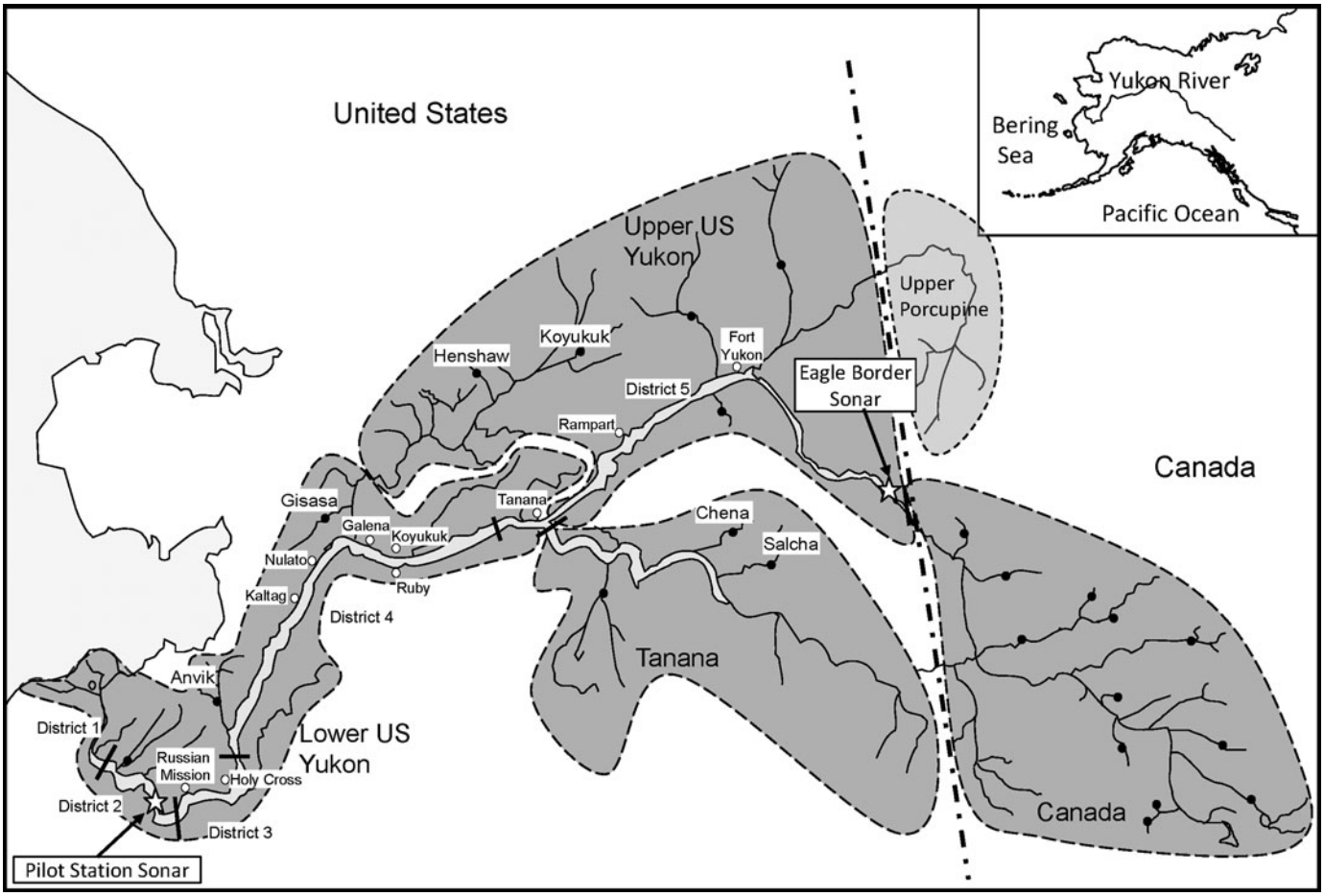

FIGURE 2. The Yukon River drainage showing fishery districts and GSI stock groups. Black solid circles indicate locations of genetic baseline samples of Chinook Salmon. White circles show locations of villages for GSI sampling.

Genetic samples of Chinook Salmon were taken from a sample size of 100–400 fish, which is sufficient to estimate a genetic stock proportion with a SD of 3–7% (see Templin et al. 2006, 2008; DeCovich and Templin 2009; DeCovich and Howard 2010, 2011; Decovich et al. 2010). At Pilot Station samples were taken from all Chinook Salmon captured in the daily test fishery and grouped into three or four temporal strata based on run pulses (Table 1). Samples of commercial fisheries were taken at several fishery opening periods where the majority of harvest occurred, except for district 2 in 2008, 2009, and 2011 and district 3 in 2009 (Table 1). Subsistence fishery harvests were sampled opportunistically by Alaska Department of Fish and Game (ADFG) staff and volunteer subsistence fishers at several communities where the majority of harvests occurred (Table 1).

Genetic stock identification of Chinook Salmon.—The proportion of various Chinook Salmon genetic stocks was estimated using genetic stock identification with the mixed-stock analyses (GSI-MSA) technique, employing microsatellites (2005) and single-nucleotide polymorphism (SNP) markers (2006–2011) (see Templin et al. 2006, 2008; Decovich and Templin 2009; Decovich and Howard 2010; Decovich et al. 2010). Genetic data were collected from the fishery samples as individual multilocus genotypes for 13 microsatellites in 2005 (Templin et al. 2006), 26 SNPs in 2006–2007 (Templin et al. 2008; Decovich and Templin 2009), and 42 SNPs in 2008–2011 (Decovich and Howard 2010, 2011; Decovich et al. 2010). Stock composition estimates for the stock groups of management interest were generated using the statistical packages SPAM (Debevec et al. 2000) in 2005–2007 and BAYES (Pella and Masuda 2001) in 2008–2011.

For the Yukon River Chinook Salmon, stock composition estimates were made for four groups: (1) lower Yukon (Lower), (2) Tanana, (3) upper U.S. Yukon (Upper), and Canada. For each year fishery samples were analyzed, the baseline data were evaluated to ensure that stock grouping was identifiable with mean correct allocation of >90% for the 100% simulation test (Seeb et al. 2000). Regardless of the above historical changes in GSI-MSA techniques, the stock groupings of Lower, Tanana, Upper, and Canada consistently met this 90% threshold. However, the mixed-stock analysis lacks several baseline populations, notably Porcupine River, Yukon Territory, which accounts for 2–4% of

TABLE 1. Total commercial and subsistence harvest of Chinook Salmon in the Yukon River at each district upriver from Pilot Station, and the number of genetic samples collected at Pilot Station and upriver commercial and subsistence fisheries at each district.

	Year						
Sample location	2005	2006	2007	2008	2009	2010	2011
Pilot Station (number of strata)	3	4	3	3	4	3	3
Total samples	671	551	540	711	867	370	571
District 2							
Commercial (total harvest)[a]	13,413	19,844	13,306	2,111	226	4,153	46
Number sampled/total fishery periods	3/3	4/6	5/9	1/5	0/1	6/7	0/11
% harvest in sampled periods	100	90.1	80.8	24.6	0	94.6	0
Total samples	1,128	1,466	1,357	100	0	450	0
Subsistence (total harvest)	3,462	3,873	4,583	4,881	2,459	3,440	3,828
Total samples	0	0	0	0	0	0	198
District 3							
Commercial (total harvest)		315	190				
Total samples		106	0				
Subsistence (total harvest)	5,131	5,689	4,651	5,855	2,924	4,299	4,134
Number sampled/total communities	0/3	0/3	1/3	1/3	1/3	1/3	0
% harvest by sampled communities	0	0	62.4	42.9	59.7	72.1	0
Total samples	0	0	204	133	238	197	0
District 4							
Subsistence (total harvest)	13,653	11,719	11,624	10,229	8,344	12,697	9,717
Number sampled/total communities	3/7	4/7	5/7	5/7	5/7	4/7	3/7
% harvest by sampled communities	56.3	57.0	75.7	68.8	76.9	66.2	45.3
Total samples	927	606	903	750	1,234	744	570
District 5							
Commercial (total harvest)	1,469	1,839	1,241				
Number sampled/total fishery periods[b]	–/3	–/3	3/3				
Total samples	367	472	395				
Subsistence (total harvest)	14,431	14,463	17,339	9,904	7,312	7,843	8,978
Number sampled/total communities	0/9	1/9	2/9	2/9	3/9	3/9	2/9
% harvest by sampled communities	0	30.0	33.2	41.6	59.1	58.9	34.9
Total samples	0	285	927	599	752	592	487

[a]Total district 2 commercial harvest. Of that total, 20% of harvest was assumed to occur upriver from Pilot Station.
[b]A dash "–" indicates sampling periods are unknown.

the run (Figure 2; Eiler et al. 2004, 2006a, 2006b). Those populations were more likely to be misallocated to Canada stock.

Genetic mark–recapture estimation of the Yukon River Chinook salmon.—Run size of the Canada stock at Pilot Station (N_c) was estimated by summing the passage of Chinook Salmon at the Eagle border sonar (E_c) and harvests of the Canada stock between Pilot Station and Eagle ($C_{k=1}$) as:

$$\hat{N}_c = \hat{E}_c + \hat{C}_{k=1} \tag{6}$$

and

$$\hat{C}_k = \sum_{i,j} (\hat{C}_{c,i,j} \cdot \hat{P}_{c,i,j,k}) + \sum_{i,j} (\hat{C}_{si,j} \cdot \hat{P}_{s,i,j,k}), \tag{7}$$

where k is the stock identification number (1 = Canada, 2 = Lower, 3 = Tanana, and 4 = Upper), $C_{c,i,j}$ is the number of Chinook Salmon harvested by commercial fisheries in the ith district during the jth fishery period, $P_{c,i,j,k}$ is the proportion of the kth stock in the commercial harvest at the ith district during the jth fishery period, $C_{s,j}$ is the number of Chinook Salmon harvest by subsistence fisheries at the ith district and jth village, and $P_{s,j,k}$ is the proportion of the kth stock in subsistence harvest at the ith district and jth village.

For subsistence harvests of communities without genetic samples, we assumed that the genetic proportion was the same as that of the nearest sampled community and that the harvest of communities near Eagle were 100% Canada stock. For commercial fisheries where the genetic proportion of a fishery period

TABLE 2. Estimated escapement (E_c) of Canada stock Chinook Salmon in the Yukon River at Eagle, run size (N_c) and proportion (p_c) at Pilot Station, and Chinook Salmon passage estimates by genetic mark–recapture N and Pilot Station sonar N_{sonar} in years 2005–2011. Values in parentheses are SEs.

Year	E_c	N_c	p_c	N	N_{sonar}
2005	81,528 (353)	107,442 (1,924)	0.42 (0.030)	255,121 (19,958)	159,441 (30,134)
2006	72,691 (245)	97,469 (787)	0.41 (0.027)	237,678 (16313)	169,403 (13,383)
2007	41,697 (143)	68,726 (1,287)	0.37 (0.030)	185,548 (15,742)	125,553 (12,256)
2008	38,097 (116)	55,741 (903)	0.35 (0.024)	157,746 (11,371)	130,643 (9,555)
2009	69,957 (172)	81,361 (571)	0.37 (0.029)	222,402 (18,256)	122,990 (13,023)
2010	35,074 (82)	52,293 (1,572)	0.41 (0.077)	128,859 (27,366)	113,410 (83,091)
2011	51,271 (135)	66,225 (1,514)	0.35 (0.030)	191,155 (18,372)	123,369 (10,831)

was missing, the proportion of the nearest fishery period was substituted.

At Pilot Station, the proportion of Canada stock ($P_{k=1}$) passage was estimated as

$$\hat{P}_k = \frac{\sum_j (\hat{N}_j \cdot \hat{P}_{j,k})}{\sum_j \hat{N}_j}, \tag{8}$$

where N_j are sonar estimates of Chinook Salmon passage at Pilot Station at the jth period and $P_{j,k}$ is the proportion of kth stock at the jth period.

From the above, genetic mark–recapture estimates of Chinook Salmon run size at Pilot Station (N) were calculated as

$$\hat{N} = \frac{\hat{N}_c}{\hat{P}_{k=1}}. \tag{9}$$

Stock-specific run size, escapement, and exploitation rate of all four genetic stock groups were also estimated using equations (3–5) described above.

Variance of the above estimates was calculated using a parametric bootstrap simulation of 10,000 replications (Efron and Tibshirani 1993). In this simulation, variances associated with both run size or harvest estimates and genetic proportion estimates were incorporated. Estimates of the subsistence harvest and Canada stock Chinook Salmon run size at Eagle were assumed to be normally distributed with the reported survey CV (7–10%). Harvest of the commercial fishery was assumed to be without error (CV = 0). Coefficients of variation of Chinook Salmon passage at Pilot Station were generally 7–15%, except in 2010 when CV was 70% (Table 2). The original CV of the genetic stock proportion incorporated errors associated with both sampling and genetic stock identification (i.e., identifying each stock correctly) (Templin et al. 2006, 2008; Decovich and Templin 2009; Decovich and Howard 2010, 2011; Decovich et al. 2010). For bootstrap approximation of genetic proportion CV, we used the multinomial distribution, Mult(n, $p_1, \ldots p_k$), $0 \leq p_i \leq 1$, $\sum p_i = 1$, where n is a sample size. Because this approximation considers only sampling error (i.e., each stock was correctly identified), we adjusted the sample size (n) so that bootstrap CV matched the original CV.

Comparison of estimates between genetic and radiotelemetry mark–recapture.—We compared the consistency of estimates of genetic mark–recapture with those from radiotelemetry mark–recapture conducted during the 2002–2004 periods (Spencer et al. 2009). Radiotelemetry generated estimates of Chinook Salmon run size upriver from Russian Mission just upriver from Pilot Station (N_R), as well as run size at the U.S.–Canada border passage (Canada: E_c) and Tanana River escapement (Tanana: E_t) (Table 3; see Spencer et al. 2009). From those, total escapement (E_{total}) and escapement of the US stocks (E_{US}) can be estimated as $E_{\text{total}} = N_R - C$, and $E_{\text{US}} = E_{\text{total}} - E_c$, and escapement of Lower + Upper stock (E_{l+u}) can be estimated as $E_{l+u} = E_{\text{US}} - E_t$. Then, we calculated the following indices: (1) proportion of total escapement among Canada (E_c/E_{total}), Tanana (E_t/E_{total}), and Lower + Upper stock (E_{l+u}/E_{total}) and (2) proportion of Lower + Upper stock escapement to the U.S. escapement (E_{l+u}/E_{US}). Further, for the Tanana stock, we calculated the proportion of Chena + Salcha rivers escapement to Tanana River escapement (Chena + Salcha escapement/E_t).

Assuming that the stock composition of run and harvests did not change greatly between the 2002–2004 and 2005–2011 periods, those estimates should be similar between radiotelemetry and genetic mark–recapture methods.

TABLE 3. Radiotelemetry mark–recapture estimates of Chinook Salmon in the Yukon River in years 2002–2004 modified from Spencer et al. (2009).

Population	2002	2003	2004
Large salmon[a]	125,255	261,545	229,739
Small salmon[b]	77,423	48,342	
Total (N_R)	202,678	309,887	229,739
Canada (E_c)[c]	66,530	90,037	59,415
Tanana (E_t)[c]	22,436	53,034	50,803
U.S. harvest (C)	66,530	434,450	45,017

[a]For 2002–2003, ≥650 mm from mideye to caudal fork; for 2004, ≥520 mm.

[b]For 2002–2003, 520–650 mm, length stratification was not done in 2004.

[c]For 2002–2003, original estimates using ≥650 mm (Spencer et al. 2009) were expanded to ≥520 mm, based on sampled length distributions at recapture sites.

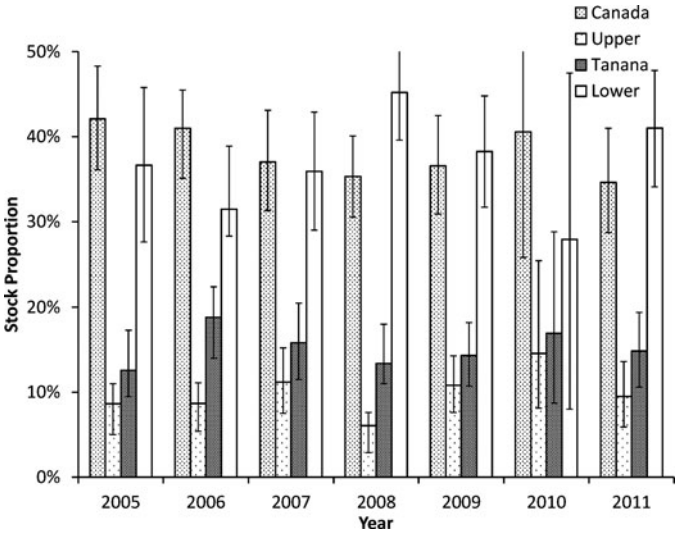

FIGURE 3. Estimated proportions of four stocks of Chinook Salmon at Pilot Station on the Yukon River. The vertical error bars show the range of bootstrap 95% confidence intervals.

RESULTS

The estimated Canada stock passage at Pilot Station (N_c) ranged from 52,293 (2010) to 107,442 (2005) with CVs ranging from 1% to 4% (Table 2). The estimated proportion of Canada stock at Pilot Station (p_c) ranged from 0.35 to 0.42 with SEs ranging from 0.024 to 0.030, except for 0.077 in 2010 (Table 2; Figure 3). This high SE in 2010 is due to the high CV of the Pilot Station sonar run size (N_{sonar}) estimate (Table 2). From those data, genetic mark–recapture estimates of Chinook Salmon run size (N) at Pilot Station ranged from 128,859 (2010) to 255,121 (2005) with CVs ranging from 6% to 9%, except for 19% in 2010. Estimates of genetic mark–recapture Chinook Salmon run size (N) were consistently 20–80% higher than the Pilot Station sonar (N_{sonar}) estimates (Table 2).

Among the four genetic stock groups, the proportion of Canada stock at Pilot Station was the highest (35–42%), followed by Lower (27–45%), Tanana (13–19%), and Upper (5–15%) (Figure 3). Among the U.S. stocks, the Lower stock had the largest run sizes, ranging from 34,708 to 93,497 with CVs ranging from 13% to 61%, followed by Tanana (21,118–44,765; CV, 15–36%) and Upper (9,567–24,084; CV, 16–29%) (Figure 4). Similarly, estimates of escapement were the highest for the Lower stock (33,768–88,533; CV, 13–39%), followed by Tanana (14,481–38,723; CV, 18–38%) and Upper (5,829–21,153; CV, 21–37%). The stock-specific exploitation rate upriver from Pilot Station was the highest for Canada (14–39%) and Upper (12–39%), followed by Tanana (10–34%) and the Lower stock (4–6%) (Figure 5).

Comparing the estimates of genetic mark–recapture with those of radiotelemetry mark–recapture, genetic mark–recapture appeared to show a higher escapement proportion of Lower + Upper stocks and a lower proportion of Canada and Tanana stocks (Table 4). Consistently, the proportion of Lower + Upper stock escapement in the U.S. stock escapement was also higher for genetic mark–recapture than for radiotelemetry. On the other hand, the proportion of the Chena + Salcha rivers stock to Tanana stock escapement was higher for radiotelemetry (Table 4). However, the mean estimates of genetic and radiotelemetry mark–recaptures were close, and the range of all estimates overlapped between the two methods.

TABLE 4. Comparison of average proportion and range (in parentheses) for radiotelemetry mark–recapture (RTMR) and genetic mark–recapture (GMR) of Yukon River Chinook Salmon.

Stock	RTMR (%) 2002–2004	GMR (%) 2005–2011
Canada escapement	35.0 (32.2–39.0)	33.7 (29.1–38.0)
Tanana escapement	20.2 (13.1–27.5)	14.7 (12.2–19.6)
Lower + Upper escapement	44.8 (40.3–47.9)	51.5 (43.2–58.1)
Lower + Upper in U.S. escapement	69.3 (59.5–78.5)	77.7 (68.8–83.2)
Chena + Salcha in Tanana	56.9 (50.0–70.5)	51.7 (35.2–63.0)

DISCUSSION

We presented an application of a genetic mark–recapture technique for the estimation of salmon total and stock-specific run sizes in a large river system, i.e., for Chinook Salmon of the Yukon River. The primary advantages of this approach over the traditional mark–recapture technique are the elimination of the effects of tagging fish and the ability of genetic mark–recapture to simultaneously estimate stock-specific run size, escapement, and exploitation rates. Further, genetic mark–recapture can be conducted using preexisting projects and data. In this study, this technique made it possible to estimate run size, escapement, and exploitation rate of the Yukon River Chinook Salmon by stocks for the first time. Those data make it possible to understand the contributions of individual stocks to the long-term stability of the populations and sustainability of the fisheries (Hilborn et al. 2003; Chaput 2004; Crozier et al. 2004; Peterman 2004; Carlson et al. 2011). Simultaneously, this technique has specific data requirements and assumptions that need to be considered for application. In the following, we discuss points to be considered when applying this technique.

For successful application of this technique, the following conditions are imperative: (1) presence of a genetic stock that can be identified accurately, (2) accurate estimate of the upriver run and escapement of the "marked" stock, (3) accurate estimates of the proportion of target genetic stock at the lower river, and (4) accurate estimates of harvests and their genetic stock proportions between the lower and upper rivers. In this regard, this study had an advantage in that the Canada stock was genetically identifiable, its upriver abundance was

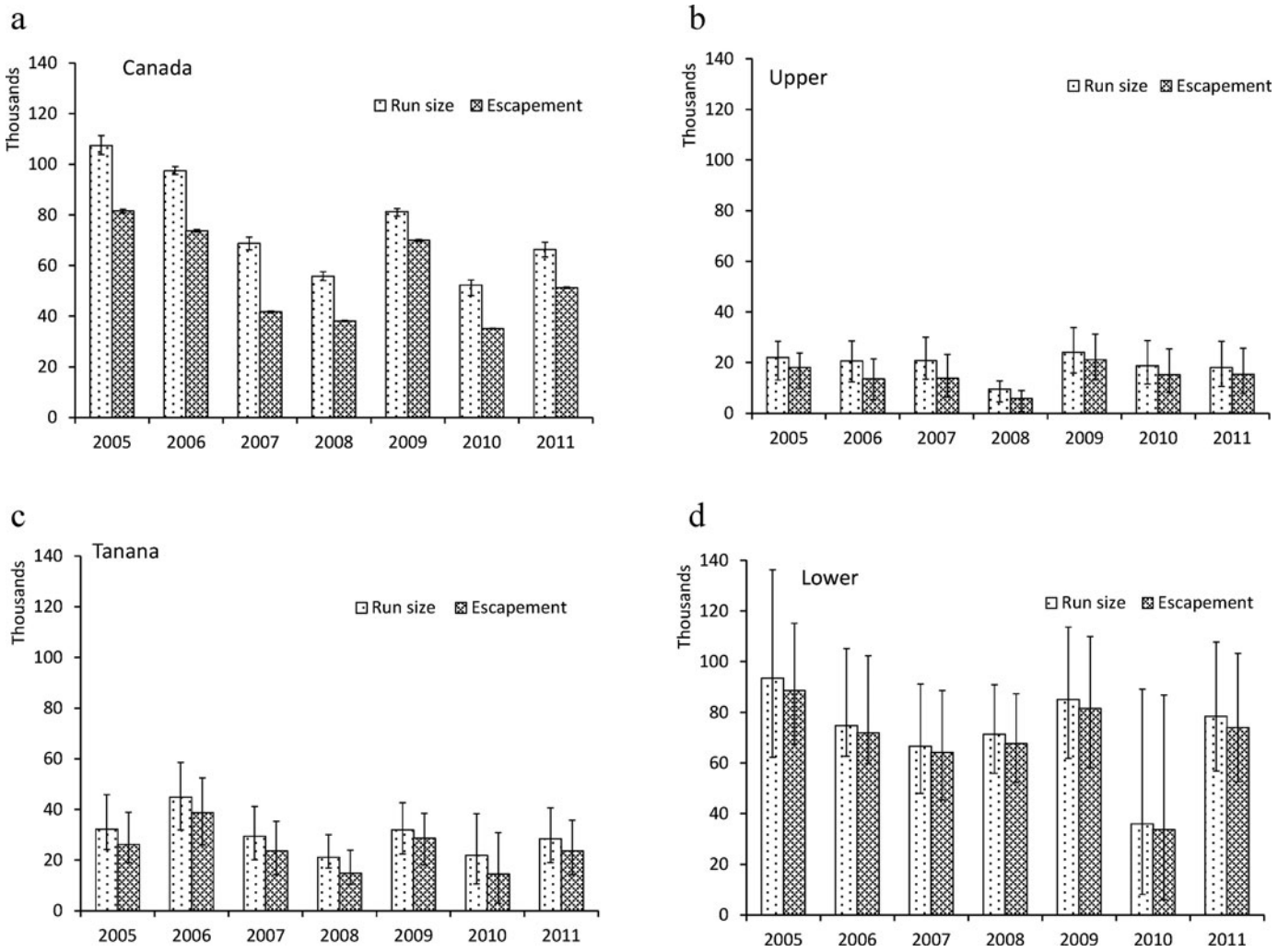

FIGURE 4. Genetic mark–recapture estimates of Chinook Salmon run size at Pilot Station and escapement by stock: (**a**) Canada, (**b**) Upper, (**c**) Tanana, (**d**) Lower. The vertical error bars show the range of bootstrap 95% confidence intervals. Escapement is defined as run size minus harvest in the U.S. portion upriver from Pilot Station.

accurately counted at Eagle, and its harvests and run proportion at the lower river have been monitored. Thus, application of genetic mark–recapture estimates was a simple extension of currently available data. We acknowledge that any of those data requirements can be challenging for many situations; however, conditions 1 and 2 are imperative. In many cases, not all the spawning tributaries within a genetic stock are monitored. This makes it difficult to estimate run size of the "marked" stock. For instance, in this study, application of genetic mark–recapture estimates was not possible using Lower, Tanana, or Upper stocks as "marked" because of the lack of ability to estimate their escapement (Figure 2). When direct escapement of the "marked" genetic stock is unavailable, additional escapement estimation techniques will be needed.

Even when the required data were available, ensuring the accuracy of genetic stock proportions in the lower river run and upriver harvests is challenging, primarily because of potential biases associated with sampling. Morphology, run timing, and within-river migration routes (e.g., bank orientation, swimming depth) may differ among stocks (Quinn 2005), and every kind of fishing gear is selective to fish of particular lengths and swimming behaviors (Hubert et al. 2012). In this study, Chinook Salmon at Pilot Station were sampled using gill nets of multiple mesh sizes at three locations of the river section (near shore left and right banks, and offshore) twice daily (Carroll et al. 2007; Carroll and McIntosh 2008), which minimized potential sampling biases. Further, we estimated seasonal genetic proportion using stratification equation (8). For stratification, we used the Chinook Salmon sonar passage estimates. While sonar passage estimates of Chinook Salmon are known to be underestimated (JTC 2013; Table 2), we assumed that run timing was accurate. Alternatively, run timing can be estimated using test-fishery CPUE; however, an assumption of CPUE as a proxy of run abundance is also challenged (Harley et al. 2001).

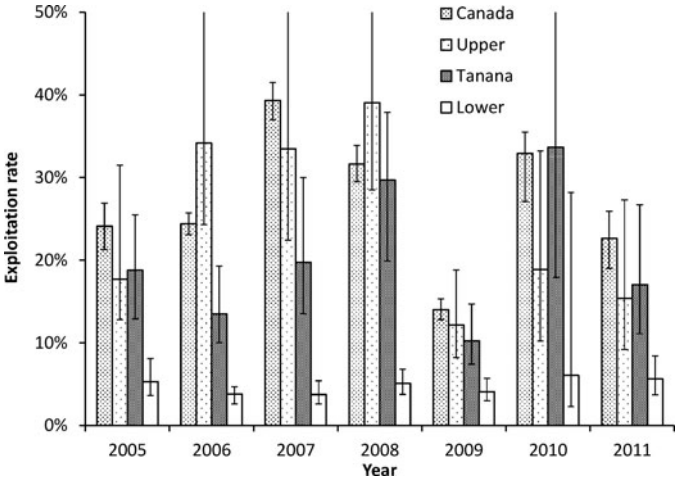

FIGURE 5. Estimated exploitation rate of four individual Chinook Salmon stocks upriver from Pilot Station on the Yukon River. The vertical error bars show the range of bootstrap 95% confidence intervals. Exploitation rate is defined as harvest in the U.S. portion upriver from Pilot Station divided by run size at Pilot Station.

Obtaining representative genetic samples for upriver harvests is also challenging, especially when fisheries occur at multiple locations and times and with different fishing gears. In this study, the majority of upriver harvests were subsistence fisheries where each household fishes using their preferred fishing gears at their preferred time and location. Since the harvest samples were collected opportunistically by individual volunteer fishers (JTC 2013), it remains unknown whether those samples are true representatives of the harvests of entire communities and districts.

We believe that the influence of the above potential sampling biases is minimal in our study because of the similarity of stock composition between radiotelemetry mark–recapture and genetic mark–recapture (Table 4). However, without this comparison, it would have been difficult to evaluate whether estimates of the genetic mark–recapture were biased. Thus far, no methods have been developed for detecting and correcting those biases, and further work is needed.

Finally, geographical boundaries of genetic stocks may change as techniques of GSI-MSA advance. While biological–management stock is defined based on geographic closeness of spawning tributaries (e.g., Canada stock is defined as a group of fish spawning in tributaries in Canada), genetic stock grouping is based on statistical similarity of genetic characteristics among sampled baseline populations (e.g., Canada stock is defined as a group of fish that have similar genetic characteristics as those spawning in tributaries in Canada; Figure 2). Statistical genetic grouping is influenced by (1) the number and distinctiveness of sample baseline populations, (2) the number and distinctiveness of genetic markers, and (3) statistical analytical methods. For instance, in 2013 the inclusion of more SNPs and baseline populations made it possible to separate upper Koyukuk spawners (Hanshaw and Kyoukuk; Figure 2) from the Upper stock and to identify a new U.S.–Canada border stock (ADFG, unpublished data). Because this change of genetic grouping will have a significant influence on the interpretation of stock status, such as abundance and exploitation rate, it is imperative to ensure historical consistency of genetic stock grouping.

For the Yukon River Chinook Salmon, an application of the genetic mark–recapture enabled us to estimate stock-specific run size, escapement, and exploitation rate for the first time. The results were consistent with current understandings of Yukon River Chinook Salmon, such as the Pilot Station sonar underestimation of Chinook Salmon run size (Tables 2, 4), that upriver stocks (i.e., Canada and Upper) had higher exploitation rates than the Lower stock (Criddle 1996; Criddle and Streletski 2000) and that Chena and Salcha rivers are the major spawning grounds of the Tanana river stock. Underestimation of the Chinook Salmon run size at the Pilot Station sonar site has been known and was also observed in comparison with radiotelemetry mark–recapture (Spencer et al. 2009). While its main cause is unknown, it is suspected to be underrepresentation of Chinook Salmon compared with other species in the daily test fishery (e.g., catchability of Chinook Salmon is lower than that of other species). This, however, is not an issue at Eagle sonar because no fish migrate concurrently with Chinook salmon at that site (Crane and Dunbar 2009a, 2009b, 2011; Dunbar and Crane 2007).

A notable and unexpected finding was the large proportion of Lower stock and their low exploitation rate (Figures 3–5). This was consistent with radiotelemetry mark–recapture results (Table 4), but was opposite from the findings of Eiler et al. (2004, 2006a, 2006b) in which about 20% of the radio-tagged fish moved to lower river spawning tributaries. Few major spawning tributaries of Lower river stock are monitored upriver from Pilot Station, such as in the Anvik, Nulato, and Gisasa rivers (Figure 2). Escapement on Anvik and Nulato rivers is monitored opportunistically by aerial survey (2,000–4,000 fish for both rivers combined), while that of Gisasa river is monitored at the weir (1,000–3,000 fish) (JTC 2013). Aerial surveys generally underestimate escapements (Holt and Cox 2008), and the number of radio-tagged fish that moved into the Anvik and Nulato rivers was about 6.5 times higher than the number that moved into Gisasa river (Eiler et al. 2004, 2006a, 2006b). However, even with this adjustment, total monitored Lower stock escapements would be 7,000–23,000 fish. This suggests that less than half of the Lower stock escapement (33,000–89,000) was observed, which also contradicts Eiler et al. (2004, 2006a, 2006b), in which about 67% of radio-tagged fish among Lower stock tributaries was observed in the three rivers. Those discrepancies between genetic mark–recapture and radiotelemetry may be due to radio-tagged Chinook Salmon being caught by gill nets of 8.5-in mesh size (Eiler et al. 2004, 2006a, 2006b). Nets having large mesh size are selective to capturing larger (i.e., longer) fish (Bromaghin 2005), and the length of the spawning Chinook Salmon in the lower river tended to be smaller than those spawning upriver (Schumann and DuBois 2011).

This discrepancy also raises an issue of verifying the mark–recapture estimates, especially when the estimates appear to challenge current understandings of population status and stock structure. Since those findings may also influence the current fishery management scheme, further work is needed, especially to investigate the potential spawning locations of the Lower stocks, to resolve the discrepancies.

In conclusion, we have presented a concept of the genetic mark–recapture technique, its application to the stock-specific estimation of the Yukon River Chinook Salmon, and considerations of potential biases and uncertainties. As stock-specific data are fundamental for mixed-stock fishery management (Hilborn et al. 2003; Chaput 2004; Crozier et al. 2004; Peterman 2004; Carlson et al. 2011), further development and application of this technique are needed.

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