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ARTICLE

Conservation Risk and Uncertainty in Recovery Prospects for a Collapsed and Culturally Important Salmon Population in a Mixed-Stock Fishery

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Abstract
Mixed-stock fisheries simultaneously exploit populations that may differ in their conservation status, and uncertainty in stock-specific harvest rates can hamper evaluations of recovery prospects for depressed populations. These difficulties are exemplified in the Sockeye Salmon population from the Atnarko watershed, which collapsed in the early 2000s, causing cultural and economic hardship. A recovery plan identified the incidental harvest of Sockeye Salmon by mixed-stock fisheries in the Atnarko as a potential, but poorly understood, impediment to recovery. We reconstructed harvest rates for salmon in Indigenous and commercial fisheries and used an age-structured state-space model of stock–recruit dynamics to predict how a range of future mixed-stock harvest rates would influence recovery. Under recent harvest rates, there is a 50–60% chance that the population will grow to exceed a recovery goal of 15,000 spawners over the next four generations. Eliminating the harvest of Sockeye Salmon altogether increased predicted

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recovery prospects to a maximum of 69%, suggesting that factors other than fisheries are contributing to the lack of recovery (e.g., ocean conditions) and that harvest management alone is unlikely to lead to recovery with a high degree of certainty. We developed a generalized migration, harvest, and catch monitoring simulation model to quantify how different monitoring scenarios might improve estimates for mixed-stock harvest rates. Increasing the number of specimens collected for genetic samples improved the harvest rate estimates for each stock caught in the mixed-stock fisheries, particularly for the smallest stocks, and relative to single sampling events conducted near the peak of the return migration, weekly sampling improved estimates only slightly but provided insurance against missing the peak of the return migration. Our study highlights collaborative research initiated and directed by the Nuxalk Nation to promote the recovery of a depressed stock that is inherent to traditional foods, thereby contributing to a global effort to integrate Indigenous cultural values with biological conservation.

> I believe the salmon is the heart of everything—the heart of our culture, the heart of our traditions, and the heart of our traditional economy. [Nuxalk Nation Hereditary Chief Quatsinas (Edward Moody); from Winbourne 1998.]

Balancing the social and economic benefits of harvesting a diversity of fish stocks, considering the overharvest of weak stocks that are incidentally caught in mixed-stock fisheries, is a persistent challenge to the sustainability of many fisheries around the globe (Hilborn et al. 2012, 2015; Link 2017). This challenge is acute in Pacific salmon fisheries that target comigrating stocks. Mixed-stock fisheries that harvest high salmon biodiversity can benefit from the stability in harvests that arise through portfolio effects (Hilborn et al. 2003; Schindler et al. 2010; Nesbitt and Moore 2016), yet this benefit may also come at the cost of collapse to individual stocks that are unable to withstand a given harvest rate (Pestes et al. 2008; Walters et al. 2008).

Understanding the extent to which the incidental harvest of depressed salmon populations in mixed-stock fisheries influences their recovery potential has become increasingly important in recent years. For example, in Western Canada over a dozen Chinook Salmon *Oncorhynchus tshawytscha* (COSEWIC 2018a), Coho Salmon *Oncorhynchus kisutch* (COSEWIC 2016), Sockeye Salmon *Oncorhynchus nerka* (COSEWIC 2017), and steelhead (COSEWIC 2018b) populations have been assessed as being at risk of extinction by the Committee on the Status of Endangered Wildlife in Canada (COSEWIC). These populations are subject to varying degrees of harvest in mixed-stock fisheries, and the Canadian Species at Risk Act requires that recovery potential assessments be conducted to quantitatively determine the extent to which harvest influences prospects for recovery. These assessments are challenged by multiple uncertainties, including those surrounding estimates for population parameters and the magnitude of mixed-stock harvest rates.

Pacific salmon are central to the ecosystems, economies, and cultures of the Northeast Pacific. Returning adult salmon transport marine-derived nutrients to coastal marine food webs (Vélez-Espino et al. 2015) and terrestrial flora and fauna (Reimchen 2000; Schindler et al. 2003; Hocking and Reynolds 2011). In coastal communities, salmon support commercial and recreational fisheries, and their abundance indirectly supports tourism and recreation. Salmon are also of cultural importance, particularly for First Nations (Trosper 2003) who have been living with and benefitting culturally and economically from salmon for at least seven thousand years (Cannon and Yang 2006). Indigenous communities in coastal British Columbia are disproportionately affected by the overharvest of weak salmon stocks in mixed-stock fisheries because their relationship to the resource is place-based and culturally grounded in traditions that span many centuries (Turner and Berkes 2006; White 2006). Further, many case studies illustrate how the loss of access to traditional foods affects the physical and social health of Indigenous communities (Burgess et al. 2005; Turner et al. 2013; Talaga 2018).

The importance of salmon, the cultural and economic consequences of their declines, and the challenges of mixed-stock fisheries are exemplified by the Sockeye Salmon population in the Atnarko watershed (hereafter, "Atnarko"), which is located in the Nuxalk Ancestral Territory of British Columbia (Figure 1).

Sockeye Salmon have been harvested from Atnarko by the Nuxalk for millennia and, along with other Pacific salmon species, they are an essential component of food fisheries that support a healthy community and the cultural integrity of the Nuxalk Nation. Through the 1970s and 80s, annual returns of Sockeye Salmon to the Atnarko River supported multiple fisheries (i.e., recreational, commercial, and Indigenous) that regularly caught more than 30,000 fish, with an average of 30,000 fish also making it to the spawning grounds. However, beginning in the late 1990s, the number of Sockeye Salmon returning to the system collapsed and the abundance of fish returning to spawn has remained severely depressed ever since (Figure 2).

The collapse of Sockeye Salmon throughout Atnarko and their subsequent failure to recover has led to cultural and economic hardship for the Nuxalk Nation and non-First Nation communities that have also historically benefitted from a commercial fishery. In response, a recovery

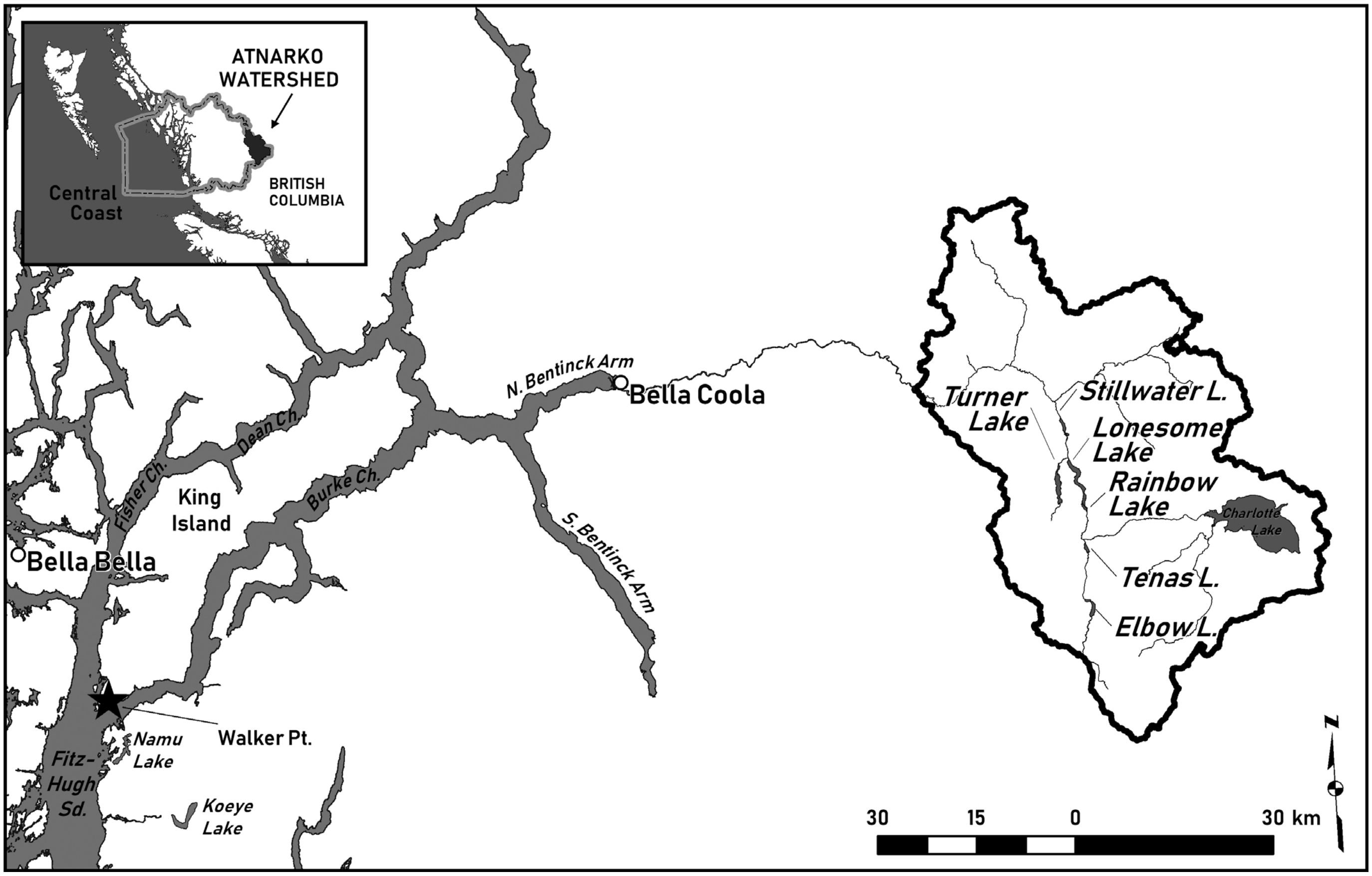

FIGURE 1. The Atnarko watershed and Sockeye Salmon nursery lakes within it. The Atnarko River flows 43 km through five connected Sockeye Salmon nursery lakes (Elbow, Rainbow, Tenas, Lonesome, and Stillwater) before joining the Talchako River to become the Bella Coola River. Note that Charlotte Lake is inaccessible to Sockeye Salmon. The marine waters shown constitute those in Fisheries Management Area 8, and Walker Point is indicated by a black star.

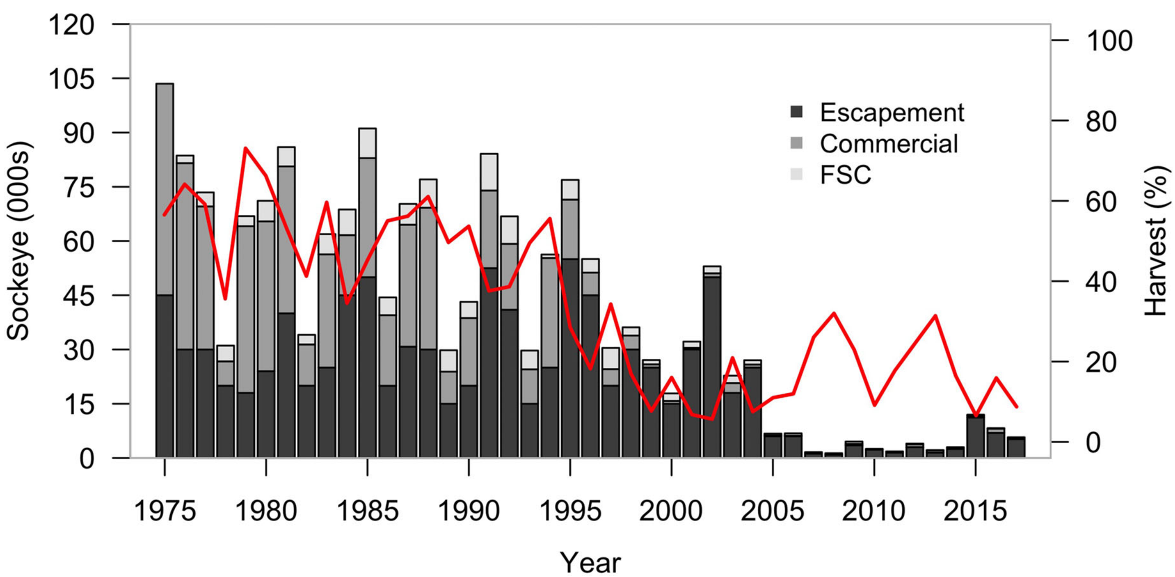

FIGURE 2. Total reconstructed escapement and harvest rates by commercial and Food Social and Ceremonial (FSC) fisheries for Sockeye Salmon in the Atnarko watershed from 1975 to 2017. Harvest rates are depicted by the red line.

plan was developed by the Nuxalk Nation in collaboration with Fisheries and Oceans Canada (DFO) and others involved in the monitoring, management, and scientific study of Sockeye Salmon in Atnarko. The recovery plan synthesized the available data, reviewed the evidence for factors potentially limiting survival, and identified actions that could be taken to promote recovery (Connors and Atnarko Sockeye Recovery Planning Committee 2016). Broad-scale declines in Sockeye Salmon survival across British Columbia (Peterman and Dorner 2012) suggest that common mechanisms that are operating at sea such as the changing ocean climate (Malick et al. 2017) and competition with increasing abundances of other salmon (Ruggerone and Connors 2015), coupled with disturbances affecting freshwater survival and productivity (including forest fires and severe floods), likely have contributed to the depressed state of Sockeye Salmon in Atnarko (Connors and Atnarko Sockeye Recovery Planning Committee 2016). The recovery plan identified the incidental harvest of Sockeye Salmon in commercial gillnet and seine fisheries that target other species as well as harvest in Indigenous fisheries for food, social, and ceremonial (FSC) purposes as a potential, but poorly understood, impediments to recovery.

Here we describe a project that was undertaken to (1) expand the genetic baseline of information on Sockeye Salmon in Atnarko to improve stock composition estimates in mixed-stock salmon fisheries and estimates of historic harvest rates for Sockeye Salmon, (2) develop and parameterize an age-structured state-space model of Sockeye Salmon stock–recruit dynamics in Atnarko and use closed loop simulation to evaluate the extent to which a range of plausible future harvest rates could influence prospects for the recovery of the Sockeye Salmon population, and (3) provide recommendations for First Nation-led monitoring of Sockeye Salmon in Atnarko to better understand and mitigate the effects of incidental harvest on this stock.

METHODS

Life History, Population Structure, Historic Population Size, and Harvest

Data are available for Sockeye Salmon spawner abundance and catches in Atnarko from the mid-1970s to present. Spawning Sockeye Salmon have been enumerated by using a variety of methods, including stream walks and aerial surveys.[1] From 1972 to 2004 the average annual escapement of Sockeye Salmon to the Atnarko River was more than 32,000 fish, with an average harvest rate of 40%. The Sockeye Salmon population in Atnarko collapsed in 2005, and over the ensuing ten years escapement averaged just 2,840 fish, prompting fisheries closures and conservation concerns (Figure 2).

We reconstructed annual estimates of population age-structure by using scale samples that were collected from fish that were caught in the lower Bella Coola FSC fishery and on the spawning grounds above the Atnarko River. In total there were 33 years of age-composition information from 1975 to 2017 (Figure 3). While age composition varied among run years, 4-year-old fish were consistently the most abundant age-class, comprising an average of 66% of spawners. Age-5 fish made up an average of 33% of spawners, while 3- and 6-year-old fish represented only 1% of the total samples that had been collected over the 46 years.

The structure of the Sockeye Salmon population in the Atnarko and Bella Coola watershed remains another source of uncertainty. Three distinct juvenile life histories (lake rearing, stream type, and ocean type) are represented in the population (reviewed in Connors and Atnarko Sockeye Recovery Planning Committee 2016). Fish spawning in the lower Atnarko River below Stillwater Lake are thought to be primarily ocean-type or stream-rearing, and their historical contribution to the population may have been as high as 30% of total recruitment. Fish that spawn in the lakes above Stillwater Lake are considered to be lake-rearing.

Harvest Reconstruction and Genetic Stock Identification

We reconstructed the harvest rates for Sockeye Salmon in Atnarko from databases for commercial and FSC catch that are maintained by DFO. Historic estimates for harvest rates from 1975 to 2007 were previously summarized in the Atnarko Recovery Plan, along with preliminary estimates through 2014 (Connors and Atnarko Sockeye Recovery Planning Committee 2016). In-river catches of Sockeye Salmon in Atnarko by Nuxalk First Nation fishers have been monitored throughout the time series, but harvest estimates from 2007 to present in the recovery plan did not account for FSC catch in marine areas or for bycatch of Sockeye Salmon in commercial fisheries that were targeting other species. Therefore, we updated the total harvest estimates to reflect all of the potential sources of fishing mortality including those occurring in directed commercial and FSC fisheries as well as incidental mortality in fisheries that were targeting other Sockeye Salmon populations and species from 1975 to 2017. We note that marine FSC catch reporting is voluntary, so the reported FSC harvests are likely underestimated.

Working with DFO staff in the Bella Coola office, we compiled postseason reviews and other data on Sockeye Salmon interceptions in Fisheries Management Area 8 (Figure 1), which includes the marine waters in which Sockeye Salmon from Atnarko are most likely to be intercepted. Previous genetic stock identification work had estimated that

[1]Beginning in 2015, spawner surveys no longer occurred below Lonesome Lake; therefore, we used the historic ratio of spawners above and below Stillwater Lake (4.65; CV = 1.27) to estimate spawner abundance below Lonesome Lake during 2015–2017.

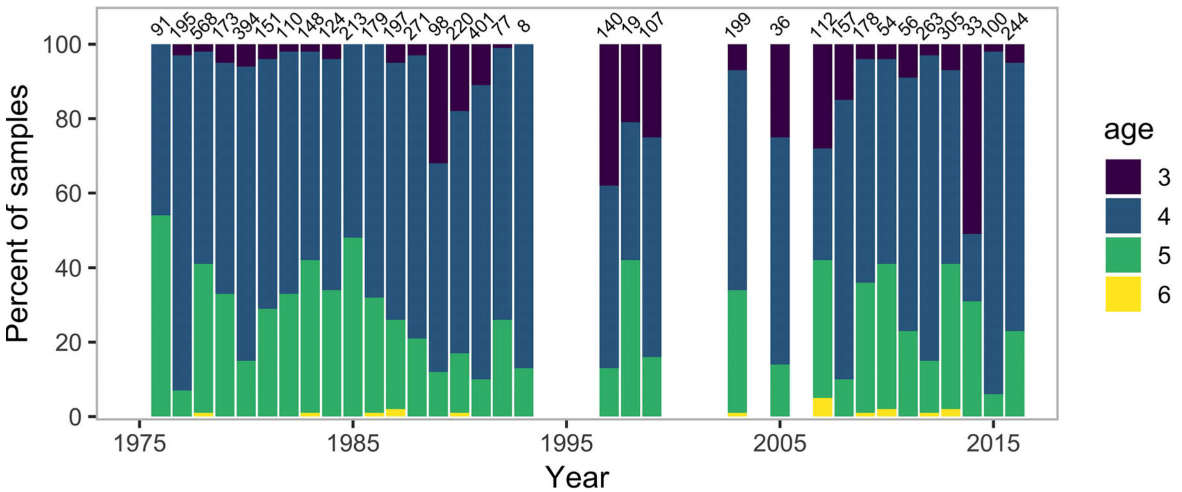

FIGURE 3. Age composition of returning adult Sockeye Salmon from Atnarko. The estimates were derived from biological samples (number denoted above each bar) that were taken from fish on the spawning grounds or from those harvested in FSC fisheries. The years with no FSC or escapement samples are left blank.

Atnarko-bound fish made up 13% of the Sockeye Salmon that were caught south of Walker Point in Area 8-3, and 6% of the salmon that were caught north of Walker Point (from 94 fish sampled in 2003; Connors and Atnarko Sockeye Recovery Planning Committee 2016). To further quantify the stock composition Sockeye Salmon in catch from Area 8, we extracted genetic material from the adipose fins of 89 adult Sockeye Salmon that had been collected by Nuxalk Fisheries in Fitz Hugh Sound during the summer of 2008. These samples were analyzed to determine stock-identification by using a stock-specific microsatellite genetic baseline that had previously been shown to be effective in assigning Sockeye Salmon to their population of origin, including those from Atnarko (Beacham et al. 2005). These fish were assigned to 21 genetically distinct populations, with Sockeye Salmon from the Bella Coola–Atnarko watershed contributing 14% (SD 3.8; Table S2 available separately online in the Supporting Information). Despite the uncertainty associated with these catch composition estimates (e.g., due to timing, location, and sample size), they were consistent with the previous work by DFO, which found that Sockeye Salmon from Atnarko made up 13% of the catch in the relevant management area (Area 8-3; Figure 1).

We used the above estimates for the stock composition of Sockeye Salmon in mixed-stock fishery catch to reconstruct historic catch rates for Sockeye Salmon from Atnarko in marine FSC fisheries and commercial bycatch in fisheries that were targeting other salmon species. In recent years, some Sockeye Salmon that have been caught incidentally in commercial fisheries have been released, so we assumed 30% and 50% postrelease mortality for seine- and gillnet-caught Sockeye Salmon, respectively, and applied these values to recorded Sockeye Salmon releases (Donaldson et al. 2011; Patterson et al. 2017).

After accounting for marine FSC harvest and commercial bycatch, the harvest rates for Sockeye Salmon from Atnarko during the last 10 years have ranged from 6% to 32%, with an estimated average of 18.5%. These estimates were relatively robust to assumptions about release mortality. Assuming no release mortality resulted in harvest rate estimates that ranged from 6% to 28%, with an average estimate of 16%, and assuming 100% release mortality resulted in harvest rate estimates that ranged 7% to 36%, with an average estimate of 20%.

Stock-Recruitment Estimation

In order to forward-simulate the dynamics of Sockeye Salmon in Atnarko under a range of alternative future harvest rates, we first developed an age-structured state-space stock–recruitment model that was fit to all available data (i.e., time series of catch, spawner abundance, and age composition). Our approach, which closely follows that of Fleischman et al. (2013), consisted of a state-space stock–recruitment model that allows for temporal variability in productivity and age-at-maturity. This approach allows for the appropriate representation of process variation and observation error and more realistic incorporation of multiple sources of uncertainty than do traditional stock–recruitment models..

Process model.— The process model, or system equations, component of our state-space model specifies productivity and age at maturity by cohort (i.e., brood year). Returns of Sockeye Salmon from the Atnarko watershed (R) from 1975–2017 were treated as unobserved states and modeled as a function of spawner abundance (S), assuming a Ricker (1954) stock–recruitment relationship with serially correlated lognormal process variation:

$$\ln(R_y) = \ln(S_y) + \ln(\alpha) - \beta S_y + \nu_y, \quad (1)$$

where α is productivity (intrinsic rate of growth), β is the magnitude of within brood-year density-dependent effects, and ν reflects interannual variation in survival, which was assumed to be correlated (ϕ) over time:

$$\nu_y = \phi\nu_{y-1} + \varepsilon_y, \quad \varepsilon_y \sim \text{Normal}(0, \sigma_R), \quad (2)$$

where ε_y is independent normally distributed process variation in survival with a standard deviation of σ_R. The first 6 years of observed returns (1969–1974) that were not linked to observations of spawner abundance in the stock–recruitment relationship (equation 1) were modeled as draws from a lognormal distribution with mean ln (R_0) and standard deviation σ_{R0}.

The number of Sockeye Salmon from Atnarko that returned to spawn in year y and age a was the product of the total return from brood year $y - a$ and the proportion of fish from brood year $y - a$ that returned at age a:

$$N_{y,a} = R_{y-a}p_{y-a,a}, \quad (3)$$

where the vector of age-at-maturity proportions were drawn from a common Dirichlet distribution, realized by generating independent gamma variates ($g_{y,a}, a \in 3:6$) and dividing by their sum (Fleischman et al. 2013):

$$p_{y,a} = \frac{g_{y,a}}{\sum_a g_{y,a}}, \quad (4)$$

where the gamma variates are drawn from a gamma distribution with shape k_a and inverse scale equal to 1. This gamma distribution was parameterized according to Gelman et al. (2004), where the k_a are the age-specific hyperparameters of the Dirichlet distribution that determine the expected proportions (π_a) of salmon returning at age:

$$\pi_a = \frac{k_a}{\sum_a k_a}. \quad (5)$$

Spawning escapement (S_y) was then equal to the number of adult salmon returning to spawn prior to fisheries (N_y) and harvest (H_y), which was modeled as the product of total run size and the harvest rate (U_y) experienced ($0 \ll 1$), which serves to constrain S_y to be nonnegative:

$$H_y = N_y U_y. \quad (6)$$

Data and observation model.— Because we had no quantitative estimates for observation error in spawner abundances that were specific to the Atnarko watershed, we assumed a 50% coefficient of variation (CV) for spawner observations from 1975 to 2014, which is generally consistent with the upper bound on observation error estimates from the same techniques in other systems (Cousens et al. 1982). We assumed a 100% CV from 2015–2017 to account for the fact that spawner counts were expanded to account for a reduction in the spatial extent of spawner surveys in recent years. Observed spawner abundance was therefore assumed to be lognormally distributed with parameters ln($S_{O,y}$) and $\sigma_{S_{O,y}}$, with the CVs converted to lognormal variance following Evans et al. (1993):

$$\sigma^2_{S_{O,y}} = \ln[\text{CV}^2(S_{O,y}) + 1]. \quad (7)$$

As with spawner observations, we had no direct quantitative estimates of observation error in harvest, so we assumed that harvest had a 15% CV, which is considered reasonable given the relatively precise estimates of commercial harvest that are typically generated for Sockeye Salmon on the Central Coast of British Columbia. For the years after 1999, which lacked a commercial fishery, we assumed a higher CV of 30% due to the increased uncertainty in harvest estimates that are derived from multiple sources. This level of uncertainty is consistent with the uncertainty in stock-assignments from genetic analysis of mixed-stock fishery catch (Table S1). We assumed that the harvest observations were lognormally distributed with parameters ln($H_{O,y}$) and $\sigma_{H_{O,y}}$, with the CV converted to lognormal variance as per equation (7).

Age composition by return year was assumed to be observed with error, where uncertainty in age proportions in a given year was generated by specifying an effective sample size (ESS). For years with age data, we set the ESS equal to the true sample size divided by the maximum sample size across all years (593) multiplied by 250. This procedure yields multinomial sample sizes that are expected to produce uncertainty that is roughly equivalent to that which would be anticipated from the average number of fish sampled in a given year from a population with age proportions and classes similar to that of fish in Atnarko (i.e., CVs of 95, 8, 15, and 95% for ages 3, 4, 5, and 6, respectively). For years with no empirical estimates for age composition, we set the ESS equal to 25 to account for the fact that age composition uncertainty was much higher in these years. We note that previous work has found that population parameter estimates from state-space analyses of spawner-recruitment data for Pacific salmon are generally not sensitive to the choice of ESS (e.g., Fleischman and McKinley 2013).

Model fitting.— We fit the model described in equations (1)–(7) in a Bayesian estimation framework. Prior probabilities for most unknowns in the model were specified to be uninformative (Table 1), except for β, which was constrained to avoid biologically implausible negative

TABLE 1. Parameters and associated prior and posterior distributions; median (95% credible intervals). A description of the parameters that were used in the models is described in the main text along with their associated prior distributions and marginal posterior estimates.

Parameter	Description	Prior	Posterior
S	Spawner abundance		
R	Recruitment		
N	Adult salmon returning to spawn prior to any harvest in fisheries		
H	Total harvest in fisheries		
U	Harvest rate		
$\log_e(\alpha)$	Population productivity (recruits-per-spawner at small population size)	~U (0,3)	1.07 (0.14–2.53)
β	Magnitude of within brood-year density dependent effects on survival	~U(0,10)	3.11×10^{-5} (1.37×10^{-5}–4.97×10^{-5})
ϕ	Strength of correlation in survival from one year to the next	~U(-1,1)	0.88 (0.69–0.98)
σ_R	Inter-annual variation in survival (SD units)	~U(0,100)	0.48 (0.27–1.15)
$\gamma_{3:6}$	Age-at-maturity proportions	~Dirichlet (0.25,0.25,0.25,0.25)	0.09 (0.07–0.12) 0.64 (0.60–0.68) 0.25 (0.22–0.29) 0.02 (0.01–0.02)

values, which would imply that the population could grow at an increasing rate as it expanded. Joint posterior probability distributions for all unknowns in the model were generated using a Markov chain–Monte Carlo (MCMC) procedure in the JAGS sampler, interfaced through R (Plummer 2017). We ran six chains for 250,000 iterations after a burn-in of 50,000, and we thinned at every fifth iteration. Convergence was assessed by examining the potential scale reduction factor () and assumed to have occurred if was less than 1.1 (Gelman and Rubin 1992). This Gelman–Rubin statistic compares within-chain variance to between-chain variance to diagnose convergence.

Forward Simulations

With estimates of historic spawner abundance, age composition, carrying capacity, and temporal variation in survival for Sockeye Salmon from Atnarko, we then simulated these dynamics forward in time across a range of plausible future harvest rates. To achieve this we simulated future population trajectories by iterating the process model in equations (1)–(3) forward over 20 years (approximately 4 generations), thereby generating a posterior predictive distribution of future states, conditioned on the historical data. By simulating the salmon dynamics in this manner, we ensured that predicted future spawner abundance and age structure were conditioned on the incomplete cohorts at the end of the data series (i.e., those cohorts from which one or more older age-classes have not yet returned to spawn) and that uncertainty in the stock–recruit relationship was propagated (i.e., by drawing from the posterior distributions of each estimated parameter in each iteration of the simulation).

We simulated 10,000 future trajectories for each of 20 different harvest rates, ranging from 0–40%, and then summarized the results by quantifying the probability of exceeding the provisional (1) limit reference point (4,000 spawners) and (2) recovery goal (15,000 spawners) (Connors and Atnarko Sockeye Recovery Planning Committee 2016) over the last 10 years of the simulation. This limit reference point corresponds to the spawner abundance predicted to result in recovery to S_{MSY} under equilibrium conditions in one generation in the absence of fishing (S_{gen}; Holt et al. 2009), and it is meant to indicate the population size at which the need for management intervention is high. This proposed limit reference point is slightly higher than what is typically assumed to be a minimum population size from a genetic perspective in Pacific salmon (Allendorf et al. 1997). The recovery goal set by the recovery planning committee corresponds to the spawner abundance that was previously predicted to maximize long-term yield from the system (S_{MSY}) and is assumed to correspond to a minimum spawner abundance that is required to support cultural uses, provide livelihood opportunities, and fulfill the population's ecological role in the system.

Sensitivity Analyses

We ran several sensitivity analyses to quantify the extent to which our assumptions about observation error and the composition of mixed-stock catch influenced inferences about recovery prospects. The first sensitivity analysis doubled the magnitude of spawner and harvest observation error and increased the magnitude of uncertainty in age composition by dividing the baseline effective sample size in half. The second sensitivity analysis assumed that the precollapse composition the of mixed-stock catch of Sockeye Salmon from Atnarko was double that in the years following the collapse when genetic samples were available for estimating catch composition.

Simulations to Inform Future Catch Monitoring

We simulated a catch monitoring program to characterize general trade-offs between precision of catch composition or harvest rate estimates and the sampling effort associated with different marine catch sampling regimes (i.e., the number and frequency of samples taken from Sockeye Salmon that are caught). To do so, we simulated a group of 10 populations (roughly the number of Sockeye Salmon populations that are likely to be harvested in Area 8) and then derived estimates for catch composition and harvest rates for the populations, assuming that they were either of equal (5,000 fish) or variable size (500, 1,000, 2,000, 3,000, 4,000, 6,000, 8,000, 10,000, 15,000, and 20,000 spawners), the latter corresponding to the approximate range of Sockeye Salmon population sizes in the region. The return timing of each population through the fishing area was simulated to occur over a six-week period by randomly generating 10 multinomial distributions with return probabilities of 0.1, 0.2, 0.3, 0.2, 0.15, 0.05 (assuming an effective sample size of 100 and again roughly corresponding to the spread of return timing of Sockeye Salmon in the region). These proportions were then multiplied by the total run size for each population to determine the numbers of fish that were exposed to fishing in the area during each week of the six-week return migration. We simulated the fisheries harvest process by assuming that the mixed-stock harvest rate was constant across all populations and across the six run weeks (20%) and that fish were caught randomly from the population and without replacement by the fishers.

To evaluate the trade-offs associated with different sample frequency and sizes, we simulated the catch process and resulting estimates for population-specific harvest rates for two possible sampling protocols: (1) sampling once on a randomly selected week during the peak migration (week 2, 3, or 4) for five different sample sizes (60, 120, 240, 360, or 600 fish) or (2) sampling weekly with six different weekly sampling sizes (10, 20, 40, 60, or 100 fish). Both protocols produced the same number of total samples, allowing us to directly isolate and quantify the benefits of weekly sampling versus increased sample sizes. The estimated contribution of individual stocks to total harvest and associated uncertainty were generated by rerunning the fishing and sampling process 1,000 times. We then estimated the stock-specific harvest rates and associated uncertainty across a range of observation error (CV = 0, 0.2, 0.5) in both total catch and escapement estimates. In our model, total catch was multiplied by the estimated contribution of each population in the catch sample to produce an estimate of total harvest for each stock. In some model iterations where individual populations were subjected to high harvest rates and observation error was high, population-specific harvest estimates occasionally exceeded total run size. Since actual harvest rates cannot exceed 100%, we fixed estimated harvest rates to be 95% in these instances and estimated mean harvest rates across simulation runs accordingly.

All code and data required to reproduce our analyses are archived in Connors (2019).

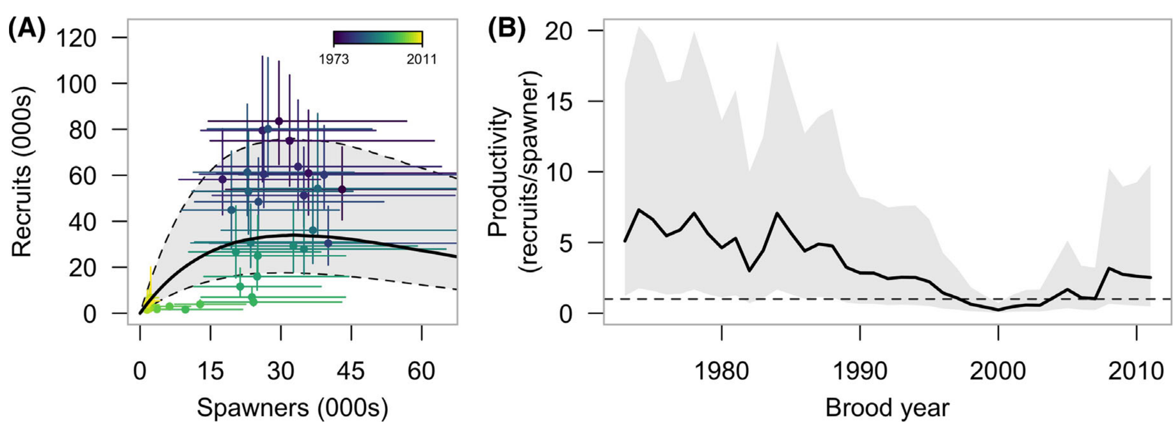

FIGURE 4. Panel **(A)** shows the relationship between recruitment and spawner abundance for Sockeye Salmon in Atnarko from 1975 to 2017. The error bars are 95% credible intervals from the Bayesian state-space age-structured model. The thick black line is the predicted relationship between spawner abundance and recruitment along with 80% credible intervals. Panel **(B)** shows the estimated productivity of Sockeye Salmon in Atnarko over time {exp[sum of ln(α) and log residuals]} along with 80% credible intervals from the Bayesian state-space age-structured model. The dashed line illustrates replacement.

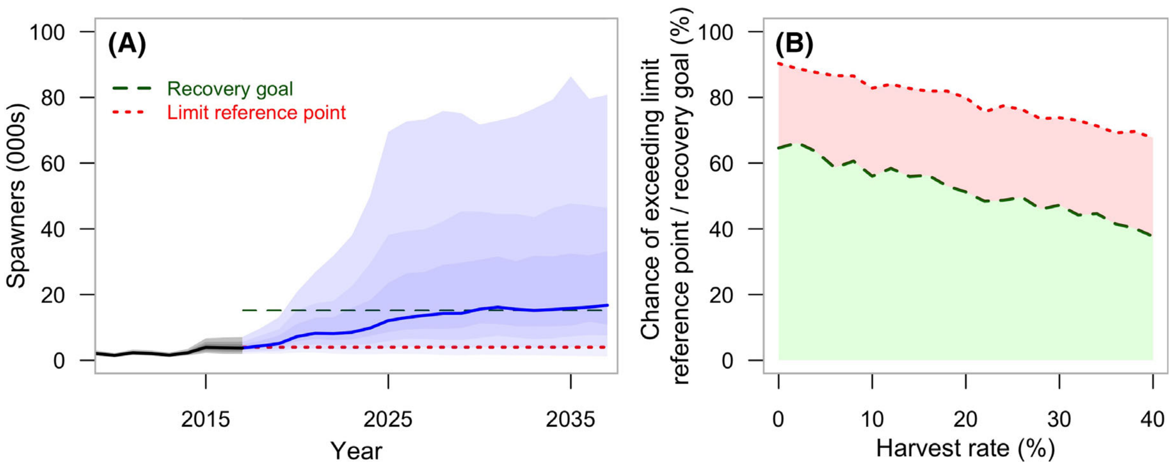

FIGURE 5. Panel **(A)** shows the predicted median (solid lines) for Sockeye Salmon spawner abundance in Atnarko over the next four generations, assuming an annual mixed-stock harvest rate of 15%. The shaded areas are the 40th, 60th, and 80th percentiles to illustrate uncertainty in the projections. Panel **(B)** shows the percentage of forward projections, where average spawner abundance over the last 10 years exceeded the limit reference point (4,000 spawners; red dotted line) or recovery goal (15,000 spawners; green dashed line) across a range of future harvest rates.

RESULTS

Sockeye Salmon in Atnarko have exhibited relatively low productivity over the past four decades (2.54 recruits/spawner at low population sizes; 95% CI [1.14, 9.55]; see Table 1), and they have a predicted equilibrium population size of 57,000 (95% CI [30,204, 201,524]). These estimates and the overall shape of the stock–recruitment relationship, however, are uncertain (Table 1 and Figure 4A). We found evidence for strong serial correlation in survival ($\phi = 0.68$) and clear evidence of nonstationary productivity where the Atnarko salmon population exhibited a period of below average survival in the early 2000s that likely contributed to the depressed spawner abundance that has been observed ever since (Figure 4B). However, productivity appears to have rebounded in recent generations, suggesting that with sufficient numbers of fish returning to the spawning grounds the population has the potential to recover.

Our simulations predicted a moderate influence of future harvest rates on recovery potential for Sockeye Salmon in Atnarko (Figure 5A and B). Our forward simulations predicted a high probability (>0.75) that salmon will increase in abundance and remain above the proposed limit reference point (4,000 spawners) regardless of future harvest rates (up to the maximum 40% harvest rate examined;

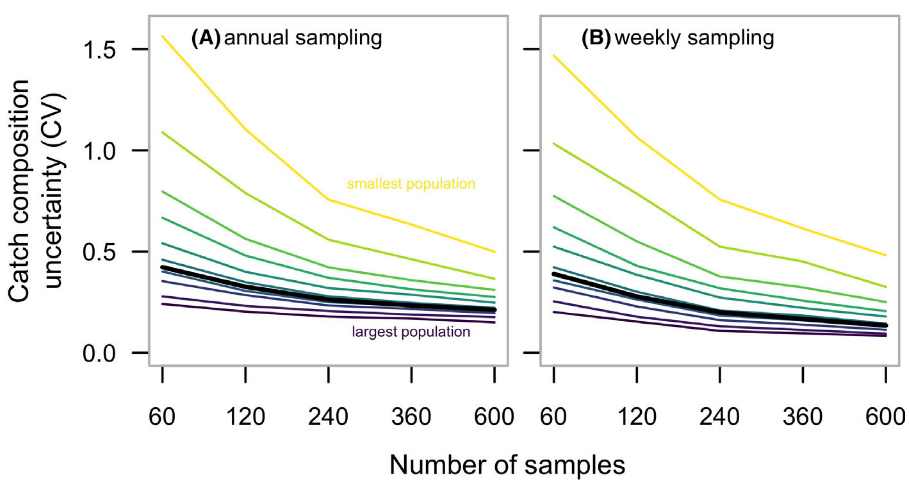

FIGURE 6. Relationships between sample size and the coefficient of variation (CV) in estimated stock-composition for catch sampling protocols involving either **(A)** a single annual sample or **(B)** weekly samples. The thick black line is the mean estimated CV when all of the populations are of equal size (5,000 fish). The colored lines are the CVs of stock-composition estimates from catch samples consisting of populations of variable size (500–20,000 fish). The highest CVs in (B) are associated with the smallest population sizes, and vice versa.

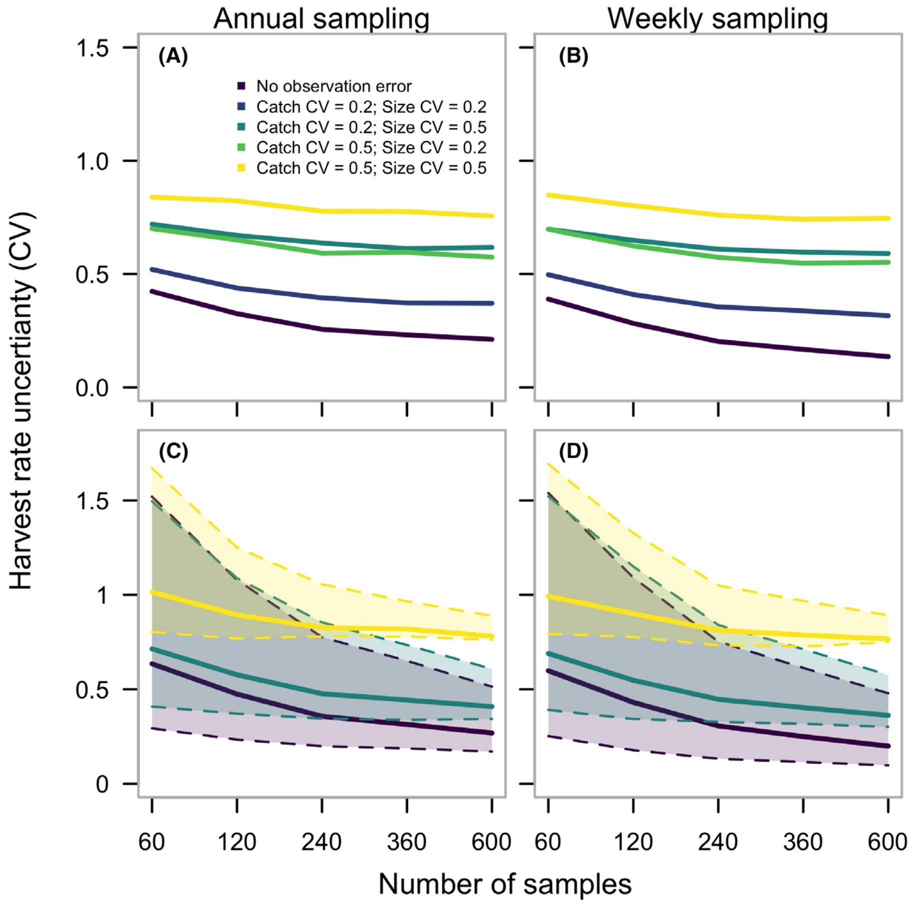

FIGURE 7. Relationships between sample size and the coefficient of variation (CV) in estimated harvest rate based on either **(A** and **C)** a single annual sample or (B and D) weekly samples across 5 levels of observation error in total catch and escapement. For the simulations with variable population sizes (C and D), the solid lines represent the average CV across all populations and the dashed lines represent CVs for the largest (lower dashed line) and smallest (upper dashed line) populations under differing levels of observation error (colors corresponding to legend in [A]).

Figure 5B). However, at harvest rates in the range of those that have been experienced in recent years (15–30%), there is only a 50–60% chance that Sockeye Salmon will recover and exceed the recovery goal (15,000 spawners) in Atnarko over the next 4 generations (Figure 5B). If future harvest rates are higher, the chances of recovery are predicted to be even lower (e.g., less than a 50% chance for recovery at harvest rates greater than 30%). Eliminating the harvest of Sockeye Salmon in the Atnarko River watershed altogether is predicted to result in further increases in the chances of recovery (up to a maximum of 69%; Figure 5A and B).

Our catch sampling simulations highlighted that increasing the number of specimens that are collected for genetic samples that are taken from fishery catches improves the precision of estimates for catch composition and harvest rates and that observation error in total catch and escapement can increase uncertainty in harvest rates (Figures 6 and 7). Variability in the size of the populations contributed to greater uncertainty in catch composition and harvest rate estimates, particularly at lower levels of sampling intensity. Smaller populations were less likely to be sampled in fishery catches and therefore had the greatest uncertainty in their harvest rates, while larger populations were better sampled, producing greater relative certainty in harvest estimates. Consequently, uncertainty in harvest rate estimates were both larger when there was greater variation in population sizes, regardless of the sampling design (Figure 7). However, estimates for harvest rates for small populations improved dramatically when more samples were taken. We tested the effects of increasing aggregate harvest rates from 20% to 50% and found no difference in the estimates for stock composition, so we only report results under the 20% harvest scenario below.

We found that weekly sampling yielded more precise harvest rate estimates than did single sampling events near the peak of the return. However, for all of the levels of overall sample size or variation in population size that we examined, the increases in precision were small (Figure 7). For example, when populations varied in size and observation error was moderate (CV = 0.2 for catch and escapement), sampling 40 fish per week (240 total) produced a nearly equivalent harvest rate CV (0.442) to that for sampling 360 fish in a single event (0.441). However, further increases in sample size produced minimal reductions in uncertainty, particularly when observation error was high. Across the range of sampling frequency and population sizes that we considered, increasing the sample size from 60 to 240 fish resulted in large reductions in harvest rate uncertainty, particularly for small populations, with more gradual increases in precision with increasing sample numbers thereafter (Figure 7C and D).

The point estimates for the Atnarko stock–recruitment parameters were largely insensitive to alternative assumptions about (1) the magnitude of observation error in spawner abundance and harvest, or the magnitude of uncertainty in age composition, and (2) the precollapse composition of mixed-stock catch for Sockeye Salmon from Atnarko, though uncertainty in the parameter estimates predictably increased when we assumed higher observation error. Nonetheless, increased uncertainty did not strongly influence the predicted probabilities of recovery compared with those predicted under our baseline uncertainty assumptions, though predicted recovery potential was slightly lower when the magnitude of precollapse mixed-stock harvest rates was assumed to be twice as large as postcollapse rates (Figure S1 available separately online in the Supporting Information).

DISCUSSION

Mixed-stock fisheries challenge the sustainability of marine fisheries for salmon. While targeting multiple comigrating populations of salmon can provide stability in commercial (Hilborn et al. 2003) and Indigenous FSC fisheries (Nesbitt and Moore 2016), these benefits may come at the cost of increased risk to small or low-productivity populations. For example, by-catch of nontarget stocks in fisheries for the abundant Sockeye Salmon in the Babine River has been implicated in the declines of several smaller populations in the Skeena River watershed (Walters et al. 2008). Similarly, Sockeye Salmon in the Atnarko watershed are still captured incidentally by Indigenous FSC fishers and commercial fisheries that target other species.

Our results suggest that, across a range of plausible harvest rates, directed FSC and incidental commercial harvest of Sockeye Salmon from Atnarko can reduce recovery prospects, but the reduction is not so much that these fish are at immediate risk of extinction due to small population sizes. Prospects for recovery depend on the magnitude of future harvest rates, and our findings emphasize the importance of limiting the incidental harvest of Sockeye Salmon from Atnarko by fisheries that are targeting other species or populations. Across a range of plausible future harvest rates, there was a high probability (>5%) that salmon spawner abundance in Atnarko would increase to and remain above a proposed limit reference point of 4,000 fish. However, under those harvest rates, there is only a 50–60% chance that the population will grow to exceed a recovery goal of 15,000 spawners over the next four generations. Eliminating harvests altogether would increase the probability of meeting the recovery goal to a maximum of 69%, which suggests that factors other than fisheries (e.g., ocean conditions) are contributing to the depressed state of Sockeye Salmon in Atnarko. Therefore, harvest management alone is unlikely to be sufficient for population recovery with a high degree of certainty, and other actions that were identified by the Atnarko Recovery Plan should be considered concurrently with improved harvest management. These actions include research to resolve life-history characteristics of Sockeye Salmon in Atnarko (e.g., through expanded spawner surveys, improved baseline genetic sampling that uses single nucleotide polymorphisms instead of microsatellite markers, and otolith readings to characterize life histories to inform appropriate scales of management and limiting factors); freshwater habitat assessment (to identify any freshwater factors that may need intervention); and the assessment and synthesis of existing data from over 10 years of conservation enhancement efforts (to inform the conservation enhancement efforts that are underway).

Accurate estimates for catch provide a foundation for understanding harvest effects, giving managers the ability to implement fisheries closures and take other actions (e.g., gear restrictions, release policies) to minimize the harvest of populations that are of conservation concern. We simulated catch monitoring in a salmon fishery that is similar to the one that occurs for Sockeye Salmon in Area 8 to provide insights into some design considerations for future catch-sampling efforts. Our results showed that estimates for the stock composition of Sockeye Salmon that are caught in a mixed-stock fishery will be uncertain when the population size is variable, but increased sample sizes, and to a lesser extent weekly samples, can reduce the uncertainty around the contribution of different stocks to total harvest rates, with the smallest (rarest) stocks showing the largest reductions in uncertainty with increasing sampling effort. The findings are based on simulations that assumed that annual sampling occurred near the peak of the return migration (i.e., within 2 weeks of it) and that the salmon populations have similar (but not identical) migrating timing through the mixed-stock fishery. In instances where carrying out a single annual sampling event near the peak of the return migration is difficult and/or when there are large differences among populations in return timing, the benefits of weekly sampling are likely to be larger. Further, weekly sampling provides insurance against missing the peak of the return migration, which would be risked by single sampling events. Our results also suggest that monitoring programs should attempt to sample a minimum of 200 to 300 fish from a given fishing area if they hope to characterize catch composition with any degree of certainty (e.g., less than 100% CV for the smallest stocks). In contrast, sample size is predicted to have less of an influence on uncertainty in stock-specific harvest rate estimates across a broad range of observation error in both harvest and spawner abundance, except for small stocks where increasing sampling effort is predicted to result in substantial reductions in uncertainty in the estimates for harvest rates. In addition to considering predicted increases in the precision of catch composition and mixed-stock harvest rate estimates, the design of each catch sampling program should also consider the financial and logistical costs of weekly versus annual collection of data as well as improved estimates for total harvest or escapement when deciding on the most appropriate sampling protocol.

We made several simplifying assumptions about escapement enumeration, harvest rates, and future productivity regimes in order to conduct our analyses. First, we assumed that changes in the methodologies that were used to estimate escapement rates for Sockeye Salmon in Atnarko over time have not led to time-varying bias in the estimates for spawner abundance. It is possible that changes in survey design could have downwardly biased the spawner estimates in recent years if enumeration programs changed or detection probabilities for spawning fish declined as total abundance declined. The spatial extent of spawner surveys has contracted in recent years, with no counts occurring in the Atnarko River below Lonesome Lake. We attempted to account for this reduction in sampling effort by expanding the estimates of abundance above the lake using the historic ratio of spawning Sockeye Salmon above and below Lonesome Lake. Second, our harvest reconstructions were based in part on reported FSC catch in Area 8 and releases (in recent years) of Sockeye Salmon that were caught as bycatch in commercial fisheries. It is possible that our harvest estimates are biased downward due to the voluntary nature of catch reporting for marine FSC, which, in turn, may lead to underestimates of total recruitment, productivity, and recovery prospects. As a result, we consider our forward projections to be biologically conservative. Third, we simulated future variation in survival by assuming it was serially correlated over time and did not exhibit regime-like periods of depressed (or elevated) productivity in the future. This is likely to be reasonable given that productivity appears to have improved after an early period of depressed survival (Figure 4B). However, if there are persistent directional changes in survival, forward projections of recovery potential that are parameterized with contemporary measures of population performance would not necessarily be accurate. Lastly, we assumed that our estimates of age composition, brood-year survivals, and estimates of spawner abundance were robust to any changes in the life histories of Sockeye Salmon in Atnarko over time. Unaccounted changes in the relative contributions of ocean, river, and lake life histories to the composition of returns have the potential to bias estimates for productivity and population size.

Our findings have implications for catch monitoring, fisheries, recovery planning, and the role of First Nations in fishery management for the Sockeye Salmon populations of British Columbia. High uncertainty in the estimates for contemporary harvest rates for the Sockeye Salmon population in Atnarko emphasize the importance of improving estimates for catch composition in salmon fisheries in the marine waters of Area 8. In recent years, 75% of the total estimated Sockeye Salmon harvest in Atnarko has been attributed to FSC and commercial fisheries in the marine approaches, so more accurate estimates of the composition of this catch would greatly improve our understanding of the extent to which marine fisheries jeopardize the recovery of Sockeye Salmon in Atnarko. Stock-assignments of mixed-stock catch samples are currently generated by using microsatellite markers, which can have relatively low assignment probabilities and a genetic baseline that is derived from ~300 samples that are collected on the spawning grounds or in terminal FSC catches. These baseline samples show some genetic evidence of population differentiation among sampling locations, and future research and assessment efforts should seek to improve the baseline sample collection and develop a single nucleotide polymorphism baseline that would have lower misassignment error rates than those that occur with microsatellites.

Approaches to characterizing salmon stock–recruitment relationships and evaluating recovery prospects often assume that spawner abundance is an independent variable and that the annual values for spawner abundance and resulting recruitment rates (based on harvest rate and age composition) are measured without error. However, spawner abundance is not an independent variable because it is dynamically linked to previous recruitment events and estimates of spawner abundance, harvest, and age-composition are all measured with error. Failure to consider the recruitment–spawner linkage that is inherent in the data may lead to biased estimates of stock–recruitment parameters, particularly for stocks with low intrinsic productivity (i.e., “time series bias”; Walters 1985; Korman et al. 1995), while spawner estimates measured with error can lead to “errors-in-variables bias” (Walters and Ludwig 1981; Kehler et al. 2002; Kope 2006). The approach that we have described provides a more complete assessment of uncertainty in the key life history parameters of interest, and it likely helps to reduce bias due to time series and error-in-variables problems. Most importantly, this approach allows for a more complete propagation of uncertainty in the forward simulations. As a result our general approach has broad relevance to recovery potential assessments of salmonid populations that are plagued by multiple sources of uncertainty, including populations that are at risk of extinction in Western Canada (COSEWIC 2016, 2017, 2018a, 2018b) where formal processes for quantifying recovery potential across a range of mixed-stock harvest rates are underway.

The monitoring and management of marine resources in coastal British Columbia is increasingly driven by the values and needs of Indigenous communities (Salomon et al. 2015), and these communities are playing a central role in the collection of information on culturally important resources (e.g., Frid et al. 2016; Moore et al. 2016). In light of the challenges posed by mixed-stock fisheries and recent declines in Sockeye Salmon productivity, there has been considerable interest among First Nations in coastal British Columbia in developing scientific tools to support community-led management and conservation of salmon (e.g., Atlas et al. 2017). One initiative of immediate relevance is more accurate estimation for catch rates and stock composition in Sockeye Salmon fisheries. Our work highlights opportunities for these First Nations to play a leading role in catch monitoring and management for marine-based fisheries that may incidentally capture Sockeye Salmon in Atnarko. This information would provide a stronger foundation for understanding and managing harvests of Sockeye Salmon in Atnarko while contributing the baseline information that is required to support community-led management of salmon from other populations. More generally, our study illustrates the collaborative research that has been initiated and directed by the Nuxalk Nation to inform monitoring and management actions that may promote the recovery of a depressed stock that is inherent to traditional foods, thereby contributing to a global effort to integrate Indigenous cultural values with biological conservation (Berkes 2018).

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SUPPORTING INFORMATION

Additional supplemental material may be found online in the Supporting Information section at the end of the article.