

Mortality of Atlantic salmon after catch and release angling: assessment of a recreational Atlantic salmon fishery in a changing climate

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Abstract: Human activities have the potential to accelerate population-level decline by contributing to climate warming and decreasing the capacity of species to survive warming temperatures. Here we build a predictive model to test interactions between river warming and catch and release mortality in recreational fisheries for Atlantic salmon (*Salmo salar*) by compiling and analyzing published data. We then test whether warming has occurred in rivers where angling occurs and whether angling opportunities have been restricted through increased river closures due to high water temperatures. We find that catch and release mortalities are low (<0.05) at cool river temperatures (<12 °C). At river temperatures often leading to fishery closures (between 18 and 20 °C), mortalities range from 0.07 to 0.33 (mean = 0.16). River temperatures on the east and southeast coasts of Newfoundland have warmed, leading to an increase in fishery closures in recent years. By contrast, river temperatures in southern Labrador have warmed slightly, with only one documented river closure. Accordingly, increasing temperatures will increase the frequency of river closures and likely result in higher mortality in caught and released Atlantic salmon in rivers that remain open to catch and release angling at warm water temperatures.

Résumé : Les activités humaines ont le potentiel d'accélérer les déclinés de populations en participant au réchauffement climatique et en réduisant la capacité des espèces de survivre à des températures en hausse. Nous élaborons un modèle prédictif pour examiner les interactions entre le réchauffement des rivières et la mortalité associée à la pêche avec remise à l'eau dans la pêche sportive au saumon atlantique (*Salmo salar*), en compilant et en analysant des données publiées. Nous vérifions ensuite si un réchauffement s'est produit dans les rivières où une pêche a lieu et si les occasions de pêche ont été restreintes par l'augmentation du nombre de fermetures de rivière en raison de températures de l'eau élevées. Nous constatons que les taux de mortalité associés à la pêche avec remise à l'eau sont faibles (<0,05) quand la température de la rivière est faible (<12 °C). À des températures de la rivière menant souvent à des fermetures de la pêche (de 18 à 20 °C), les taux de mortalité vont de 0,07 à 0,33 (moyenne = 0,16). Les températures de rivières sur les côtes est et sud-est de Terre-Neuve ont augmenté, entraînant une augmentation du nombre de fermetures de la pêche ces dernières années. En comparaison, les températures de rivières dans le sud du Labrador n'ont augmenté que légèrement, une seule fermeture de rivière étant documentée. Ainsi, la hausse des températures fera augmenter la fréquence des fermetures de rivières et se traduira vraisemblablement par des taux de mortalité accrus des saumons atlantiques remis à l'eau dans les rivières qui demeurent ouvertes à la pêche avec remise à l'eau malgré une hausse des températures de l'eau. [Traduit par la Rédaction]

Introduction

Average global air temperature has increased 0.74 °C since 1906, with 17 of the 18 warmest years on record occurring since 2001 (IPCC 2018) and with projections of further increases reaching 1.8 to 4.0 °C by year 2100 (Hein et al. 2012; Taylor et al. 2018; IPCC 2018). A well-documented consequence of climate change is increased frequency of extreme events, including intense heat waves (Stillman 2019) and drought (Lennox et al. 2019). High lati-

tude environments have changed faster than those in lower latitudes (Prowse et al. 2006), emphasizing the need to evaluate potential consequences of climate change on a regional scale.

Poikilotherms, such as most fishes, cannot regulate their body temperature metabolically; therefore, their physiology is directly influenced by environmental temperature fluctuations (Brett 1971). Consequently, culturally, commercially, and recreationally important species will be influenced by warming. Here we focus on

Received 8 November 2019. Accepted 14 April 2020.

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Atlantic salmon (*Salmo salar*), which is indigenous to eastern North America and western Europe, and is an important species for commercial, recreational, and subsistence fisheries (MacCrimmon and Gots 1979; Bradbury et al. 2015).

Atlantic salmon abundance has declined across much of the North Atlantic despite closures and (or) restrictions of fisheries (Parrish et al. 1998; Chaput 2012; Lehnert et al. 2019). While retention fisheries still occur, which target salmon during their upstream spawning migration, voluntary and mandatory release of caught salmon is increasing (ICES 2019). Among fisheries managers and conservation organizations, catch and release has been accepted as a management tool (Brownscombe et al. 2017) allowing for the recreational fishery and associated social and economic benefits to continue, even when stock abundance is low, based on past evidence of minimal mortality of fish after release (Tufts et al. 1991; Wilkie et al. 1996; Lennox et al. 2017a). Yet given the high numbers of caught and released fish (ICES 2019) and the declining abundance of Atlantic salmon (Lehnert et al. 2019), the use of catch and release as a management tool is sometimes challenged and re-evaluated (Dempson et al. 2002; Bartholomew and Bohnsack 2005; Arlinghaus et al. 2007).

Whereas much of the mortality following catch and release can be attributed to angler practices, gear and bait types, and angler experience, water temperature also influences survival (Cooke and Wilde 2007; Havn et al. 2015; Lennox et al. 2017a). Many Atlantic salmon are caught by anglers during the warmest months (July and August) and consequently are exposed to physiologically stressful and potentially lethal water temperatures (Huntsman 1942; Breau 2013). Mortality rates of Atlantic salmon following catch and release have been reported between 0% and 12% at water temperatures ≤ 18 °C (Dempson et al. 2002; Thorstad et al. 2007). At water temperatures > 18 °C, substantial increases in mortality are likely (Gale et al. 2013; Havn et al. 2015; Lennox et al. 2017a), because the synergistic effects of high water temperature and lower dissolved oxygen, with exhaustive exercise during the capture process, can impede the fish's aerobic and anaerobic recovery (Wilkie et al. 1996, 1997; Arlinghaus et al. 2007; Breau 2013). To ensure effective catch and release management, we should consider predicted warming in river temperatures when making management decisions to ensure conservation. Indeed, to some extent this does occur; fisheries managers (e.g., Fisheries and Oceans Canada, DFO) implement river closures to angling when water temperature exceeds a predetermined threshold; however, the threshold value can be variable and subjective.

Given the predicted increases in the frequency and intensity of high water temperature events, documented declines in Atlantic salmon abundance, and ongoing debate on the use of catch and release angling as an effective management tool (Bartholomew and Bohnsack 2005; Arlinghaus et al. 2007), our focus was on the role of water temperature in the management of recreational Atlantic salmon angling. We first (i) analyzed the probability of mortality at a given water temperature for caught and released Atlantic salmon, based on a compilation of published data across the distribution range of Atlantic salmon. Then, using Newfoundland and Labrador, Canada, as a case study, we (ii) estimated the total number of Atlantic salmon expected to have died following catch and release during the fishing season for select rivers. We did this by combining estimates of the number of caught and released salmon from angler survey data with river temperature data and probable mortality for caught and released fish at the different water temperatures. Finally, we (iii) examined regional and temporal trends (~1978 to 2018) for river temperatures during the angling season and number of days rivers were closed to angling due to high water temperatures and (or) low water levels.

Methods

Predicting the probability of mortality at a given water temperature for caught and released Atlantic salmon

Mortality and water temperature data were compiled following an extensive literature search of all available published peer-reviewed studies investigating the effects of recreational catch and release angling on the survival, physiology, and behavior of Atlantic salmon (Table 1). Although, we are aware of one other published peer-reviewed catch and release study (e.g., Whoriskey et al. 2000), water temperature data were not available and therefore not useable for our purposes. For each study, mortality estimates following catch and release, mean water temperature for the study, fishing gear type, and life history stage were recorded (salmon that had spent one (1SW) or multiple winters at sea (MSW), 1SW–MSW if both were used in a study, and kelt, which is a salmon that spawned the previous fall). Studies from which published data were analysed took place in Canada, Ireland, United Kingdom, Norway, and Finland. Most data were collected from studies that used salmon anglers familiar with proper angling and handling procedures. Field studies often involved cooperation between researchers and recreational anglers fishing from riverbanks, and researchers tagged salmon with internal or externally attached acoustic or radio tags prior to release or placing fish in cages to monitor their fate (Table 1). Notably, some of the studies have excluded salmon from results that were critically injured during capture because of regional regulations that prevent the release of wounded fish. Where this occurs, it is outlined in the Methods section in each of the published papers and denoted in Table 1. Laboratory studies primarily involved simulations of the catch and release process in tanks, either by chasing the fish to exhaustion (chase) or manually hooking the fish in the jaw and retrieving it with standard fishing gear. To investigate the effects of methodologies among studies not generally associated with catch and release (e.g., substantial handling associated with experimental procedures, tagging, anesthetic, or confinement), we also recorded whether studies included a non-angled control group (Table 1). Additional data recorded for each of the non-angled control groups included capture method (seine, bag nets, angling, but 7 months prior), holding environment, and procedure (confinement, internal or external tags; Table 1).

Catch and release mortality model

Factors reported differed across studies, preventing inclusion of all variables of possible interest in the catch and release mortality model. A general linear mixed effects model with a binomial distribution (number of dead versus number of live fish) was developed, using the function “glmmadmb” in the package glmmADMB (Skaug et al. 2014) in R (R Core Team 2017). A binomial distribution allowed studies to be weighted based on sample size of fish (larger sample sizes equals greater effect in the model). Temperature (included as mean water temperature of the study and used as a measure of temperature at time of capture) was included as a polynomial term to allow curvature in the relationship between probability of mortality and water temperature. We further included reference (the literature source) as a random effect to control for differences in methodology among studies and to control for multiple estimates of mortality at various water temperatures from a single study (non-independence of measures).

Estimating the number of Atlantic salmon expected to have died following catch and release during the fishing season for select rivers

The number of retained and the number of caught and released Atlantic salmon in Newfoundland and Labrador was estimated using data from the DFO license stub program (O'Connell et al. 1998). Anglers were provided with a logbook upon purchase of a fishing license to record information regarding their fishing ac-

Table 1. Published data from studies investigating the effect of catch and release angling for Atlantic salmon and associated data used in a catch and release model to predict the probability of catch and release mortality (Prob. mortality) at a given water temperature (min., mean, and max. temperatures of the study).

Point No.	Temperature (°C)			Sample size	Prob. mortality	Type	Technique	Reference
	Min.	Mean	Max.					
Catch and release mortality values								
1	0.40	1.20	2.60	11	0.00	Kelt	Barbless-treble-lure-angling-internal tag	Halttunen et al. 2010
2	0.40	1.20	2.60	13	0.08	Kelt	Barbless-treble-lure-angling-external tag	Halttunen et al. 2010
3	3.00	4.00	5.00	89	0.01	Kelt	Barbed-single-fly-angling-cage	Bielak 1996
4	3.00	4.00	5.00	24	0.00	Kelt	Barbed-single-fly-angling-cage	Brobbel et al. 1996
5	5.00	5.50	6.00	20	0.00	1SW-MSW	Barbed-single-fly-angling-cage	Davidson et al. 1994
6	4.00	6.00	5.00	20	0.00	1SW-MSW	Barbed-single-fly-angling-cage	Booth et al. 1995
7	7.00	8.00	9.00	6	0.00	1SW	Barbed-single-fly-angling-internal heart tag	Anderson et al. 1998
8	8.40	9.40	10.40	5	0.00	1SW	Barbed-treble-lure-angling-external tag	Mäkinen et al. 2000
9*	8.40	9.60	10.70	38	0.05	1SW-MSW	Barbed-treble-fly/lure-angling-external tag	Lennox et al. 2017b
10	9.00	10.00	12.00	8	0.50	1SW	Barbed-treble-lure-angling-external tag	Gargan et al. 2015
11	9.50	11.70	13.90	8	0.00	1SW	Barbless-single-fly-angling-cage	Dempson et al. 2002
12	12.00	12.00	12.00	10	0.00	1SW	None-none-chase-cage	Wilkie et al. 1997
13	10.00	12.25	14.50	30	0.00	1SW-MSW	Barbed-treble-fly/lure-angling-external tag	Thorstad et al. 2003
14	11.00	13.00	16.00	48	0.02	1SW	Barbed-double/treble-fly-angling-external tag	Gargan et al. 2015
15	13.00	13.00	14.00	3	0.33	1SW-MSW	Barbed-single-lure-angling-external tag	Gargan et al. 2015
16	13.00	13.00	14.00	12	0.00	1SW-MSW	Barbed-single/double/treble-fly-angling-external tag	Gargan et al. 2015
17	8.00	13.00	18.00	27	0.11	1SW-MSW	Barbed-treble-fly/lure-angling-external tag	Lennox et al. 2015
18*	13.00	14.00	15.00	40	0.05	1SW-MSW	Barbed-treble-fly/lure-angling-external tag	Lennox et al. 2016
19	11.60	14.50	16.40	20	0.00	MSW	Unknown-unknown-fly-angling-internal gastric tag	Richard et al. 2014
20	14.00	15.95	17.90	20	0.10	1SW	Barbless-single-fly-angling-cage	Dempson et al. 2002
21	15.00	16.00	17.00	25	0.12	1SW	Barbed-single-fly-angling-cage	Brobbel et al. 1996
22	15.50	16.50	17.50	5	0.00	1SW	Barbed-single-fly-angling-internal heart tag	Anderson et al. 1998
23*	16.30	17.30	19.70	60	0.20	1SW-MSW	Barbed-double/treble-fly/lure-angling-external tag	Havn et al. 2015
24	18.90	17.60	20.20	19	0.11	1SW	None-none-chase-gastric tag	Lennox et al. 2019
25	18.00	18.00	18.00	16	0.00	1SW	None-none-chase-cage	Tufts et al. 1991
26	18.00	18.00	18.00	10	0.00	1SW	None-none-chase-cage	Wilkie et al. 1997
27	18.00	19.95	21.90	20	0.10	1SW	Barbless-single-fly-angling-cage	Dempson et al. 2002
28	18.00	20.00	22.00	5	0.80	1SW	Barbed-single-fly-angling-internal heart tag	Anderson et al. 1998
29	19.40	20.00	21.10	23	0.13	1SW	Barbed-double/treble-fly/lure-angling-external tag	Havn et al. 2015
30	18.00	20.00	22.00	10	0.40	1SW	Barbed-single-fly-angling-cage	Wilkie et al. 1996
31	22.00	22.00	22.10	1	0.00	1SW	Barbless-single-fly-angling-cage	Dempson et al. 2002
32	23.00	23.00	23.00	10	0.30	1SW	None-none-chase-cage	Wilkie et al. 1997
Control mortality values								
1	0.40	1.20	2.60	17	0.00	Kelt	Angled-internal tag (7–10 months earlier)-released	Halttunen et al. 2010
2	0.40	1.20	2.60	17	0.00	Kelt	Angled-internal tag (7–10 months earlier)-released	Halttunen et al. 2010
6	5.00	5.50	6.00	20	0.00	1SW-MSW	Seine-cage-undisturbed	Davidson et al. 1994
11	9.50	11.70	13.90	5	0.00	1SW	Box trap-cage-undisturbed	Dempson et al. 2002
12	12.00	12.00	12.00	16	0.00	1SW	Hatchery-cage-undisturbed	Wilkie et al. 1997
8	8.00	13.00	18.00	33	0.00	1SW-MSW	Bag net at sea-external tag-released	Lennox et al. 2015
17	11.60	14.50	16.40	20	0.00	MSW	Box trap-anaesthetic-internal tag-released	Richard et al. 2014
20	14.00	15.95	17.90	8	0.00	1SW	Box trap-cage-undisturbed	Dempson et al. 2002
24	18.90	17.60	20.20	18	0.06	1SW	Box trap-internal/external tags-released	Lennox et al. 2019
26	18.00	18.00	18.00	16	0.00	1SW	Hatchery-cage-undisturbed	Wilkie et al. 1997
27	18.00	19.95	21.90	7	0.00	1SW	Box trap-cage-undisturbed	Dempson et al. 2002
32	23.00	23.00	23.00	16	0.00	1SW	Hatchery-cage-undisturbed	Wilkie et al. 1997

Note: Point No. refers to the data point reference on Figs. 1 and 2. An asterisk (*) denotes studies that excluded critically injured fish in previous analyses given that regional legislation prevented the release of critically wounded fish (two mortalities were added to Point 9, one to Point 18, and eight to Point 23 as mentioned in these papers). Sample size for each study is given, as well as type of fish (1SW and MSW, salmon that had spent one or multiple winters at sea, respectively; 1SW-MSW, both were used in the study; kelt, salmon that had spawned the previous fall). The technique column describes the hook used (barbed or barbless; single, double, or treble), capture method (fly, lure, none; i.e., no hooking was used), angling or chase (i.e., simulated angling), and how the fate of the fish was assessed following release (internal tag, external tag, cage, genetics of offspring). The reference for each study is given. Non-angled control estimates of mortality, if available, are given at the bottom of the table.

tivities. When completed in full, logbook information included date, river name, number of fish retained and (or) released, and number of hours fished. Salmon abundance data were obtained from DFO records from the Newfoundland and Labrador Atlantic salmon abundance monitoring program. Salmon counting fence facilities are assembled in designated rivers from May to September and are a barrier to upstream-migrating Atlantic salmon, allowing for counts of returning salmon to be completed as fish

swim through designated openings outfitted with various camera-based systems.

We estimated the total number of fish expected to have died following catch and release for six rivers in Newfoundland and two rivers in Labrador where catch statistics, water temperature information, and salmon abundance were available for the 2016 fishing season. Using data for daily number of fish released from anglers' logbooks, daily water temperatures, and results from the

catch and release mortality model, we estimated the expected mortality across various water temperatures. The 2016 data were used because of the uncertainty associated with angler participation after unprecedented declines in salmon abundance in 2017 (DFO 2018) and changes to the cost of licenses and subsequent management measures in 2018 and 2019 (e.g., changes in warmer water protocols and maximum number of fish retained and released). Only logbook data that contained daily entries for river, date, and number of fish released were included. The number of fish estimated to have died daily as a result of catch and release were summed to give monthly estimates of mortality. To scale the data (i.e., adjust for stub returns that were not completed in full and were missing dates of capture and release) and provide rough estimates of mortality for the entire fishing season, we used the total number of fish estimated to have been released from the 2016 salmon season and multiplied it by the proportion of fish calculated above to have been released per month. Estimates were compared with the current protocol for Newfoundland and Labrador, established by DFO, assuming 10% mortality for caught and released Atlantic salmon (Dempson et al. 2002) and as a percentage of total salmon abundance per river. Values expressed as a percentage of total salmon abundance per river were calculated by dividing the number of fish retained, the number of fish released, the number of fish predicted from the model to have died following catch and release, and the assumed 10% mortality for a caught and released Atlantic salmon by the total salmon abundance for a given river in 2016, and multiplying by 100 (Table 2).

Regional and temporal trends for river temperatures

Water temperature data for monitored rivers with sufficient time series of data to support an analysis ($n = 13$ of 16 rivers) were obtained from DFO records from the Newfoundland and Labrador Atlantic salmon abundance monitoring program. Water temperatures were taken in the morning (~0800) and afternoon (~1600) to approximate the range of low to high values salmon would experience. River temperature trends in July and August across years for rivers of Newfoundland and Labrador were modelled using a general additive mixed effects model in the package *mcgv* and the function “*gamm*” (Wood 2011) in R (R Core Team 2017). River was included as a random effect (because rivers were repeatedly sampled through time) with a temporal autocorrelation term across years. We included time of day (morning or afternoon) as a covariate, modelled as a spline fit with a $k = 4$. In addition, we analyzed data excluding years <2010 to test for a significant recent trend in river temperature using a general least squares regression that included time of day as a covariate.

Regional and temporal trends for river closures due to high water temperatures and (or) low water levels

For more than 40 years, Atlantic salmon rivers in Newfoundland and Labrador, have been periodically closed to angling by fishery managers due to high water temperatures and low water levels. River closure data, prior to 1982, were obtained from archived DFO management records. Closure data from 1982 to 2018 were obtained from DFO anglers' notices and annual stock status reports, which often included detailed reasons for, and dates of, river closures. The potential number of days salmon rivers were open to angling each year (1975–2018) for each salmon fishing area was calculated by multiplying the number of scheduled salmon rivers open to angling for a given salmon fishing area by the number of days in the season, including those rivers that were open for catch and release only (as described in Dempson et al. 2001). The percentage of days closed to angling was determined by dividing the number of days salmon rivers were closed by the potential number of angling days for an entire season and multiplying by 100. River closure, for our purpose, relates to a river closed for fishing due to high water temperature and (or) low

water level (i.e., for environmental reasons and not for reasons associated with stock conservation measures).

Trends in percentage of days fishing was closed for the salmon season across rivers of Newfoundland were examined using a general additive mixed effects model. To identify whether the trend across salmon fishing areas has been increasing or decreasing for years ≥ 2010 , we used a general linear mixed effects model (GLMM) in the package *MASS* (Venables and Ripley 2002) in R (R Core Team 2017) with a Poisson distribution and salmon fishing area included as a random intercept. Models were run for both the entire time series of data and for years ≥ 2010 to compare overall and more recent trends in river closures due to high water temperatures and (or) low water level. To date we are only aware of one river closure in Labrador (Shinney's River in 1999) for environmental reasons; therefore, no formal analysis for Labrador was needed.

Results

Predicting the probability of mortality at a given water temperature for caught and released Atlantic salmon

Catch and release mortality for Atlantic salmon was highly variable across studies, ranging from 0 to 0.80 for mean water temperatures between 1.2 and 23.0 °C (Table 1; Fig. 1), albeit with 66% of published data having mortalities of ≤ 0.10 (Table 1). Mortality among non-angled control groups ranged from 0 to 0.06 (mean = 0.005; Table 1; Fig. 2). Results of our catch and release mortality model were unequivocal, showing that the probability of mortality following catch and release increases with increasing water temperature (GLMM, $z = 5.07$, $n = 32$, $p < 0.001$; Fig. 1).

Estimating the number of Atlantic salmon expected to have died following catch and release during the fishing season for select rivers

The 10% estimate for catch and release mortality currently assumed in Newfoundland and Labrador by DFO was for the most part representative of lower (95% CI) estimates predicted by our catch and release model for select rivers during the 2016 angling season (Table 2). Catch and release mortalities in relation to total abundance of adult salmon per river were highly variable and ranged from 0% (Torrent River) to 7.2% (Harry's River) for Newfoundland (mean = 1.5%) and 0.2% (Sand Hill River) to 7.6% (Paradise River) for Labrador (mean = 1.7%).

Regional and temporal trends for river temperatures

Average monthly river temperatures in July and August for the nine monitored rivers in Newfoundland, with sufficient time series for analyses, showed a warming trend over time (July: GAMM, $t = 30.07$, $n = 29\ 861$, $p < 0.001$; August: GAMM, $t = 34.79$, $n = 25\ 124$, $p < 0.001$). When data were limited to years ≥ 2010 , river temperatures in July, did not change (GAMM, $t = 0.65$, $n = 5084$, $p = 0.51$), whereas river temperatures in August warmed (GAMM, $t = 9.62$, $n = 3971$, $p < 0.01$). All monitored rivers (3 of 3) on the east (Salmon Fishing Area; SFA 5) and (1 of 1) southeast (SFA 9) coasts of Newfoundland warmed in both July and August for years ≥ 2010 (Fig. 3), whereas monitored rivers on the south (SFA 11), west (SFA 13), and north coasts (SFA 14A) did not change (SFA 11) or cooled (SFA 13 and 14A; Fig. 3).

Overall, river temperatures in July for the four monitored rivers in Labrador did not change over time (GAMM, $t = 0.92$, $n = 5090$, $p = 0.36$), whereas river temperatures in August warmed (GAMM, $t = 7.97$, $n = 5012$, $p < 0.001$). When data were limited to years ≥ 2010 , river temperatures in July (GAMM, $t = -6.50$, $n = 1640$, $p < 0.001$) and August (GAMM, $t = -13.02$, $n = 1442$, $p < 0.001$) both cooled with half (2 of 4) of the rivers cooler (SFA 2; Fig. 4) in July and all rivers (4 of 4) cooler in August (SFA 1 and 2; Fig. 4).

Table 2. The number of Atlantic salmon estimated to have been retained, released, and predicted by a model to have died after catch and release (C+R) in rivers across Newfoundland and Labrador, Canada, for each month of the fishing season, as a proportion of salmon abundance (percentage of run size in parentheses) and as a total for 2016.

Month	Salmon count (% of run size)	No. retained (% of run size)	No. released (% of run size)	Temp. (°C, mean)	No. of C+R morts estimate (LCI, mean, UCI) (% of run size)	Assumed no. of C+R morts (10%) (% of run size)
Newfoundland angling season, 2016						
Campbellton River						
June	1 064 (35.8)	82 (2.8)	75 (2.5)	15.7	3 (0.1), 6 (0.2), 13 (0.4)	8 (0.2)
July	1 553 (52.2)	246 (8.3)	117 (3.9)	20.1	10 (0.3), 24 (0.8), 51 (1.7)	12 (0.4)
August	350 (11.7)	57 (1.9)	32 (1.1)	20.8	3 (0.1), 8 (0.2), 15 (0.5)	3 (0.1)
September	4 (0.1)	4 (0.1)	21 (0.7)	15.4	1 (<0.1), 2 (<0.1), 3 (0.1)	2 (<0.1)
Season total	2 971 (100)	389 (13.1)	245 (8.2)	18.0	17 (0.6), 40 (1.3), 82 (2.8)	25 (0.8)
Exploits River						
June	5 375 (22.9)	867 (3.7)	937 (4.0)	16.0	39 (0.2), 76 (0.3), 175 (0.7)	94 (0.4)
July	15 892 (67.7)	2 853 (12.2)	2 322 (9.9)	18.8	158 (0.7), 359 (1.5), 799 (3.4)	232 (1.0)
August	2 192 (9.3)	455 (1.9)	607 (2.6)	21.1	62 (0.3), 156 (0.7), 306 (1.3)	61 (0.3)
September	0 (0)	44 (0.2)	149 (0.6)	No record	No record	15 (<0.1)
Season total	23 459 (100)	4219 (18.0)	4 015 (17.1)	No record	No record	402 (1.7)
Harry's River						
June	3 624 (85.2)	108 (2.5)	288 (6.8)	13.8	8 (0.2), 16 (0.4), 30 (0.7)	29 (0.7)
July	629 (14.8)	449 (10.6)	605 (14.2)	18.5	39 (0.9), 87 (2.0), 196 (4.6)	61 (1.4)
August	0 (0)	150 (3.5)	208 (4.9)	19.5	16 (0.4), 38 (0.9), 81 (1.9)	21 (0.5)
September	0 (0)	21 (0.5)	10 (0.2)	No record	No record	1 (<0.1)
Season total	4 253 (100)	728 (17.1)	1 111 (26.1)	No record	No record	112 (2.6)
Middle Brook River						
June	120 (5.1)	33 (1.4)	2 (0.1)	16.7	0 (0), 0 (0), 0 (0)	0 (0)
July	1 832 (77.5)	183 (7.7)	63 (2.7)	21.3	7 (0.3), 17 (0.7), 33(1.4)	6 (0.3)
August	406 (17.2)	8 (0.3)	7 (0.3)	23.2	1 (<0.1), 3 (0.1), 5 (0.2)	1 (<0.1)
September	6 (0.3)	8 (0.3)	7 (0.3)	20.1	1 (<0.1), 1 (<0.1), 3 (0.1)	1 (<0.1)
Season total	2 364 (100)	233 (9.9)	78 (3.3)	20.3	9 (0.4), 21 (0.9), 41 (1.7)	8 (0.3)
Terra Nova River						
June	724 (12.8)	35 (0.6)	7 (0.1)	15.6	0 (0), 1 (<0.1), 1 (<0.1)	1 (<0.1)
July	4 173 (74.0)	138 (2.4)	125 (2.2)	19.2	9 (0.2), 21 (0.4), 46 (0.8)	13 (0.2)
August	689 (12.2)	62 (1.1)	68 (1.2)	20.5	6 (0.1), 15 (0.3), 31 (0.5)	7 (0.1)
September	51 (0.9)	7 (0.1)	14 (0.2)	16.7	1 (<0.1), 1 (<0.1), 3 (0.1)	1 (<0.1)
Season total	5 637 (100)	242 (4.3)	214 (3.8)	18.0	16 (0.3), 38 (0.7), 81 (1.4)	22 (0.4)
Torrent River						
June	72 (1.8)	111 (2.8)	1 (<0.1)	11.4	0 (0), 0 (0), 0 (0)	0 (0)
July	3 503 (86.9)	629 (15.6)	13 (0.3)	14.9	0 (0), 1 (0), 2 (<0.1)	1 (<0.1)
August	433 (10.7)	131 (3.2)	1 (<0.1)	16.9	0 (0), 0 (0), 0 (0)	0 (0)
September	23 (0.6)	No record	No record	13.9	No record	No record
Season total	4 031 (100)	872 (21.6)	15 (0.4)	14.3	0 (0), 1 (<0.1), 2 (<0.1)	1 (<0.1)
Labrador angling season, 2016						
Paradise River						
June	0 (0)	10 (9.5)	11 (1.0)	15.2	0 (0), 1 (1.0), 2 (1.9)	1 (1.0)
July	80 (76.2)	1 (1.0)	34 (2.9)	15.0	1 (1.0), 2 (1.9) 5 (4.8)	3 (2.9)
August	25 (23.8)	0 (0)	6 (1.0)	15.6	0 (0), 0 (0), 1 (1.0)	1 (1.0)
September	0 (0)	No record	No record	No record	No record	No record
Season total	105 (100)	11 (10.5)	51 (4.9)	No record	1 (1.0), 3 (2.9), 8 (7.6)	5 (4.8)
Sand Hill River						
June	49 (2.4)	0 (0)	18 (0.9)	12.4	0 (0), 1 (<0.1), 1 (<0.1)	2 (0.1)
July	1 788 (87.0)	27 (1.3)	164 (8.0)	12.9	4 (0.2), 8 (0.4), 13 (0.6)	16 (0.8)
August	217 (10.6)	No record	No record	13.5	No record	No record
September	0 (0)	No record	No record	No record	No record	No record
Season total	2 054 (100)	27 (1.3)	182 (8.9)	No record	4 (0.2), 9 (0.4), 16 (0.7)	18 (0.9)

Note: No record refers to missing data (i.e., incomplete temperature record or no record of a fish being retained or released). Number of C+R morts estimate are given as lower 95% confidence interval (LCI), mean, and upper 95% confidence interval (UCI). Assumed morts (10%) refers to the current protocol for Newfoundland and Labrador, established by Fisheries and Oceans Canada, assuming 10% mortality for caught and released Atlantic salmon in the recreational fishery.

Regional and temporal trends for river closures due to high water temperatures and (or) low water levels

The number of rivers closed to angling due to high water temperatures and (or) low water levels in Newfoundland varied annually, with 131 of 158 rivers experiencing closures in some years.

Overall, there was no change over time (Fig. 5; GLMM, $t = 0.69$, $df = 512$, $p = 0.49$). When restricting the data to years ≥ 2010 , there was an increase in the percentage of days closed to angling (GLMM, $t = 5.68$, $df = 83$, $p < 0.01$), with rivers on the east coast of the island (SFAs 4, 5, and 6) showing the greatest increase in closures (Fig. 5).

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Fig. 1. The relationship between probability of mortality and mean water temperature of the study as a measure of temperature at time of capture, partitioned by life history type (A) and fishing gear type (B), for a caught and released anadromous Atlantic salmon using a general linear mixed effects model with a binomial distribution. Data were collected using published studies from across North America and Europe and included only the anadromous life histories of Atlantic salmon (1SW and MSW, salmon that had spent one or multiple winters at sea, respectively; 1SW–MSW, both were used in the study; kelt, salmon that had spawned the previous fall), caught using various gear types and techniques to assess fate of fish following release. Numbered data points refer to the study reference with additional information for each study presented in Table 1. Grey line represents the mean and the shaded curved area represents upper and lower 95% confidence intervals (CIs). [Colour online.]

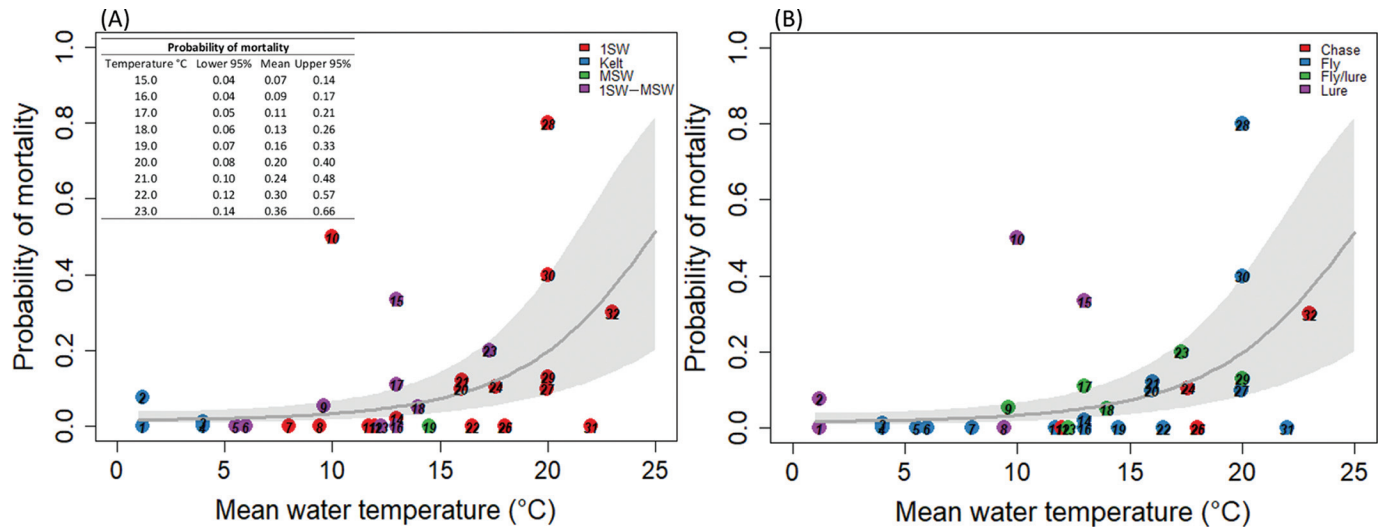
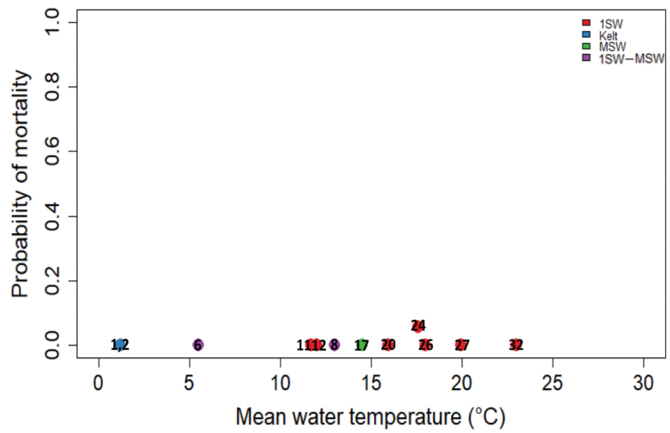


Fig. 2. The relationship between probability of mortality and mean water temperature of the study as a measure of temperature at time of capture for non-angled control groups from studies investigating the effects of catch and release angling on the survival, behavior, and physiology of Atlantic salmon. Data were collected using published studies from across North America and Europe and caught using various fishing gear types and techniques to assess fate of fish following release. Numbered data points refer to the study reference with additional information for each study presented in Table 1. Coloured data points refer to life history of the salmon (1SW and MSW, salmon that had spent one or multiple winters at sea, respectively; 1SW–MSW, both were used in the study; kelt, salmon that had spawned the previous fall). [Colour online.]



Closures across all salmon fishing areas in 2017 and 2018 were the highest recorded since 1987. This result seems consistent with patterns in river temperatures described above in July and August for Newfoundland. Consistent with the cooling trend for monitored rivers and years described above in July and August for Labrador, we are only aware of one river closure in Labrador (Shinney’s River, SFA 2 in 1999) for environmental reasons.

Discussion

We found that high river temperatures increased the probability of mortality for a caught and released Atlantic salmon. As the fight time of a fish increases, so do levels of extracellular acidosis and blood and muscle lactate. These physiological responses cause a decreased extracellular pH, plasma bicarbonate, adenosine triphosphate, and glycogen that all considerably decrease likelihood of recovery following capture (Tufts et al. 1991; Booth et al. 1995; Brobbel et al. 1996; Wilkie et al. 1996, 1997). When the catch and release process is paired with high water temperatures and resultant lower dissolved oxygen, the combination becomes synergistic, and the complete exhaustion of aerobic and anaerobic muscular fuels, scope, and cardiac function are possible (Wood et al. 1983; Wilkie et al. 1996; Anderson et al. 1998; Breau 2013). Following release, this can lead to increased vulnerability to predation (Raby et al. 2014), onset of disease (Breau 2013), and an overall higher probability of mortality (Bartholomew and Bohnsack 2005; Arlinghaus et al. 2007).

River closures to salmon angling are sometimes implemented when water temperature exceeds a predetermined threshold. Rivers in Newfoundland and Labrador that permit salmon retention are closed to angling during the day when water temperature is >20.0 °C across 2–3 days. Rivers that are catch and release only are closed to angling during the day when water temperature is >18 °C across 2–3 days. Rivers in New Brunswick, Canada, are closed to angling when water temperature is ≥20 °C on 2 consecutive days (DFO 2012; Breau 2013). Whereas retention fishing for Atlantic salmon remains open for rivers in Ireland when water temperature is above 18 °C, the practice of catch and release is discouraged, although this remains on a river by river basis. In Norway, rivers are sometimes closed to angling when water temperature increases and water levels decrease, or catch and release is discouraged, but like Ireland, this is decided subjectively case by case.

Mortality estimates predicted by our catch and release mortality model suggest that at mean water temperatures between 0 and 12 °C (±95% CI) catch and release mortalities range from 0.01 to 0.05 (mean = 0.03), and at temperatures between 12 and 18 °C these

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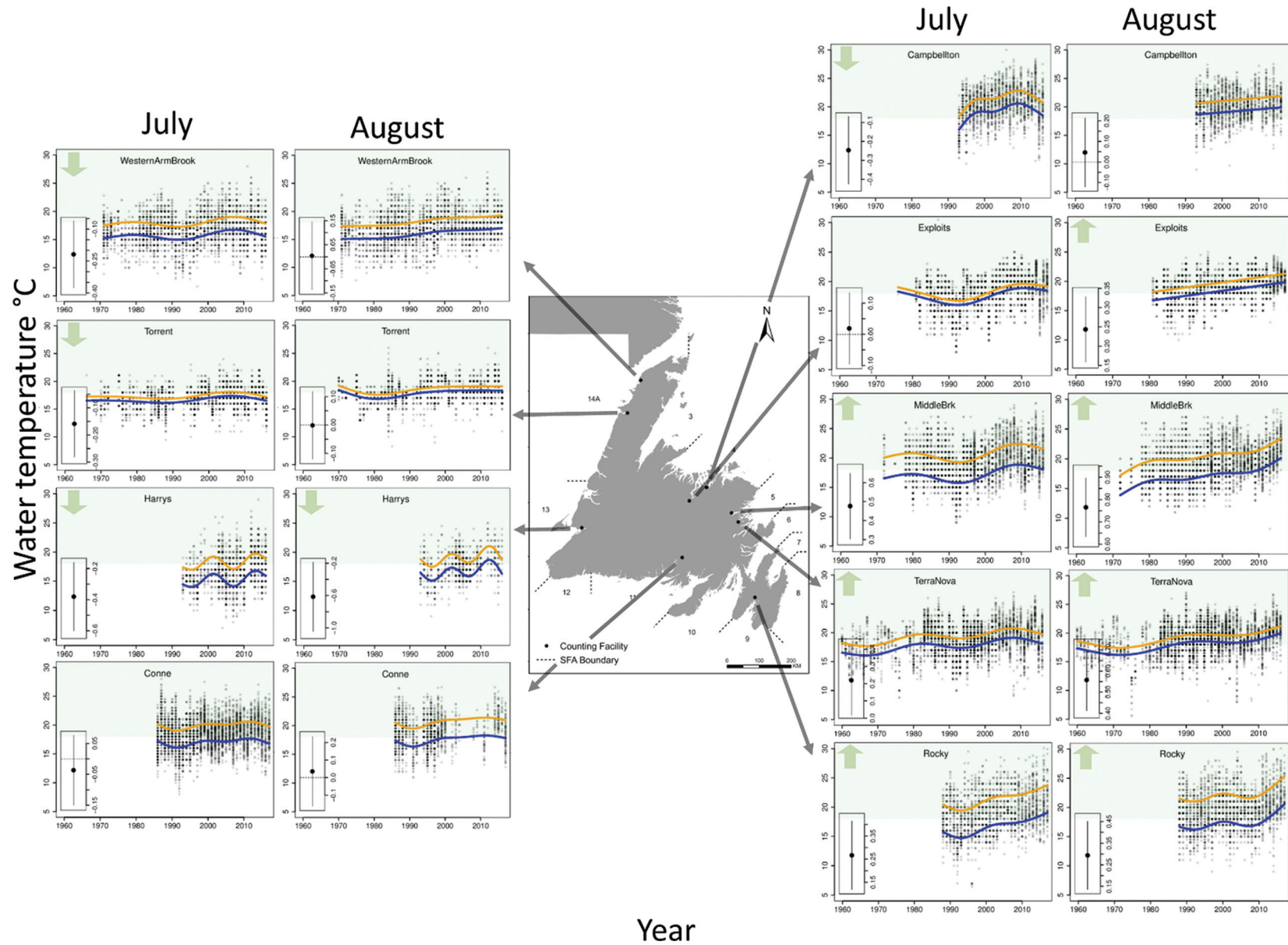
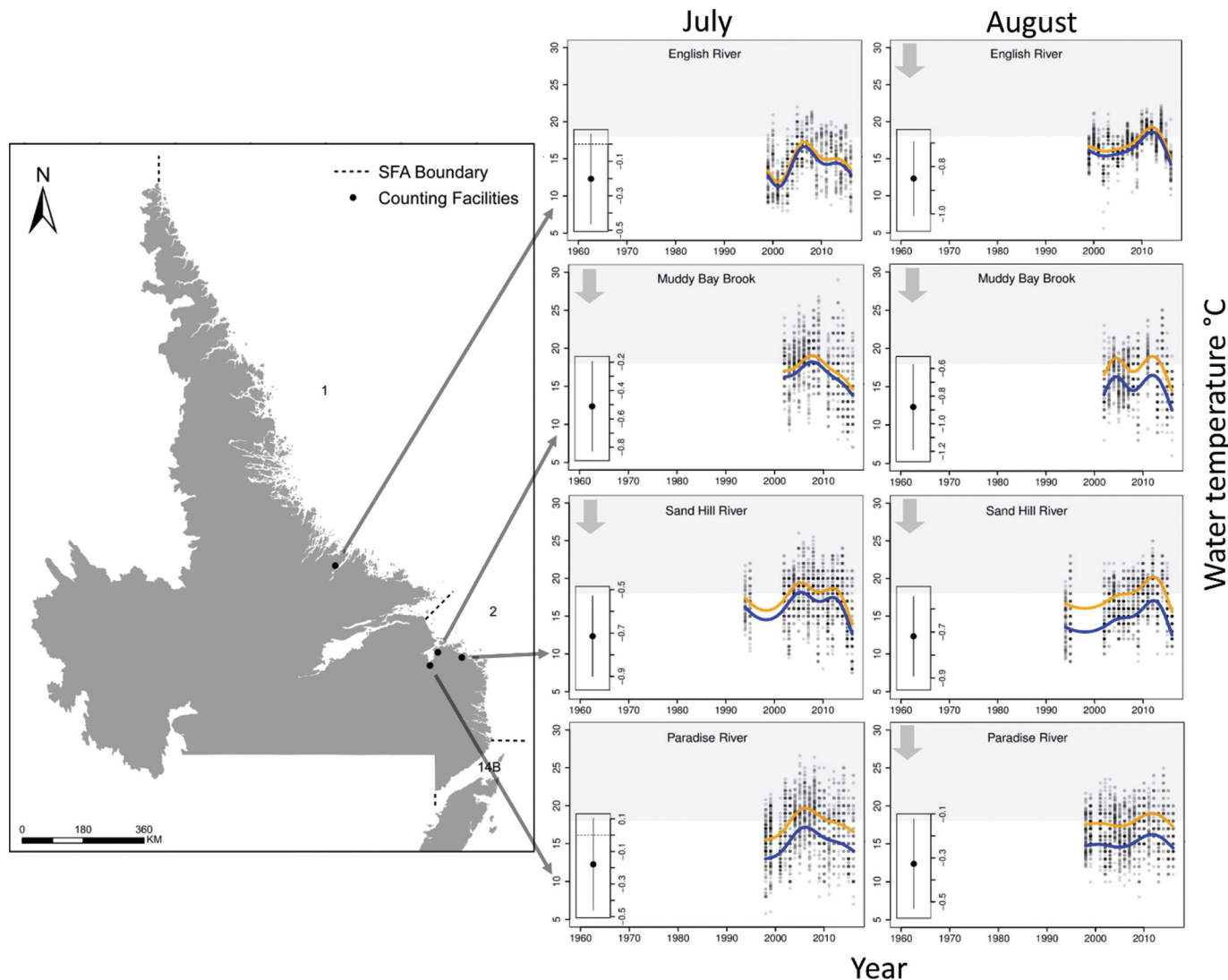


Fig. 3. The relationship between July and August river temperatures and year for nine monitored rivers in Salmon Fishing Areas 3, 4, 5, 9, 11, 13, and 14A in Newfoundland, Canada. Data points represent river temperatures taken at 0800 and 1600. The blue line represents river temperatures at 0800 across years, and the orange line represents river temperatures at 1600 across years. The shaded green area represents daily river temperatures above 18 °C. The window in the left bottom corner of each panel refers to the 95% confidence intervals (CIs) generated using a liner mixed effects model on data ≥ 2010 . Windows that contain 95% CIs that do not cross zero represent a statistically significant ($p < 0.01$) trend in river temperature for years ≥ 2010 . Green arrows in the upper left corner of the panel refer to the direction of the significant trend in river temperature if found. Map produced using ArcGis 10.7.1. [Colour online.]

Fig. 4. The relationship between July and August river temperature and year for four monitored rivers in Salmon Fishing Areas 1 and 2 in Labrador, Canada. Data points represent daily river temperatures taken at 0800 and 1600. The blue line represents river temperatures at 0800 across years, and the orange line represents river temperatures at 1600 across years. The shaded grey area represents daily river temperatures above 18 °C. The window in the left bottom corner of each panel refers to 95% confidence intervals (CIs) generated using a liner mixed effects model on data ≥ 2010 . Windows that contain 95% CIs that do not cross zero represent a statistically significant ($p < 0.01$) trend in river temperature for years ≥ 2010 . Grey arrows in the upper left corner of the panel refer to the direction of the significant trend in river temperature if found. Map produced using ArcGis 10.7.1. [Colour online.]



mortalities range from 0.04 to 0.16 (mean = 0.08). At temperatures between 18 and 20 °C, mortalities ranged from 0.07 to 0.33 (mean = 0.16), and at 20 to 25 °C mortalities range from 0.14 to 0.61 (mean = 0.35). However, owing to relatively large variation in mortality among studies ≥ 19 °C, specific predictions at these high temperatures should be interpreted with caution due to the possibility of inherent variability (e.g., differences in run timing between countries, gear types, life history types) in the processes driving relatively higher mortality.

Variation among studies ≥ 19 °C suggests that some experimental procedures may themselves have a synergistic relationship with water temperature (Wilkie et al. 1996, 1997; Anderson et al. 1998), as considerably higher mortalities occurred at higher temperatures compared with equivalent procedures (e.g., insertion of heart rate tags) at lower temperatures. Anderson et al. (1998), using Atlantic salmon with implanted heart rate tags, observed 0% mortality at mean water temperatures of 8.0 and 16.5 °C but 80% mortality at 20.0 °C. Wilkie et al. (1996, 1997) found a similar

pattern in mortality, with 0% mortality at 12.0 and 18.0 °C, but 40% mortality at 20.0 °C and 30% at 23 °C. Other sources of variation may be explained by differential susceptibility of populations to catch and release mortality (Gargan et al. 2015) or simply a result of low sample sizes at higher water temperatures (Dempson et al. 2002; Havn et al. 2017). Two aspects that could confound the interpretation of our results include (i) the inclusion of results from the Anderson et al. (1998) study due to their use of heart rate tags, which may have increased mortality at the warmest temperatures, and (ii) the increased mortality associated with the addition of critically wounded fish in the Norwegian data, intended for release, but euthanized after capture due to regional legislation. Model predictions with and (or) without the Anderson et al. (1998) study and the critically wounded fish are available for comparison (see Table 3) but do not alter our conclusions.

While a considerable amount of variation was found among studies and across temperature ranges within a single study, there are also several caveats among our model predictions, for example,

Fig. 5. The relationship between environmental closures (percentage of days rivers were closed to angling) and year (1975–2018) for each Salmon Fishing Area in Newfoundland, Canada (SFAs 3–14A). The solid black line represents the average trend in percent days closed across years. The dotted black line represents 95% confidence intervals for the model. Map produced using ArcGIS 10.7.1.

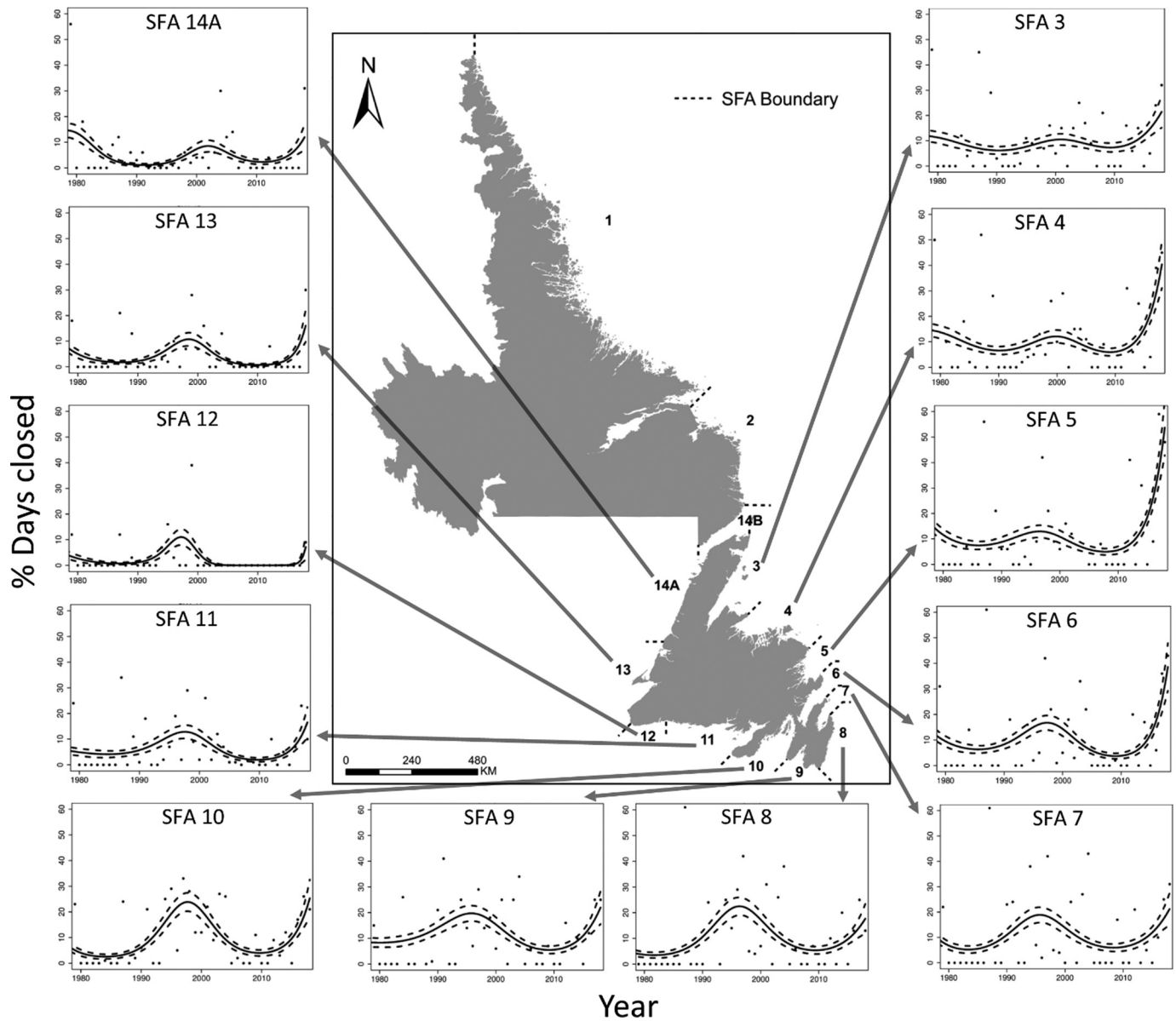


Table 3. A sensitivity analysis showing how the inclusion (Yes) or exclusion (No) of data from Anderson et al. (1998) and (or) critically wounded fish, not included previously in published studies, affects the probability of mortality for a caught and released Atlantic salmon.

Temp. (°C)	Probability of mortality (LCI, mean, UCI)			
	Yes/Yes	No/Yes	Yes/No	No/No
15.0	0.04, 0.07, 0.14	0.03, 0.07, 0.14	0.02, 0.05, 0.13	0.03, 0.06, 0.11
16.0	0.04, 0.09, 0.17	0.04, 0.08, 0.17	0.03, 0.07, 0.16	0.03, 0.07, 0.13
17.0	0.05, 0.11, 0.21	0.04, 0.10, 0.21	0.03, 0.09, 0.21	0.04, 0.08, 0.17
18.0	0.06, 0.13, 0.26	0.05, 0.14, 0.25	0.04, 0.11, 0.26	0.04, 0.10, 0.20
19.0	0.07, 0.16, 0.33	0.06, 0.17, 0.31	0.05, 0.14, 0.34	0.05, 0.12, 0.25
20.0	0.08, 0.20, 0.40	0.07, 0.21, 0.37	0.06, 0.18, 0.43	0.06, 0.15, 0.32
21.0	0.10, 0.24, 0.48	0.08, 0.25, 0.45	0.07, 0.23, 0.53	0.07, 0.18, 0.39
22.0	0.12, 0.30, 0.57	0.09, 0.25, 0.53	0.09, 0.29, 0.63	0.08, 0.22, 0.47
23.0	0.14, 0.36, 0.66	0.11, 0.31, 0.62	0.11, 0.37, 0.73	0.10, 0.27, 0.57

Note: Yes/No scenarios are presented as a combination of Anderson et al. (1998) study included-excluded / critically wounded fish included-excluded. Probability of mortality is shown as lower 95% confidence interval (LCI), mean, and upper 95% confidence interval (UCI).

the use of mean water temperature recorded for each study as a measure of water temperature at time of capture. Although most studies had minimum and maximum water temperatures within ± 2 °C, some had a greater range (Richard et al. 2014; Lennox et al. 2015; Gargan et al. 2015), which could be problematic when inferring mortality estimates across narrow water temperature ranges. Future experimental studies should focus less on the effects of handling and air exposure (which should be obsolete assuming best practices are followed) and more on understanding water temperature profiles of study rivers. Specifically, this includes better information regarding the precision and accuracy of how fine-scale water temperature data are collected, how it could be better incorporated into models, including how water temperatures leading up to the time of capture and following release influence mortality.

DFO in Newfoundland and Labrador currently assumes 10% catch and release mortality, whereas 3% and 6% mortality are applied to the annual catch and release estimates for the Miramichi and Restigouche rivers by DFO Gulf Region (Breau 2013). For ethical animal welfare reasons, legislation in some parts of the world (e.g., Norway) only allows for release of uninjured and viable fish and for wounded fish to be euthanized. Mandatory catch and release is used less in fishing regulations in Norway than in Canada, and there are no rivers or periods where salmon angling in Norway is solely mandatory catch and release. However, in many rivers where there is mandatory release of groups of salmon (e.g., large females), a wounded fish that is euthanized by the angler for animal welfare reasons has to be given to the proprietor of the river location and often donated. Because there is no benefit to the angler (i.e., no fish), the harvesting of a fish that otherwise should have been released (i.e., not critically wounded) is less likely to occur.

According to estimates predicted by our catch and release mortality model, the assumption of 10% mortality after catch and release used by DFO in Newfoundland and Labrador is representative of low to mean estimates of mortality. Furthermore, the modelling exercise also highlights that although retention and catch and release estimates of salmon (on an individual river basis) were similar, the mortality associated with catch and release is low in comparison with harvest mortality and salmon abundance and demonstrates the importance of applying estimates of catch and release mortality to real-world fisheries data (i.e., catch statistics) when evaluating the effectiveness of catch and release.

The influence of water temperature on the survival of Atlantic salmon following catch and release angling, in combination with increases in global air temperature over the last several decades, highlight the importance of understanding the effect of climate change on river temperatures when evaluating the benefit of catch and release. In our study, we found significant differences in the response of rivers to climate-mediated temperature change at both regional and local scales. Regionally we found that average monthly river temperatures in July and August for Newfoundland warmed over time, whereas river temperatures in southern Labrador warmed slightly over time but for August only. On a local scale, we found that rivers on the east and southeast coasts of Newfoundland warmed in both July and August, whereas monitored rivers on the south, west, and north coasts did not change or even cooled in recent years. Because the salmon season in many parts of the world coincides with the warmest months, slight increases in water temperature in the summer suggest that an increase in mortality due to the catch and release fishery is probable (assuming that catchability of fish remains the same) given a scenario of future increase in air temperature. A corresponding increase in economic disruption as a result of increased environmental closures would also be anticipated (assuming warm water closure protocols remain the same or exist). To some extent, this seems to be occurring, as evidenced by the increase in the percentage of days closed to angling in Newfoundland in recent years.

Although there remains a level of uncertainty around the predicted global temperature increase as a result of climate change, it is certain that climate change is occurring (Powell 2016). Increases in precipitation and extreme hot days are likely to occur in greater frequency, duration, and intensity (Hansen et al. 2012; Steffen et al. 2018). Together, changes in precipitation and extreme hot days will likely have an impact on recreational fisheries, especially those involving cold-water species. Therefore, if planning to retain a fish, doing so during days when water temperatures are highest, not practicing catch and release when water temperatures are high, and the adoption of best practices during catch and release will become increasingly important in ensuring the sustainability of recreational fisheries. Furthermore, improved levels of engagement that regulatory agencies have with anglers and greater communication among scientists, anglers, and management are also increasingly important to ensure the most comprehensive catch statistics are used in analyses and the latest developments in catch and release science are available.

The present analyses highlights (i) the increasing need for adaptive management considerations in recreational catch and release fisheries in response to climate change, (ii) the increased need to educate anglers in “best practice” during catch and release angling in response to changes in river temperatures, and (iii) that changes in river temperatures have restricted recreational Atlantic salmon fishing opportunities.

Acknowledgements

We thank Keith Clarke, Jonathon Carr, participants of the 2019 CSAS Regional Advisory process for Atlantic salmon (especially Don Hutchens, David Meerburg, and Blair Adams), which took place March 2019 in St. John’s, Newfoundland, Canada, as well as two anonymous reviewers for their valuable insight and contribution to an early version of the manuscript.

References

- Anderson, W.G., Booth, R., Beddow, T.A., McKinley, R.S., Finstad, B., Økland, F., and Scruton, D. 1998. Remote monitoring of heart rate as a measure of recovery in angled Atlantic salmon, *Salmo salar* (L.). *Hydrobiologia*, **371**: 233–240. doi:10.1023/A:1017064014274.
- Arlinghaus, R., Cooke, S.J., Lyman, J., Policansky, D., Shwab, A., Suski, C., et al. 2007. Understanding the complexity of catch-and-release in recreational fishing: an integrative synthesis of global knowledge from historical, ethical, social, and biological perspectives. *Rev. Fish Sci. Aquac.* **15**(1–2): 75–167. doi:10.1080/10641260601149432.
- Bartholomew, A., and Bohnsack, J.A. 2005. A review of catch-and-release angling mortality with implications for no-take reserves. *Rev. Fish Biol. Fish.* **15**(1–2): 129–154. doi:10.1007/s11160-005-2175-1.
- Bielak, A.T. 1996. A discussion document on the implications of catch-and-release angling for Atlantic salmon, with particular reference to water temperature-related closures. DFO Atl. Fish. Res. Doc. 96/117. p. 17.
- Booth, R.K., Kieffer, J.D., Tufts, B.L., Davidson, K., and Bielak, A.T. 1995. Effects of late season catch and release angling on anaerobic metabolism, acid-base status, survival and gamete viability in wild Atlantic salmon (*Salmo salar*). *Can. J. Fish Aquat. Sci.* **52**(2): 283–290. doi:10.1139/f95-029.
- Bradbury, I.R., Hamilton, L.C., Rafferty, S., Meerburg, D., Poole, R., Dempson, J.B., et al. 2015. Genetic evidence of local exploitation of Atlantic salmon in a coastal subsistence fishery in the Northwest Atlantic. *Can. J. Fish. Aquat. Sci.* **72**(1): 83–95. doi:10.1139/cjfas-2014-0058.
- Breau, C. 2013. Knowledge of fish physiology used to set water temperature thresholds for in season closures of Atlantic salmon (*Salmo salar*) recreational fisheries. DFO Can. Sci. Advis. Sec. Res. Doc. 2012/163.
- Brett, J.R. 1971. Energetic responses of salmon to temperature. A study of some thermal relations in the physiology and freshwater ecology of sockeye salmon (*Oncorhynchus nerka*). *Am. Zool.* **11**: 99–113. doi:10.1093/icb/11.1.99.
- Brobbe, M.A., Wilkie, M.P., Davidson, K., Kieffer, J.D., Bielak, A.T., and Tufts, B.L. 1996. Physiological effects of catch and release angling in Atlantic salmon (*Salmo salar*) at different stages of freshwater migration. *Can. J. Fish Aquat. Sci.* **53**(9): 2036–2043. doi:10.1139/cjfas-53-9-2036.
- Brownscombe, J.W., Danylchuk, A.J., Chapman, J.M., Gutowsky, L.F.G., and Cooke, S.J. 2017. Best practices for catch-and-release recreational fisheries — angling tools and tactics. *Fish. Res.* **186**(Part 3): 693–705. doi:10.1016/j.fishres.2016.04.018.
- Chaput, G. 2012. Overview of the status of Atlantic salmon (*Salmo salar*) in the North Atlantic and trends in marine mortality. *ICES J. Mar. Sci.* **69**(9): 1538–1548. doi:10.1093/icesjms/fss013.

- Cooke, S.J., and Wilde, G.R. 2007. The fate of fish released by recreational anglers, Chapter 7. In *By-catch Reduction in the World's Fisheries*. Edited by S.J. Kennelly. Springer, The Netherlands. pp. 181–234.
- Davidson, K., Haybrook, J., Hambrook, M., Bielak, A.T., and Sheasgreen, J. 1994. The effects of late season angling on gamete viability and early fry survival in Atlantic salmon. *Can. Tech. Rep. Fish. Aquat. Sci.* **1982**: 1–12.
- Dempson, J.B., O'Connell, M.F., and Cochrane, N.M. 2001. Potential impact of climate warming on recreational fishing opportunities for Atlantic salmon, *Salmo salar* L., in Newfoundland, Canada. *Fish. Manage. Ecol.* **8**(1): 69–82. doi:10.1046/j.1365-2400.2001.00225.x.
- Dempson, J.B., Furey, G., and Bloom, M. 2002. Effects of catch and release angling on Atlantic salmon, *Salmo salar* L., of the Conne River, Newfoundland. *Fish. Manage. Ecol.* **9**(3): 139–147. doi:10.1046/j.1365-2400.2002.00288.x.
- DFO. 2012. Temperature threshold to define management strategies for Atlantic salmon (*Salmo salar*) fisheries under environmentally stressful conditions. DFO Canadian Science Advisory Secretaria, Sci. Adv. Rep. 2012/019.
- DFO. 2018. Stock Assessment of Newfoundland and Labrador Atlantic Salmon – 2017. DFO Canadian Science Advisory Secretaria, Sci. Adv. Rep. 2018/034.
- Gale, M.K., Hinch, S.G., and Donaldson, M.R. 2013. The role of temperature in the capture and release of fish. *Fish. Fish.* **14**: 1–33. doi:10.1111/j.1467-2979.2011.00441.x.
- Gargan, P.G., Stafford, T., Økland, F., and Thorstad, E.B. 2015. Survival of wild Atlantic salmon (*Salmo salar*) after catch and release angling in three Irish rivers. *Fish. Res.* **161**: 252–260. doi:10.1016/j.fishres.2014.08.005.
- Haltunen, E., Rikardsen, A.H., Thorstad, E.B., Næsje, T.F., Jensen, J.L.A., and Aas, O. 2010. Impact of catch-and-release practices on behavior and mortality of Atlantic salmon (*Salmo salar* L.) kelts. *Fish. Res.* **105**: 141–147. doi:10.1016/j.fishres.2010.03.017.
- Hansen, J., Sato, M., and Ruedy, R. 2012. Perception of climate change. *Proc. Natl. Acad. Sci. USA.* **109**: E2415–E2423. doi:10.1073/pnas.1205276109.
- Havn, T.B., Uglem, I., Solem, Ø., Cooke, S.J., Whoriskey, F.G., and Thorstad, E.B. 2015. The effect of catch-and-release angling at high water temperatures on behaviour and survival of Atlantic salmon (*Salmo salar*) during spawning migration. *J. Fish Biol.* **87**(2): 342–359. doi:10.1111/jfb.12722. PMID:26179562.
- Havn, T.B., Økland, F., Teichert, M.A.K., Heermann, L., Borcherding, J., Sæther, S.A., et al. 2017. Movements of dead fish in rivers. *Anim. Biotelemetry*, **5**: 7. doi:10.1186/s40317-017-0122-2.
- Hein, C.L., Öhlund, G., and Englund, G. 2012. Future distribution of Arctic char *Salvelinus alpinus* in Sweden under climate change: effects of temperature, lake size and species interactions. *Ambio*, **41**(Suppl. 3): 303–312. doi:10.1007/s13280-012-0308-z. PMID:22864703.
- Huntsman, A.G. 1942. Death of salmon and trout with high temperature. *J. Fish. Res. Board Can.* **5**: 485–501. doi:10.1139/f40-051.
- ICES. 2019. Working Group on North Atlantic Salmon (WGNA). ICES Scientific Reports, **1**(16): 368. doi:10.17895/ices.pub.4978.
- IPCC. 2018. Global Warming of 1.5°C. An IPCC Special Report on the impacts of global warming of 1.5 °C above pre-industrial levels and related global greenhouse gas emission pathways, in the context of strengthening the global response to the threat of climate change, sustainable development, and efforts to eradicate poverty. Edited by V. Masson-Delmotte, P. Zhai, H.O. Connors, J.B.R. Matthews, Y. Chen, X. Zhou, M.I. Gomis, E. Lonnoy, T. Maycock, M. Tignor, and T. Waterfield. Intergovernmental Panel on Climate Change, Geneva.
- Lehnert, S.J., Kess, T., Bentzen, P., Kent, M.P., Lien, S., Gilbey, J., et al. 2019. Genomic signatures and correlates of widespread population declines in salmon. *Nat. Commun.* **10**: 2996. doi:10.1038/s41467-019-10972-w. PMID:31278264.
- Lennox, R.J., Uglem, I., Cooke, S.J., Næsje, T.F., Whoriskey, F.G., Havn, T.B., et al. 2015. Does catch-and-release angling alter the behaviour and fate of adult Atlantic salmon during upriver migration? *Trans. Am. Fish. Soc.* **144**(2): 400–409. doi:10.1080/00028487.2014.1001041.
- Lennox, R.J., Cooke, S.J., Diserud, O.H., Havn, T.B., Johansen, M.R., Thorstad, E.B., and Uglem, I. 2016. Use of simulation approaches to evaluate the consequences of catch and release angling on the migration behaviour of adult Atlantic salmon (*Salmo salar*). *Ecol. Model.* **333**: 343–350. doi:10.1016/j.ecolmodel.2016.04.010.
- Lennox, R.J., Cooke, S.J., Davis, C.R., Gargan, P., Hawkins, L.A., Havn, T.B., et al. 2017a. Pan-Holarctic assessment of post-release mortality of angled Atlantic salmon *Salmo salar*. *Biol. Cons.* **209**: 150–158. doi:10.1016/j.biocon.2017.01.022.
- Lennox, R.J., Havn, T.B., Thorstad, E.B., Liberg, E., Cooke, S.J., and Uglem, I. 2017b. Behaviour and survival of wild Atlantic salmon *Salmo salar* captured and released while surveillance angling for escaped farmed salmon. *Aquac. Environ. Interact.* **9**: 311–319. doi:10.3354/aei00235.
- Lennox, R.J., Crook, D.A., Moyle, P.B., Struthers, D.P., and Cooke, S.J. 2019. Toward a better understanding of freshwater fish responses to an increasingly drought-stricken world. *Rev. Fish Biol. Fisher.* **29**(1): 71–92. doi:10.1007/s11660-018-09545-9.
- MacCrimmon, H.R., and Gots, B.L. 1979. World distribution of Atlantic salmon, *Salmo salar*. *J. Fish. Res. Board Can.* **36**: 422–457. doi:10.1139/f79-062.
- Mäkinen, T.S., Niemelä, E., Moen, K., and Lindström, R. 2000. Behaviour of gill-net and rod captured Atlantic salmon (*Salmo salar* L.) during upstream migration and following radio tagging. *Fish. Res.* **45**(2): 117–127. doi:10.1016/S0165-7836(99)00107-1.
- O'Connell, M.F., Cochrane, N.M., and Mullins, C.C. 1998. An analysis of the licence stub return system in the Newfoundland Region, 1994–1997. Canadian Stock Assessment Secretariat Res. Doc. 98/111.
- Parrish, D.L., Behnke, R.J., Gephard, S.R., McCormick, S.D., and Reeves, G.H. 1998. Why aren't there more Atlantic salmon (*Salmo salar*)? *Can. J. Fish. Aquat. Sci.* **55**(Suppl. 1): 281–287. doi:10.1139/d98-012.
- Powell, J.L. 2016. The consensus on anthropogenic global warming matters. *Bull. Sci. Tech. Soc.* **36**(3): 157–163. doi:10.1177/0270467617707079.
- Prowse, T.D., Wrona, F.J., Reist, J.D., Gibson, J.J., Hobbie, J.E., Lévesque, L.M., and Vincent, W.F. 2006. Climate change effects on hydroecology of Arctic freshwater ecosystems. *Ambio*, **35**(7): 347–358. doi:10.1579/0044-7447(2006)35[347:CCEOHO]2.0.CO;2. PMID:17256639.
- R Core Team. 2017. R: A language and environment for statistical computing [online]. Available from <https://www.r-project.org>.
- Raby, G.D., Packer, J.R., Danylchuk, A.J., and Cooke, S.J. 2014. The understudied and underappreciated role of predation in the mortality of fish released from fishing gears. *Fish. Fish.* **15**: 489–505. doi:10.1111/faf.12033.
- Richard, A., Bernatchez, L., Valiquette, E., and Dionne, M. 2014. Telemetry reveals how catch and release affects prespawning migration in Atlantic salmon (*Salmo salar*). *Can. J. Fish. Aquat. Sci.* **71**(11): 1730–1739. doi:10.1139/cjfas-2014-0072.
- Skaug, H., Fournier, D., Bolker, B., Magnusson, A., and Nielsen, A. 2014. Generalized linear mixed models using AD model builder. R package version 0.8.0.
- Steffen, W., Rockström, J., Richardson, K., Lenton, T.M., Folke, C., Liverman, D., et al. 2018. Trajectories of the Earth System in the Anthropocene. *Proc. Natl. Acad. Sci. USA.* **115**(33): 8252–8259. doi:10.1073/pnas.1810141115. PMID:30082409.
- Stillman, J.H. 2019. Heat waves, the new normal: summertime temperature extremes will impact animals, ecosystems, and human communities. *Physiology*, **34**(2): 86–100. doi:10.1152/physiol.00040.2018. PMID:30724132.
- Taylor, M.A., Clarke, L.A., Centella, A., Bezanilla, A., Tannecia, S.S., Jones, J.J., et al. 2018. Future Caribbean Climates in a World of Rising Temperatures: The 1.5 vs 2.0 Dilemma. *J. Clim.* **31**: 2907–2926. doi:10.1175/JCLI-D-17-0074.1.
- Thorstad, E.B., Næsje, T.F., Fiske, P., and Finstad, B. 2003. Effects of hook and release on Atlantic salmon in the River Alta, northern Norway. *Fish. Res.* **60**(2–3): 293–307. doi:10.1016/S0165-7836(02)00176-5.
- Thorstad, E.B., Næsje, T.F., and Leinan, I. 2007. Long-term effects of catch-and-release angling on Atlantic salmon during different stages of return migration. *Fish. Res.* **85**(3): 330–334. doi:10.1016/j.fishres.2007.02.010.
- Tufts, B.L., Tang, Y., and Boutilier, R.G. 1991. Exhaustive exercise in “wild” Atlantic salmon (*Salmo salar*): acid-base regulation and blood transport. *Can. J. Fish. Aquat. Sci.* **48**(5): 868–874. doi:10.1139/f91-103.
- Venables, W.N., and Ripley, B.D. 2002. *Modern Applied Statistics with S*. Fourth Edition. Springer, New York.
- Whoriskey, F.G., Prusov, S., and Crabbe, S. 2000. Evaluation of the effects of catch-and release angling on the Atlantic salmon (*Salmo salar*) of the Ponoï River, Kola Peninsula, Russian Federation. *Ecol. Fresh. Fish.* **9**(1–2): 118–125. doi:10.1034/j.1600-0633.2000.90114.x.
- Wilkie, M.P., Davidson, K., Brobbel, M.A., Kieffer, J.D., Booth, R.K., Bielak, A.T., and Tufts, B.L. 1996. Physiology and survival of wild Atlantic salmon following angling in warm summer waters. *Trans. Am. Fish. Soc.* **125**(4): 572–580. doi:10.1577/1548-8659(1996)125<0572:PASOWA>2.3.CO;2.
- Wilkie, M.P., Brobbel, M.A., Davidson, K., Forsyth, L., and Tufts, B.L. 1997. Influences of temperature upon the postexercise physiology of Atlantic salmon (*Salmo salar*). *Can. J. Fish. Aquat. Sci.* **54**(3): 503–511. doi:10.1139/f96-305.
- Wood, C.M., Turner, J.D., and Graham, M.S. 1983. Why do fish die after severe exercise? *J. Fish Biol.* **22**: 189–201. doi:10.1111/j.1095-8649.1983.tb04739.x.
- Wood, S.N. 2011. Fast stable restricted maximum likelihood and marginal likelihood estimation of semiparametric generalized linear models. *J. Royal Stat. Soc. Ser. (B)*, **73**(1): 3–36. doi:10.1111/j.1467-9868.2010.00749.x.