Original Article

Population-specific mortality in coho salmon (*Oncorhynchus kisutch*) released from a purse seine fishery

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Coastal commercial fisheries targeting Pacific salmon inevitably capture a mix of co-migrating species and genetically distinct populations within each species, only some of which are sufficiently abundant to sustain exploitation. Species-specific release measures are implemented as a conservation measure, but there remains little understanding of the resulting mortality. A purse seine fishery for Pacific salmon in British Columbia, Canada, was simulated with the goal of estimating post-release mortality for coho salmon, a species commonly released from commercial fisheries. Landed coho salmon ($n = 220$) were tagged with acoustic transmitters and tracked along their coastal approach and into freshwater. Survival analyses accounting for variable migration pathways among populations revealed population-specific survival, with the population of greatest conservation concern having the best survival. Condition assessments revealed scale loss to be the strongest predictor of success. Physically exhausted fish, identified via reflex impairment tests, also experienced higher mortality. Results highlight the complexity of estimating release mortality in mixed-population commercial fisheries and are discussed in the context of management implications.

Keywords: bycatch, coho salmon, commercial fisheries, fish populations, Fraser River, Pacific salmon, purse seine, release mortality, scale loss, telemetry.

Introduction

Fisheries operating in coastal waters of British Columbia (BC, Canada) encounter several species of co-migrating Pacific salmon (*Oncorhynchus* spp.), each comprised of hundreds of reproductively isolated populations that are adapted to the specific requirements of their migration and rearing area (Crossin *et al.*, 2004a; Eliason *et al.*, 2011). This genetic and phenotypic heterogeneity is a major contributor to their persistence, increasing their resilience to anthropogenic disturbances such as, for example, fisheries (Hilborn *et al.*, 2003). Pacific salmon fisheries in Canada are managed by Fisheries and Oceans Canada (colloquially and herein referred to as DFO). Their primary goal is to protect populations and species of conservation concern, and secondarily,

where and when possible, allow for harvest of abundant populations; referred to as the "selective fishing strategy," this is often achieved through species-specific mandatory release (DFO, 2001).

Openings for most mixed-population commercial Pacific salmon fisheries in Canada are dictated by numbers of non-target salmon encountered, the pre-determined level of allowable fishing mortality for all species encountered, the catch composition, and an estimate of assumed release mortality given the capture scenario for non-target salmon (e.g. gear, location, species; DFO, 2015). Release mortality estimates, primarily generated from short-term (<48 h) holding studies, have consequently been applied to all non-target salmon species encountered in Pacific

salmon fisheries. The limitations of holding studies, however, are well documented (Rogers et al., 2014) and biotelemetry provides an appropriate alternative (but see limitations in Donaldson et al., 2008).

Mortality of caught-and-released fish is frequently unquantified (Hall et al., 2000), but the importance of sustainably managing these large commercial fisheries cannot be overlooked—the purse seine fleet in BC produces the largest proportion of landings (Butler, 2005) and is becoming the dominant gear type for salmon (Haas et al., 2016). Additionally, because greater mixing of populations of Pacific salmon occurs with increasing distance from natal waters (Beacham et al., 2005), coastal fisheries inevitably encounter many genetically distinct populations.

The topic of release mortality has been most contentious for Fraser River (FR) coho salmon (Oncorhynchus kisutch). A crash of the Interior Fraser River (IFR) coho salmon population in the 1990s, believed to have been caused partly by overfishing, resulted in an unprecedented moratorium on coho salmon harvest and introduction of the selective fishing measures still enforced today (Chittenden et al., 2010). Despite these dramatic management actions, however, IFR coho salmon remain of conservation concern (DFO, 2016).

In the Strait of Juan de Fuca (JDF), an anomalously high estimate of release mortality was applied to coho salmon discarded from purse seine fisheries. The estimate, 70% mortality over 24 h, was generated from a captivity study (J.O. Thomas & Associates Ltd., 2002) that was later criticized for excessive transport and handling of study fish—factors that did potentially inflate the observed mortality. Additionally, given evidence of population-specific responses to capture stress among Pacific salmon (Donaldson et al., 2010, 2012) and that effects of capture do persist beyond the first 24 h (Wilson et al., 2014), a rigorous assessment of release mortality should also account for genetic diversity and encompass long-term mortality.

As a precursor to this research, Raby et al. (2015) conducted an exploratory pilot-scale telemetry study paired with a marine holding study to evaluate mortality of coho released from purse seines in this area. Conducted in a year of low abundances, lacking from the Raby et al. (2015) study was an evaluation of the effect of realistic fishing conditions, and sufficient sample sizes to detect potential population-specific differences. We therefore conducted an experimental purse seine fishery that simulated commercial practices, and launched a large-scale acoustic telemetry study with the objective of providing realistic release mortality estimates for genetically distinct coho salmon populations, while also examining the role of technical factors associated with the capture process.

Material and methods
Sampling and tagging
All fish handling was conducted in accordance with the Canadian Council of Animal Care guidelines and approved by University of British Columbia's institutional Animal Care and Use Programme. Research was executed in DFO management Area 20 in the Canadian waters of the Strait of JDF (Figure 1) from 26–29 August 2013, aboard a commercial purse seine vessel (specifications in Raby et al., 2015). Fourteen sets were conducted. The vessel was modified to rapidly release all pink salmon (Oncorhynchus gorbuscha, the "target" species) and other bycatch while retaining coho. The time elapsed from the net being deployed to closure

(tow time) ranged from 20 to 41 min (mean 33.5 min) after which the net was pursed and lifted. The median estimated number of salmon captured per set was 880 (min = 90, max = 3500); total time to sort the catch took from 1.5 min for the smallest set to 30.5 min for the largest (median = 13 min 20 s). There were no fishery openings in Area 20 during the time of research, and therefore no risk of recapture by other vessels for fish released with tags. Pink salmon were nonetheless abundant. All fishing and tagging occurred northwest (i.e. seaward) of the first line of acoustic receivers ("JDF line," Figure 1). A total of 220 coho were released with acoustic transmitters.

Fish were transferred from the pursed net to a sorting table using an industry-standard brailer, a large dip net operated with a hydraulic winch. Coho to be tagged were transferred by the crew from the sorting table to fish totes with circulating seawater; all other fish were immediately released via a wet chute. Fishing and sorting was conducted by an experienced crew and researchers were given access to the deck for fish processing upon completion of fishing. Given an a priori expectation of relatively low abundances of IFR coho and high abundances of enhanced populations (i.e. supplemented by stocking of hatchery-reared fish), the crew was instructed to prioritize selection of coho likely to be wild (i.e. those with intact adipose fins) during sorting. Enhanced fish were also tagged to ensure all transmitters were used during the limited time available for fishing.

Processing of study fish occurred in a padded, V-shaped trough continuously supplied with seawater immediately upon completion of sorting. First, impairment was assessed using reflex action mortality predictors (Davis, 2010). Five reflexes were assessed categorically (0 = unimpaired, 1 = impaired) and an index was assigned to each fish based on the total proportion of reflexes impaired. Reflexes, described in Raby et al. (2012), included tail grab (TG), body flex (BF), head complex (HC), vestibular-ocular response (VOR), and orientation (OR). Following impairment assessment, injury was quantified by categorically determining the presence and severity of injuries including net marks, scale loss and other injuries. All injury observations were combined as a proportion (i.e. total value/highest possible value). Further details of scoring of both metrics available in Supplementary Material.

Fork length (FL) was measured and a clip of tissue (∼0.5 g) from either the adipose (when present) or dorsal fin was taken and stored in 95% ethanol for later determination of population via analyses of microsatellite loci (as in Beacham et al., 2011). Non-lethal biopsies for blood and gill tissue (as in Cooke et al., 2005) were collected randomly from 80 tagged fish for a different study. The physiological data resultant from the biopsies are not included in analyses. There were no statistical differences in impairment, survival, or migratory behaviour among biopsied and non-biopsied fish (survival: Fisher Exact, $p = 0.224$; Impairment: Mann-Whitney-Wilcoxon, $W = 5121$, $p = 0.941$; Time to the JDF line: Mann-Whitney-Wilcoxon, $W = 2248$, $p = 0.544$), justifying the inclusion of biopsied fish in statistical models with unsampled fish.

The acoustic transmitters (Model V8-4X; Vemco, Bedford, Nova Scotia, Canada) were affixed using identical methods to Raby et al. (2015). Each tag transmitted a unique code every 25–65 s with an expected minimum battery life of 47 days, which is sufficient time to cover the expected period between release and last detection. The maximum detection period (i.e. from release to last detection) was 37.5 days (mean 8 days).
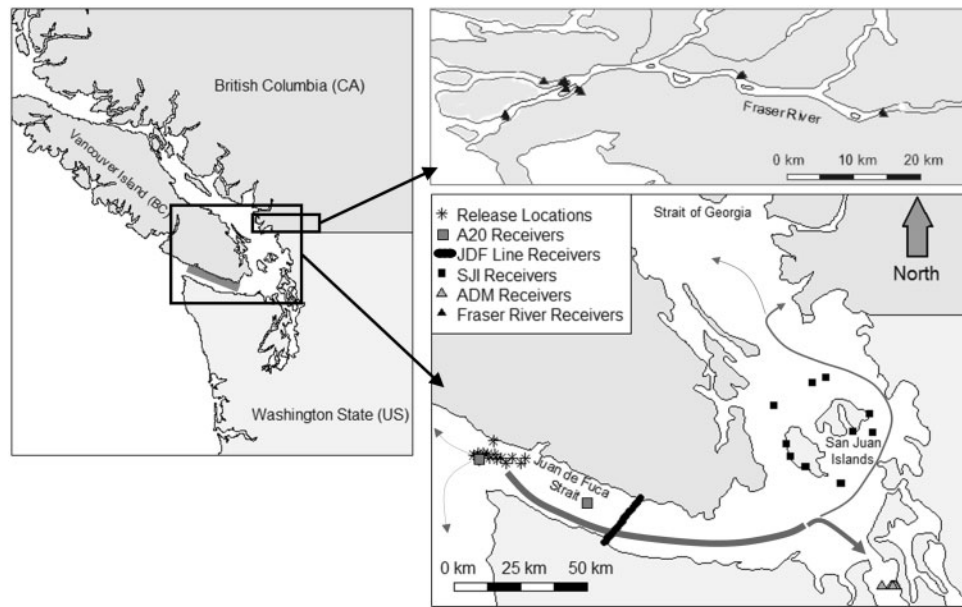
Figure 1. An experimental purse seine fishery was conducted in DFO management Area 20, indicated by the shaded area in left panel. Detection points for tagged coho released from the fishery included a receiver line spanning the Strait of JDF, two receivers near location of release (A20), clusters of receivers in the ADM Inlet and around the SJI, and within the FR, as far as 78 rkm upstream. Gray arrows represent the different migration pathways expected from the populations encountered and are scaled to represent the proportion of tagged fish expected to use each route.

Multiple fish were tagged per set (median of 16 fish; range = 7–28) and study fish were inevitably held for variable amounts of time (median 31 min; range = 2–78 min). This holding time was not significantly correlated with indices of impairment (Spearman Rank, $p = 0.209$) or injury (Spearman Rank, $p = 0.785$) and thus was not considered in further analyses.

Post-release acoustic telemetry tracking

Acoustic telemetry receivers were deployed in six distinct groups, or "arrays" (Figure 1). The largest receiver array, referred to herein as the JDF line, was comprised of 30 receivers spanning the width of the strait from Sheringham Point (Canada, 48°22′35.2″N, 123°55′15.7″W) to Bonila Point (US, 48°13′22.0″N, 124°6′28.3″W). Previous genetic testing within this region suggests that most coho salmon populations encountered in the fishing area will cross the JDF line en-route to their natal watersheds (Beacham *et al.*, 2011; Raby *et al.*, 2015). Additional detection points included receivers deployed northwest of the JDF line ($n = 2$, A20 receivers), dispersed in the waters surrounding the San Juan Islands (SJI, $n = 10$), and in the Admiralty Inlet (ADM) at the entrance to Puget Sound ($n = 6$; Figure 1). Given the dispersed nature of receivers between the JDF line and the FR, the likelihood of detection in these areas was not expected to be high. The data are nonetheless valuable for determining efficiency of the JDF Line and for estimates of long-term mortality.

For FR populations, long-term mortality was quantified via in-river receivers, divided into three groups [locations expressed as river kilometres (rkm) from river entry]. The first group includes receivers encountered within the FR in the North ($n = 4$, rkm 17) and South ($n = 5$, rkm9) arms. Subsequent upstream receivers were deployed in the Derby Reach (rkm 49) and near the town of Mission (rkm 78). These receiver stations have been used previously with very high detection efficiency (Crossin *et al.*, 2009; Drenner *et al.*, 2015).

Data analyses

The mark-recapture software programme MARK was used to evaluate survival and detection probability (i.e. the likelihood of tag transmissions being detected as the fish pass receivers; White and Burnham, 1999). All other data analyses were performed with R Studio V0.99.903 (R Core Team, 2016). As applicable, both univariate and multivariate normality was checked with Shapiro-Wilk tests and collinearity among response variables was tested using variance inflation factors (cut-off of 2.0; Zuur *et al.*, 2010).

DNA

Microsatellite analyses identified study fish to individual spawning streams. Given the large number identified ($n = 33$), many with only a few individuals, fish were categorized by major population grouping per Beacham *et al.* (2011). Fish for which population could not be identified ($n = 7$) and from populations not expected to encounter the deployed receivers based on their expected migratory paths ($n = 6$) were excluded from analyses. Three fish identified as belonging to Puget Sound populations were detected as far as the last detection point in the FR; potentially misidentified, these fish were also excluded.

Migration characteristics

Time residing within the JDF (JDF time) was calculated as the difference between release and last detection on JDF line receivers. The JDF time variable could not be transformed to meet normality and was ranked; with no duplicate values, each fish was assigned a unique value. JDF line receivers were numbered 1 (Northwest, Canada) through 30 (United States). Using receiver position as a numerical value, mean receiver location was calculated for each fish. Receivers were also clustered into North, North-Central, Central, South-Central, and South groupings with

Table 1. Population groupings of tagged coho salmon and the receiver arrays encountered along their expected migration pathways (indicated by "X") following release from a commercial purse seine vessel.

Population grouping	Expected array encounters					*n*	Population	Proportion of sample	Proportion wild
	A20	JDF	SJI	ADM	FR				
Puget Sound	x	x	x	x	–	142	North	0.53	0.69
							South and Central	0.08	0.52
							Hood Canal	0.04	0.89
FR	x	x	x	–	x	IFR=18;	Interior	0.08	1.00
						LFR=21	Lower	0.10	1.00
Other BC	x	x	x	–	–	25	South Coast BC	0.06	0.64
							Vancouver Is. E	0.05	0.90
	Excluded from analyses					14	Various	0.06	0.4

Survival models were run both with IFR and LFR individuals pooled and as separate groups. Receiver arrays included those near release (A20), the JDF line, receivers around the SJI, in the ADM and in the FR. Excluded fish include those that may have been misidentified (*n* = 3) or could not be identified (*n* = 7) in genetic analyses, as well as those belonging to populations not expected to encounter deployed receivers (i.e. west Vancouver Island and Columbia River; n = 6).

6 receivers per grouping. The mean number of individual fish detected on each receiver was compared among receiver groupings using a Kruskal-Wallis (KW) test. Non-parametric *post hoc* pairwise comparisons between receiver groups were performed using a Tukey-Kramer-Nemenyi test.

Survival and detection probability

Fish classified as mortalities for the total estimated immediate and short-term percent mortality include those tagged fish not detected on the JDF line as well as any untagged fish that were found dead prior to tagging; 95% upper and lower confidence intervals (CIs) around this estimate were derived from a binomial exact test of the probability of success (i.e. survival to JDF line) of the total number (i.e. number tagged and number of immediate mortalities) in a Bernouilli experiment (R Core Team, 2016).

For tagged fish, survival and detection probability was evaluated using a pool of spatially based Cormack-Jolly-Seber (CJS) mark-recapture models with the objective of measuring post-release survival by genetically distinct population. Population groupings, created given expected differences in migration pathways (and the receivers encountered), included: FR, Other BC (South Coast of BC and the eastern shore of Vancouver Island) and Puget Sound (Table 1). Models were also run with the FR group divided into Lower Fraser River (LFR) and IFR groups, given known genetic differentiation and good detection histories for both groups. Detection histories were created by expected migration route, resulting in variable migration pathways among groups. Variable migration pathways preclude traditional CJS model structuring (Lebreton *et al.*, 1992); such a model structure is termed "nested" (Melnychuk, 2009). Methods generally followed Melnychuk (2009), except that groups shared a common release point and differed in destination (further details available in Supplementary Material).

A pool of candidate models (*n* = 20) with varying model structures (e.g. fully independent or fully shared parameter estimates for each population grouping) were ranked based on Akaike Information Criterion (AIC) adjusted for sample size (AICc). Final parameter estimates were derived by model averaging (AICc model weighting), permitting evaluation of the most parsimonious model (Burnham and Anderson, 2003). The CJS model produced estimates for each population grouping at each array

(detection probability) and between each receiver interval (survival probability). Distances between arrays varied considerably, ranging from an estimated average of 17 km (from release to A20 receivers) to ∼100 km (JDF line to SJI array). Consequently, survival estimates were distance-corrected, whereby survival for each 10 km migrated within each reach was calculated.

Population-specific differences in fish characteristics

A two-way factorial MANOVA was used to explore differences in migratory characteristics (i.e. JDF time and mean receiver position) for survivors to the JDF line among population and origin (hatchery or wild). Given the non-normal and ordinal nature of injury and impairment indices, individual KW tests were used to assess differences among population and origin. In both cases, the dataset was simplified to include only population groupings with > 10 individuals (i.e. LFR, IFR, Puget Sound, and South Coast BC).

Predictors of mortality

Potential predictors of mortality to the JDF line included impairment, injury, FL, and set size (i.e. estimated total number of fish caught). Time to brail and sort the catch, directly dependent on set size, were not included. Predictors of mortality were not explored to other detection points given variable migration pathways, reduced sample sizes and low detection probabilities. All parameters were included in a logistic regression model with an outcome of survival to JDF line. Impairment and injury indices were further broken down into their individual binary components in an additional logistic regression model, reduced using backwards stepwise methods. Goodness of model fit was tested in all cases using a Hosmer-Lemeshow test. Predictors of mortality were also tested for effects on migratory behaviour.

Results

Of the 321 coho captured during the study period, 220 were tagged. There were 12 additional fish found dead prior to tagging and sampling, equating to an immediate mortality rate of 4%. Throughout, normally distributed values are presented as mean ± standard deviation and non-parametric values are presented as a median with range.

Condition at capture

Most fish handled were categorized as having no injury (54%). Only three individuals were assigned an injury index of 1—i.e. had severe scale loss, net marks, and at least one other external injury. Median impairment index was 0.2 (range = 0–0.6; aside from immediate mortalities, no fish had impaired VOR or HC reflexes. The most commonly impaired reflexes were TG and BF and few fish (8%) had impaired OR.

Origin of study fish

The majority (75%) of the tagged fish were presumed to be of wild origin (i.e. adipose fin intact). It is notable however that given our preference for tagging wild fish, this ratio is not representative. Most tagged fish originated from Puget Sound populations (65%) and of the 19% of study fish destined for the FR, 46% were from IFR populations (8% of sample; Table 1). Among population groupings, there were no significant differences in FL [ANOVA, $F_{(3)} = 1.039$, $p = 0.377$], impairment (KW, $H_{(3)} = 3.979$, $p = 0.263$) or injury [KW, $H_{(3)} = 0.482$, $p = 0.923$]. Similar results were observed in a comparison between hatchery and wild fish [FL: T-test, $T_{(101)} = -0.816$, $p = 0.417$; impairment: KW, $H_{(1)} = 0.0770$, $p = 0.781$; injury: KW, $H_{(1)} = 0.145$, $p = 0.703$].

Migratory characteristics

Migratory characteristics varied considerably among individuals. It took a mean of 4.6 ± 4.2 days (min = 1.01, max = 26.8) to reach the JDF line, 43–63 km from release depending on location of release and receiver of first detection. Among FR fish, it took a mean of 13.6 ± 4.4 days to reach river entry. Time within the JDF was also variable, ranging from <24 h to over 30 days (median = 79 h). Significant differences were observed in the number of fish detected by receiver grouping (KW; $p < 0.001$), with more fish detected by the southern receiver group than the central ($p < 0.001$) and north ($p = 0.001$) groupings (Figure 2). Migratory characteristics (i.e. JDF time and mean receiver position) did not differ significantly among populations [Factorial MANOVA, $F_{(3)} = 1.840$, $p = 0.0919$, Pillai's Trace = 0.0839) or origin (i.e. hatchery/wild, $F_{(1)} = 0.466$, $p = 0.629$, Pillai's Trace = 0.00740].

Survival and detection probability

The most parsimonious CJS model (AICc weight = 0.50) suggested that survival was group-specific but did not vary among receiver intervals, and that detection probability was described by an interaction between population group and receiver interval (summary in Table 2; all model combinations in Supplementary Table S1). There was little support for combining IFR and LFR fish when estimating survival parameters (i.e. the highest AICc weight with the two populations combined was 0.23 whereas was 0.50 when separate; Table 2), indicating that survival significantly differed between these two populations.

Model averaged parameter estimates suggest that detection probability at the JDF line and within the FR was 100% for all groups (i.e. no fish passed undetected). Detection probability at the A20 group, comprised only of 2 receivers in a large area, was expectedly poor for all populations (<15%). For those expected to encounter the ADM and SJI receiver groupings, detection probability was estimated at <50%. Exact detection probabilities
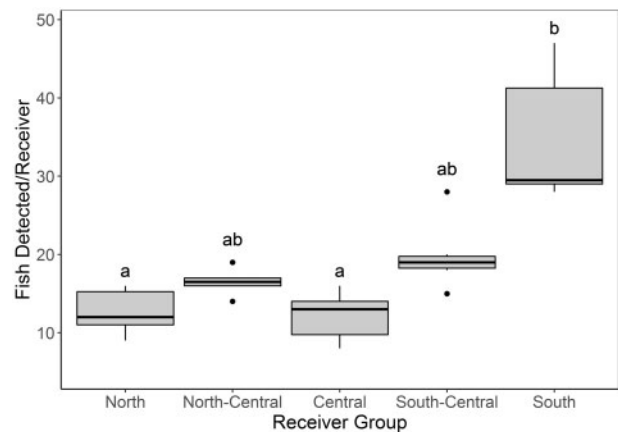

Figure 2. Number of tagged coho salmon detected by receiver grouping within the JDF line. Center line indicates the median, top and bottom of the box represent the 25th and 75th percentile, respectively, and the vertical lines of the box indicate the range excluding outliers, which are shows as points. Letters denote statistical differences.

by group at each detection location are provided in Supplementary Table S2.

Of the 209 fish expected to cross the JDF line, 141 were detected there. Estimated immediate and short-term mortality for coho captured in this fishery was 36.1% (LCI = 29.9%, UCI = 42.9%) over a median of 4.6 days. Given 100% detection efficiency at the JDF line for all populations, this estimate can be interpreted as accurate. The raw percentage of fish detected on the JDF line following release was highest among the IFR population (77%), followed by Puget Sound (68%), South BC populations (64%) and was lowest for LFR fish (57%). This pattern of survival being highest for IFR fish and lowest for LFR fish held true for the entire migration in terms of both cumulative proportion surviving (Figure 3c) as well as proportion surviving within each reach [Figure 3a and b (distance-corrected); raw model estimates in Supplementary Table S2]. Estimated cumulative survival between release and the last receiver array (Mission, B.C.) was 42.3 and 14.2% for IFR and LFR populations, respectively. Estimates were consistently similar among other BC and Puget Sound populations, being higher than those for LFR and lower than those for IFR. Most mortality occurred prior to reaching the JDF line. Accounting for the large distances between the JDF line and FR, estimated reach-specific survival was quite high for all groups (i.e. >95% per 10 km travelled; Figure 3). Survival to JDF was similar among wild (62%) and hatchery (65%) fish.

Predictors of survival

Both impairment and injury were significant predictors of survival to the JDF line (Table 3). Analysis of individual predictors revealed that only scale loss and BF were significant (p-value's < 0.01, Table 3; full model outputs in Supplementary Table S3). Model predicted survival ranged from $86 \pm 3.5\%$ for fish in the best condition (i.e. unimpaired BF and no scale loss) to $25 \pm 8.8\%$ for fish in the worst condition (i.e. impaired BF and severe scale loss) and scale loss had the strongest effect on survival. The prevalence of scale loss differed among populations overall (chi-square, $p = 0.0387$; Figure 4), but these differences were

Table 2. A subset of the model pool of CJS survival models ($n = 20$) fit to acoustic data where survival (S) and detection probability (p) were modelled as a function of fish population grouping (POP, a. Interior Fraser, b. Lower Fraser, c. Other BC, and d. Puget), cluster of population groupings (CLUS, a. all FR fish, b. Other BC, and c. Puget) and acoustic receiver array (ARRAY).

Model	S pooled[a]	p pooled[b]	AICc	ΔAICc	AICc Weights	nPar
S (POP) p(CLUS * ARRAY)	No	Yes	755.7	0.0	0.50	13
S(CLUS * ARRAY) p(CLUS * ARRAY)	Yes	Yes	757.3	1.5	0.23	17
S(POP) p(CLUS * ARRAY)	No	No	757.9	2.2	0.17	17
S(POP * ARRAY) p(CLUS * ARRAY)	Yes	Yes	760.8	5.1	0.04	22
S(CLUS) p(CLUS * ARRAY)	No	Yes	762.1	6.3	0.02	12
S(CLUS * ARRAY) p(CLUS * ARRAY)	No	Yes	763.6	7.8	0.01	21
S(CLUS)p(CLUS * ARRAY)	No	No	764.2	8.4	0.01	16
S(POP) p(POP * ARRAY)	No	Yes	764.3	8.6	0.01	17

Models without an AICc weighting are not shown here ($n = 12$, see Supplementary Table S1). The most parsimonious model (AICc weight = 0.50) included POP to estimate survival and an interaction or CLUS and ARRAY to estimate detection probability.
[a]Pooled only in first two intervals ("Release" to "Area 20" and "Area 20" to "JDF").
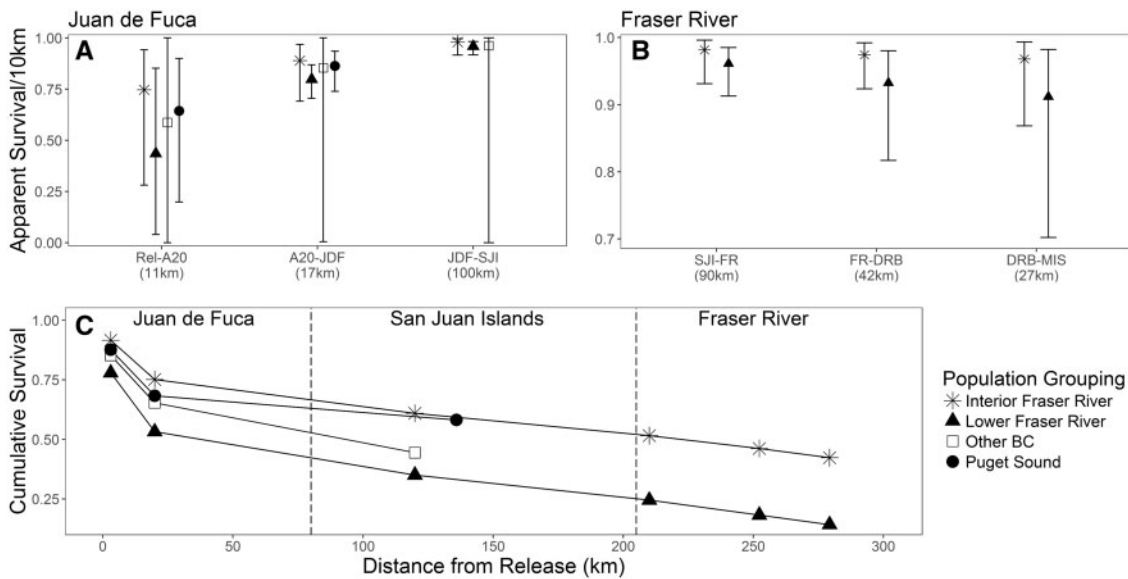[b]Pooled only for first two receiver stations ("Area 20" and "JDF").

Figure 3. Reach-specific and cumulative survival by population grouping of coho salmon released from a purse seine fishery, determined by nested CJS modeling. Distance-corrected reach-specific survival (i.e. survival at each interval, accounting for differences in distances) for each population grouping through the Strait of JDF (a) is provided for receiver intervals including the release (REL) and detections by receivers in the fishing area (A20), the JDF line, and receivers clustered around the SJI. Within the FR (b), detection of FR populations occurred at receivers at river entry (FR), Derby (DRB), and Mission (MIS). Error bars represent upper and lower 95% CIs. High error around "Other BC" is a result of low detection efficiencies, small sample sizes, and relatively high mortality. Cumulative proportion surviving by distance from release (c) was determined by multiplying reach specific estimates for each population grouping given detection histories; error associated with the reach-specific model outputs are not multiplicative and thus were not carried though.

small and *post hoc* comparisons were insignificant. There were no differences among populations in impairment of the BF reflex.

Migration time to the JDF line differed significantly with injury [KW, $H_{(3)} = 9.945$, $p = 0.02$] and scale loss categories [KW, $H_{(2)} = 11.065$, $p = 0.00396$] but not reflex impairment [KW, $H_{(3)} = 5.029$, $p = 0.169$]. Fish with 'little to no' scale loss took the least about of time to reach the JDF line ($n = 115$, mean time to JDF line = 132.2 ± 14.0 h) and times were similar among fish categorized as having "moderate" and "severe" scale loss ($n = 21$, 189.2 ± 39.4 h and $n = 8$, 174.7 ± 51.0 h, respectively). *Post hoc* analyses only revealed significant differences among the "little to no" and "moderate" scale loss categories ($p = 0.0088$). The number

classified as having "severe" scale loss was small, only a proportion of which survived to the JDF line ($n = 8$).

Discussion
Post-release mortality
The estimated rate of immediate and short-term mortality in this study of 36.1% (LCI = 29.9%, UCI = 42.9%), after a median of 4.6 days is lower than the 24-h mortality estimate applied by management to coho salmon released from purse seines in Area 20 at the time of study (70%). In response to this research and that of the precursor study, Raby *et al.* (2015), the estimate of

Table 3. Model outputs from logistic regressions evaluating predictors of mortality to the JDF line among tagged coho salmon.

Model	Parameters	Estimate	SE	Z-value	Sig.	OR	LCI	UCI
Overall mortality predictors (full model)	Overall Model	4.656	2.026	2.298	**0.0216**	–	–	–
	FL	0.005	0.003	−1.424	0.154	0.995	0.999	1.000
	Injury	−2.944	0.743	−3.960	**<0.0001**	0.053	0.0115	0.216
	Impairment	−2.985	0.892	−3.345	**<0.001**	0.051	0.0083	0.280
	Set size	0.0001	0.0002	0.433	0.665	1.000	0.990	1.000
Condition mortality predictors (reduced)	Overall Model	1.849	0.293	6.276	**<0.0001**	–	–	–
	Scale Loss 1	−1.262	0.382	−3.304	**<0.001**	0.283	0.132	0.597
	Scale Loss 2	−1.971	0.508	−3.880	**<0.001**	0.139	0.0487	0.365
	BF	−0.985	0.338	−2.918	**<0.01**	0.373	0.190	0.716

Model 1 (top) includes all expected predictors of mortality. Model 2 (bottom) includes all categorical condition parameters collected and used backwards step-wise methods to reduce predictors (reduced model shown). Odds ratio (OR) provided for each parameter with lower and upper 95% CIs (LCI and UCI).
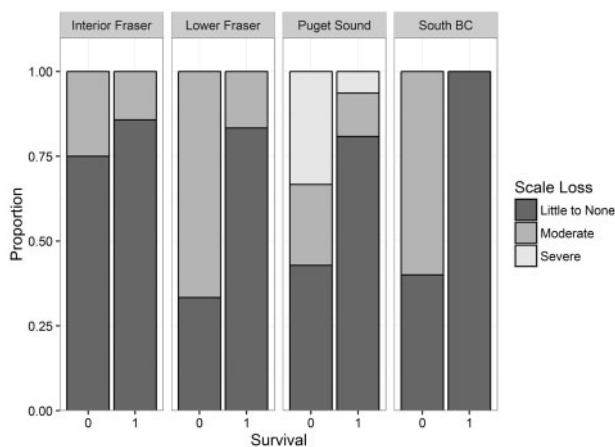

Figure 4. Proportion of total sample of each population grouping that was either detected on the JDF line (survivor, 1) or not (mortality, 0) and the magnitude of scale loss observed, categorized as little to none (<5%), moderate, or severe (>50%).

release mortality used in management models to determine harvest levels was reduced in 2014 from 70 to 50%. Despite very similar methodology, the Raby *et al.* (2015) study generated a lower estimate of mortality: 21% to the JDF line. This between-study discrepancy is not surprising; in the initial study sample sizes were small (*n* = 50), fishing occurred during a time of low abundances (the largest set was 83 fish compared with a median of 880 here), and fish were brailed into a water-filled recovery tote rather than onto a sorting table as would occur in a commercial fishery. The current study therefore provides what is, to date, the most robust mortality estimate for coho salmon released from purse seine fisheries.

Still, the short-term mortality observed may not encompass the full effects of the capture event, some of which may be slow to develop. Cumulative and interacting effects such as temperature-mediated disease progression (Miller *et al.*, 2014) and the impact of capture-induced injuries on spawning success (Baker and Schindler, 2009; Baker *et al.*, 2013), are potential long-term effects of capture and release. Nguyen *et al.* (2014) only detected an effect of injury after two weeks in an in-river telemetry study evaluating the relative contribution of injury and exhaustion to post-release mortality in Pacific salmon. Baker and Schindler (2009) observed failed reproduction in over half of the sockeye

arriving to spawning grounds with signs of gillnet entanglement, despite having nearly completed the migration. Although in both these studies fish sustained gillnet injuries, typically more severe than those resulting from seines, results propose that latent mortality is likely to occur.

There is no established point in time after a fish is released at which its mortality can no longer be attributed to the fishery, but it was notable that cumulative mortality from release to last detection for FR fish was quite high: 58% for IFR coho and 86% for LFR coho. Our telemetry-tagged fish would have encountered a multitude of other stressors after release and throughout migration. The estuarine stage of the return migration and freshwater transition is thought to be particularly difficult due to osmotic challenges (Shrimpton *et al.*, 2005), exposure to warmer pathogen-rich waters (Miller *et al.*, 2014), and predation pressure from pinnipeds (Wright *et al.*, 2007). The high mortality from release to last detection observed in this study is likely the result of a combination of unavoidable en-route stressors in addition to the latent effects of capture, the relative contribution of which would be near impossible to evaluate. Additionally, although there were no fisheries in the area of capture, fisheries of various gear types were operating in the Puget Sound and FR.

Population-specific differences

Mortality was consistently lowest for IFR coho, the population of greatest conservation concern. The largest divergence in survival was between the two FR population complexes that, despite some overlap in habitat use, are genetically very distinct. Contiguous salmon spawning habitat in the FR watershed is divided by Hell's Gate, a narrow canyon 128 rkm from river entry. Habitat used by LFR coho is limited to areas downstream of Hell's Gate, whereas IFR coho migrate through the Lower Fraser to spawn mostly in the Thompson River watershed, which drains into the FR 35 rkm upstream of Hell's Gate.

In sockeye salmon, populations spawning longer distances from the ocean generally have higher gross somatic energy densities at the onset of river migration compared with short distance migrants, and tend expend less somatic energy per unit of migratory difficulty (Crossin *et al.*, 2004b). Because overcoming the effects of acute stress requires the use of finite energy reserves (Bonga, 1997), availability of additional energy resources may confer a certain resiliency. Consistent with this hypothesis, Donaldson *et al.*, (2010) exposed two co-migrating FR sockeye populations (Chilko and Adams-Shuswap) to capture stress at river entry. Those from the Chilko population, having the longer

migration, were better able to cope with stressors. Likewise, IFR coho are probably energetically prepared for a more challenging migration than LFR coho and may also be expected to have greater capacity to overcome challenges in general, including capture stress. There is no clear explanation for the observed reduced survival in LFR relative to IFR coho but two not mutually exclusive hypotheses may apply: (i) IFR are better adapted to cope with acute stress given the longer and more challenging migration ahead, and (ii) IFR have more capacity in the form of stored energy to respond to the acute stress of capture.

Predictors of survival

Post-release migratory success was largely driven by scale loss, despite being a relatively minor dermal injury compared with those resulting from other commercial gear types (e.g. gillnetting injuries, Baker et al., 2013; Uhlmann and Broadhurst, 2015). That scale loss also influenced migration behaviour, with scaled fish delaying in the capture area, indicates the potential for sub-lethal fitness outcomes (Wilson et al., 2014). Having been associated with reduced success in other species [e.g. Atlantic herring (Clupea harengus), Olsen et al., 2012; sardine (Sardina pilchardus), Marçalo et al., 2010; garfish (Hyporhamphus australis), Butcher et al., 2010], the effects of capture-induced scale loss are well documented.

The mucus and scales act as a primary line of defense in fish, without which their skin is highly susceptible to injury, pathogen attachment and infection (Caipang et al., 2011). If scale loss is severe enough to damage the neuromasts of the lateral line, swimming, schooling, and predator evasion behaviour can also be affected (Montgomery et al., 1995; Olsen et al., 2012). For example, experimentally de-scaled herring failed to maintain cohesive shoals, a behaviour important to avoiding predation (Olsen et al., 2012). Scale loss is also known to compromise osmoregulatory function (Zydlewski et al., 2010; Olsen et al., 2012), which could be especially impactful for Pacific salmon upon their approach to freshwater. Investigations of scale regeneration time have not been undertaken to our knowledge in Pacific salmon but Guerreiro et al., (2013) estimate 3–6 days for sea bass (Dicentrarchus labrax). In rainbow trout (O.mykiss), genomic signatures indicating wound healing are not present until 1–2 weeks following injury (Schmidt et al., 2016). If dermal injuries persist, return migrants will be considerably more susceptible to fungal infections (e.g. saprolegnia spp.) and other diseases once in freshwater (Van West, 2006; Baker and Schindler, 2009). Therefore, a failure to regenerate scales prior to river entry and/or any damage resulting in dysfunction of the lateral line could have serious fitness consequences to salmonids (Smith and Monroe, 2016).

It was curious that we failed to see a relationship between set size with condition or mortality. Longer crowding time and higher catch densities typically result in increased stress, behavioural impairment, and mortality in purse seine fisheries (Marçalo et al., 2010; Tenningen et al., 2012). Salmon seine vessels in B.C. are required to brail a few hundred fish at a time onto a sorting table, rather than employing the faster but more damaging method of hauling the catch over the stern (Farrell et al., 2000). It is possible that, even in the larger sets, the brailing method minimized the relationship between catch size and mortality. However, with only 14 sets of which there was great variability in catch volume, statistical power was limited; the effect of set size and composition warrants further study for this fishery.

Limitations to mortality estimates

Several uncontrolled factors inevitably influenced results. First, rates of natural mortality among Pacific salmon are largely unknown (though see Martins et al., 2011) and unreported fishery removals may have occurred. We received tag returns from hatcheries and recreational fishers from the Puget Sound area, but none from Canadian waters. Fisheries were closed in the study area, meaning tag reporting biases were not a factor in the short-term mortality estimates, but are a relevant consideration for estimates derived from receivers beyond the JDF line. However, with Area 20 fisheries closed, released fish were not exposed to the repeated capture that could occur during openings.

Unquantified mortality could also be attributed to researcher handling and/or transmitter presence. External tags do create drag, potentially influencing swimming performance (Mellas and Haynes, 1985) and a fish losing its tag would have appeared as a mortality, over-inflating estimates. There is very little published on loss rates for externally-mounted tags but where documented, tag loss has not occurred until weeks after attachment (e.g. Sutton and Benson 2003). The so-called "observer effect" is another well-known limitation to bycatch research (Benoît and Allard, 2009). We replicated a commercial opening to the best of our abilities but the crew was not under the same pressures as in a typical fishery where efficiency is maximized and careful handling of bycatch may not be prioritized. Additionally, vessels effects (see Stram and Ianelli, 2015) including differences in infrastructure (e.g. brailer size, presence of sorting table and/or chute), crew experience, or handling protocols were not accounted for.

Management implications and conclusions

The release of fish following fisheries capture can be a valuable conservation tool in commercial fisheries, but properly accounting for mortality is essential. Findings of reduced release mortality relative to levels currently used in management models is promising, and instinctively suggests that harvests of target species in the area could be increased. However, low abundances of IFR coho persist despite aggressive management actions following their decline (DFO, 2015), and recovery is known to be slow among exploited fish populations following a dramatic reduction (Hutchings and Reynolds, 2004).

As a result, fisheries encountering coho in both the United States and Canada are conservatively managed to minimize fishing mortality of IFR coho. Release mortality estimates, along with expected total coho encounters, fishing effort, and the expected proportion of IFR coho, are all considered in bilateral models that estimate fishing mortality given various harvest scenarios (DFO, 2015). However, currently lacking from these models is consideration of temporal variability in the monitoring of fishery-induced mortality (Patterson et al., 2017). Adopting 24-h mortality estimates has become standard practice, but the low observed long-term survival may challenge this practice. Moreover, behavioural data suggests that coho salmon may hold in the fishing area, enhancing the probability of recapture given a commercial opening. Such fishery context-specific information is also not considered in management models (Patterson et al., 2017). We have very little knowledge of the effects of repeated capture but it would inevitably induce further injury and impairment, reducing the probability of survival with every capture event. Addressing these issues will improve our understanding fishery impacts in

general and especially to populations of conservation concern such as IFR coho.

Supplementary data

Supplementary material is available at the ICESJMS online version of the article.

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