

Location-specific consequences of beach seine and gillnet capture on upriver-migrating sockeye salmon migration behavior and fate¹

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Abstract: Fish released after capture, or fish interacting with gear but escaping, sometimes experience fishing-related incidental mortality (FRIM). For adult Pacific salmon migrations, knowing the magnitude of FRIM is important to estimate escapement accurately and to understand the total impact of a specific fishery. To determine how multiple gear types are associated with FRIM at different levels of maturity, we captured sockeye salmon (*Oncorhynchus nerka*) by both gill net and beach seine at three locations along their migration route (10%, 26%, and 72% of a 500 km freshwater migration) and determined their migratory success using biotelemetry. FRIM was higher for fish captured by gill net except at the location closest to spawning grounds. In addition, salmon captured by gill net at the lower river locations temporarily delayed migration, potentially indicating a requirement for lengthier recovery time compared with beach-seined fish. These results provide the first empirical and parallel comparison of these two common in-river fishing methods for salmon, revealing clear differences in FRIM between the two fishing methods in lower river fisheries and the importance of maturity.

Résumé : Les poissons relâchés après leur capture et les poissons interagissant avec des engins, mais qui s'en échappent sont parfois l'objet d'une mortalité accidentelle liée à la pêche (MALP). En ce qui concerne les migrations de saumons du Pacifique adultes, il importe de connaître l'ampleur de la MALP pour estimer avec exactitude l'échappement et l'impact total d'une pêche. Afin d'établir comment différents engins sont associés à la MALP pour différents degrés de maturité, nous avons capturé des saumons sockeyes (*Oncorhynchus nerka*) au filet maillant et à la senne de plage en trois endroits le long de leur route de migration (représentant 10 %, 26 % et 72 %, respectivement, d'une migration de 500 km en eau douce) et déterminé leur succès de migration à l'aide de la biotélémetrie. La MALP était plus importante pour les poissons capturés au filet maillant, sauf à l'endroit situé le plus près des lieux de frai. En outre, les saumons capturés au filet maillant dans les lieux situés dans le cours inférieur de la rivière retardaient temporairement leur migration, ce qui pourrait indiquer qu'ils ont besoin d'une plus longue période de récupération que les poissons capturés à la senne de plage. Ces résultats fournissent la première comparaison empirique et parallèle de ces deux méthodes répandues de pêche en rivière et font ressortir des différences nettes sur le plan de la MALP entre les deux méthodes pour les pêches dans le cours inférieur de rivières, ainsi que l'importance de la maturité. [Traduit par la Rédaction]

Introduction

As Pacific salmon (*Oncorhynchus* spp.) undertake migrations to natal spawning areas, they are fished in marine and freshwater (hereinafter “in-river”) fisheries. Prior to and during spawning migrations, fisheries managers are tasked with estimating total mortality (natural mortality plus fisheries captures) to ensure that a sufficient number of salmon return to spawning grounds (spawning escapement) and perpetuate populations (Patterson et al. 2017a). While the number of fish removed by in-river fisheries can be directly estimated, delayed mortality resulting from damage inflicted during unobserved encounters with and escape from fishing gear (Baker and Schindler 2009) is difficult to estimate. Likewise, spawning escapements for species or populations that co-mingle with those targeted for harvest, but for which

release is mandated due to conservation concerns, can also be impacted by delayed mortality. Regardless of whether fish are intentionally released or experience unobserved entanglement, we hereinafter refer to the phenomenon of contact with fisheries gear followed by continued migration as “nonretention” and the associated mortality as “fishing-related incidental mortality”, or FRIM (Patterson et al. 2017a). Without accurately accounting for FRIM, anticipated spawning escapement targets for populations may not be achieved, negatively affecting future production (Baker et al. 2014), and accurate accounting of total mortality for a given population is not possible (Patterson et al. 2017b).

Among the in-river Pacific salmon fishery gears (angling, drift and set gill nets, fish wheels, dip nets, beach seines, and fish weirs) used in the Fraser River watershed, British Columbia (Canada's largest producer of Pacific salmon), fishers use gill nets and beach

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seines to capture the majority of fish. Historically (and during abundant years in modern times), commercial fishers used gill nets in the Lower Fraser River, and both gill nets and beach seines are commonly employed by Indigenous Peoples in their in-river fisheries. Gill nets entangle fish, which often results in suffocation, lacerations, removal of mucus, and constriction (Kojima et al. 2004; Baker and Schindler 2009). Estimates of successful arrival at spawning areas for fish captured by gill nets in the lower sections of large rivers range from 43% (sockeye salmon (*Oncorhynchus nerka*) in the Fraser River; Donaldson et al. 2010) to 57% (Chinook salmon (*Oncorhynchus tshawytscha*) in the Columbia River; Vander Haegen et al. 2004). Beach seines corral fish into shallow water and, provided the net is kept at adequate depth while fish are removed, handling time can be minimal and little more than removal of mucus is expected to occur (Raby et al. 2014). Even so, local oxygen is depleted in nets if fish density is high (Raby et al. 2014). Researchers have found survival rates in large rivers to range from 52% (sockeye salmon in the Fraser River; Donaldson et al. 2011) to 74% (coho salmon (*Oncorhynchus kisutch*) in the Fraser River; Raby et al. 2012) for salmon captured by beach seine. However, Fisheries and Oceans Canada (DFO) estimates postrelease survival at 40% and 95% for gill net and beach seine caught salmon, respectively (DFO 2017). To date, no study has simultaneously compared FRIM resulting from beach seine and gillnet capture.

Sublethal effects, alterations to behavior, growth, or reproduction resulting from stress or injury (Wilson et al. 2014), are under-emphasized compared with physiological changes and mortality rates in studies of fisheries gear impacts. For semelparous salmon with unidirectional migrations, a behavioral alteration such as migratory delay is a measurable sublethal impact that can limit reproductive opportunities (Dickerson et al. 2005) or prolong exposure to unfavorable river conditions (e.g., temperatures (Martins et al. 2011), infectious agents (Wagner et al. 2005), fisheries). Salmon often delay migration following capture and tagging, likely due to recovery from that stressful experience (Liedtke and Rub 2012; Bernard et al. 1999). In several studies, migratory delay varied among multiple fisheries gear used to capture fish (Mäkinen et al. 2000; Donaldson et al. 2011; Nguyen et al. 2014). While FRIM is an obvious measurement of the negative potential consequences of nonretention, the total impact of a stressor cannot be assessed without acknowledgment of sublethal effects (Patterson et al. 2017a).

The occurrence of FRIM and sublethal effects depends upon the biological context under which capture occurs, including the physiological condition, disease state, and maturity of the captured fish (Brobbel et al. 1996; Raby et al. 2015; Patterson et al. 2017a). For example, the morphology and physiology of a migrating salmon changes rapidly and substantially along its migration route (e.g., absorption of scales (Kacem et al. 1998), consumption of endogenous energy (Gilhousen 1980), thickening of the epidermis (Robertson and Wexler 1960), development of secondary sexual characteristics, alterations to immune function (Dolan et al. 2016), and changes in physiological parameters such as hormones and ions (Shrimpton et al. 2005; Baker and Vynne 2014)). Indeed, mature fish in their spawning areas are highly resilient to net entanglement and air exposure (Raby et al. 2013). Thus, the distance along the migration as a proxy for maturity and physiological condition must be considered as a factor potentially influencing FRIM. However, no studies have evaluated the survival of released salmon captured across the migratory corridor for a single population complex during a single spawning migration, although the impact of nonretention has been experimentally compared between salmon at different states of maturity (Brobbel et al. 1996).

Temperature is the most important environmental factor influencing salmon migration (Lee et al. 2003b; Goniea et al. 2006). For example, while the thermal optimum for aerobic scope of migrating adult sockeye salmon varies by population (Eliason et al. 2011),

and mortality increases above 18 °C (Martins et al. 2011), many salmon pathogens become virulent above 16 °C (Richter and Kolmes 2005) and pathogen-associated mortality and sublethal impacts have been demonstrated in multiple studies featuring high water temperature (Benda et al. 2015; Wagner et al. 2005). Nevertheless, the impact of multiple fishing gears has, to our knowledge, only once been compared under high water temperature scenarios (Donaldson et al. 2011).

In view of the above knowledge gaps that are important to FRIM, we compared the impacts on survival and migration rates of capture by beach seine and gill net for late-run Fraser River sockeye salmon at three locations along the migration route. In addition, we repeated the study with summer-run sockeye salmon at the second location to examine the influence of high water temperature. We visually assessed injury after capture and used radio-telemetry to determine the survival and migration rate to the natal spawning area. The null hypothesis for each fishing location was that visible injury, survival to spawning grounds, and migration rate would not differ between sockeye salmon captured by beach seine or gill net. We also tested the null hypothesis that visible injury would not vary for each fishing gear among capture locations.

Methods

Fish collection, biopsy, and tagging

Handling, biopsy, and tagging were performed according to The University of British Columbia animal care and use permit, A12-0250. The late-run Shuswap sockeye salmon population was studied in 2014 ($N = 348$) and the predominantly summer-run mixture of populations in 2015 ($N = 281$). Microsatellite analysis was conducted at the DFO Pacific Biological Station (Nanaimo, British Columbia) to determine population origin by variation in the major histocompatibility complex (Beacham et al. 2004). This molecular technique required a 6 mm tissue punch from the adipose fin to be taken from each fish (Beacham et al. 2004). Populations tagged in 2015 included Chilko (50%), Nadina (30%), Stellako (10%), Tachie (5%), Bowron (3%), other small populations (2%).

In 2014, fishing crews collected sockeye salmon at McMillan Island (48 river kilometres (hereinafter, rkm) from the mouth of the Fraser River, 23–25 September), Peters Road (131 rkm, 30 September – 2 October), and at Savona, immediately downstream of Kamloops Lake (363 rkm, 7–8 October) (Fig. 1). In 2015, fish were only captured at Peters Road (29–31 July and 4–6 August). The rarity of river characteristics that allowed use of both beach seine and gill net, paired with the ability to find local fishing crews that employ both gears, partially dictated our choice of locations. Nevertheless, the three locations represent recent entry to fresh water (McMillan Island), transition from the lower river to the Fraser canyon and faster-moving water (Peters Road), and close proximity to the natal river where maturity should be relatively advanced (Savona). The number of fish radio-tagged at each capture location are presented by sex, capture method, mean fork length (FL), and mean netscore (see below) in Table 1.

At each location, fish were captured using both gill net and beach seine. Fishers were instructed to capture and handle fish using these gears as they normally would if fishing during a period when bycatch is expected and release would be mandated for some species (for example, when regulations require the release of the Early Stuart River sockeye salmon population during the opening period for summer Chinook salmon, *O. tshawytscha*). At McMillan Island and Peters Road, gill nets were drifted with the current from boats (drift net). At McMillan Island, the gill net was attached to a large boat and a smaller boat moved along the net, with fishers removing fish soon after (5–10 min) they were captured and placing them in a tote full of river water. At Peters Road, a single boat drifted a gill net for 5 min and then retrieved the net, and disentangled salmon were placed in a tote full of river water.

Fig. 1. Map of stationary radio receivers (circles) and tagging locations (red and white icons) used for studies of migrating adult sockeye salmon in the Fraser River, British Columbia, in 2014 and 2015. Yellow circles represent receivers used in only 2014, green circles represent those used in 2014 and 2015, and pink circles represent those used in only 2015. Geospatial data used to create this map are from the British Columbia Freshwater Atlas. [Colour online.]

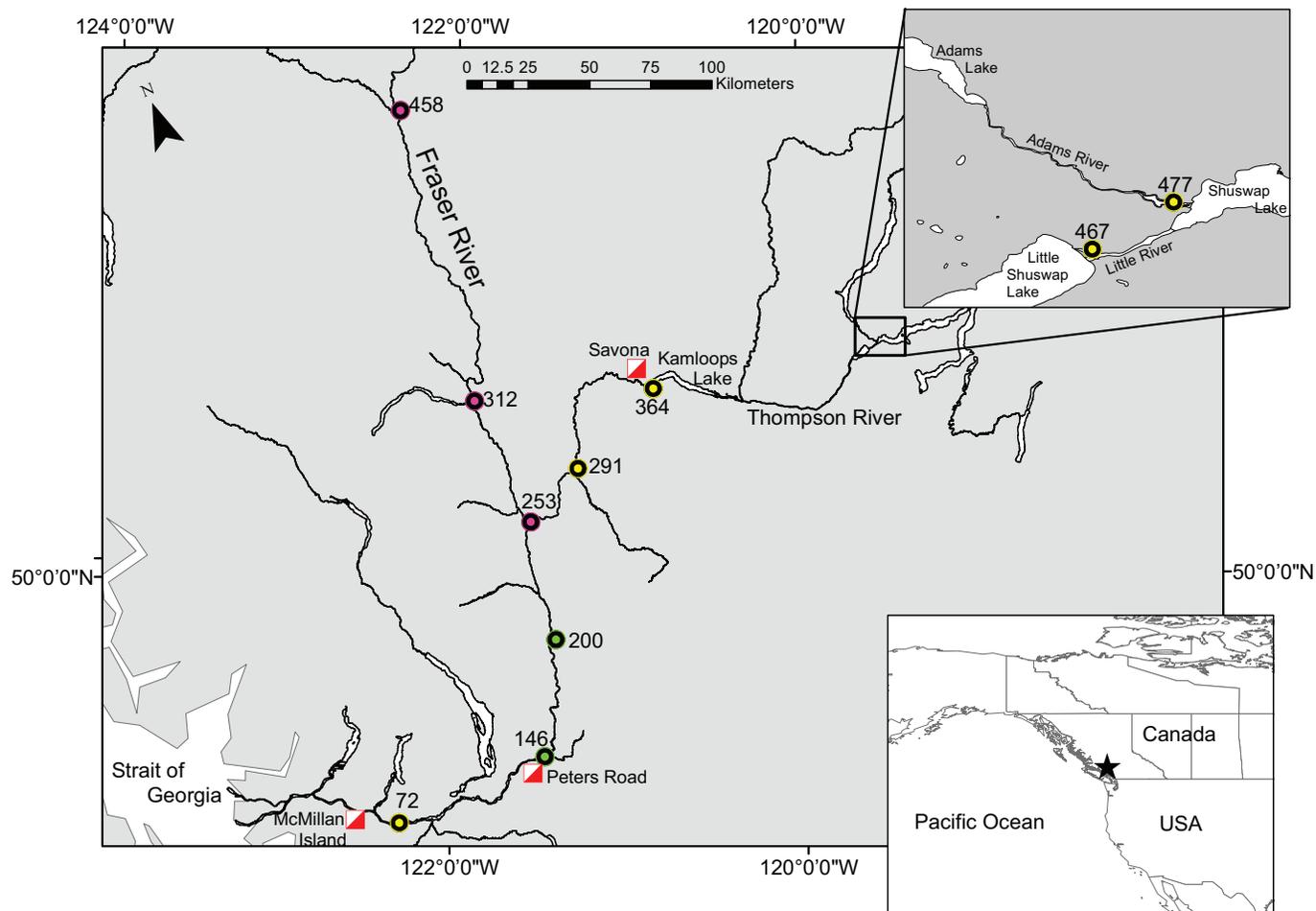


Table 1. Summary information for releases of radio-tagged late-run Shuswap sockeye salmon captured by beach seine or gill net in the Fraser and Thompson rivers, British Columbia (2014 and 2015).

Year	Location	Date	Fishing gear	Sex	N	Mean (±SD) fork length (cm)	Mean (±SD) netscore (0–3)
2014	McMillan Island (rkm 48)	23–25 Sept.	Beach seine	Female	27	59.1 (1.8)	0.37 (0.69)
			Beach seine	Male	9	61.6 (1.6)	0.22 (0.44)
			Gill net	Female	37	58.7 (2.5)	1.86 (0.71)
	Peters Road (rkm 131)	30 Sept. – 2 Oct.	Gill net	Male	36	62.2 (2.5)	1.03 (0.77)
			Beach seine	Female	52	58.5 (2.4)	0.23 (0.42)
			Beach seine	Male	22	61.2 (2.2)	0.45 (0.51)
			Gill net	Female	42	58.5 (1.8)	1.79 (0.61)
	Savona (rkm 363)	7–8 Oct.	Gill net	Male	16	61.3 (2.1)	1.38 (0.81)
			Beach seine	Female	35	59.7 (2.3)	0.06 (0.24)
			Beach seine	Male	19	63.6 (2.1)	0.11 (0.46)
Gill net			Female	33	58.2 (1.9)	1.52 (0.67)	
2015	Peters Road (rkm 131)	29–31 July and 4–6 Aug.	Gill net	Male	20	62.3 (2.4)	0.45 (0.60)
			Beach seine	Female	106	57.5 (2.2)	0.69 (0.61)
			Beach seine	Male	59	59.1 (3.0)	0.66 (0.66)
			Gill net	Female	62	58.1 (1.9)	2.29 (0.76)
			Gill net	Male	25	59.3 (2.4)	2.00 (0.87)

Note: Netscore represents the severity of observable wounds caused by the capture experience (0 = no injury; 1 = minimal net marking; 2 = moderate net marks around head, no exposed flesh; 3 = extensive net marks from head to dorsal fin, exposed flesh).

Table 2. Stationary telemetry receivers used to detect migrating sockeye salmon in the Fraser and Thompson rivers, British Columbia (2014 and 2015).

Site No.	2014		Estimated ρ		2015		Estimated ρ
	River km	Description	McMillan 2014	Peters Road 2014	River km	Description	Peters Road 2015
1	72	Mission	0.17	—	—	—	—
2	146	Hope	0.51	0.61	146	Hope	0.90
3	199	Hell's Gate	1.00*	1.00*	199	Hell's Gate	1.00*
4	291	Spence's Bridge	1.00*	1.00*	253	Lytton	0.52
5	364	Savona	0.57	0.32	312	Lillooet	0.83
6	467	Little and Adams rivers	1.00*	1.00*	458	Chilcotin River	1.00*

Note: Table includes distance from ocean (river km), location names, and probability of detection for each release group as determined by Cormack-Jolly-Seber modelling. Asterisks indicate that receiver efficiency was "fixed" to permit parameter identification in Program MARK.

At Savona, the river conditions required the use of a gill net fixed in place in a large eddy (set net). After the floats on the gill net were noticed to bob (indicating an entangled fish), the gill net soaked for an additional 5 min and then fish were removed from the net. Gillnet mesh size at all locations was 13.3 cm. At each location, beach seines were drawn using motor boats and nets were pulled by hand into knee-deep water, where fish were removed using dip nets. The mesh size of the beach seines was such that sockeye salmon did not become entangled behind the operculum. After capture, fish were held in pens in (flowing water, 1 m deep) prior to biopsy, tagging, and release. Median holding times, from after capture to tagging, were 84 min for beach seine (range: 4–230 min) and 44 min for gill net (range: 3–130 min). Since as many as 80 fish were caught in a single beach seine (Savona), more time was required to process all fish at this site.

The biopsy and tagging process was identical for all fish and very similar to that of Teffer et al. (2017). The median biopsy time required was 2.5 min (range: 1.4–6.6 min). Fish could not be anesthetized because of the possibility of recapture and human consumption. During biopsy and tagging, a technician held a fish in the trough while other technicians performed the biopsy and tagging procedure. Fork length was measured and sex was determined from secondary sexual characteristics. Blood was drawn from the caudal vasculature using a heparinized vacutainer, and a small gill sample (2–3 mm of three to four gill filament tips) was removed with sterilized end clippers. Biopsies were taken for another study and the data are not present herein. A Pisces 5 radio tag (43 mm length \times 16 mm diameter, 15.2 g in air, 5 s burst rate; Sigma Eight Inc., Newmarket, Ontario) was placed in the stomach, immediately behind the esophageal sphincter with the wire antenna hanging out of the fish's mouth. A haphazardly distributed proportion of the radio tags (64% in 2014 and 37% in 2015) had an Ibutton thermochron model DS1921Z logger (6 mm height \times 16 mm diameter, 3.3 g in air, 30 min recording; Maxim Integrated, San Jose, California) affixed to them to record the water temperature experienced by each fish. Acquisition of these data requires recovery of the ibutton. To provide an indication of water temperature experienced by fish prior to tagging, water temperature collected by DFO near Hope (rkm 150) was incorporated (see Patterson et al. 2007).

Damage caused in the capture process (netscore) was assessed for each fish (0 = no visible damage; 1 = minimal net marking; 2 = moderate net marks around head, no exposed flesh; 3 = extensive net marks from head to dorsal fin, exposed flesh). An elastic visual identification tag (aka "spaghetti" tag, Northwest Marine Technology, Shaw Island, Washington) was looped through the musculature posterior to the dorsal fin to identify fish in spawning areas or those captured by fishers. Radio and spaghetti tags were labeled with contact information so that tags could be returned and information regarding date and location of capture could be relayed.

Radiotelemetry

In 2014, fixed radiotelemetry receivers (Orion, Sigma Eight Inc., or SRX600, Lotek), each equipped with either a three- or four-element Yagi antenna, were positioned at strategic locations along the Fraser and Thompson rivers (Fig. 1; Table 2). In 2015, some of the same sites were used but additional receivers were positioned along the mainstem Fraser River (Fig. 1; Table 2). Reception range was tested by placing a radio tag 1 m underwater on both sides of the river channel where possible. For the late-run Shuswap population (2014), the Little River (rkm 467) and Adams River (rkm 477) receivers were considered in aggregate as the final receiver location since spawning occurs upstream of both of these receivers and in other tributaries to Shuswap Lake (inset Fig. 1; Table 2). In 2014, mobile tracking was performed in the lower 10 km of the Adams River by boat using a Lotek SRX 600 (Newmarket, Ontario, Canada) with a three-element Yagi antenna.

Radio detections were filtered for each individual fish so that detections at a given receiver separated by more than 2 min (likely false positives) or less than 5 s (pulse rate of radio tags) were removed. The detection history for each fish was plotted against receiver location so that false detections could be identified and removed. For a given fixed receiver "X", detection efficiency was determined by the mark-recapture analysis described below as the number of fish detected at receiver X, divided by the total number of fish known to have passed receiver X, independent of detection at receiver X (by release, detection, or capture). Low detection efficiencies (<80%) typically occurred when receivers malfunctioned or when the river was deep and wide (site 1, Table 2) or receivers were positioned too far from the river (site 4, 2015). Individuals detected during mobile tracking in 2014 on the Adams River ($N > 100$) were used to determine that detection efficiency for the Little River and Adams River receivers combined was 100%. Similarly, detection efficiency for the Chilcotin confluence receiver in 2015 was also 100%, based on upstream detections and tag returns.

Researchers recovered tags during mobile tracking on spawning grounds and from voluntary reports by fishers. In 2014, 11 sockeye salmon tagged at the Lower Fraser River release locations were reported from recaptures in net and recreational fisheries in the Fraser and Thompson rivers. The Kamloops Lake (rkm 364) purse seine fishery run by the Secwepemc Fisheries Commission captured another 12. The sockeye salmon tagged in 2015 experienced substantially more fishery openings and effort (Table 3), and fishers reported 37 tags, with 81% of these captured between the Hope and Hell's Gate receivers (rkm 146–200).

Statistical analyses

Visible injury

As netscore is an ordinal variable, rank sum tests were conducted for between-group comparisons. Netscore was compared for each sex, year, and location combination. Pairwise compari-

Table 3. Weekly effort for the combination of First Nations Food, Social, and Ceremonial and Economic Opportunity fisheries during the periods of late-run Shuswap (2014) and summer-run (2015) Fraser River tagged sockeye salmon migration.

Week ending date	Hope to Sawmill Ck.			Sawmill Ck. to Texas Ck.		Texas Ck. to Kelly Ck.		Thompson River	
	Gill net	Dip net	Beach seine	Gill net	Dip net	Gill net	Dip net	Gill net	Dip net
28 Sept. 2014	—	82	8	252	—	NA	NA	—	252
5 Oct. 2014	—	—	—	—	—	NA	NA	34	269
12 Oct. 2014	—	—	—	—	—	NA	NA	5	118
2 Aug. 2015	180	—	—	1320	24	240	144	NA	NA
9 Aug. 2015	6645	—	—	8702	134	2100	756	NA	NA
16 Aug. 2015	315	—	—	4848	—	1488	336	NA	NA

Note: Effort represents a count of the nets participating multiplied by the number of hours licensed. Gill net is a combination of drift and set nets. Dashes indicate that the fishery either was closed or there were no observed participants. NA indicates that the river reach was not applicable to the population monitored in that year given its migration route.

sons of rank sums (Kruskal–Wallis test) with p values adjusted for multiple comparisons were implemented using Dunn's test with the R statistical software (R Core Team 2017) package “dunn.test” (Dinno 2017). The Benjamini–Hochberg adjustment was used to control the false discovery rate (Benjamini and Hochberg 1995).

Survival

The explanatory variable of interest was fishing method (beach seine versus gill net). In 2014, survival to spawning was defined as detection at the last receiver group. In 2015, survival was defined as detection at the Chilcotin receiver. Although spawning habitat is still several hundred river kilometres upstream of these locations, this length of migration was adequate for determining survival differences between groups. Differences in survival between seine and gillnet capture was tested with a series of Cormac–Jolly–Seber (CJS) models using Program MARK within the RMARK interface in R statistical software (White and Burnham 1999; Laake 2013; R Core Team 2017). CJS models allow the estimation of apparent survival (ϕ) as a function of the probability of detection (ρ) and based on maximum likelihood estimation. Three sets of models were run, one for each Lower Fraser River tagging location and year combination. Owing to an inadequate number of receivers between release and the spawning area, CJS modeling could not be applied to the Savona tagging location. Here, a series of generalized linear models were fit (see below).

For the McMillan Island tagging location, receiver sites 1 through 6 were included in the analysis, and for the Peters Road group, sites 2 through 6 were included. Fish that were captured and reported by in-river fisheries were censored at the receiver downstream of (prior to) their capture location. For each model set, we used the RELEASE goodness of fit function within Program MARK to test two assumptions: every marked animal present in the population at time i has the same probability of recapture, and every marked animal in the population immediately after time i has the same probability of surviving to time $i + 1$. Overdispersion was evaluated using the median \hat{c} method in Program MARK, with 100 replicates at 15 points (White and Burnham 1999).

Sex and FL were included as covariates because sex can be associated with survival (Jeffries et al. 2012; Martins et al. 2012; Teffer et al. 2017) and body size is associated with vulnerability to gill nets (Peterson 1954) and other capture-and-release scenarios (Davis 2002). In a single-cohort CJS model with detections over a spatial extent (e.g., a salmon migration), the parameter “time” represents variability occurring between detection locations. For all models, both survival and probability of detection were varied by time since it was expected that detection probability varied between sites, and we were interested in determining how survival varied between river reaches. For each tagging location, a full model was fit that included capture method, sex, body size, and time as explanatory variables for both ϕ and ρ . This model was used to plot survival estimates and determine overdispersion

(without FL, since individual covariates cannot be included in the determination of median \hat{c} ; (White and Burnham 1999). The full model and all nested models were compared using Akaike's information criterion for small populations, adjusted for overdispersion (QAIC_c; Burnham and Anderson 2003).

Because parameter estimates that approach boundaries (0 or 1) can confound analyses in Program MARK and result in unidentified parameters, especially in the case of small sample sizes, several model parameters were fixed for each set of models. We fixed ρ to 1 for the last time interval based on 100% detection efficiency at site 6 in both years. This allowed the estimation of the last ϕ parameter, which is usually not possible in CJS models since the final ρ is generally unknown. In addition, ρ was fixed to 1 for Hell's Gate and Spence's Bridge (sites 3 and 4 in 2014) due to perfect efficiency at these locations (Table 2).

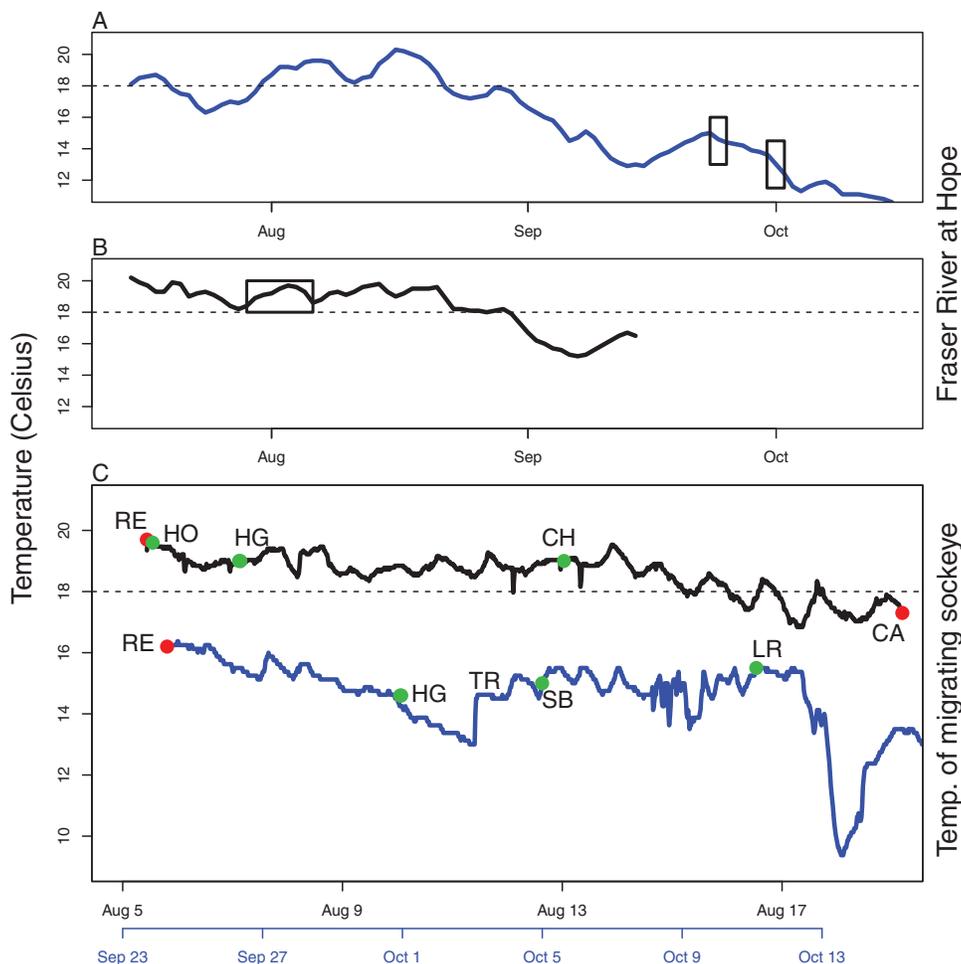
For the Savona tagging location in 2014, a series of generalized linear models (GLMs, binomial distribution) were compared by AIC_c for migratory success against the final receiver group. A full model included fishing method, sex, and body size to all nested models and a null model containing no explanatory variables. To meet the assumption of multicollinearity, we estimated the variance inflation factor to be sure that it was below 4 for all variables (O'Brien 2007). We determined that overdispersion for the full model was negligible (1.04). A Hosmer–Lemeshow goodness of fit test indicated that the model fit was appropriate (Hosmer et al. 1997).

Migration time and rate

The same explanatory variables (fishing method, sex, body size) were applied to accelerated failure time (AFT) models of migration time to determine whether fishing method was associated with migration time. For the Lower Fraser tagging locations in 2014 and 2015, migration time from release to the Hell's Gate receiver (rkm 200, the first receiver with 100% detection efficiency) was modeled. Migration time was calculated as the difference between time of release and the first detection at Hell's Gate. For the 2014 groups, migration time from Spence's Bridge (rkm 291) to Little River (rkm 467) was also modeled (insufficient data for modeling migration time of 2015 fish beyond Hell's Gate). This was calculated as the difference between the first detection at Spence's Bridge and the first detection at Little River. Migration time to Hell's Gate was investigated separately from migration time through the Thompson River because we were interested in whether delay occurred shortly after capture and also if there was a difference in delay by treatment further along the migration when many unsuccessful fish had already been removed. For the Savona tagging group, migration time was from release (rkm 363) to Little River.

To meet the assumption of the appropriate error distribution for all AFTs, distributions were selected via AIC after each model was fit using the loglogistic, lognormal, logistic, exponential, Weibull, and Gaussian distributions (Swindell 2009). The two dis-

Fig. 2. Temperatures experienced by sockeye salmon migrating through the Fraser River in 2014 and 2015. Panels A (2014) and B (2015) show water temperature recorded at Hope; rectangles indicate tagging periods (McMillan Island and Peters Road in 2014, Peters Road in 2015). Panel C shows water temperatures recorded by thermal loggers attached to gastric radio tags in individual sockeye salmon in 2014 (blue line) and 2015 (black line). Locations determined by radiotelemetry are indicated by points. For 2014, RE = release at McMillan Island, HG = Hell's Gate, TR = entry to Thompson River, SB = Spence's Bridge, LR = Little River. For 2015, RE = release at Peters Road, HO = Hope, HG = Hell's Gate, CH = Chilcotin River, CA = capture by gill net at rkm 702. In all panels, the temperature at which sockeye salmon begin to experience elevated mortality (18 °C; Martins et al. 2011) is indicated by a dashed line. [Colour online.]



tributions with the lowest AIC values were visually assessed by plotting the negative log of the Cox–Snell residuals against time, and the distribution demonstrating better agreement with a line through the origin with a slope of 1 was selected.

In addition to the AFT analysis, we created boxplots of migration rates comparing fishing method for river reaches between receivers with relatively abundant detections. Migration rate was calculated as the distance between a given receiver and the next upstream receiver divided by the time difference between first detection at the two receivers. The group means were compared using Welch two-sample *t* tests for each year, reach, and tagging group combination.

Results

Water temperature data collected at Hope and temperature profiles from fish tagged at the Peters Road location indicate the temperatures experienced by fish prior to and following tagging in 2014 and 2015 (Fig. 2). The late-run Shuswap population (2014) rarely experienced water temperatures above 16 °C, while the

mixture of summer-run populations (2015) consistently experienced water temperatures above 18 °C between river entry and the Chilcotin River receiver.

Controlling for capture location and sex, gillnet capture always resulted in a significantly higher netscore than beach seine ($p \leq 0.01$) except in the case of male sockeye salmon at Savona ($p = 0.12$; refer to online Supplementary material, Table S1²). Netscore differed by sex only for gillnet capture at McMillan Island and Savona, where females had significantly higher netscore than males ($p < 0.001$ for both). In 2014, netscore for gillnet-captured male sockeye salmon was lower at Savona compared with gillnet-captured males at both McMillan Island and Peters Road ($p = 0.02$ and 0.002 , respectively). Although netscore at Peters Road was higher in all groups for 2015 compared with 2014 (Table 1), the only significant difference was beach seine capture for females ($p < 0.001$).

Survival

For all the experimental fishing performed in the Lower Fraser River, capture by gill net was associated with lower survival than

²Supplementary data are available with the article through the journal Web site at <http://nrcresearchpress.com/doi/suppl/10.1139/cjfas-2017-0474>.

Table 4. Top five models (determined by QAIC_c rank) of survival for four sockeye salmon release groups.

Tagging location	Model structure		No. of parameters	QAIC _c	Δ QAIC _c	Weight
	φ parameters	ρ parameters				
McMillan Island, 2014	Fork length + fishing method + time	Time	9	422.44	0.00	0.24
	Sex + fork length + fishing method + time	Time	10	422.94	0.51	0.19
	Fork length + fishing method + time	Sex + time	10	424.24	1.80	0.10
	Fork length + fishing method + time	Fork length + time	10	424.28	1.84	0.10
	Fork length + fishing method + time	Fishing method + time	10	424.51	2.07	0.09
Peters Road, 2014	Time	Time	6	684.05	0.00	0.19
	Fishing method + time	Time	7	685.16	1.10	0.11
	Fork length + time	Time	7	685.76	1.71	0.08
	Time	Fishing method + time	7	685.82	1.76	0.08
	Sex + time	Time	7	686.03	1.98	0.07
Peters Road, 2015	Fishing method + time	Time	8	318.09	0.00	0.26
	Fishing method + time	Fishing method + time	10	319.73	1.64	0.11
	Sex + fishing method + time	Time	9	319.75	1.66	0.11
	Fork length + fishing method + time	Time	9	319.94	1.86	0.10
	Fishing method + time	Sex + time	9	320.15	2.06	0.09
Savona, 2014 (logistic regression)	~1	—	1	122.9	0.00	0.32
	Sex	—	2	124.0	1.10	0.18
	Fishing method	—	2	124.5	1.55	0.15
	Fork length	—	2	125.0	2.06	0.11
	Sex + fishing method	—	3	125.6	2.72	0.08

Note: φ parameters were associated with survival probability, and ρ parameters were associated with detection probability. Since time consists of multiple detection sites, it adds >1 parameter to the total number of model parameters (No. of parameters), but sites where ρ was fixed (perfect detection) do not contribute to this number. Cormack-Jolly-Seber models were created for the Lower Fraser River locations, and logistic regression models were created for the Savona tagging location.

beach seine. For all tagging locations, ρ for the top model was always time (Table 4), which reflects the variation in detection probability between receivers (Table 2). Based on uncorrected detections and accounting for fisheries captures, 71% of beach seined and 35% of gillnetted fish captured and tagged at McMillan Island were detected at the final receiver group. The top model for fish tagged at McMillan Island included body size ($\beta = 0.27$, 95% confidence interval (CI) = 0.14–0.41), fishing method ($\beta = -1.73$, 95% CI = -2.54 – -0.92), and time (Table 4; Figs. 3, 4). Although a competing model ($\Delta\text{QAIC}_c = 0.51$) for this tagging location included sex (Table 4), males and females had a similar likelihood to survive ($\beta = 0.16$, 95% CI = -0.66–0.99). Sex was not a statistically significant factor in any of the top models, despite a consistent (and sometimes large) numerical difference (Fig. 3).

For the Peters Road tagging location in 2014, 62% and 46% of beach-seined and gillnetted fish (calculated as above) were detected at the final receiver group. The top CJS model only included time, indicating that differences among the river reaches accounted for more variation in survival than fishing method at Peters Road. As seen in CJS modeling for all tagging releases (Fig. 3), survival was lowest between the Hope (rkm 146) and Hell's Gate (rkm 200) receivers, followed by the final river reaches monitored (Savona receiver (rkm 364) to Little River (rkm 467) receiver in 2014, Lillooet receivers (rkm 312) to Chilcotin receiver (rkm 458) in 2015). The next competing model ($\Delta\text{QAIC}_c = 1.10$) included fishing method as a predictor of φ, and the effect of gillnetting was significantly negative ($\beta = -0.57$, 95% CI = -0.01 – -1.13).

For the Peters Road tagging location in 2015, survival was very low with only 9% and 2% of beach-seined and gillnetted fish (calculated as above) detected at the Chilcotin receiver (rkm 458). The top model included fishing method ($\beta = -1.95$, 95% CI = -2.46 – -1.44) and time (Table 4). The next competing model ($\Delta\text{QAIC}_c = 1.64$) included fishing method as a significant predictor of the probability of detection, with the effect of gillnetting being significantly negative. In another competing model including sex as a predictor of survival, sex was not significant.

For the Savona tagging location in 2014, 82% and 75% of beach-seined and gillnetted fish (calculated as above) were detected at the final receiver group. For GLM models (instead of CJS) com-

pared by AIC_c, the null model had the lowest AIC, suggesting none of the explanatory variables adequately explained the probability of survival to Little River (rkm 467). The next three models by AIC included one of each of the explanatory variables used to create the full model, but none were significantly associated with survival (Table 4).

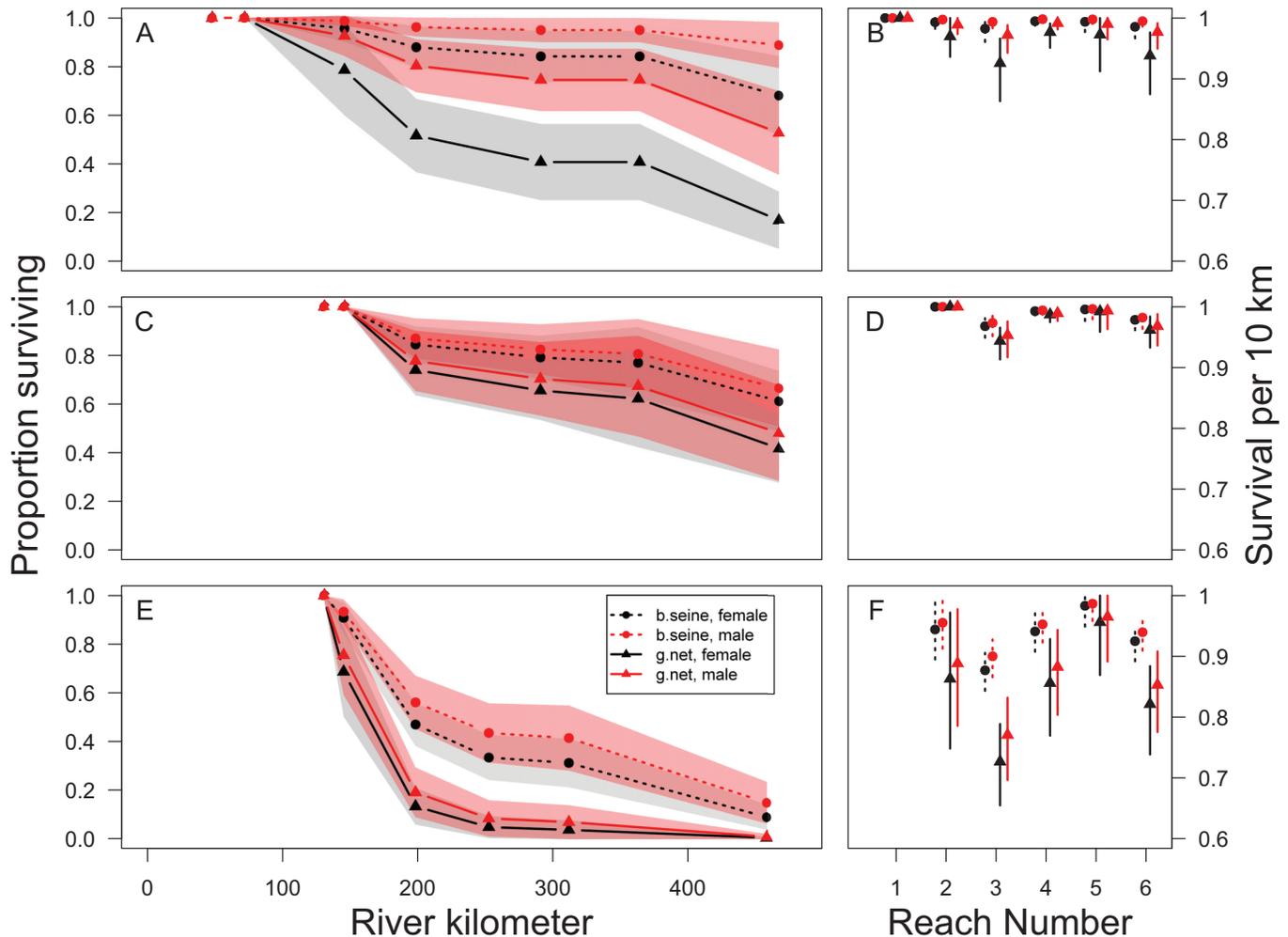
Migration rate

For the Lower Fraser River release groups in 2014, gillnet capture significantly slowed migration to Hell's Gate (rkm 200) but not beyond to the spawning areas (Fig. 5; Table 5). Neither body size nor sex was significantly associated with migration rate in any models.

To complete migration from the tagging location to Hell's Gate, late-run sockeye salmon tagged at McMillan island in 2014 took a median 6.88 days (95% CI = 6.78–7.74 days) and 7.64 days (7.12–8.18 days) for beach-seined and gillnet-caught fish, respectively. The same values for fish tagged at Peters Road in 2014 were 4.82 days (4.74–4.95 days) and 5.91 days (5.52–6.88 days). While parameter estimates were similar for the Peters Road location in 2014 and 2015, there was no significant effect of fishing method on migration time to Hell's Gate in 2015 (Table 5). AFT models for the Lower Fraser River tagging locations indicated that gillnetted fish would take from 15% (McMillan 2014, 95% CI = 6%–27%) to 21% (Peters Road 2014, 95% CI = 14%–35%) longer than beach-seined fish to complete this section of migration. The observed difference for migration times in the Lower Fraser River did not persist in the Thompson River for the groups tagged in the Lower Fraser River in 2014. In contrast, beach-seined fish migrated from the Savona tagging location to the Little River 13% (0%–28%) slower than gillnetted fish (Table 5; Fig. 5).

A comparison of migration rates (Fig. 6) showed that sockeye salmon caught by beach seine at both release locations in both years migrated significantly faster to the Hope receiver (rkm 146) than fish caught by gill net (McMillan: $p = 0.04$; Peters Road, 2014: $p < 0.001$; Peters Road, 2015: $p < 0.001$). Thereafter, migration rate was not different between the groups except for the Peters Road group where in the following river reach, gillnet-caught fish migrated significantly faster than beach-seined fish ($p = 0.001$).

Fig. 3. Plots of cumulative survival (left) and distance-normalized survival across river reaches (right) for female and male Fraser River sockeye salmon captured by beach seine or gill net at McMillan Island (A, B), Peters Road in 2014 (C, D), and Peters Road in 2015 (E, F). To show survival estimates across multiple river reaches, grouped by sex and capture method, but with confidence intervals, a full Cormack–Jolly–Seber model was created for each tagging group (ϕ = fishing method + sex + time, ρ = fishing method + sex + time). These estimates were generated using the “deltamethod.special” function in RMark. [Colour online.]



Discussion

Although it is often assumed that gillnet capture is a more deleterious fishing method than beach seining for adult Pacific salmon encountering these gear types during their freshwater spawning migration (Raby et al. 2015; DFO 2017), this study provides the first side-by-side, empirical comparison of the two fishing methods where treatments were true capture experiences (as opposed to simulations). Similar to a study where gillnet capture was simulated (Nguyen et al. 2014), we found that sockeye salmon released following capture by gill net in the Lower Fraser River had elevated mortality, higher physical damage, and slowed migration rate relative to those captured by beach seine. In contrast with those captured early in their freshwater migrations, fish captured by gill net at the furthest upstream location experienced survival similar to, migrated to spawning grounds faster than, and, in the case of male fish, displayed physical damage indistinct from that of beach-seined fish. These results indicate that gill nets generally cause more damage and mortality than beach seines, but the relative impact of these gears changes as salmon undergo physical and physiological alterations during migration. In light of our results, we suggest that FRIM can be reduced substantially under certain conditions, for example, the use of beach seines instead of gill nets will, in most cases, reduce FRIM until Pacific

salmon have reached a level of maturity where they have greater resilience to capture (i.e., terminal fisheries).

Two findings in this study point towards the differences between beach-seined and gillnet-captured salmon that likely lead to elevated mortality for the latter. As evidenced by netscore, the physical damage caused by gill nets was almost always greater. Open wounds provide points of entry for infectious agents (Svendsen and Bøggwald 1997), and visible damage caused by contact with nets has been associated with mortality (Baker and Schindler 2009; Olsen et al. 2012). The second finding indicating a difference between the two capture methods was the temporary migratory delay that occurred for gillnet-caught fish. The stress response, anaerobic exercise, and asphyxiation are all experiences that cause an increase of lactate in fish blood and tissue (Farrell et al. 2000; Kojima et al. 2004), and deep respiration accompanied by reduced movement is required for a return to homeostasis (Høgåsen 1998; Lee et al. 2003a). The gillnet capture experience may include burst swimming, constriction, asphyxiation resulting from the net sealing the operculum closed, and air exposure while removing fish from nets. From this list (assuming a net mesh appropriate for the target or bycatch species), the beach seine method employed herein (not dragging the beach seine onto the shore) likely only features burst swimming. We

Fig. 4. Predicted survival estimates based on fork length for sockeye salmon captured at McMillan Island by beach seine or gill net. These estimates are derived from the best model (by QAIC_c rank): ϕ = fishing method + fork length + time, ρ = time. Survival was estimated for the reach from the Hope receiver (rkm 146) to the Hell's Gate receiver (rkm 199), which was the river reach with the highest mortality and greatest difference in survival between beach-seined and gillnetted fish. [Colour online.]

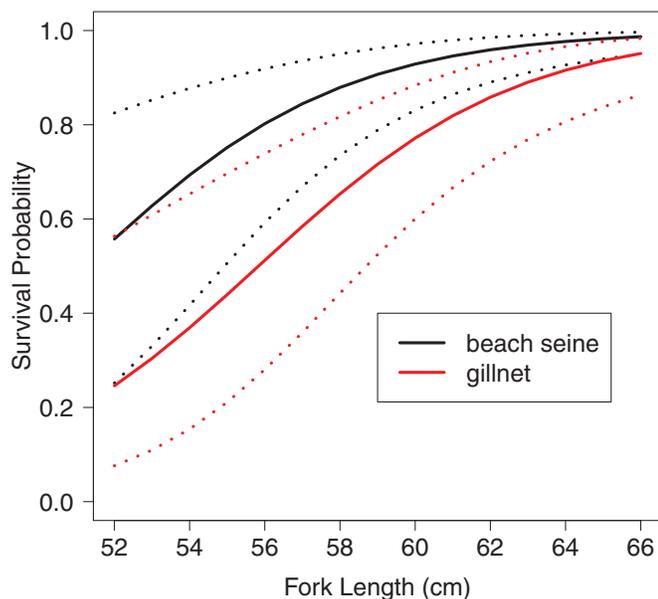


Fig. 5. Kaplan–Meier plots of migration times to Hell's Gate (left) and Little River (right) for beach-seined and gillnetted sockeye salmon tagged at McMillan Island (A, B), Peters Road in 2014 (C, D), Peters Road in 2015 (E), and Savona (F). The starting point was the Spence's Bridge receiver for panels B and D and the tagging location for all other panels. A single asterisk next to the title letter of a panel indicates significance at $p < 0.05$, and two asterisks indicate $p \leq 0.001$. [Colour online.]

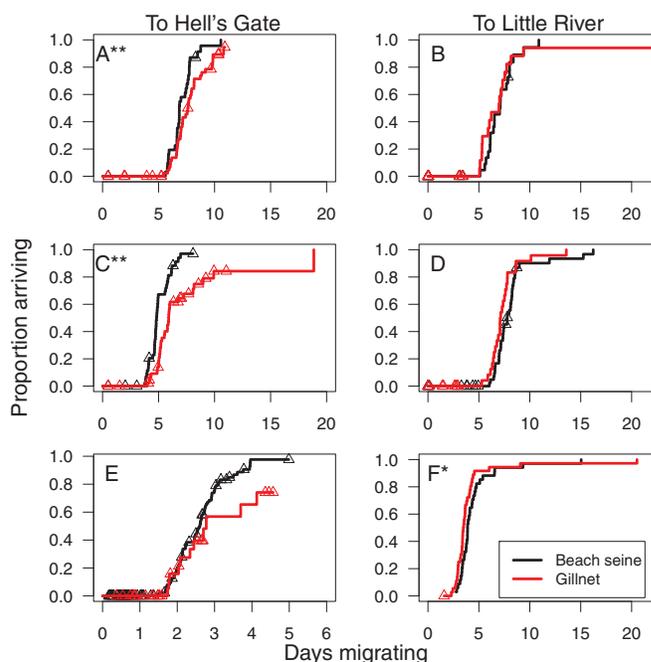


Table 5. Model results for accelerated failure time models applied to sockeye salmon captured by beach seine and gill net (GN).

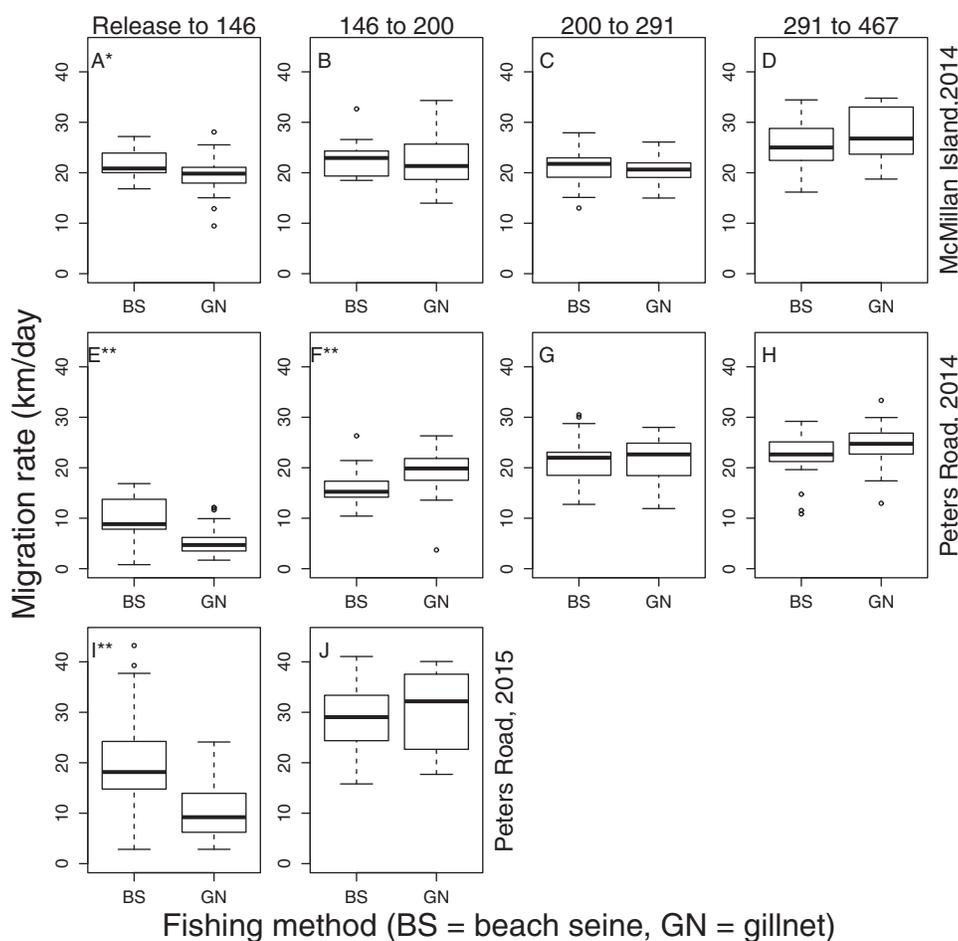
Tagging group to receiver	Survival distribution	N obs. (events)	Model parameter	Explanatory variables		
				Sex (M)	Fishing method (GN)	Fork length (cm)
McMillan Island, 2014, to Hell's Gate	Lognormal	109 (76)	β	-0.08	0.15	-0.02
			SE	0.05	0.05	0.01
			p	0.14	0.001	0.09
Peters Road, 2014, to Hell's Gate	Loglogistic	131 (105)	β	-0.06	0.21	-0.01
			SE	0.05	0.04	0.01
			p	0.25	<0.001	0.26
Peters Road, 2015, to Hell's Gate	Lognormal	180 (86)	β	-0.09	0.15	-0.004
			SE	0.06	0.08	0.01
			p	0.13	0.08	0.70
McMillan Island, 2014, Spence's Bridge to Little River	Loglogistic	68 (37)	β	-0.02	-0.05	-0.01
			SE	0.07	0.07	0.02
			p	0.80	0.40	0.63
Peters Road, 2014, Spence's Bridge to Little River	Loglogistic	94 (63)	β	-0.03	-0.06	0.003
			SE	0.05	0.04	0.01
			p	0.53	0.12	0.76
Savona, 2014, to Little River	Loglogistic	107 (70)	β	-0.09	-0.13	-0.003
			SE	0.09	0.06	0.02
			p	0.34	0.04	0.84

Note: Significance for explanatory variables at $p < 0.05$ are indicated in bold font.

suggest that the delay of gillnet fish relative to beach seine fish was symptomatic of a need for additional recovery time and indicative of a more severe physiological impact (Jain et al. 1998; Donaldson et al. 2010, 2011) that could have long-term consequences in the form of increased consumption of stored energy and impaired immune defense (Maule et al. 1989; Lupes et al. 2006).

An important caveat to our comparisons of FRIM between gillnet and beach seine capture is that the highest number of fish captured in a given beach seine set in this study (~100) was low compared with the number of salmon (>1000) in large sets where Raby et al. (2014) found oxygen levels to drop and asphyxiation occurred as a result. Interestingly, Raby et al. (2014) did not find catch size to be a significant predictor of survival to spawning

Fig. 6. Boxplots comparing migration rates ($\text{km}\cdot\text{day}^{-1}$) between sockeye salmon captured by beach seine (BS) and gill net (GN), radio-tagged, and released in the Fraser River, British Columbia. Capture location and year is indicated on the right side of each row of plots. Sample sizes for BS and GN, respectively, are as follows: A = 17, 30; B = 16, 23; C = 34, 34; D = 21, 16; E = 41, 38; F = 36, 26; G = 58, 36; H = 39, 24; I = 171, 35; J = 82, 8. A single asterisk next to the title letter of a panel indicates significance at $p < 0.05$, and two asterisks indicate $p \leq 0.001$. Comparisons were not available for migration beyond rkm 200 in 2015 due to low survival.



grounds, although it was positively associated with an index of reflex impairment. The beach seine capture conducted in our study is likely more representative of a “best-case scenario” where catch size was low and nets were kept in deeper water while fish were removed. However, the case is the same for gillnet capture; if fish densities were such that we would capture over 1000 fish per beach seine, we would expect to catch many more fish in gillnet drifts, and fish would spend more time entangled in gill nets as others are disentangled. We therefore maintain that although our results should not be applied to all scenarios involving gill nets and beach seines, in many circumstances gill nets will cause more FRIM than beach seines.

Although the survival for sockeye salmon captured and tagged during high water temperatures (2015) was lower than that of those tagged under cooler conditions (2014) and the difference in survival between fishing methods was magnified (see β estimates for fishing method), there are several caveats that prevent us from definitively ascribing these phenomena to temperature. First, we tagged the Late Shuswap population in 2014 and a mixture of summer-run populations in 2015, and previous studies have demonstrated that response to capture stressors may vary between populations (Donaldson et al. 2010, 2012). Second, in-river fisheries pressure was considerably higher in 2015 compared with 2014, and fisheries openings occurred in close temporal and spatial proximity to our tagging dates. Regardless, many studies have confirmed the impact of temperature on adult Pacific salmon in

the laboratory (Gale et al. 2011; Eliason et al. 2011) and by using biotelemetry (Gonia et al. 2006; Mathes et al. 2010). A study combining multiple years and populations of sockeye salmon in the Fraser River also identified this phenomenon (Martins et al. 2011). Furthermore, chronic stress has been shown to hinder wound healing (Mateus et al. 2017), and the stressful elevated water temperatures experienced by the 2015 sockeye salmon therefore likely exacerbated the impact of gillnetting. Although not confirmed by a statistical comparison in this study, we suggest that high water temperatures contributed to the low survival and greater difference between the impacts of beach seine and gill net observed in 2015.

Salmon skin thickens as Pacific salmon migrate upstream (Robertson and Wexler 1960), and scales are reabsorbed, more so for males than females (Kacem et al. 1998). As salmon approach spawning grounds, cortisol levels increase (Robertson et al. 1961; Baker and Vynne 2014). These factors may lead to lower incidence of FRIM for fish captured close to spawning grounds, since the integument is harder to rupture and stressors will cause minimal departure from baseline cortisol levels (Raby et al. 2013). Indeed, netscore at the furthest upstream capture location (Savona) was lowest for all fishing method and sex combinations, although the difference was significant only for gillnet-captured males. The summer-run sockeye salmon captured in 2015, which were the least mature fish based on their life history strategy (late-run Shuswap salmon mature more while milling in the estuary, while

summer-run fish typically enter the Fraser River immediately; Hinch et al. 2012), had the highest netscores for all combinations. In addition, the development of secondary sexual characteristics at Savona may have prevented males from becoming badly entangled in gill nets. We noticed that many males were snagged by their teeth, which were much larger at Savona than in the lower river, or were prevented from becoming entangled around their operculum by the development of their dorsal hump. Although the GLM analysis indicated that fishing method was not associated with survival to spawning grounds, there are two caveats to this result. The migration from Savona to spawning grounds was relatively short and characterized by slow-moving water, which may have been an inadequate distance and rigor to invoke FRIM. Additionally, fishing by gill net at Savona was conducted using a set net, and entangled fish were brought to shore, disentangled, and immediately placed in netpens after 5 min of struggle (whereas fish gillnetted in the lower river were often entangled for 5–10 min and were transported to netpens by boat). The capture experience at Savona might have been less stressful and damaging than drift gillnetting in the Fraser River, and the fact that gillnet fish arrived at spawning grounds in substantially less time than beach seined fish suggests that salmon captured by beach seine at this location required a longer recovery period. Although the finding that there was no difference in survival between the two capture treatments at Savona corroborates one of the few other studies that examined FRIM in close proximity to spawning grounds (Raby et al. 2013), we encourage more experiments to determine how broadly this phenomenon applies.

The top model for the first tagging location included body size as a significant explanatory variable, with larger fish more likely to survive than smaller fish. When a variety of fish sizes are corralled in a beach seine, smaller fish might be more likely to receive injury or be crushed than larger fish, as has been observed in other net gears that corral fish (Neilson et al. 1989; Davis et al. 2001). A study comparing the selectivity of different gillnet mesh sizes showed that 13.3 cm gill nets (used in this study) were most selective for Fraser River sockeye salmon with fork lengths of 58–60 cm (Peterson 1954). It is likely that fish in this size range and below experienced greater damage, since removal from gill nets would have been more difficult due to tighter entanglement around the operculum or anterior to the dorsal fin (median FL for population = 60 cm).

A design limitation of our study is that we only estimated survival to spawning areas and have no measures of actual spawning success (e.g., failed spawning is indicated by egg retention in females) for our experimental groups. Baker and Schindler (2009) found that while sockeye salmon with gillnet injuries arrived very close to the mouth of their spawning stream, 98%, 92%, 33%, and 10% of fish with no, minor, moderate, and major injuries (respectively) entered the spawning stream. Of those that did enter, moderate and severely injured fish died rapidly, limiting spawning opportunities. These results indicate the importance of measuring spawning success when studying the impacts of FRIM, and we encourage the collection of these data in future studies.

In summary, we have provided evidence that gillnet capture in the Lower Fraser River causes greater injury and subsequent mortality for sockeye salmon than beach seine capture. Our findings of the interaction of gear type, injury, and location address a key information gap regarding the role of salmon maturity in migration success and behavior (Patterson et al. 2017b). In some cases, prioritizing the use of one gear type over another may reduce FRIM to an acceptable level so that Pacific salmon fisheries can persist, and this approach will become more common as climate change proceeds. We caution that managers must give adequate consideration to the underlying context of capture (environmental and biological) for a given fishery, because this is sometimes more important than the gear type employed. Ultimately, our findings will contribute to improved science advice given to man-

agers regarding FRIM and lead to improved accounting of fishing-related mortality (Patterson et al. 2017a).

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