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Recreational fisheries-related injuries and body size affect travel rate and post-release mortality in marine migrating coho salmon (*Oncorhynchus kisutch*)

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ABSTRACT

Although many coho salmon (*Oncorhynchus kisutch*) caught in recreational fisheries are harvested, a substantial number of salmon are released after capture. Mortality rates of coho salmon released from recreational fisheries are largely unknown in the marine environment. This two-year study investigated factors associated with post-release mortality and travel rate of coho salmon in a marine recreational fishery in British Columbia, Canada. Adult coho salmon were recreationally angled in the marine environment, affixed with acoustic tags, and tracked during their return migration to natal spawning streams using a network of acoustic receivers. We found post-release mortality to the first point of detection (~50 km from release) was 31.5% (95% CI: 26.1 – 37.4%; n = 279). Scale loss, eye damage, bleeding, and smaller body size of coho salmon were associated with increased odds of mortality. Scale loss and smaller body size were also associated with slower migration rate post-release. Air exposure up to five minutes was not found to be a driving factor in mortality or travel rate. These fishing-related injuries can cause immediate physiological and behavioural disturbances, increase vulnerability to predation, infection, and disease, and delay migration as the fish recovers. Smaller coho salmon may also be less capable of overcoming capture stress. Our study highlights the importance of quantifying mortality of wild fish in their natural environment, and we suggest that small changes to fishing practices (e.g., smaller hook sizes, less handling, etc.) could make large differences in release survival thus encouraging a more sustainable recreational fishery.

1. Introduction

Catch-and-release (C&R) fishing is often used as a conservation measure in the management of recreational fisheries to protect species and populations of concern (Wydoski, 1977). The intended outcome of C&R is that released fish will survive to be caught again or survive and ultimately contribute to the spawning population. However, actual C&R-related mortality estimates are largely unknown for many fisheries and vary among fisheries (reviewed in Bartholomew and Bohnsack, 2005; Arlinghaus et al., 2007). Moreover, many C&R mortality estimates are generated by simulating fisheries in the lab and holding fish in captivity which is not representative of C&R scenarios in the field (Cooke et al., 2013). As a result, published mortality estimates may not reflect reality, complicating the ability to develop biologically meaningful management measures for wild fish populations (Coggins et al., 2007). Knowledge of C&R mortality and its drivers provide opportunities to improve fishing practices and thus reduce mortality and improve biological outcomes for fish (Brownscombe et al., 2017).

Pacific salmon (*Oncorhynchus* spp.) are ecologically, culturally, socially, and economically valuable across their entire range. In British Columbia, Canada (BC), Pacific salmon are commonly targeted in recreational, commercial, and First Nations fisheries. Unfortunately, wild

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Pacific salmon are experiencing coast-wide declines along the west coast of North America, and many populations are currently designated as Endangered or Threatened (Beamish et al., 2010; Zimmerman et al., 2015; COSEWIC, 2016; Connors et al., 2020; Welch et al., 2020). Given that Pacific salmon species and populations are often co-migrating while homing (Cook et al., 2018a), protecting populations and species of conservation concern while allowing fishing opportunities can be difficult. Recreational Pacific salmon fisheries in BC are managed by Fisheries and Oceans Canada (DFO). To allow for harvest opportunities and meet spawning escapement targets, DFO operates under the 'selective fishing strategy' which encourages the release of non-target fish 'alive and unharmed' (DFO, 2001). Currently, DFO incorporates estimates of C&R mortality to inform fisheries management of non-harvest fisheries mortality (DFO, 2016), which has been recognized as a critical input into stock assessment for decades (Ricker, 1976). Any mortality that occurs throughout, or because of, the fishing, capture, and handling event excluding fish that are harvested is considered Fisheries-Related Incidental Mortality (FRIM). Examples include mortality from fish that encounter fishing gear and do not survive after escaping, fish that die upon capture but are not harvested, and fish that die post-release (Patterson et al., 2017). Studying post-release mortality is notoriously challenging, and many previous studies have attempted to quantify post-release mortality by using short-term holding studies (Davis, 2002; Rogers et al., 2014). While holding studies are critical to investigate the physiological mechanisms driving post-release mortality and can eliminate factors such as post-release predation, confining fish in unrealistic conditions can exacerbate fish stress and potentially confound mortality estimates (Raby et al., 2015b). There are also numerous factors during C&R events that can have both acute and chronic impacts on fish fitness that can lead to mortality. Namely, fish condition, angler behaviour, predators, and environmental context can have major roles in determining fish mortality (Bartholomew and Bohnsack, 2005; Cooke and Suski, 2005; Arlinghaus et al., 2007; Raby et al., 2015a). Lack of information on the impacts of different environmental and anthropogenic factors in realistic conditions, long-term mortality rates beyond immediate release, and differences in responses among Pacific salmon stocks all add to the general challenges of calculating FRIM (DFO, 2016; Patterson et al., 2017).

Coho salmon (*Oncorhynchus kisutch*) have been a focal species on the topic of fisheries mortality for decades (Cox-Rogers et al., 1999; Farrell et al., 2001; Cook et al., 2018a; Teffer et al., 2019). The crash of the once thriving Interior Fraser River (IFR) coho salmon population in the 1990 s led to fisheries closures and catch restrictions that remain today in BC's Pacific salmon fisheries, and the population was designated as Endangered in 2002 and re-designated as Threatened in 2016 (Bradford and Irvine, 2000; Beamish et al., 2010; COSEWIC, 2016). Coho salmon are frequently targeted for harvest in several fisheries, and many are also released as bycatch, either voluntarily or due to management restrictions protecting populations of conservation concern like the IFR coho salmon (DFO, 2023). Two recent studies investigated post-release mortality of coho salmon bycatch in marine commercial purse seine fisheries (Raby et al., 2015b; Cook et al., 2018a). Raby et al. (2015b) and Cook et al. (2018a) used acoustic telemetry to quantify mortality of coho salmon in the Salish Sea and found 20% and 36.1% short-term mortality, respectively. These studies also identified factors influencing post-release mortality (scale loss, reflex impairment, population) and were critical in revising the post-release mortality estimates for this fishery (DFO, 2023). For recreational fisheries, current marine post-release mortality estimates for coho salmon are mainly derived from short-term (0–24 hours) holding studies (e.g., Cox-Rogers et al., 1999), and a 10% release mortality rate (includes fish that die pre-release [upon or after capture] and post-release) is applied in stock assessments for coho salmon in all marine recreational fisheries in British Columbia (DFO, 2023). Release mortality is also integrated into tools such as the Fishery Regulation Assessment Model (FRAM) used in United States coho fisheries management (SMAW, 2023), where estimates were similarly derived from short-term holding studies (WDF, 1993; STT, 2000) and range from 7% to 23% for marine recreational coho fisheries. Biotelemetry allows long-term tracking of fish in their natural environment and provides an opportunity to obtain longer-term and thus more accurate estimates of C&R mortality, as well as other post-release behaviours such as travel rate (Pollock and Pine, 2007; Donaldson et al., 2008). However, there has been no direct telemetry research to assess post-C&R mortality rates nor the factors that influence C&R mortality and travel rates for coho released from marine recreational fisheries.

The objectives of this study were to use acoustic telemetry to determine levels of post-release mortality and to investigate angling-related and biological factors that are associated with post-release mortality and travel rate of coho salmon in a marine recreational fishery. This is the first study on marine recreational C&R mortality of adult coho salmon in their natural environment. Quantifying mortality rates and understanding how factors influence behaviour and survival of C&R migrating adult coho salmon will provide information essential to developing management tools and fishing best practices to reduce mortality of wild Pacific salmon.

2. Material and method

2.1. Fish collection and tagging

Between September 1–18, 2020, and August 23 – September 3, 2021, adult coho salmon were caught in DFO management Area 20 in the Canadian waters of the Strait of Juan de Fuca (median water depth = 169.5 m, range = 14.3 – 257 m). Coho salmon were caught via angling with a rod and reel, trolling with down-riggers (median depth= 15.2 m, range = 0 – 45.7 m) aboard guided fishing boats at various popular recreational fishing locations where homeward migrating adult coho salmon were known to be located at that time of year (Fig. 1). To ensure C&R mortality estimates were representative of the fishery, anglers were not restricted as to gear type, capture location, nor landing method, aside from being required to use barbless hooks and fishing within areas open to the fishery in accordance with management regulations. Coho salmon were either targeted directly or caught as bycatch during a concurrent study targeting Chinook salmon. All coho salmon were captured during daylight hours, and the median sea surface temperature (SST) was 11.8°C (range = 11.1°C – 14.5°C; measured every 30 minutes) in 2020 and 13.2°C (range = 12.7°C – 13.7°C; measured daily at the start of tagging) in 2021. In 2020, two boats angled side-by-side; one boat was used for angling and the second boat was used for both angling and tagging. When the angling boat caught a coho salmon the fish was landed with a knotless, vinyl-coated, catch-and-release landing net. The fish was kept underwater in the net and passed to the tagging boat for processing. In 2021, both angling and tagging were conducted on the same boat. We intended to accurately represent anglers participating in the fishery, so all boats included at least one professional fishing guide and 2–3 anglers/fish handlers whose level of expertise ranged from novice to experienced. To track legal-sized adult coho salmon in this region that were expected to be migrating to their natal rivers to spawn (age 2–3), our only restriction was to tag coho salmon over 30 cm (COSEWIC, 2016). In many southern BC fisheries management zones where an aggregate of populations is expected to be intercepted, there is a mark-selective fishery in place for coho salmon, where only marked (clipped adipose fin indicating hatchery origin) fish can be retained. In 2020, we only tagged coho salmon that were unmarked (presumed wild) to increase the chances of release if a tagged coho salmon was recaptured in the recreational fishery; however, both unmarked and marked coho salmon were tagged in 2021 because the number of reported recaptures of our tagged coho salmon in 2020 was low (n = 7; 3.5% of 2020 release). In both years, we did not select for coho salmon based on any body condition metrics (e.g., injuries).

An angling interaction commenced when a coho salmon struck the

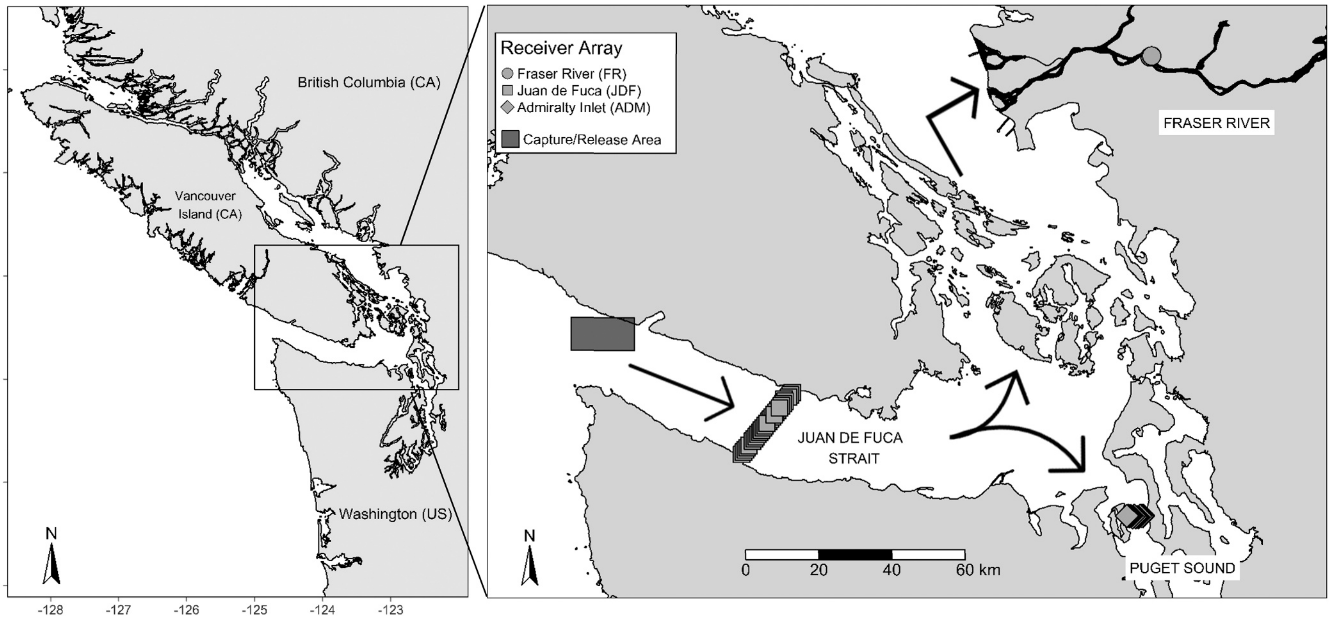

Fig. 1. In 2020 and 2021, adult coho salmon were captured via angling and released with acoustic tags in the Juan de Fuca Strait (JDF) on the west coast of Vancouver Island. Acoustic receivers in JDF, Admiralty Inlet at the entrance of Puget Sound (ADM), and the lower Fraser River (FR) were used to estimate post-release mortality of tagged coho salmon along their return migrations in Canada and the United States. Receivers are maintained by the Ocean Tracking Network (JDF receivers), National Oceanic and Atmospheric Administration (ADM receivers), and Kintama Research (FR receivers). Arrows indicate the expected direction of migration for coho salmon detected on these receivers. Detection radius of acoustic receivers is not reflected by symbols on the map.

lure and concluded when the fish was netted (median angling event duration = 1 min), using the same tactics employed by local anglers and under the instruction of the angling guide. The coho salmon was either landed with a landing net or brought directly on board with no net involved (i.e., pulling the fish on board via the fishing line while still hooked). To investigate the impact of air exposure on post-release mortality, a subset of fish was subjected to an experimental air exposure treatment upon landing (Table 1). In 2020, we imposed an air exposure treatment ranging from 0–180 seconds to mimic the capture and landing experience of an average fisher, informed by survey data collected through the FishingBC smartphone application, where angling event information is provided by public anglers participating in the fishery (Johnston, unpublished data). Air exposure range was extended in 2021 to 0–300 seconds, to further investigate thresholds of air exposure on post-release mortality. Control fish were placed directly into the sampling cooler, while air-exposed coho salmon were placed

Table 1
Results for the 1) generalized linear model (binomial with logit link) with post-release mortality as the response variable, and 2) generalized linear model (gamma distribution with log link) with travel rate (km/day) as the response variable. Predictors in bold indicate significant associations with the response variable. Predictor variables included air exposure (0–300 s), bleeding (0–2), eye injury (absent or present), fork length (cm), scale loss (0–3), year (2020 or 2021), number of fins damaged (0–7), sex (female or male), and hook location (corner, top jaw, bottom jaw, or foul).

Response	Predictor	Odds Ratio	z-value	p-value	95% CI min	95% CI max
POST-RELEASE MORTALITY (DETECTED/NOT DETECTED)	Intercept	6.0717	1.4484	0.1475	0.5289	69.7048
	Air Exposure	0.9968	1.4357	0.1511	0.9925	1.0012
	Bleeding	**2.3775**	**3.3700**	**0.0008**	**1.4367**	**3.9342**
	Eye Injury (Present)	**2.7709**	**2.8463**	**0.0044**	**1.3735**	**5.5899**
	Fork Length	**0.9424**	**2.4957**	**0.0126**	**0.8994**	**0.9873**
	Scale Loss	**1.9374**	**3.6257**	**0.0003**	**1.3550**	**2.7699**
	Sex (Male)	0.9232	0.3830	0.7018	0.6134	1.3896
	Year (2021)	0.8916	0.4420	0.6585	0.5360	1.4831
	Hook Location (Top Jaw)	1.1384	0.4381	0.6613	0.6375	2.0328
	Hook Location (Bottom Jaw)	0.9130	0.3206	0.7485	0.5234	1.5926
	Hook Location (Foul)	1.5326	0.6859	0.4928	0.4525	5.1908
	# of Fins Damaged	0.9899	0.2263	0.8210	0.9069	1.0806

Response	Predictor	Coefficient	z-value	p-value	95% CI min	95% CI max
POST-RELEASE TRAVEL RATE (KM/DAY)	Intercept	2.0469	4.7510	0.0000	1.2025	2.8913
	Air Exposure	0.0000	0.1270	0.8990	-0.0005	0.0005
	Bleeding	-0.0345	0.4715	0.6373	-0.1779	0.1089
	Eye Injury (Present)	-0.0304	0.4086	0.6828	-0.1759	0.1152
	Fork Length	**0.0191**	**2.5443**	**0.0109**	**0.0044**	**0.0339**
	Scale Loss	**-0.2308**	**3.9053**	**0.0001**	**-0.3467**	**-0.1150**
	Sex (Male)	0.0100	0.2057	0.8370	-0.0851	0.1051
	Year (2021)	-0.1537	1.2385	0.2155	-0.3970	0.0896
	Hook Location (Top Jaw)	-0.0052	0.1481	0.8823	-0.0743	0.0639
	Hook Location (Bottom Jaw)	0.0025	0.1007	0.9198	-0.0469	0.0519
	Hook Location (Foul)	0.0035	0.0790	0.9370	-0.0829	0.0899
	# of Fins Damaged	-0.0048	0.3385	0.7350	-0.0326	0.0230

unrestrained on the boat deck and air-exposed up to 180 seconds in 2020 and up to 300 seconds in 2021 (Table S1). Once the air exposure treatment was complete, the fish was placed in a cooler (79 cm × 34 cm × 37 cm) filled with fresh seawater for the duration of processing and tagging. Reflex impairment (Raby et al., 2012), fork length (FL; nearest half cm; Fig S1), hook location, and the presence and severity of injuries (fin damage, scale loss, bleeding, eye damage) were assessed (Table S2). Injuries were assessed visually and grouped using the following guidelines: scale loss (0 = < 5%, 1 = 5–10%, 2 = 10–35%, 3 = > 35%), bleeding (0 = none or small ooze from hook wound, 1 = notable/light bleed, 2 = significant/heavy bleed), eye damage (0 = absence, 1 = presence), and number of fins damaged (damaged in any way [0–7]). Hook location was identified as corner mouth, top jaw, bottom jaw, or foul (anywhere other than jaw or mouth). Details on how reflex impairment and hook location were evaluated are available in Supplementary Material. When necessary, coho salmon were held still throughout the tagging and sampling process by loosely holding the caudal peduncle with one hand and placing the other hand in front of the fish's eyes. Other data such as pre-existing wounds, sea lice presence, lure type (e.g., hoochies, spoons, plugs, bait, with or without flashers), net usage, hook size and type (3/0–6/0; siwash and octopus), handling time, and predator presence were recorded (Table S3), but are not included in subsequent analyses because of low variability and to avoid overfitting our models.

A tissue sample was taken from the adipose or caudal fin and affixed to a Whatman sheet for Genetic Stock Identification (GSI), Parentage-based tagging (PBT), and sex identification (Beacham et al., 2017, 2020). Coho salmon were assigned to conservation units in Canada and reporting groups in the United States if probability of assignment was 80% or greater (Beacham et al., 2020). To include as many coho salmon as possible in our analyses, we optimized the 80% cutoff by aggregating fish to a region if we were not able to assign them to a single conservation unit or reporting group. For example, if a fish had a 60% and 20% probability of originating from Boundary Bay and East Coast Vancouver Island conservation units, respectively, we could still assume they will pass the JDF receiver array. A small amount (2–3 mm) of gill tissue was sampled from the tips of 2–3 gill filaments in 2020 for additional genomic analyses which are not included in this paper. This type of biopsy approach has been used extensively by our group over the past 20 years with no evidence that it affects behaviour or survival of adult salmon (Cooke et al., 2005).

Acoustic tags (Model V13 and V7; Innovasea, Bedford, Nova Scotia, Canada) were attached externally to coho salmon behind the dorsal fin using a "backpack"-style method whereby a thin plastic cord was inserted with a needle through the skin and musculature, with the tag attached via an end-cap and the cord secured in a small loop using a crimping tool (Raby et al., 2015b; Fig. 2). This tag attachment approach was used instead of gastric because these fish are still feeding, or surgical because of the extra time needed for anesthesia and recovery prior to release. External tag attachments like ours are commonly used and have generally been shown to have little influence on adult salmon survival (Dick et al., 2018; Naughton et al., 2018; Runde et al., 2022). In a companion study conducted over three years on adult Chinook salmon (*Oncorhynchus tshawytscha*), we have found that angled and released fish which were in excellent physical condition upon release (e.g., no/minor injuries) and were not air-exposed, had 97% survival (n= 64) for at least two weeks during passage through another set of acoustic arrays (Johnston and Hinch, unpublished data), suggesting that this tagging technique has minimal, if any, impact on survival. Despite the likely minimal impact of our tagging process, we are unable to classify mortality unrelated to the capture event (e.g., natural mortality, tagging effects, tag loss, unreported harvest mortality) and we have further elaborated on this in Section 4.2 of the discussion.

Fig. 2. External "backpack" attachment of acoustic transmitters on coho salmon.

Each tag transmitted a unique code, randomly every 80–160 sec, with battery life estimated at 50–632 days, except for two tags that had a shorter estimated battery life; however, both of these tagged fish were detected on all expected receivers (as determined by GSI) so they were included in all analyses. Based on previous studies conducted in Area 20 at a similar time of year (Raby et al., 2015b; Cook et al., 2018a), tag life was adequate to cover the expected period of detection (for coho salmon with known GSI). After sampling and tagging, coho salmon were released as quickly as possible regardless of their condition. The entire measurement and tagging process took 2–8 min (median = 4 min; rounded to the nearest minute).

2.2. Receiver arrays and migration pathways

Upon release, coho salmon were tracked using an existing network of acoustic receivers located at multiple locations frequented by returning migrating coho salmon in this area. In this study, we focus on three main receiver lines crossing Juan de Fuca (JDF) Strait, Admiralty Inlet at the entrance of Puget Sound (ADM), and the lower Fraser River (FR) near Maple Ridge, BC (Fig. 1). These receiver lines were chosen because a large proportion of coho salmon were expected to migrate past these locations (Table S4); depending on the population, the fish were expected to pass the JDF receivers first, then either FR or ADM (Fig. 1).

The JDF line consisted of 28 and 29 receivers, in 2020 and 2021, respectively (48.2247°N, 124.1140°W to 48.3764°N, 123.9260°W); the ADM line consisted of 13 and 9 receivers, in 2020 and 2021 respectively (48.0733°N, 122.6814°W to 48.0731°N, 122.6220°W); the FR line consisted of 2 sets of paired receivers in both 2020 and 2021 (49.2016°N, 122.5958°W to 49.2036°N, 122.5901°W). Detection data from additional receivers throughout the Salish Sea were available to evaluate migration pathways, detection efficiency of main receiver lines, and potential multi-year detections (Fig S2); however, these additional receivers were not used to estimate mortality due to low detection efficiency and/or because few fish were expected to pass these receivers based on GSI/PBT.

We used this extensive network of acoustic receivers throughout the Salish Sea to estimate detection efficiency at the JDF, FR, and ADM receiver lines (Fig S2). To determine detection efficiency of the JDF receiver line, we used all receivers east of the JDF receivers, towards the FR and Puget Sound. Detection efficiency of both the ADM and FR receiver lines were determined by checking detection on a second set of receivers further into Puget Sound and the FR, respectively. Receiver lines between the northeast coast of Vancouver Island and mainland BC were used to confirm that no coho salmon bypassed the JDF receiver array by migrating northward around Vancouver Island (Fig S2).

2.3. Data Analyses

A summary of all sample sizes used throughout the study and described in the sections below, is available in Table S5.

2.3.1. Post-release mortality estimates

We analyzed the influence of capture and handling on post-release mortality of tagged adult coho salmon returning to the Salish Sea (JDF, ADM, and FR receiver arrays). We used GSI and PBT results to determine the expected migration paths and detection points for each coho salmon and used absence of detection on expected receiver arrays as a proxy for mortality because detection efficiency was relatively high (60–100%) for all receiver arrays. Post-release mortality estimates were calculated by dividing the number of coho salmon detected on a given receiver array by the number of coho salmon expected to swim past an array. Coho salmon that were released alive with acoustic tags, fish that were confirmed mortalities prior to or upon release, and fish that were dead upon capture (prior to bringing on board) were all included in our post-release mortality estimates. We calculated binomial confidence intervals (CI; 95%) for post-release mortality estimates using the Clopper-Pearson exact method (Clopper and Pearson, 1934).

2.3.2. Population differences in post-release mortality and travel rate

Using GSI and PBT, 239 coho salmon were identified to a minimum of 41 individual spawning streams representing 12 conservation units in Canada and 7 reporting groups in the United States (Table S4). Coho salmon not expected to pass the JDF receiver array ($n = 20$) were removed from the analyses (i.e., coho salmon from the Columbia River, Oregon, Juan de Fuca-Pachena, or west coast of Vancouver Island units). There were 84 coho salmon that could not be identified to a population group (i.e., conservation or reporting group), and those that could not be aggregated to a region ($n = 22$) were removed from analysis. We chose to analyse the influence of population groups on post-release mortality and travel rate in separate analyses to increase the sample size within larger post-release mortality and travel rate models. Two outliers were also removed from analysis due to anomalously high travel rates. One tag was presumed a false detection because of a single detection on the JDF array soon after release (0.56 days to travel 47.9 km); having a single detection is unlikely for a coho salmon given the receiver detection radius and reasonable swimming speed. The second tag was suspected to be a predator swallowing a tag based on swimming speed to the JDF receivers (88.3 km/day). We used a binomial generalized linear model (GLM) (logit link) to assess the relationship between population and mortality to the JDF receiver array ($n = 215$), and a KW test to assess the relationship between population and travel rate (km/day) to the JDF receiver array ($n = 149$ survivors).

2.3.3. Predictors of post-release mortality

We used a binomial GLM (logit link) to assess the relationship of various injury and biological factors, and mortality to the JDF receiver array ($n = 271$). The initial 10 independent variables of interest included year, sex, eye injury, scale loss, hook location, bleeding, air exposure, number of fins damaged, fork length, and reflex impairment. We used Spearman's rank correlation and the vif function in the car package (verson 3.1–2; Fox and Weisberg, 2019) to test explanatory variables for multicollinearity and used a generalized variance-inflation factor (GVIF) of 3 as our threshold (Zuur et al., 2010). Air exposure and reflex impairment were highly correlated (Spearman's rank correlation, $r_s = 0.75$; Fig S3) and no independent variables had GVIF values that exceeded 3. Since air exposure was our experimental treatment, reflex impairment was removed from the model leaving nine independent variables. There did not appear to be any difference in mortality across tagging dates, so tagging date was not included in the model. To determine the most parsimonious model, we used model selection via Akaike's information criterion corrected for small sample sizes and overdispersion ($QAIC_c$). We used the "dredge" function in the "MuMIn" package to evaluate all possible variable combinations and ranked candidate models based on $QAIC_c$ weight. To account for model uncertainty, all models comprising 95% of model weights were extracted and variable coefficients were averaged from this subset of best models. We used 95% CI and full average estimates, where a value of zero was applied for a variable when it was not included in one of the candidate models (Burnham and Anderson, 2002; Grueber et al., 2011). An association between the response variable and an explanatory variable was determined when the 95% CI of an explanatory variable did not overlap zero.

2.3.4. Predictors of post-release travel rate

We used a GLM (gamma distribution with log link) to assess the relationship of the same 9 injury and biological factors listed above, and travel rate (km/day) to the JDF receiver array ($n = 186$ survivors). Travel rate was calculated with the time and distance between release and first detection on the JDF array. The same variable selection and model averaging approach was used as in the post-release mortality model above; however, no overdispersion factor was required for the AICc estimates. We did not include tagging date in the model for three reasons: 1) we were more interested in interannual differences in travel rate rather than tagging date, 2) tagging dates differed between years, so year and tagging date would be highly colinear, and 3) there did not appear to be any difference in travel rate across tagging dates when visually assessed.

All statistical analyses were conducted in R version 4.2.2 (R Development Core Team, 2022). Statistical significance was set at $\alpha = 0.05$ and statistical tests were chosen after evaluating model assumptions using diagnostic plots of residuals. Median values are presented in data summaries when data distribution is skewed.

3. Results

We captured 559 coho salmon during the study and processed 403 of them for tagging (200 in 2020 and 203 in 2021). We did not process coho salmon that were undersized (< 30 cm), hatchery (in 2020, when we were prioritizing tagging wild-origin fish), or when the tagging boat was unable to take the fish for tagging. We did not select for coho salmon based on any body condition metrics (e.g., injuries). One coho salmon was dead on arrival, four coho salmon were confirmed mortalities upon release (processed for tagging but no acoustic tag attached), 319 were released alive with acoustic tags, and an additional 80 coho salmon were measured, sampled, and tagged with a spaghetti tag (i.e., no acoustic tag) in 2020 to increase the chances of tag recapture, and gather extra information on injury rates and GSI. We had nine fish with acoustic tags recaptured in total (three in 2020 and six in 2021), and four fish with spaghetti tags recaptured in 2020. All recaptured coho salmon were caught past their final expected receivers except two fish headed to the FR which were included in our long-term mortality estimate.

3.1. Fish origin

Hatchery origin was determined by both visual (adipose fin clipped) and genetic marking (PBT) and was found to be 31.5% ($n = 403$) across the two years of study (Table S4). Of the coho salmon expected to pass the JDF receiver line, there were no significant differences in FL between hatchery and wild coho salmon (KW, $H_1 = 0.002$, $p = 0.964$), nor population groups (KW, $H_{14} = 15.691$, $p = 0.333$). The majority of coho salmon originated from Puget Sound (42.4%) and the Fraser River (20.8%). Smaller numbers of coho salmon originated from the East Coast of Vancouver Island and the Strait of Georgia (7.2%), Howe Sound and Burrard Inlet (5.5%), West Coast Vancouver Island (3.5%), Boundary Bay (2.5%), Columbia River (1.5%), Elwha River (0.5%), Oregon (0.3%), or were of unknown origin (15.9%) (Table S4).

3.2. Injuries and air exposure

Of the 403 coho salmon processed for tagging, 22 coho salmon (5.5%) had zero observable injuries (i.e., no fin damage, scale loss, bleeding, nor eye injury) and 156 coho salmon (38.7%) had at least one severe injury (i.e., highest category of scale loss, bleeding, and/or presence of eye injury). Of the 271 coho salmon used in the post-release mortality binomial GLM, there were no significant differences in FL among air exposure (KW, $H_8 = 7.019$, $p = 0.535$), scale loss (KW, $H_3 = 2.582$, $p = 0.461$), bleeding (KW, $H_2 = 2.821$, $p = 0.244$), nor eye injury groups (KW, $H_1 = 1.601$, $p = 0.206$). There were significant differences in FL among groups of coho with different numbers of fins damaged, and Tukey's HSD test generally indicated that fish with more than one fin damaged were larger than fish with one or no fins damaged (Fig S4).

3.3. Detection efficiency

Detection efficiency was estimated to be 100% for both the JDF (95% CI: 96.7 – 100%) and FR (95% CI: 71.5 – 100%) receivers, because all coho salmon detected at further receivers were previously detected on the JDF (n = 111) and FR (n = 11) receiver lines. Detection efficiency of the ADM line was 100% (95% CI: 54.1 – 100%; n = 6) in 2020; however, due to unexpected changes to receiver locations or possibly differences in migration paths, 6 out of 15 coho salmon that were detected on subsequent receivers in Puget Sound in 2021 were not detected on the ADM line. Therefore, we estimated detection efficiency for the ADM line in 2021 to be 60.0% (95% CI: 32.3 – 83.7%), which was used as a correction factor for the 2021 mortality estimate.

3.4. Post-release mortality and travel rate to JDF, FR, and ADM receivers

Immediate mortality (upon capture or prior to release) was 1.5% ($n_{total} = 324$, $n_{mortality} = 5$). All subsequent post-release mortality estimates also include immediate mortalities. Post-release mortality to the JDF line was 31.5% (95% CI: 26.1 – 37.4%; $n_{tagged} = 279$, $n_{mortality} = 88$), for coho salmon expected to pass the JDF receivers. Survivors were first detected on the JDF line after a median 3.3 days (min = 1.1, max = 22.6 days), swimming at a median rate of 15.6 km/day (min = 2.5 km/day, max = 49.2 km/day) to the JDF line which was a median of 50.1 km away (min = 42.1, max = 60.5 km) from release. Mortality to the JDF receivers was 29.9% (95% CI: 23.4–35.9%; n = 218) and 38.1% (95% CI: 26.1–51.2%; n = 63), for wild and hatchery fish, respectively. Post-release mortality to the FR was 77.4% (95% CI: 63.8 – 87.7%; $n_{tagged} = 53$, $n_{mortality} = 41$), and survivors took a median 13.4 days (min = 9.5, max = 47.9 days) to reach the first point of detection in the lower FR. In 2020, post-release mortality to the ADM line was 56.0% (95% CI: 34.9 – 75.6%; $n_{tagged} = 25$, $n_{mortality} = 14$), while in 2021 post-release mortality was 55.1% (95% CI: 43.4 – 66.4%; $n_{tagged} = 78$, $n_{mortality} = 43$ [corrected for 60% detection efficiency]). Because detection efficiency was different between 2020 and 2021 at ADM, we report the mortality estimates separately. Over both years fish detected on the ADM receivers took a median 9.0 days (min = 4.0, max = 82.2 days) to reach the ADM receiver line.

3.5. Factors influencing post-release mortality to the JDF line

We averaged candidate models that comprised 95% of all model weights, which included combinations of all 9 independent variables (i.e., year, sex, eye injury, scale loss, hook location, bleeding, air exposure, number of fins damaged, fork length). The 95% CI of the full model averaged estimates for bleeding, eye injury, scale loss, and fork length did not cross zero, indicating a significant association with post-release mortality (Fig. 3, Table 1). Model-averaged parameter estimates suggested that increased severity of bleeding and scale loss, presence of eye injuries, and smaller fork length were associated with increased odds of post-release mortality to the JDF line (Table 1). Coho salmon with an eye injury have 2.77 times (95% CI = 1.37 – 5.59, p = 0.0044) greater odds of post-release mortality than coho salmon without an eye injury. Every decrease of 1 cm FL is associated with 1.06 times (95% CI = 1.11 – 1.01, p = 0.0126) increase in the odds of post-release mortality. Going up from 1 level of scale loss to the next (i.e. 0–5% → 5–10% → 10–35% → >35%) is associated with 1.94 times (95% CI = 1.36 – 2.77, p = 0.0003) greater odds of post-release mortality. Going up from 1 level of bleeding to the next (i.e. none → minor → major) is associated with 2.38 times (95% CI = 1.44 – 3.93, p = 0.0008) greater odds of post-release mortality (Table 1).

We analyzed differences in post-release mortality among 12 population groupings with a minimum of 2 individuals: Boundary Bay, East Coast Vancouver Island and Georgia Strait, Hood Canal, Howe Sound and Burrard Inlet, Lillooet, Interior Fraser River, Lower Fraser River, North Thompson River, Lower Thompson River, North Puget Sound, Mid-Puget Sound, and South Puget Sound. There was no significant difference in post-release mortality to the JDF line among these 12 population groupings (p = 0.65; Fig S5).

3.6. Factors influencing travel rate to the JDF line

We averaged models that comprised 95% of all model weights, which included combinations of all 9 independent variables (i.e., year, sex, eye injury, scale loss, hook location, bleeding, air exposure, number of fins

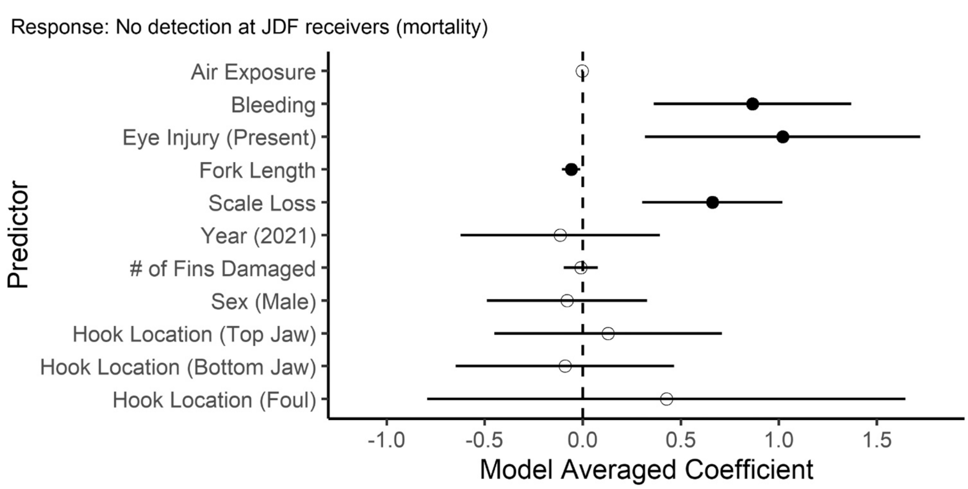

Fig. 3. Full model-averaged coefficients (log odds; untransformed) from a generalized linear model (binomial with logit link) of coho salmon post-release mortality (detected/not detected). Coho salmon were tagged in the Canadian waters of the Juan de Fuca Strait and tracked to the first point of detection (Juan de Fuca receiver array; Fig. 1) in 2020 and 2021. Predictor variables included air exposure (0–300 s), bleeding (0−2), eye injury (absent or present), fork length (cm), scale loss (0−3), year (2020 or 2021), number of fins damaged (0−7), sex (female or male), and hook location (corner, top jaw, bottom jaw, or foul). Filled circles indicate variables that are significantly different from zero and horizontal lines indicate the 95% confidence interval for each variable.

damaged, fork length). The 95% CI of the full model averaged estimates for scale loss and fork length did not cross zero, indicating a significant association with travel rate (Fig. 4, Table 1). Model-averaged parameter estimates suggested that increased severity of scale loss and smaller fork length are associated with a slower travel rate to the JDF line. We analysed differences in travel rate among the same 12 population groupings used in post-release mortality analyses listed above. There was no significant difference in travel rate to the JDF line among these 12 population groupings (KW, $H_{11} = 3.401$, $p = 0.98$; Fig S5).

4. Discussion

This study is the first to quantify post-release mortality of adult coho salmon in their natural environment after a marine recreational fisheries event. Our study used acoustic telemetry to investigate anthropogenic and biological factors that may be associated with post-release mortality of angled coho salmon. We found post-release mortality to the first point of detection was 31.5% (95% CI: 26.1% – 37.4%). Our mortality estimate is greater than the 10% post-release mortality derived from short-term holding studies, and currently used in the management of marine recreational coho salmon fisheries in southern BC where this study was conducted (DFO, 2023). Most current post-release mortality estimates used in fisheries management of Pacific salmon are based only on short-duration (~24 hour) holding studies (Cox-Rogers et al., 1999), whereas our post-release mortality estimate is based on survival in their natural environment after a median 3.3 days and ~50 km from the release point. Therefore, our study provides a more realistic *in-situ* estimate of adult coho salmon mortality in the marine environment, post-release from a recreational fisheries event. Tracking coho salmon in their natural environment eliminates confounding factors related to confinement but given the longer duration and absence of an untagged control, our estimates may also encompass mortality unrelated to the capture event (e.g., natural mortality, tagging effects, unreported harvest mortality; further elaborated on in Section 4.2 of the discussion). Natural mortality is difficult to calculate due to the nature of tagging studies and remains unknown for return-migrating salmon during the marine phase (Patterson et al., 2017). We assert that a considerable portion of the release mortality in our study can be associated with the C&R event given the fisheries-related injuries associated with increased odds of mortality to the first point of detection in our study (i.e. JDF receivers), which was reached by tagged fish in a median of 3.3 days.

Our mortality estimate is similar to Cook et al. (2018a) who found coho salmon released as bycatch in a commercial purse seine fishery had 36.1% (95% CI: 29.9–42.9%) post-release mortality after a median of 4.6 days to the same first point of detection (i.e., JDF receiver line). Our longer term mortality estimates to the FR (77.4%) and ADM (56.0% and 55.1%) were also consistent with previous studies (Raby et al., 2015b; Cook et al., 2018a). The types of potential stressors and injuries (e.g., hypoxia, scale loss) for fish caught via purse seine are similar to an angling event (Cook et al., 2018a, 2019), but our comparable post-release mortality estimates were surprising given the longer handling time associated with purse seine fishing and suggests that the ability for coho salmon to cope with even minimal handling may be low.

4.1. Predictors of post-release mortality and travel rate

We found that scale loss, bleeding, and eye injuries were associated with increased odds of post-release mortality between release and the first point of detection about 50 km away. Mortality has been linked to scale loss for numerous fish species (Marçalo et al., 2008; Butcher et al., 2010; Olsen et al., 2012) including coho salmon (Cook et al., 2018a). Scales, skin, and mucus act as physical barriers to the outside environment and are the primary defense against injuries and pathogens (Wainwright and Lauder, 2017; Reverter et al., 2018). Scale loss can initiate physiological disturbances, which can cascade further, cause changes in behaviour and fitness, and potentially lead to delayed mortality (Olsen et al., 2012; Cook et al., 2019). Pacific salmon are more vulnerable to scale loss and injuries during their ocean phase before they begin scale resorption to prepare for upriver migrations (Baker et al., 2013). Scale loss and dermal injuries can make salmon more vulnerable to infection and disease, particularly as they begin their freshwater migration (Svendsen and Bogwald, 1997), and may cause decreased ability to osmoregulate (Zydlewski et al., 2010; Olsen et al., 2012), all of which can lead to pre-spawn mortality and decreased spawning success (Baker and Schindler, 2009).

Bleeding from a fisheries injury has been recognized as a major contributing factor to post-release mortality of fish for decades (Warner, 1978; Diewert et al., 2002; Lyle et al., 2007), including Chinook (Bendock and Alexandersdottir, 1993) and coho salmon (Vincent-Lang et al., 1993) caught in recreational fisheries. Salmon are sometimes able to recover from blood loss (Cowen et al., 2007), however, bleeding can cause increased physiological strain and vulnerability to nearby predators. Similarly, increased mortality related to eye hooking injuries has been observed for Pacific salmon and other fish species (Wertheimer,

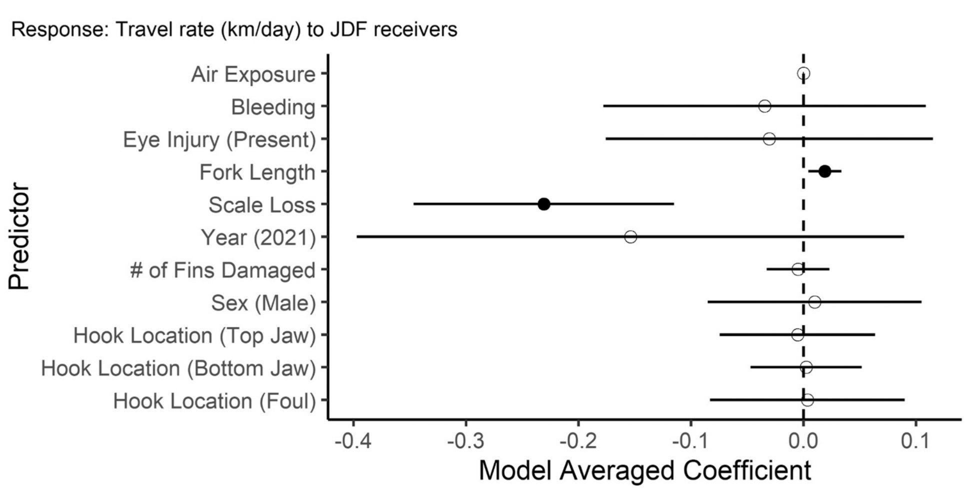

Fig. 4. Full model averaged coefficients (untransformed) from a generalized linear model (gamma distribution with log link) of coho salmon post-release travel rate (km/day). Coho salmon were tagged in the Canadian waters of the Juan de Fuca Strait and tracked to the first point of detection (Juan de Fuca receiver array; Fig. 1) in 2020 and 2021. Predictor variables included air exposure (0–300 s), bleeding (0−2), eye injury (absent or present), fork length (cm), scale loss (0−3), year (2020 or 2021), number of fins damaged (0−7), sex (female or male), and hook location (corner, top jaw, bottom jaw, or foul). Filled circles indicate variables that are significantly different from zero and horizontal lines indicate the 95% confidence interval for each variable.

1988; Muoneke and Childress, 1994). Eye injuries can result in blindness which may impact a fish's ability to evade a predator, forage for food, and navigate. However, Lindsay et al. (2004) and Fritts et al. (2023) did not identify the eye as a critical hooking location for Chinook salmon released from recreational C&R events in freshwater which could indicate an influence of migration stage and environmental context. More likely, our results differ because we are investigating detectable eye injury rather than eye hooking location; not all of the eye injuries we noted in our study were the result of a direct eye hooking location, but an incidental injury from a different hooking location (e.g., corner hooking location that grazed or punctured the eye).

The only non-injury related factor associated with post-release mortality in our study was fork length (FL), where FL was negatively associated with likelihood of mortality. Smaller fish have been found more likely to die after a fisheries encounter in many previous studies (Wertheimer, 1988; Suuronen et al., 1996; Pálsson et al., 2003; Olsen et al., 2012; Bass et al., 2018). Fish size has not been identified as a driving factor of marine post-release mortality in past studies on coho salmon (Raby et al., 2015b; Cook et al., 2018a) but has been linked with increased severity of injury when coming into contact with fishing gear, particularly nets (Raby et al., 2015b; Veldhuizen et al., 2018; Cook et al., 2019). The only injury type where we observed differences in fish size was the number of fins damaged, where larger fish generally had more fins damaged. It is interesting that the only injury associated with size was net-related, and not hook-related (i.e., eye injuries, bleeding). We used hook sizes that are often used by recreational fishers in this fishery, however, the range of hook sizes used may not have been variable enough to observe an effect. Given that severity of injuries was not greater in small coho salmon in this study, the mechanism of mortality could be related to a lower anaerobic capacity and/or ability to recover from capture stress in general (Kieffer, 2000; Davis, 2002). After release, smaller coho salmon may also be at greater risk of predation as they recover compared to larger coho salmon (Scharf et al., 2000). Although all our tagged coho salmon were of legal size for harvest in our study area ($>$ 30 cm), smaller coho salmon are often released as bycatch with the intention of harvesting a larger fish, or at times of year when coho salmon retention is closed. Higher post-release mortality for smaller coho salmon could have implications for population and fisheries productivity.

Surprisingly, we did not detect any relationship between duration of air exposure (0–300 s) and post-release mortality nor travel rate. When grouped, air-exposed fish (30–300 s) did have higher mortality (34.6% [95% CI: 27.8 – 41.8%; n = 191]) than non-air-exposed fish (23.9% [95% CI: 15.4 – 34.1%; n = 88]) between release and the JDF receiver line; however, the direction of the relationship within the levels of air exposure was not clear. Air exposure throughout a C&R event may occur during hook removal, length measurement for regulation purposes, or while taking a photo. Air exposure can be detrimental to fish survival because it quickly causes gill lamellae to collapse and inhibit gas exchange which may cause mortality (Butcher et al., 2010; Graves et al., 2016; Joubert et al., 2020) or have sublethal consequences such as decreased swimming ability and impaired reflexes (Ferguson and Tufts, 1992; Cook et al., 2018b; Twardek et al., 2018). Although air exposure was not a driving factor for post-release mortality in our study, we found that air exposure and reflex impairment were positively correlated. However, our results suggest coho salmon may be able to overcome the physiological stress from air exposure (Arlinghaus et al., 2009), in contrast to physical injuries such as scale loss and eye injuries which could take longer to recover from. Our tagged coho salmon may have been able to recover from air exposure because of the relatively cooler water temperatures (median = 11.80°C [range = 11.1°C – 14.5°C] in 2020 and median = 13.16C [range = 12.7C – 13.7C] in 2021) in the marine environment compared to warmer temperatures often experienced during freshwater fisheries events (Martins et al., 2011; Robinson et al., 2013). Aerobic scope is generally higher at colder water temperatures (Eliason et al., 2011; but see Raby et al., 2016) allowing exhausted fish to recover faster, whereas the same fish may experience latent effects and/or delayed mortality after performing exhaustive exercise in warmer water temperatures, such as in freshwater during the summer (Burnett et al., 2014).

Travel rate to the JDF receivers was negatively related to scale loss (i.e., coho salmon with greater scale loss swam slower than coho with less scale loss), potentially suggesting a greater need to recover or orient themselves post-release. Changes in normal behaviour have been suggested for fish exposed to stressors (Mäkinen et al., 2000) and experiencing capture injuries such as scale loss; however, the response can vary. For example, Olsen et al. (2012) found that herring with scale loss swam faster and had altered schooling behaviour in a laboratory environment than herring without scale loss, perhaps due to damage of the lateral line. Conversely, both Nguyen et al. (2014) and Bass et al. (2018) found that sockeye salmon with greater injuries had slower migration rates than salmon with fewer injuries during upriver migration. Our results are consistent with Cook et al. (2018a) who found coho salmon with scale loss released from a purse seine fishery, at a similar time and location, delayed migration. The negative relationship between FL and travel rate in our study may reflect a lower swimming efficiency of smaller coho salmon (Weihs, 1973; Geist et al., 2000), or the need for a longer recovery period before resuming migration. However, when travel rate was scaled for FL (i.e., body length per second), we found no relationship with FL. A limitation in our travel rate estimates is that the exact swimming path is unknown, constraining our ability to infer the behaviour associated with the migratory delay. For a portion of our tagged coho, we have evidence of indirect migration from receivers deployed on Swiftsure Bank, an area west of our tagging area at the mouth of the JDF strait. We found that of the coho we expected to pass the JDF array, 66 coho salmon were detected on the Swiftsure Bank receivers. Of these coho salmon, 26 were subsequently detected on JDF receivers, 32 were never detected on the JDF receivers, and eight were first detected on the JDF receivers and then detected on the Swiftsure Bank receivers afterwards. Therefore, our estimates of travel rate should be considered conservative.

4.2. *Limitations to post-release mortality estimates*

There is no established and accepted length of time in the literature in which post-release mortality can be distinguished from other sources of mortality (i.e., other types of fisheries-related or natural mortality), and as such, our estimates could be conservative or inflated. Our mortality estimates do not encapsulate the entire return migration and may lead to an underestimation of mortality since they only reflect mortality during a relatively short period of marine migration and, for some populations, do not account for additional mortality that can occur during estuarine or river migration to spawning grounds. Conversely, our post-release mortality estimates may be inflated because we cannot definitively confirm the cause of mortality and may also include some natural mortality and other non-capture related mortality, especially over longer time periods and distances (i.e., to FR and ADM receivers). Nevertheless, our study improves upon previous holding studies which likely underestimate true FRIM given our study was conducted over a longer period and our tagged fish were released into their natural environment. A considerable portion of the release mortality in our study can be associated with the C&R event given the fisheries-related injuries associated with increased odds of mortality to the first point of detection in our study (i.e. JDF receivers), which was reached by tagged fish in a median of 3.3 days.

Other than mortality, lack of detection may have also occurred due to tag loss, straying, or continued ocean residence. Although tag loss (including tag malfunctioning) has not been quantified for externally attached tags during marine migration for coho salmon, our study was conducted over a relatively short period of time and high tag retention rates have been observed using this method (Runde et al., 2022). The smaller coho salmon (∼30 cm) we tagged could have potentially spent another year in the ocean (Chittenden et al., 2009); however, coho salmon do return to natal spawning areas as age-2, and if not, we would have likely detected the tagged coho in the following year on the extensive network of receivers as an age-3 if the fish survived. Over both years we only observed five coho salmon detections from unexpected populations (all on the ADM receiver line); however, given we did not track coho salmon to spawning grounds, there was no clear evidence of straying. We also acknowledge that we did not have an untagged control, and our post-release mortality estimates may be elevated because they include potential tagging effects. Quantifying the consequences of the tagging process or tagging burden when tracking fish in their natural environment is impossible, but our methods were selected based on attempts to minimize such impacts, and the external tagging method we used in this study is generally associated with minimal mortality and trauma (Jepsen et al., 2015; Runde et al., 2022).

Detection efficiency was very high (i.e. 100%) for all receiver lines except ADM in 2021. There are three potential entrances to Puget Sound: through ADM Inlet, Deception Pass, or Swinomish Channel. Coho salmon from central and southern populations likely enter Puget Sound through the ADM entrance; however, salmon have been caught near Deception Pass and Swinomish Channel and out-migrating juvenile salmonids from northern Puget Sound populations (e.g., Skagit River) have been known to use all three corridors when exiting Puget Sound (Moore et al., 2015). To our knowledge, there are no studies quantifying the frequency of Deception Pass and Swinomish Channel as a migration corridor for returning migrating adult coho salmon. Therefore, for this study we have assumed all tagged coho salmon use the ADM entrance; however, detection efficiency for the ADM receiver line reported in this study should be used with caution given these uncertainties.

4.3. Management implications and future directions

Catch-and-release angling is an important management tool that can be used to balance recreational fishing opportunities and conservation of wild fish populations, such as the threatened IFR coho salmon. Still, quantifying context-specific mortality is vital to developing biologically meaningful management measures, informing best angling practices, and maintaining sustainable fish populations. In most southern BC recreational fisheries, there is a mark-selective fishery in place for coho salmon, where only marked hatchery-origin coho salmon can be harvested in an effort to conserve wild stocks by releasing them. The success of a mark-selective management method is dependent on low mortality of released fish; high mortality of released wild fish will mean a mark-selective management strategy is less likely to succeed (Lawson and Sampson, 1996). Our results reveal that over one third of coho salmon did not survive post-release from a C&R event to the first point of detection along their migration route in the Salish Sea. We emphasize that our post-release mortality estimates may also be from a combination of sources, particularly over longer durations post-release (i.e., FR and ADM receivers). Nonetheless, our post-release mortality estimate to the first point of detection in our study (i.e. JDF receivers) was only over a median 3.3 day period, and fisheries-related injuries were associated with increased odds of mortality, so we contend that much of the mortality can be attributed to the C&R event.

Our results suggest that modifications to fishing practices that reduce the number and severity of injuries could enhance survival of released fish. The main injuries associated with mortality were scale loss, bleeding, and eye injury. Large amounts of scale loss can be caused by netting, handling, and boating of the fish. Minimizing these events by releasing the fish from the line prior to handling or boating, e.g., with a gaff-release technique, should be considered. Hooking can cause considerable bleeding and injury, and in our study eye injuries were found to be a driving factor in mortality. Using proportionally smaller hooks which do not penetrate from the mouth into the eye is a potential approach to reduce eye injuries. However, further study is needed to ensure that use of smaller hooks does not yield other unanticipated consequences such as ingestion (Brownscombe et al., 2017; Skov et al., 2023). Smaller body size was also found to be a driving factor in post-release mortality and travel rate. Greater odds of mortality and reduced travel rate for smaller coho salmon could have implications given smaller coho salmon are often released voluntarily (e.g., during C&R or "highgrading" [i.e., choosing to release a smaller fish in the hopes of harvesting a larger fish]), or to remain compliant with fishing restrictions of recreational coho salmon fisheries (e.g., minimum size limits, selective fisheries, bycatch). We do not recommend highgrading, and we encourage anglers to cease fishing, shift their fishing location, or change their fishing gear (e.g., to a larger lure size) if they are having frequent encounters with smaller coho salmon. Although air exposure was not identified as a driving factor for mortality in this study, air exposure is inherently harmful to any fish (Cook et al., 2015) and can also increase chances of injury such as scale loss, and we therefore recommend air exposure be kept to a minimum.

The modifications to fishing practices that we have suggested are relatively feasible and cost-effective for anglers to adopt. Most anglers will have access to the necessary gear, and the changes in fishing practices are relatively minor and logistically easy to implement. Previous studies (Nguyen et al., 2012, 2013), personal observations, and an ongoing interview study investigating angler opinions on recreational marine Pacific salmon fisheries (Lunzmann-Cooke, unpublished) indicate that many anglers already implement the recommendations we have suggested, actively seek information on best practices, and are open to adjusting fishing practices to increase survival of released fish. Education should be available to anglers to improve fish handling and promote awareness of fishing best practices. Reporting methods such as smartphone applications (e.g., FishingBC) or creel surveys could be used to monitor fishing best practices.

Although some of the tagged coho salmon were captured as bycatch while targeting Chinook salmon, most were targeted directly via gear type and fishing location. Anglers generally choose fishing gear and locations that align with their target species, reducing the chances of bycatch; however, gear types and habitat do overlap among Pacific salmon species in recreational fisheries. We have no evidence to suggest post-release mortality estimates would differ for coho salmon caught as bycatch in other recreational trolling fisheries, and the relative similarity of gear types, as well as breadth of angler experience and gear selection, would suggest that the potential effects would be limited overall.

It is important to note that post-release mortality is just one component of fisheries-related mortality, and our estimates do not account for other types of fisheries-related mortality such as avoidance, escape, depredation, and drop-out mortality, which are more challenging to estimate but do occur and need to be quantified (Patterson et al., 2017). Sublethal impacts can also occur from any physical injury and physiological stress sustained from the C&R even if direct mortality does not occur. Sublethal impacts can include a decreased ability to cope with other stressors such as temperature, pathogens, and osmotic stress related to freshwater entry, to survive subsequent C&R events, and may have population-level effects through altered growth, reproductive output, or ability to spawn (reviewed in Wilson et al., 2014). Given the detrimental effects of warm water on Pacific salmon (Martins et al., 2011), the effects of rising water temperatures should be considered in future fisheries-related mortality estimates for the marine environment. Finally, future studies could investigate the physiological condition of captured fish to disentangle fisheries-related and some sources of natural mortality of coho salmon released from recreational fisheries during their ocean phase.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper

Data Availability

Data will be made available on request.

Acknowledgements

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.fishres.2024.107062.

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