Changes in adult Atlantic salmon (*Salmo salar*) run timing in the Miramichi River, New

Brunswick, in relation to river temperature and discharge rates over seven decades

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ABSTRACT

Atlantic salmon (*Salmo salar*) is a culturally, economically, and ecologically important species in Eastern Canada. Populations have been declining in recent decades, which can have negative implications for livelihood, ecosystems, and local tradition. Ecological factors associated with climate change in aquatic systems including temperature and river flow can alter the upstream migration behaviour of adult salmon. River entry during upstream migration for spawning, or "run timing", is a critical life history event for this species. This project found that run timing has significantly changed in the Miramichi River between 1952-2021. To investigate whether this change is associated with ecological factors in freshwater, I examined the relationship between freshwater environmental predictor variables – temperature and discharge rate – and Atlantic salmon entry to the estuary. Unlike previous work on smaller freshwater tributaries, there were no strong relationships found between entry to the estuary from the ocean and freshwater variables.

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INTRODUCTION

General background

Climate change is an ongoing threat to ecosystems and species, and it is of particular concern for species that are threatened and endangered. Changes in weather patterns and temperature may threaten the distribution and persistence of many populations (McCarty, 2001; Walther *et al.,* 2002). The effects of warming on ecosystems can already be observed and will likely be exacerbated as temperatures continue to increase and become more variable (IPCC, 2014). Potential impacts of climate change on species include shifts in timing of life history events, range, gene frequencies, and declines in population (McCarty *et al.*, 2001; Walther *et al.*, 2002; Parmesan *et al.*, 2022).

The impacts of climate change are pronounced in aquatic ecosystems (e.g. Bindoff *et al.*, 2019; Häder & Barnes, 2019). Changes in range, community composition, and biological characteristics that affect growth and survival are currently impacting many aquatic species, and fisheries are reporting decreased yield that reflects poor condition for many populations (Bindoff *et al*., 2019; Häder & Barnes, 2019). Aquatic ecosystems are vulnerable to temperature fluctuations, and changes in precipitation can alter habitat characteristics such as river discharge rates and water level, with flooding occurring earlier in the season due to earlier spring melts and lower discharge rates/water levels at higher temperatures (El-Jabi *et al.*, 2014; Parmesan *et al.*, 2022). Many aquatic organisms, including fish, are ectothermic (Talbot, 1993; Willmer *et al.*, 2009). Ectotherms are particularly vulnerable to temperature fluctuations as their body temperature is not internally regulated, but is instead influenced by the temperature of their environment. Direct effects of temperature on metabolism and indirect effects such as increased

productivity and food availability can influence growth and energy (Lennox *et al.*, 2018; Isaak & Young, 2023). Increased temperature, for example, decreases dissolved oxygen levels in water, while simultaneously increasing metabolic demands (Graham & Harrod, 2009; Lennox *et al.*, 2018; Bindoff *et al.*, 2019; Chapra *et al.*, 2021). Cold-water fish have higher dissolved oxygen requirements than warm-water fish (Chapra *et al*, 2021), and while warm-water fish are likely to experience range expansions with warming temperatures, habitat for cold-water fish will become more limited (Sharma *et al.*, 2007; Fossheim *et al.*, 2015). The most recent IPCC report on climate change (Parmesan *et al*., 2022) states that cold-water fish in freshwater environments, including salmonids, are particularly vulnerable to the impacts of warming waters.

Atlantic salmon (*Salmo salar*) are found throughout the Atlantic Ocean (Figure 1), and populations have been declining across its native range in recent decades. It is a cold-water species that tolerates a temperature range of 0-28°C, begins feeding at 6°C, and reaches an optimal growth rate at a temperature of ~16°C (Elliot, 1991; Elliot & Hurley, 1997; Handeland *et al.*, 2008). Climate change has been identified as one of the main factors threatening populations of Atlantic salmon in Canada (COSEWIC, 2010). In Eastern Canada Atlantic salmon is a financially, culturally, and ecologically important species. Its range in Canada falls in Mi'kma'ki, where salmon was historically a staple food item but it is now commonly reserved for large gatherings as a result of declining fish numbers (Denny *et al.*, 2013; Denny & Fanning, 2016).

Populations of Atlantic salmon are genetically differentiated (Verspoor *et al.*, 2005; Bourret *et al.*, 2013); thus, populations may respond differently when presented with similar environmental

challenges. There is evidence of strong relationships between variation in some genes and environmental factors – particularly temperature – indicating local adaptation within tributaries and river systems (Verspoor *et al.*, 2005). Additionally, acclimation plays a role in how most fish, including salmon, respond to environmental factors (e.g. Antilla *et al.*, 2014). Acclimation to warmer temperatures can mitigate some negative effects on metabolism and condition (Antilla *et al.*, 2014) but there is no evidence of adaptation to temperatures above the established thermal limits for Atlantic salmon (Elliot & Elliot, 2010).

Many populations of Atlantic salmon are anadromous, meaning that they live in both freshwater and marine habitats during different stages of their life, and they are an ecologically important species as they facilitate nutrient transfer between the two environments (e.g. Jonsson & Jonsson, 2003). Anadromous salmon hatch in freshwater, inhabit freshwater streams and rivers as juveniles, and migrate to cool regions of the North Atlantic Ocean to mature (Klemetsen *et al.*, 2003). Atlantic salmon life history is complex with high variance in age composition. Juveniles may stay in the river system for 2-8 years before migrating to the ocean (Scott & Crossman, 1973; Klemetsen *et al.*, 2003). A combination of environmental factors, chiefly temperature and body size, influence when smolts migrate to the marine environment (Jonsson & Ruud-Hansen, 1984; Jonsson *et al.*, 1990; Antonsson & Gudjonsson, 2002). Fish typically stay in the ocean for 1-3 years (Klemetsen *et al.*, 2003), where the majority of growth occurs (e.g., Cairns, 2003; O'Connell *et al.*, 2006), before returning to their natal rivers to breed. Mature salmon return to the freshwater system in which they hatched with extremely high fidelity (Aas *et al.*, 2010). Sea age (the number of years spent at sea) and climatic conditions are among the factors that influence when salmon migrate upstream into freshwater tributaries to spawn (Smith, Smith, &

Armstrong, 1994; COSEWIC, 2010; Valiente, Juanes, & Garcia-Vaquez, 2011). Salmon may begin to return from the ocean in late spring (May-June) and continue to enter river systems through October to early November (Cairns, 2003; Chaput & Douglas, 2012). This migration is referred to as a salmon run, and run timing and length vary by system. Spawning occurs in the fall regardless of when salmon return (Scott & Crossman, 1973; Cairns, 2003). Atlantic salmon are iteroparous and may undergo additional ocean migrations and return to their natal rivers to spawn after their first breeding event. Two important environmental factors influence the return timing of salmon from the ocean: temperature and river discharge. I will discuss these factors in turn below.

Environmental factors influencing migration

Higher water temperatures increase the energetic costs of swimming in both juvenile and adult salmon, which could have implications for migration (Enders *et al.*, 2005; Lennox *et al.*, 2018). Lennox *et al.* (2018) note that this increase in energy expenditure could influence characteristics such as run timing or instances of iteroparity in Atlantic salmon, but suggest that more work needs to be done in this area. It is well established that juvenile salmon in fresh water make use of cool refuges during high temperature events, but increasing temperatures threaten the presence of thermal refugia, which may limit the ability of salmonids to adapt to rising temperatures (Breau, *et al.*, 2007; Daigle *et al.*, 2015; Kurylyk *et al.*, 2015). Some species of salmon in the Pacific have been shown to exhibit this thermoregulatory behaviour as adults, and aggregating in cool refuges allows them to maintain a body temperature that is lower than the ambient water temperature and expend less energy on migration (Berman & Quinn, 1991; Snyder *et al.*, 2022). Recent work on adult Atlantic salmon in Quebec (Frechette *et al.,* 2018) and in the Miramichi

(Carrow, 2021) has found that adults also make use of thermal refugia, but work on adults is limited.

Temperature stress in salmon can have complex effects; for example, a study conducted in Margaree, NS, found that increased temperature aided in post-exercise recovery in Atlantic salmon but was positively correlated with post-exercise mortality (Wilkie *et al.*, 1997). There are many studies that examine the relationship between smolt migration and temperature (e.g. Hvidsten *et al.*, 1998; Vollset *et al.*, 2021; Frechette *et al.*, 2023), whereas far fewer investigate the effects of temperature on adults returning to spawn. A delay in the first day of salmon catch has been found in populations at the southernmost edge of the European distribution, which are most vulnerable to climate change, and this delay has been attributed to increasing freshwater temperature (Valiente *et al.*, 2011). Jonsson *et al.* (2007) found that when comparing eight rivers in Norway, fish from the more northern populations entered the river at higher temperatures than those from the southern populations. Thus, while there appear to be relationships between return dates of salmon and river temperatures, the effects of temperature vary among populations.

In addition to temperature, river flow is a primary influence on upstream migration timing in many salmon populations (e.g. Smith *et al.*, 1994; Trepanier *et al.*, 1996). Salmon typically show increased river entry during periods of increasing flow (Smith *et al.*, 1994; Jonsson *et al.,* 2007). This is especially true in small systems with physical barriers and high predation rates at low water levels (Smith *et al.*, 1994). Extreme flow rates, however, decrease entry, likely as a result of the increased energetic cost of swimming (Enders *et al.*, 2005; Jonsson *et al.,* 2007). Jonsson *et al.* (2007) reported that the influence of environmental conditions seemed to decrease with

increasing latitude in Norwegian populations, indicating that populations closer to the southern edge of the species distribution are more heavily influenced by factors such as temperature and flow. A recent study suggests that salmon populations with short migration windows may have more difficulty adapting to changes in the environment due to poor adaptability and a dissonance between external conditions and internal (hormonal) motivation to migrate, which may lead to migration during non-optimal conditions (Arevalo *et al.*, 2021). Because river discharge rate is associated with migration timing, size, age at maturation, and repeat spawning in salmon (Jonsson, Hansen, & Jonsson, 1991; Smith, Smith, & Armstrong, 1994; Thorstad *et al.*, 2008), the effects of climate change on flow (i.e., through precipitation and melting events) could influence biological characteristics of Atlantic salmon populations.

Study system

The Miramichi River, located in central New Brunswick, is the second largest river in Atlantic Canada, with a maximum axial length of 250 km and drainage basin of 14 000 km^2 (Cunjak & Newbury, 2005). It is considered to have the largest Atlantic salmon run in Eastern North America (Cunjak & Newbury, 2005; Chaput & Benoit, 2012), and is one of few index rivers in Atlantic Canada that has a good demographic time series dataset. Its two major branches, the Northwest (NW) branch and Southwest (SW) branch, drain into a common estuary that leads to the Gulf of St Lawrence (Chaput & Douglas, 2012).

Unlike many other Atlantic salmon populations in Eastern North America, salmon in this system return from the ocean in a bimodal fashion, with "early" (spring) run fish returning prior to September 1st and "late" (fall) run fish returning September 1st onwards (Chaput, 2010). Salmon

who mature for one year at sea before returning to spawn are referred to as grilse, or one sea winter (1SW) fish, while others may stay for two years (2SW) or longer (MSW – multi-sea winter; Gardner, 1976). Size classifications defined for commercial fisheries are relevant when discussing salmon biology, as they often relate to age and repeat spawning classifications. These classifications designate "small" salmon as fish with a fork length (the linear distance from the tip of the snout to the fork in the tail) less than 63cm – these are typically grilse, though a proportion of small salmon may be 2SW fish. By contrast, "large" salmon – those with a fork length of 63cm or greater – are typically MSW fish. Large salmon may consist of varying proportions of maiden (first-time) and repeat spawners of varying age compositions (Moore *et al.*, 1995; Chaput *et al.*, 2016). Size at maturation can have effects on survival and fecundity, whereby large/older fish typically have higher fecundity than small fish (Thorpe *et al.*, 1984; Fleming, 1996). In addition to increased fecundity, the number of large salmon in a population has implications for population growth through repeat spawning, which allows individuals to contribute to the population multiple times. Returning fish are more fecund as a result of increased growth, and repeat females have been shown to have significant reproductive contributions (Moore *et al.*, 1995). Unlike fecundity, instances of repeat spawning decrease with increasing body size, likely due to higher energy expenditure and increased mortality in larger fish (Jonsson *et al.*, 1997; Fleming, 1998; Klemetsen *et al.*, 2003).

Thermal limits for adult salmon in the Miramichi are defined as minimum temperatures exceeding 20°C for reconditioning/recovery from stress, maximum temperatures exceeding 23°C, which may act as a thermal migration barrier where fish will slow migration and seek out cooler water, and a functional lethal temperature of 25°C (Breau, 2013). The Miramichi river can

reach temperatures outside of the tolerance range for Atlantic salmon in the summer, meaning that the presence of thermal refugia for salmonids is critical, particularly for those returning in the spring (Daigle *et al.*, 2015). Water temperatures in the Miramichi are predicted to increase by at least 0.7°C within the next 30 years (El-Jabi *et al.*, 2014), and river discharge is expected to increase, with flooding occurring earlier in the season (El-Jabi *et al.*, 2016). It is therefore essential to define how salmon populations respond to changes in ecological characteristics in the Miramichi so we might anticipate how they will react to future changes. Environmental conditions may be more influential for one run than the other. Early run fish are expected to encounter higher temperatures than the late run, while late run fish migrating after the summer should be able to avoid high temperatures during migration later in the season, but may be subject to low flows as a result of heightened temperatures early in the season.

Project Overview & Objectives

The primary objectives of this project are to examine past trends in the run timing of Atlantic salmon in the Miramichi River and to assess the relationship between entry from the ocean and ecological variables in freshwater. This project examines how run timing relates to size class, water temperature, and river discharge in the returning freshwater phase of the salmon life cycle. This was completed using seven decades of salmon catch data (1952-2021) collected by the Department of Fisheries and Oceans (DFO). As one of the primary index rivers in Eastern North America, this population will provide information that may be applicable across the broader region. This work is a first step in a comprehensive approach to the assessment of changes that have occurred in Atlantic salmon populations returning to Canadian rivers. Highlighting the changes that have occurred in this system and the influence of climatic factors can help with management and conservation of populations in Atlantic Canada.

In this project, I will examine whether the median date of return to the estuary, first and last day of migration, and run duration have changed over the last seven decades. Further, I will assess whether small and large salmon within each of the runs differ in these characteristics. In line with previous work in other systems, I predict that increasing river temperature will be associated with delayed river entry in the early run and shorter run length for both the early and late runs. I expect to see an increase in migration at higher flow, but decreased migration during extreme flow, which is defined as rates over 60 m/s^3 for this project (as outlined in the methods). Catch should increase with increasing temperature to an optimum, after which it should decrease. I anticipate that temperature will influence run timing more strongly than flow in the early run, where temperatures are higher, and that the early run will respond more strongly to changes in environmental conditions than the late run. I predict that in both runs the interactive effects between river temperature and river discharge will be a strong predictor of salmon migration timing in the Miramichi River.

METHODS

Atlantic salmon dataset

Atlantic salmon catch data in the Miramichi River were collected by DFO. The available time series spans from 1952-2021, excluding 1953. Fish were collected in T-trap design trapnets, which are made of twine or mesh and installed at depths of ~2-6m with leaders extending to shore (Chaput, 2010). The leaders corral the fish to the box, where they remain until the net is fished. Trapnet locations are shown in Figure 2. Between 1952 and 1991, data were collected only at the Millbank trapnet (M14) in the main branch of the river. In 1991 the trapnet was only operated Monday through Friday, while in all other years the trapnets were fished daily.

In 1992 DFO began separate branch assessment for the Northwest and Southwest branches of the Miramichi estuary. Northwest branch data were obtained from Eel Ground (M15) between 1992 and 1997, after which the Cassilis trapnet (M05) was established, which is currently in use for the NW branch. The Eel Ground trap is operated by Eel Ground First Nation (Chaput, 2010). In the Southwest branch, an enclosure (M23) trapnet was used in 1992 and 1993. The current trapnet at Millerton (M26) was established in 1994 and is still currently in use. NW and SW catch values were combined for analyses from 1992-2021. There were four years of overlap among the trapnets in the Northwest and Southwest branches and the Millbank trapnet (1985, 1986, 1987, & 1992). Two-sample Kolmogorov-Smirnov tests were used on the cumulative count ratio within the early and late runs for these years between the Millbank and branch trapnets to determine whether the branch trapnets were appropriate to use in the time series (P>0.8 for all years).

Due to the size of the river, it is not possible to obtain absolute counts of salmon, and thus runs were sampled using partial capture techniques (Chaput, 2010). Fork length was measured for up to 30 grilse per day and for all large salmon (Chaput *et al.*, 2016).

Environmental variables

Water temperature

Water temperature data were not available for the entire time series. The best available data covering the entire time series were historical air temperature datasets from Environment and Climate Change Canada (ECCC). Air temperatures from 1952-1993 were obtained from the Miramichi A station (Climate ID 8101000; Figure 2), and temperatures from 1994 onwards were obtained from the automated Miramichi RCS station (Climate ID 8100989; Figure 2), which was installed in the same location as the original Miramichi A. Data from both stations were used to cover the entire time series. The datasets used from these stations include daily minimum, mean, and maximum air temperatures in °C. Temperature data are not available for September and October 1991, and are therefore missing from the time series.

A predictive water temperature model established for the Miramichi River by Caissie *et al.* (1998) was used to convert the air temperature datasets to approximate water temperatures. The calculated water temperatures are the sum of a baseline annual cycle for water temperature ($TA_w(t)$) and a short-term component based on air temperature ($R_w(t)$):

$$T_w(t) = TA_w(t) + R_w(t)$$

The annual component for air and water temperatures are calculated using the following equation:

$$TA(t) = a + b \sin \frac{2\pi(t-t_0)}{365}$$

where *a* and *b* are coefficients for mean temperature and seasonal cycle, respectively. The coefficients used for this project are those from Brodeur *et al.* (2015) in their report on predictive water temperature modelling in the Miramichi. The short-term component was calculated using air temperature and the calibrated regression coefficients for the day of observation (t) and the two preceding days:

$$R_w(t) = a_1 R_a(t) + a_2 R_a(t-1) + a_3 R_a(t-2)$$

where R is the difference between the observed air temperature and the value predicted by the annual cycle for air temperature. These models were calibrated using 20 years of air and water temperature data. The regression coefficients used in these calculations and detailed root mean square error/performance values/calibration methods can be found in Brodeur *et al.* (2015).

Water temperature data used in analyses were calculated using this predictive model with ECCC air temperature data. Mean water temperatures and the critical value physiological value for minimum temperatures over 20°C and maximum temperatures over 23°C were used in analyses.

River Discharge

River discharge data reported as rates (m^3/s) were obtained from ECCC historical hydrometric data (available at https://wateroffice.ec.gc.ca/map/index_e.html?type=historical). The sites used in this project are Little Southwest Miramichi River at Lyttleton (01BP001; Figure 2), which has data from the mouth of the NW branch, and Southwest Miramichi River at Blackville (01BO001; Figure 2), which has data from the SW branch. The Lyttleton site is situated near the NW trapnets (M05 & M15), while the Blackville site is adjacent to the SW trapnets (M26 & M23).

The NW site had data annually from 1951-2020, while the SW site had data from 1961-2020. Data for 2021 were not publicly available, therefore this year is excluded from flow analyses. Because salmon migrate up both the NW and SW branches of the river, the two sites were compared to ensure that the flow rates at both sites followed the same intra-annual patterns. Mean daily flow values from the NW and SW branches were compared and while absolute discharge values vary, there is significant correlation between the two sites. The mean correlation between individual years is 0.9; values for individual years can be found in Table 9 in the appendix. The NW (01BP001) data are used in this project to allow for analyses over the entire time series.

Statistical Analyses

All statistical analyses were conducted using RStudio Version 2022.02.03+492 "Prairie Trillium" for MacOS with R version 4.2.0 (R Core Team, 2022).

Run timing

Runs in the Miramichi are defined as being before or after September 1st (early/spring and late/fall runs, respectively). In 2020 the trapnets were not operated prior to September due to the Covid-19 pandemic, and as a result this year is excluded from run timing analyses. Analyses were carried out using daily catch data to characterize the two runs. Modality and skewness for run distribution were calculated using the LaplacesDemon (Statisticat, 2021) and moments (Komsta & Novomestky, 2022) packages in R. A generalized additive model (GAM) was used with the mgcv package (Wood, 2011) to assess whether changes in skewness over time were significant. Model comparisons of generalized linear models (GLMs) including run (early and late) and year as interactive effects on median return and run length were used to determine

whether these features differed between the two runs. A gaussian distribution was used for the response variable. Differences in median return dates over the time series for early and late runs, both overall and for small/large fish separately, were assessed using generalized additive models. Changes over time for date of first catch and date of last catch (as day of year – DOY) of each run were assessed using GAMs. Annual length of the early and late runs over the time series, calculated as the difference between the day of first and last catch, were analyzed using GLMs.

Environmental variables

Annual changes in minimum, mean, and maximum water temperatures were assessed using GLMs. Mean temperatures for early (weeks 18-34) and late (weeks 35-46) runs were analyzed independently because of differences in run characteristics (see Results). Behavioural thermoregulation, where salmon actively seek refuge from high temperatures, has been observed in Atlantic salmon at 23°C and when there are consecutive days over 20°C (Frechette *et al.*, 2018); thus, the number of days in a year over critical temperature limits of 20°C and 23°C were evaluated using GLMs. Although maximum temperature over 25°C is the critical critical limit for the system, 23°C is used in this project as a proxy for whether behavioural thermoregulation may occur. This threshold has been defined as a potential thermal barrier to migration in the Miramichi, where fish may delay migration (Breau, 2013; Brodeur *et al.*, 2015).

Annual changes in mean and maximum discharge rates were assessed using GLMs. These analyses used the mean annual values within the early and late runs. Discharge rates were grouped as low, high, and extreme flow to examine the number of fish caught across flow regimes. Flow regime was primarily grouped based on average values for days where fish were

migrating/trends in the river, where the low flow limit was set just below the mean and high flow was capped above the 3rd quartile. Values from previous work in other systems (Jonsson *et al.,* 1991; Smith *et al.*, 1994) were also considered when determining category values. Low days were categorized as those with NW flow rates of 20m^3/s or slower, while high and extreme were categorized as 20m^3/s-60m^3/s and greater than 60m^3/s, respectively. Flow is reported for the NW site, which can reach rates of over 800m^3/s. Differences among flow groups and between runs were compared using a two-way ANOVA and post-hoc analysis.

Size class

The size ratios (large:small) of salmon caught within the early and late runs were compared using two-sample Kolmogorov-Smirnov tests to determine whether there were differences in size class returns between the early and late runs. Model comparison among linear models for the run timing metrics described above that included size (small and large) as an interactive effect with year was used to determine that analyses would be run separately on small and large fish within the early and late runs.

Environmental variables as predictors of run timing and duration
To examine patterns among years, the relationships between number of days in a year with temperatures over 23°C and median return date and length of annual run were assessed using GLMs. Average annual temperature in May and June were assessed against the first day of annual catch in the early run to determine if river temperature at the onset of migration influenced return timing. Average annual temperatures in September and October were assessed

against the last day of catch to determine if river temperature at the end of the period influenced the last day of return timing.

To determine whether temperature or flow affected salmon movement, the combined effects of temperature and river discharge on daily catch values were examined using generalized linear mixed models (GLMMs) with the lme4 package (Bates *et al.*, 2015). The fit was assessed by examining the residuals and comparing between models. These models examined the response of catch, which represents migration behaviour, to the predictor variables of discharge rate (low, high, or extreme) and mean daily water temperature. Year was included as a random effect in all models. The quadratic and linear terms for temperature were included, as it was predicted that catch would increase with increasing temperature to an optimum, after which it would decrease. For these analyses the log10 values of catch were used. As stated in the introduction, I predicted that there would be an interactive effect between temperature and river discharge rate. Akaike Information Criterion (AICc) was used for model selection. Analyses were run separately for early and late run, as well as for large and small fish.

RESULTS

Run timing and duration

Atlantic salmon run timing in the Miramichi River is characterized by a bimodal return distribution, with an early/spring run that has a peak return density between May-August and a late/fall run that has a peak return density between September-November. The density curves for 57 of the 68 years observed had two distinct modes in their distribution (Figure 3). The skewness of each annual return density is shown in Figure 4A. Skewness changed significantly across the time series in a non-linear fashion (t = 3.631, p = 5.76e-04). The years from 1952-1967 have consistent negative skew values, indicating higher catch in the trapnets in the late run during those years. In 1968 and beyond catch bias is more skewed towards the early run. Catch was historically higher in the late run than the early run, but switched to an early run bias in the 70s-80s and has since become more variable (Figure 4). Variation from the median return date changes significantly across years (Figure 4B), and Bartlett's tests found significant differences in the variance across years within both runs (x^2=13681/15446, p < 2.2e-16).

Linear models looking at run timing factors (median return date, run duration) with run as an interactive effect determined that patterns of return are different in the early and late runs (Table 1); thus, runs were analyzed independently in subsequent analyses including size and environmental variables. The length of both runs has decreased across the time series, and the rate of change is different between the early and late run (Table 2, Figure 5C). Median return date varies between years, and as with run duration, there are differences between runs (Table 2, Figure 5D). The first day of catch in the early run and the last day of catch in the late run, which

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represent the first day of catch and last day of catch for the year, have both changed significantly in a non-linear fashion (Table 2, Figure 5A, Figure 5B).

Environmental variables

Model comparisons for environmental variables with year and run as interactive effects showed that conditions differ between the early and late runs (Table 3). Mean values for minimum, mean, and maximum annual water temperature in the early run increased by approximately 0.01°C/year (Table 4, Figure 6A). Average water temperature in the late run increased by approximately 0.01°C/year for minimum temperature and 0.02°C/year for mean and maximum temperatures (Table 4, Figure 6B). The number of days in the Miramichi with minimum water temperatures over 20°C and maximum water temperatures over 23°C increased in the early run, but there were no changes observed in the late run (Table 4, Figure 7). Because only two years in the late run had days with a minimum temperature over 20°C, this metric was excluded from further analyses.

In contrast with temperature, there were no significant changes in mean or maximum flow rate over the time series for early or late runs (Table 4, Figure 8). The number of days per year in each flow group are shown in Figure 9. A two-way analysis of variance (ANOVA) showed significant variation among the groups (F = 23.442, *df* = 2, p = 2.579e-10). Post-hoc analysis showed that between the early and late runs, there were significant differences for number of days with high (p = 2.6e-06) and extreme (p = 1.4e-09) flow, but not low flow (p = 0.320). Within the early run, there was significant variation between number of days with extreme flow and both low (p = 5.7e-09) and high (p = 2.2e-04) flow, but no significant variation between days with low and high flow (p = 0.305). Within the late run there was significant variation

between days with low and high flow (p < 2e-16), between days with low and extreme flow (p < 2e-16), and between days with high and extreme flow (p = 1.8e-07).

Salmon size – relationship to run timing

The ratio of large to small salmon returning to the Miramichi has changed significantly between 1952-2021 in a non-linear fashion (Table 5, Figure 10). The ratio of large to small fish is generally higher in recent years than earlier years with the exception of the earliest years (1952-1960) for the late run; however, overall catch is lower in recent years for both size classes (Figure 10). Kolmogorov-Smirnov testing shows that the ratios are significantly different between the two runs (p = 4.334e-08), and the ratio of large to small salmon is higher in the late run than the early run (Figure 10). As predicted, models including salmon size as an interactive effect showed that small and large salmon have different return behaviours in the early and late runs (Table 6). The patterns within each run were, therefore, also assessed by size.

The relationship between median return date of fish caught in the trapnet is significant and non-linear for all fish (Table 2), with the most change occurring for large fish in the early run (Figure 11D). Changes in the first day of return are significant for large fish in the early run, but not for small fish (Table 2, Figure 11A). Changes in the last day of return are significant for small and large fish in the late run and follow a similar pattern in both groups, whereby current migration ends earlier than it has historically (Table 2, Figure 11B). Changes in the length of the run are significant for large fish in the early run and small and large fish in the late run, with a decrease of approximately 0.2 days per year for all groups (Table 2). There have been no significant changes in run length for small fish in the early run. Run length for large fish in the early run has

decreased from approximately 110 days in the 50s to approximately 90 days in the 2010s, while run lengths for large and small fish in the late run have decreased from approximately 60 days in the 50s to approximately 50 days in the 2010s (Figure 11C).

Run timing and temperature

In contrast to my prediction, there were no significant relationships found between the first day of return and average temperatures in May or June (Table 7, Figure 12A, Figure 12B). There were also no relationships found between the last day of migration and average temperatures in October and November for small or large fish (Table 7, Figure 12C, Figure 12D). No significant relationships were found between the number of days with maximum temperatures over 23°C and median return date in the early run (Table 7, Figure 13A) or with length of either run (Table 7, Figure 13C, Figure 13D) for fish of either size. There was a weak relationship identified for median return date of small fish in the late run and number of days with maximum temperatures over 23°C, where median return date is delayed by ~1 day for every day over 23°C, and no relationship was found for large fish in the late run (Table 7, Figure 13B).

Interactive effects of river temperature and discharge on catch

Based on AIC values, the best models for small fish included the interaction between flow and both the linear and quadratic terms for temperature (Table 8). The best models for large fish included the linear and quadratic terms for temperature and the interaction between flow group and the linear term (Table 8). Catch (migration) generally increases to an optimum average water temperature, after which it declines (Figure 14, Figure 15). Catch occurs at higher temperatures in the early run than the late run. Catch is estimated to be lower in the extreme flow group and

similar within the low and high flow groups for all fish, but may be higher for large fish in the early run at low temperatures (Figure 15). The mixed models have marginal R^2 values of 0.080 for small fish in the early run, 0.160 for small fish in the late run, 0.018 for large fish in the early run, and 0.149 for large fish in the late run. The low marginal R^2 values for all models indicate that the interaction between river temperature and river discharge rate are not strong predictors of salmon entry from the ocean in the Miramichi River.

Tables

Table 1. Model comparisons of linear models for variables relating to run timing, length, and duration by year. Models for median return date and run duration include run (early run/late run) and year as interactive effects. Degrees of freedom (df), Akaike Information Criterion (AIC$_C$), differences between the weight of the best model and given model (ΔAIC$_C$), and model weight (ω_{AICc}) included. Best models are highlighted in bold.

Run factor	Model	df	logLik	AICc	ΔAIC$_C$	ω_{AICc}	R^2 (adjusted)
Median Return	**Run + Year**	**4**	**-452.871**	**914.0**	**0.00**	**0.616**	**0.902**
(Day of Run)	Run x Year	5	-452.266	915.0	0.95	0.384	
	Run	3	-460.982	928.1	14.10	0.001	
	Intercept	2	-610.629	1225.3	311.30	0	
	Year	3	-609.745	1225.7	311.62	0	
First day of run	**Year**	**3**	**-235.995**	**478.4**	**0.00**	**1**	**0.268**
	Intercept	2	-246.817	497.8	19.45	0	
Last day of run	**Year**	**3**	**-239.947**	**486.3**	**0.00**	**0.982**	**0.129**
	Intercept	2	-245.027	494.2	7.96	0.018	
Run duration	**Run x Year**	**5**	**-466.273**	**943.0**	**0.00**	**0.529**	**0.893**
	Run + Year	4	-467.470	943.3	0.23	0.471	
	Run	3	-483.328	972.8	29.82	0	
	Year	3	-613.432	1233.1	290.03	0	
	Intercept	2	-615.060	1234.2	291.19	0	

Table 2. Coefficients of GLMs and GAMs for the first and last day of the run, median return date, and duration of early/late runs (in days) for all fish and for small and large fish. GAMs were used for non-linear relationships. Includes the estimated degrees of freedom (edf), which approximates the degree of non-linearity in the relationship, and F value (GAMs) and estimate, standard error, t value, p-value, and adjusted R^2 value (GAMs & GLMs). Significant results are highlighted in bold and indicated with asterisks.

Run	Size	Run factor	Est	Std err	t value	edf	F	p-value	R^2 (adj)
Early	-	**Median**	194.147	0.745	260.6	13.4	3.567	**2.22e-04 *****	0.429
		First day	142.939	0.619	230.9	14.72	12.500	**<2e-16 *****	0.760
		Last day	1.065e-03	2.521e-03	0.422	-	-	0.674	-0.012
		Duration	-0.285	0.054	-5.303	-	-	**1.51-06 *****	0.294
	Small	**Median**	191.603	0.526	364.2	13.84	4.299	**4.20e-05 *****	0.463
		First day	0.014	0.052	0.272	-	-	0.786	-0.014
		Last day	1.039e-03	2.540e-03	0.409	-	-	0.684	-0.013
		Duration	-0.019	0.053	-0.364	-	-	0.717	-0.014
	Large	**Median**	185.618	1.132	164.0	14.61	7.796	**<2e-16 *****	0.627
		First day	143.231	0.640	223.6	11.12	15.950	**<2e-16 *****	0.756
		Last day	0.025	0.017	1.530	-	-	0.131	0.021
		Duration	-0.289	0.053	-5.405	-	-	**1.06e-06 *****	0.306
Late	-	**Median**	267.058	0.631	423.2	3.655	8.896	**6.05e-06 *****	0.365
		First day	-2.028e-04	3.203e-03	-0.063	-	-	0.95	-0.016
		Last day	296.727	0.823	360.7	4.23	8.564	**5.14e-06 *****	0.380
		Duration	-0.169	0.054	-3.157	-	-	**0.002 ****	0.121
	Small	**Median**	260.493	1.177	221.3	4.728	5.224	**3.23e-04 *****	0.461
		First day	2.208e-03	3.612e-03	0.611	-	-	0.543	-0.009
		Last day	295.169	0.782	377.5	5.258	9.183	**7.15e-07 *****	0.459
		Duration	-0.136	0.058	-2.323	-	-	**0.023 ***	0.064
	Large	**Median**	265.36	1.090	243.5	4.890	4.352	**0.002 ****	0.235
		First day	-0.010	0.015	-0.658	-	-	0.513	-0.008
		Last day	296.200	0.0824	359.4	2.965	10.870	**3.52e-06 *****	0.383
		Duration	-0.167	0.061	-2.720	-	-	**0.008 ****	0.091

Table 3. Model comparisons of linear models for environmental variables (temp and flow) with run (early/late) and year as interactive effects. Degrees of freedom (*df*), Akaike Information Criterion (AIC$_C$), differences between the weight of the best model and given model (ΔAIC$_C$), and model weight (ω_{AICc}) included. Best models are highlighted in bold.

Environmental variable	Model	df	logLik	AICc	ΔAIC$_C$	ω_{AICc}	R^2 (adjusted)
Minimum temperature	**Run + Year**	**4**	**-39084.14**	**18176.3**	**0.00**	**0.729**	**0.170**
	Run x Year	5	-39084.14	78178.3	2.00	0.268	
	Run	3	-39090.94	78187.9	11.60	0.002	
	Year	3	-40321.06	80648.1	2471.83	0	
	Intercept	2	-40326.96	80657.9	2481.64	0	
Mean temperature	**Run + Year**	**4**	**-41198.01**	**82404.0**	**0.00**	**0.727**	**0.160**
	Run x Year	5	-41197.99	82406.0	1.95	0.273	
	Run	3	-41213.96	82433.9	29.89	0	
	Year	3	-42344.95	84695.9	2291.87	0	
	Intercept	2	-42358.75	84721.5	2317.48	0	
Maximum temperature	**Run + Year**	**4**	**-42405.75**	**84819.5**	**0.00**	**0.719**	**0.161**
	Run x Year	5	-42405.69	84821.4	1.88	0.281	
	Run	3	-42420.90	84847.8	28.28	0	
	Year	3	-43561.14	87128.3	2308.77	0	
	Intercept	2	-43574.24	87152.5	2332.97	0	
Days with minimum over 20°C	**Run x Year**	**5**	**-367.606**	**745.7**	**0.00**	**0.843**	**0.442**
	Run + Year	4	-370.51	749.3	3.65	0.136	
	Run	3	-373.41	753.0	7.33	0.022	
	Year	3	-408.84	823.8	78.19	0	
	Intercept	2	-410.54	825.2	79.15	0	
Days with maximum over 23°C	**Run x Year**	**5**	**-458.87**	**928.2**	**0.00**	**0.846**	**0.818**
	Run + Year	4	-461.76	931.8	3.63	0.138	
	Run	3	-464.94	936.1	7.87	0.017	
	Intercept	2	-581.28	1166.6	238.46	0	
	Year	3	-580.67	1167.5	239.33	0	
Mean discharge rate	**Run**	**3**	**-543.90**	**1094.0**	**0.00**	**0.604**	**0.478**
	Run + Year	4	-543.75	1095.8	1.82	0.243	
	Run x Year	5	-543.13	1096.7	2.74	0.153	
	Intercept	2	-589.57	1183.2	89.25	0	
	Year	3	-589.49	1185.2	91.18	0	
Maximum discharge rate	**Run**	**3**	**-838.42**	**1683.0**	**0.00**	**0.659**	**0.240**
	Run + Year	4	-838.40	1685.1	2.09	0.232	
	Run x Year	5	-838.09	1686.6	3.62	0.108	
	Intercept	2	-858.58	1721.3	38.24	0	
	Year	3	-858.57	1723.3	40.30	0	

Table 4. Coefficients of GLMs for changes in environmental variables for early (weeks 18-34) and late (weeks 35-46) salmon runs in the Miramichi River, 1952-2021 (temperature) and 1952-2020 (river discharge). Results include changes in average minimum, mean, and maximum annual temperatures, changes in the number of days with a minimum temperature over 20°C and maximum temperature over 23°C, and changes in mean and maximum annual river discharge rates. Table includes estimate, standard error, t value, and p-value. Significant results highlighted in bold and indicated with asterisks.

Run	Environmental Variable	Estimate	Std Error	t value	p-value
Early	**Minimum temperature**	0.007	0.003	2.923	**0.005 ****
	Mean temperature	0.013	0.003	3.637	**5.32e-04 *****
	Maximum temperature	0.013	0.004	3.182	**0.002 ****
	Days with minimum over 20°C	0.063	0.027	2.291	**0.025 ***
	Days with maximum over 23°C	0.122	0.051	2.391	**0.020 ***
	Mean discharge rate	-0.088	0.083	-1.063	0.292
	Maximum discharge rate	-0.269	0.791	-0.340	0.735
Late	**Minimum temperature**	0.008	0.003	2.395	**0.019 ***
	Mean temperature	0.015	0.005	3.161	**0.002 ****
	Maximum temperature	0.016	0.005	3.329	**0.001 ****
	Days with minimum over 20°C	6.65e-04	9.97e-04	0.667	0.507
	Days with maximum over 23°C	0.007	0.012	0.584	0.561
	Mean discharge rate	0.030	0.068	0.436	0.664
	Maximum discharge rate	0.440	0.452	0.974	0.333

Table 5. GAM coefficients for size ratio (large:small) of Atlantic salmon returning to the Miramichi river, 1952-2021. Includes estimated degrees of freedom (edf), which estimates the degree of non-linearity in the relationship, F value, p-value, and adjusted R^2 value. Significant results bolded and indicated with asterisks.

Run	edf	F	p-value	R^2 (adj)
Early	7.377	5.381	**3.22e-05 *****	0.382
Late	7.302	3.122	**3.81e-03 ****	0.254

Table 6. Model comparisons of linear models for variables relating to run timing with size and year as interactive effects. Degrees of freedom (df), Akaike Information Criterion (AICC), differences between the weight of the best model and given model (ΔAICC), and model weight (ω_{AICc}) included. Best models are highlighted in bold.

Run	Run factor	Model	df	logLik	AICc	ΔAIC$_C$	ω_{AICc}	R^2 (adjusted)
Early	**Median return**	**Size x Year**	**5**	**-492.056**	**994.6**	**0.00**	**0.595**	**0.161**
		Size + Year	4	-493.584	995.5	0.89	0.380	
		Year	3	-497.387	1001.0	6.37	0.025	
		Size	3	-501.977	1010.1	15.55	0	
		Intercept	2	-505.177	1014.4	19.86	0	
	Run Duration	**Size x Year**	**5**	**-456.665**	**923.8**	**0.00**	**0.994**	**0.436**
		Size + Year	4	-462.899	934.1	10.30	0.006	
		Size	3	-470.254	946.7	22.89	0	
		Year	3	-490.549	987.3	63.47	0	
		Intercept	2	-495.449	995.0	71.18	0	
	First Day	**Size x Year**	**5**	**-460.162**	**930.8**	**0.00**	**0.995**	**0.414**
		Size + Year	4	-466.593	941.5	10.70	0.005	
		Size	3	-473.628	953.4	22.64	0	
		Year	3	-491.595	989.4	58.57	0	
		Intercept	2	-496.465	997.0	66.22	0	
	Last Day	**Size + Year**	**4**	**-262.816**	**534.0**	**0.00**	**0.343**	**0.072**
		Size x Year	5	-261.739	534.0	0.01	0.341	
		Size	3	-264.062	534.3	0.36	0.286	
		Year	3	-266.967	540.1	6.17	0.016	
		Intercept	2	-268.137	540.4	6.42	0.014	
Late	**Median return**	**Size + Year**	**4**	**-412.992**	**834.3**	**0.00**	**0.683**	**0.171**
		Size x Year	5	-412.486	835.5	1.16	0.357	
		Year	3	-419.246	844.7	10.37	0.004	
		Size	3	-420.091	846.4	12.06	0.002	
		Intercept	2	-425.754	855.6	21.29	0	
	Run Duration	**Year**	**3**	**-472.254**	**950.7**	**0.00**	**0.650**	**0.073**
		Size + Year	4	-472.134	952.6	1.89	0.253	
		Size x Year	5	-472.062	954.6	3.91	0.092	
		Intercept	2	-478.506	961.1	10.41	0.004	
		Size	3	-478.398	963.0	12.29	0.001	
	First Day	**Size**	**3**	**-249.622**	**505.4**	**0.00**	**0.532**	**0.022**
		Size + Year	4	-249.496	507.3	1.88	0.208	
		Intercept	2	-252.180	508.5	3.02	0.117	
		Size + Year	5	-249.180	508.8	3.41	0.097	
		Year	3	-252.060	510.3	4.88	0.046	
	Last Day	**Year**	**3**	**-452.485**	**911.2**	**0.00**	**0.611**	**0.124**
		Size + Year	4	-452.205	912.7	1.57	0.279	
		Size x Year	5	-452.050	914.6	3.42	0.110	
		Intercept	2	-462.167	928.4	17.27	0	
		Size	3	-461.926	930.0	18.88	0	

Table 7. Coefficients of GLMs for the relationship between run timing and temperature. Factors relating to run timing include first day of migration, last day of migration, median return date, length of migration, while temperature variables include mean temperatures for May and June for the first day of migration, mean temperatures for October and November for the last day of migration, and number of days with maximum temperatures over 23°C for median return and length of the run. Table includes the estimate, standard error, t value, and p value. Significant results are highlighted in bold and indicated with asterisks.

Run	Size	Run timing variable	Temperature variable	Estimate	Std Error	t value	p-value
Early	Small	First day of migration	Mean May temp	-0.173	0.8458	-0.205	0.839
			Mean June temp	-0.855	1.155	-0.741	0.462
		Median return date	No. days with max temp over 23°C	0.074	0.082	0.902	0.370
		Length of run	No. days with max temp over 23°C	-0.035	0.117	-0.301	0.764
	Large	First day of migration	Mean May temp	-0.779	1.098	-0.709	0.481
			Mean June temp	1.781	1.494	1.191	0.238
		Median return date	No. days with max temp over 23°C	-0.010	0.209	-0.050	0.960
		Length of run	No. days with max temp over 23°C	-0.101	0.141	-0.720	0.474
Late	Small	**Median return date**	No. days with max temp over 23°C	0.979	0.453	2.16	**0.035 ***
		Length of run	No. days with max temp over 23°C	0.299	0.578	0.517	0.607
		Last day of migration	Mean Oct temp	0.961	1.043	0.922	0.36
			Mean Nov temp	0.100	0.571	0.176	0.861
	Large	Median return date	No. days with max temp over 23°C	0.566	0.437	1.294	0.201
		Length of run	No. days with max temp over 23°C	-0.412	0.619	-0.067	0.947
		Last day of migration	Mean Oct temp	0.855	1.030	0.829	0.41
			Mean Nov temp	0.199	0.564	0.352	0.726

Table 8. Model comparison for mixed effects models for logged daily catch values including flow group and the quadratic and linear terms for mean water temperature. Degrees of freedom (df), Akaike Information Criterion (AIC$_C$), differences between the weight of the best model and given model (ΔAIC$_C$), and model weight (ω_{AICc}) included. Best models are highlighted in bold.

Size	Run	Model	df	logLik	AICc	ΔAIC$_C$	ω_{AICc}	R^2_m	R^2_C
Small									
	Early								
		Temp x Group + Temp² x Group	**11**	**-3486.137**	**6994.3**	**0.00**	**0.602**	**0.080**	**0.208**
		Temp x Group + Temp²	9	-3489.022	6996.1	1.75	0.251		
		Temp + Temp² x Group	9	-3489.551	6997.1	2.81	0.184		
		Temp + Temp² + Group	7	-3503.912	7021.8	27.51	0		
		Temp + Temp²	5	-3515.945	7041.9	47.57	0		
		Temp x Group	8	-3535.773	7087.6	93.24	0		
		Temp² x Group	8	-3545.458	7106.9	112.61	0		
		Temp + Group	6	-3596.938	7205.9	211.56	0		
		Temp² + Group	6	-3611.234	7234.5	240.15	0		
		Temp	4	-3618.221	7244.5	250.12	0		
		Temp²	4	-3636.303	7280.6	286.28	0		
		Group	5	-3641.892	7293.8	299.46	0		
		Intercept	3	-3687.983	7382.0	387.64	0		
	Late								
		Temp x Group + Temp²	**9**	**-2159.750**	**4337.6**	**0.00**	**0.793**	**0.160**	**0.468**
		Temp x Group + Temp² x Group	11	-2159.378	4340.8	3.29	0.153		
		Temp + Temp² x Group	9	-2162.437	4342.9	5.38	0.054		
		Temp + Temp² + Group	7	-2196.947	4407.9	70.37	0		
		Temp + Temp²	5	-2210.426	4430.9	93.31	0		
		Temp x Group	8	-2424.287	4864.6	527.06	0		
		Temp² x Group	8	-2436.436	4888.9	551.36	0		
		Temp + Group	6	-2484.920	4981.9	644.31	0		
		Temp	4	-2490.063	4988.1	650.58	0		
		Group	5	-2495.301	5000.6	663.06	0		
		Temp² + Group	6	-2495.295	5002.6	665.06	0		
		Intercept	3	-2504.502	5015.0	677.45	0		
		Temp²	4	-2503.908	5015.8	678.27	0		
Large									
	Early								
		Temp x Group + Temp² x Group	**11**	**-2512.264**	**5046.6**	**0.00**	**0.857**	**0.018**	**0.116**
		Temp² x Group	8	-2517.879	5051.8	5.20	0.064		
		Temp x Group	8	-2518.496	5053.0	6.43	0.034		
		Temp + Temp² x Group	9	-2517.639	5053.3	6.73	0.030		
		Temp x Group + Temp²	9	-2518.309	5054.7	8.07	0.015		
		Temp + Group	6	-2537.370	5086.8	40.17	0		
		Temp² + Group	6	-2537.648	5087.3	40.73	0		
		Temp + Temp² + Group	7	-2537.363	5088.8	42.16	0		
		Temp²	4	-2543.065	5094.1	47.55	0		
		Temp	4	-2543.240	5094.5	47.90	0		
		Temp + Temp²	5	-2543.062	5096.1	49.55	0		
		Group	5	-2543.477	5097.0	50.38	0		
		Intercept	3	-2552.223	5110.5	63.86	0		

| Size	Run	Model	df	logLik	AICc	ΔAIC_C	ω_{AICc}	R^2_m	R^2_C
Large									
	Late								
		Temp x Group + Temp^2	**9**	**-1884.692**	**3787.4**	**0.00**	**0.552**	**0.149**	**0.447**
		Temp x Group + Temp^2 x Group	11	-1882.933	3788.0	0.51	0.428		
		Temp + Temp^2 x Group	9	-1888.004	3794.1	6.62	0		
		Temp + Temp^2 + Group	7	-1912.832	3839.7	52.25	0		
		Temp + Temp^2	5	-1919.366	3848.8	61.30	0		
		Temp^2 x Group	8	-2118.621	4253.3	465.84	0		
		Temp x Group	8	-2130.153	4276.4	488.91	0		
		Temp^2 + Group	6	-2170.315	4352.7	565.21	0		
		Temp^2	4	-2175.032	4358.1	570.63	0		
		Temp + Group	6	-2187.319	4386.7	599.22	0		
		Group	5	-2188.764	4387.5	600.10	0		
		Intercept	3	-2191.081	4388.2	600.72	0		
		Temp	4	-2190.086	4388.2	600.74	0		
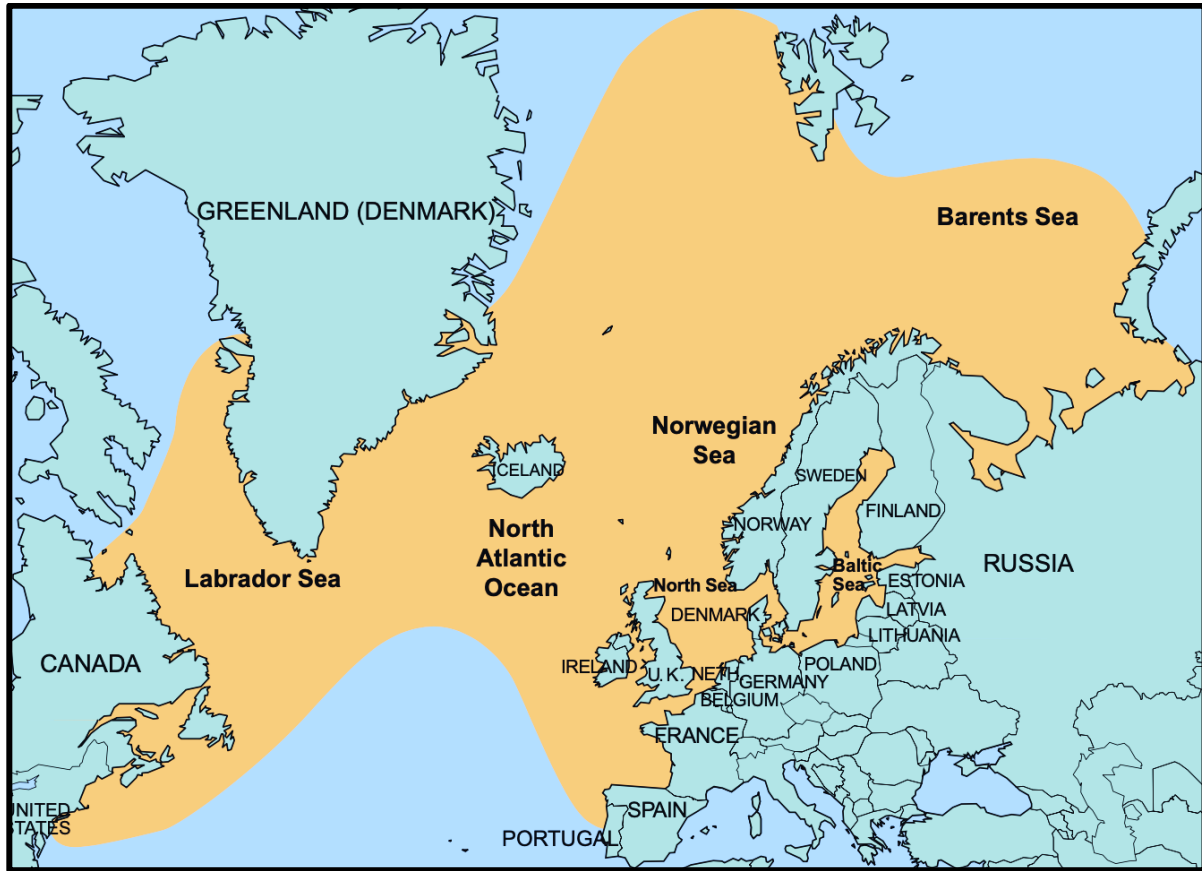
Figure 1. Assumed distribution of Atlantic salmon in the Atlantic Ocean (in yellow) and countries with spawning populations (Aas *et al.*, 2010).
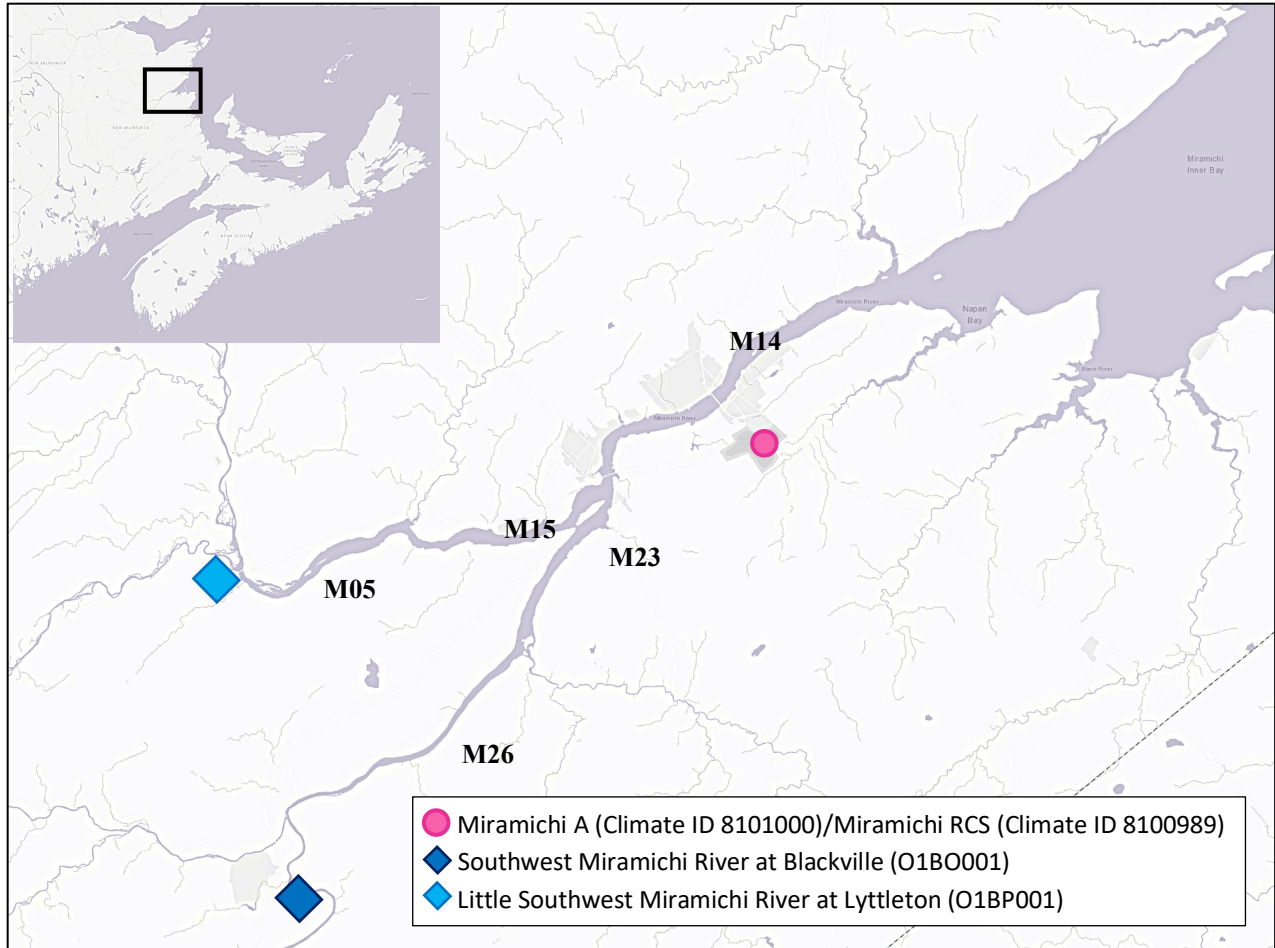
Figure 2. Map of the Miramichi River with trapnet locations numbered and environmental stations labelled. The Millbank (M14) trapnet was used prior to 1992, after which Eel Ground (M15), Cassilis (M05), Enclosure (M23), and Millerton (M26) were established as primary trapnets.
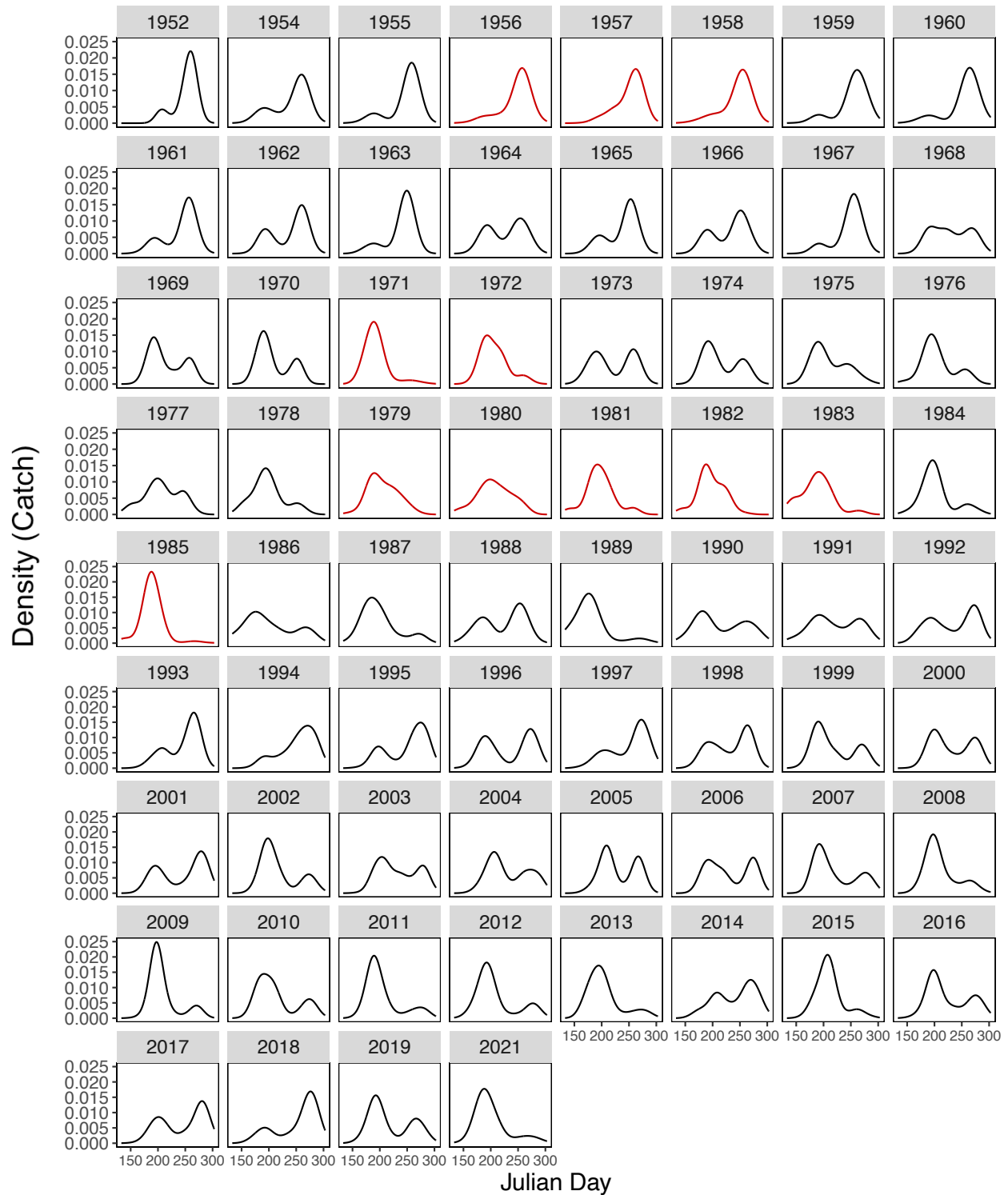
Figure 3. Annual return densities (daily catch relative to overall annual catch) by Julian day of the year for Atlantic salmon migrating into the Miramichi River estuary trapnets, 1952-2021. 2020 excluded due to missing data during the spring run. Black lines represent years with bimodal distribution, while red lines indicate years with unimodal distribution.
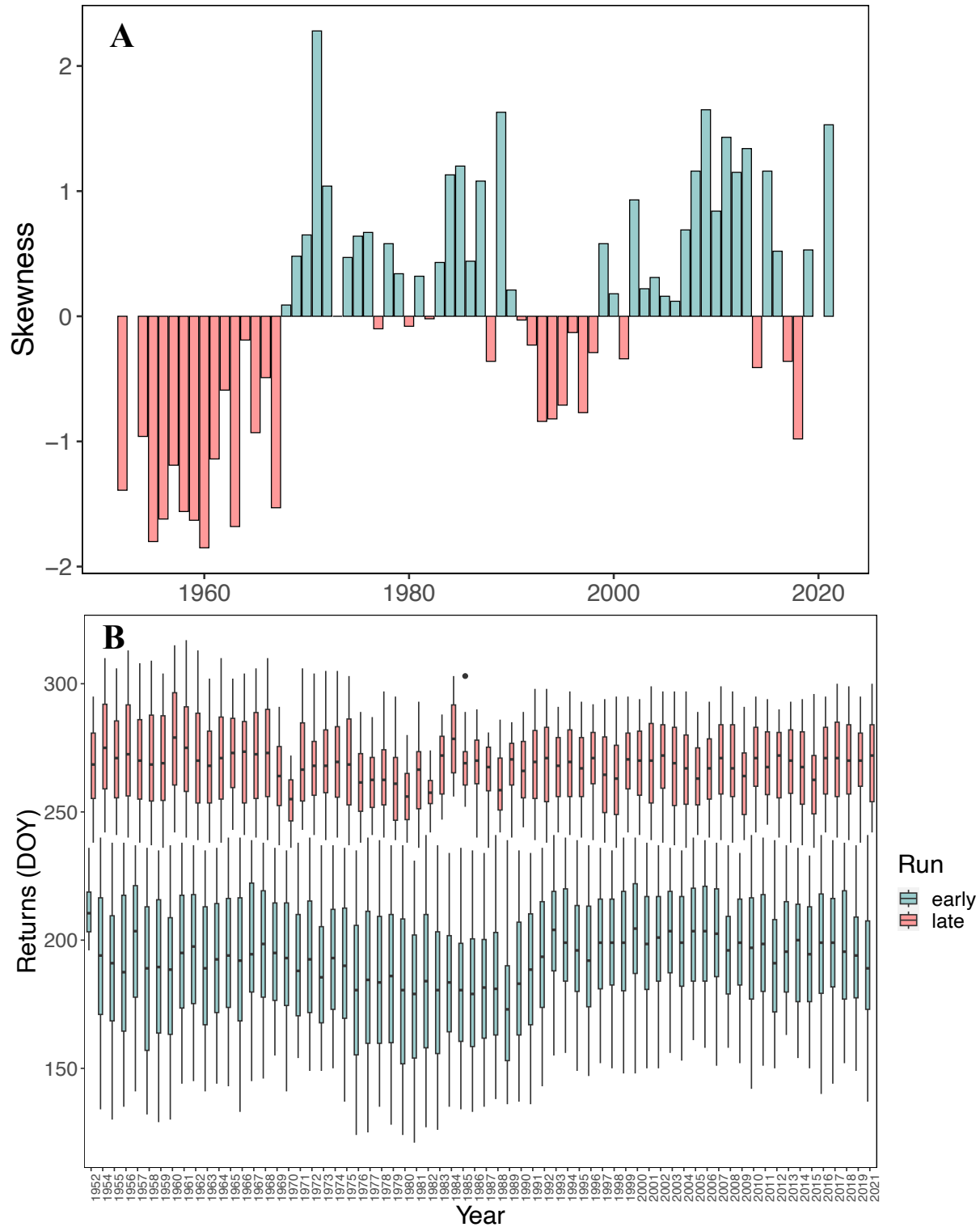
Figure 4. Skewness for return densities shown in Fig 6 (A). A positive value (blue) indicates a higher return density in the early/spring run, while a negative value (red) indicates a higher return density in the late/fall run. 2020 excluded due to missing data during the spring run. Boxplot for median return dates of salmon in the Miramichi River in the early and late runs (B).
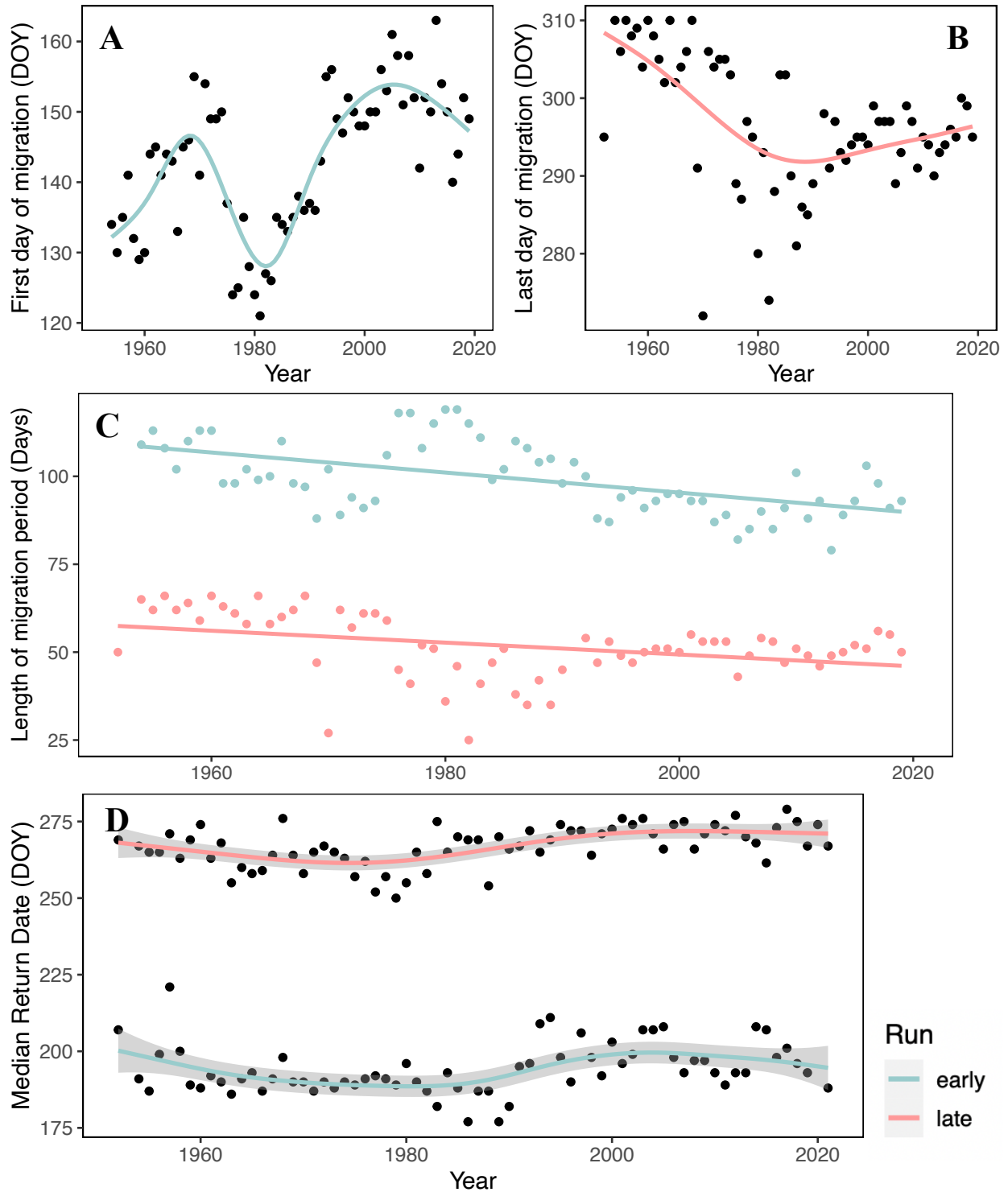
Figure 5. First (A) and last (B) days of salmon migration in the early and late runs in the Miramichi River, 1952-2021. Length of the early and late migration periods measured as the difference between the last day of migration and first day of migration, 1951- 2021 (C). Median return dates of salmon in the Miramichi in the early and late run (D).
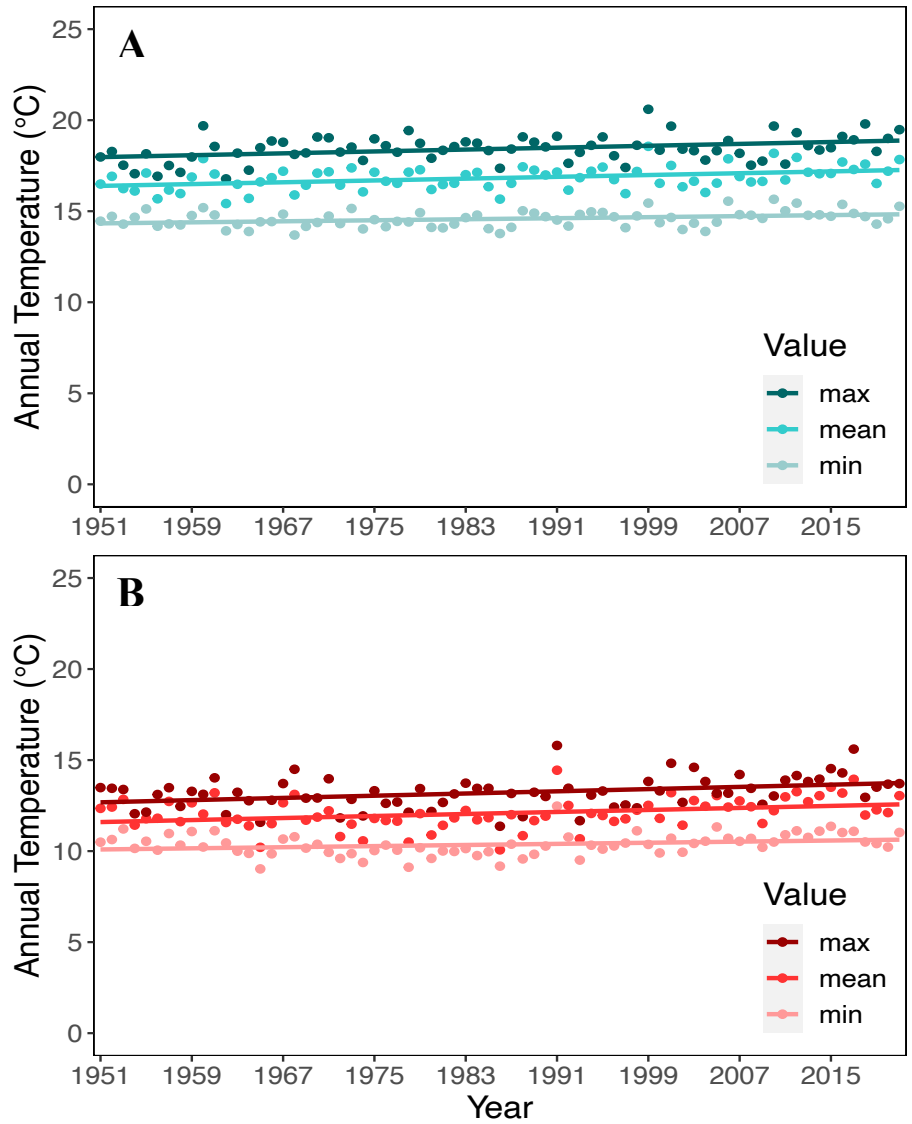
Figure 6. Mean annual water temperatures (calculated from daily minimum, mean, and maximum temperatures) in Celsius for early (A; weeks 18-34) and late (B; weeks 35-46) salmon runs in the Miramichi River, NB, 1952-2021.
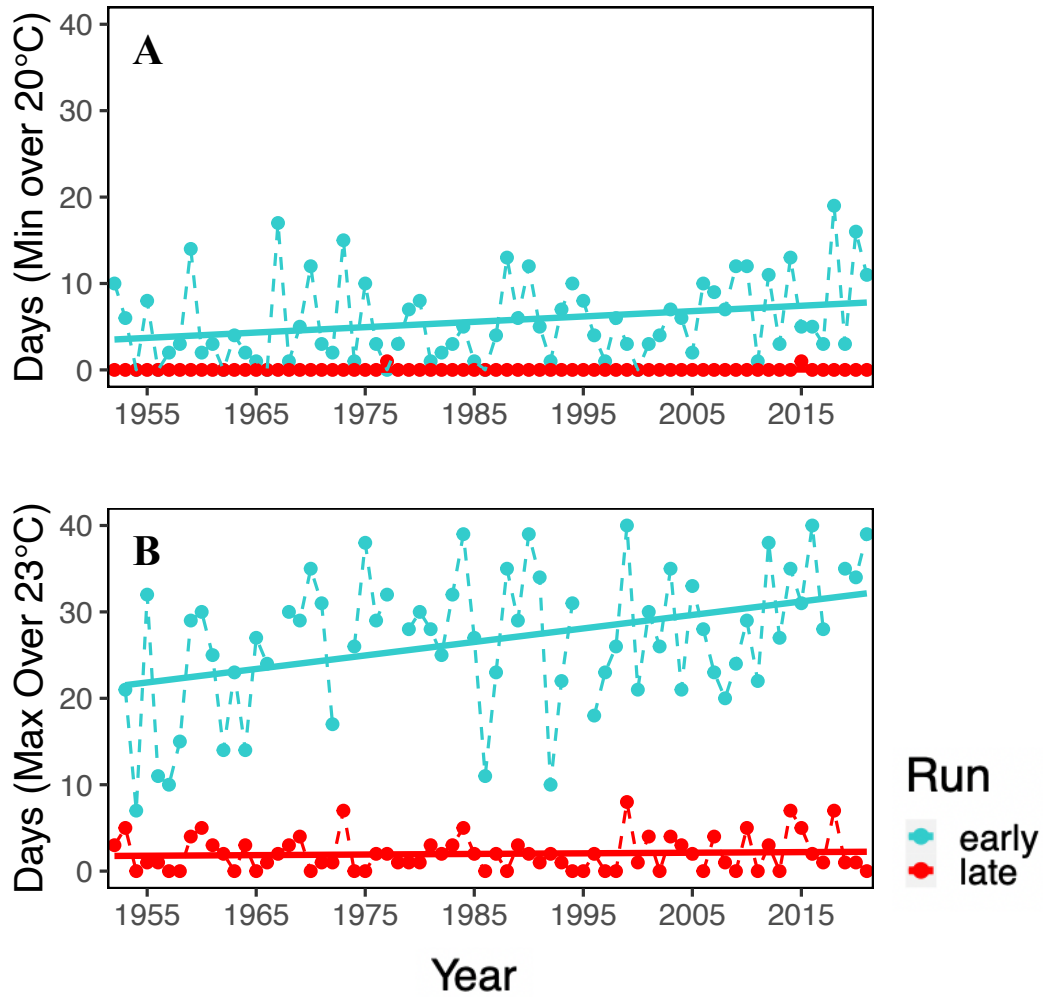
Figure 7. Number of days with minimum water temperatures over 20°C (A) and maximum water temperatures over 23°C (B) in early and late runs (weeks 18-34 and 35-46, respectively) in the Miramichi River from 1952-2021.
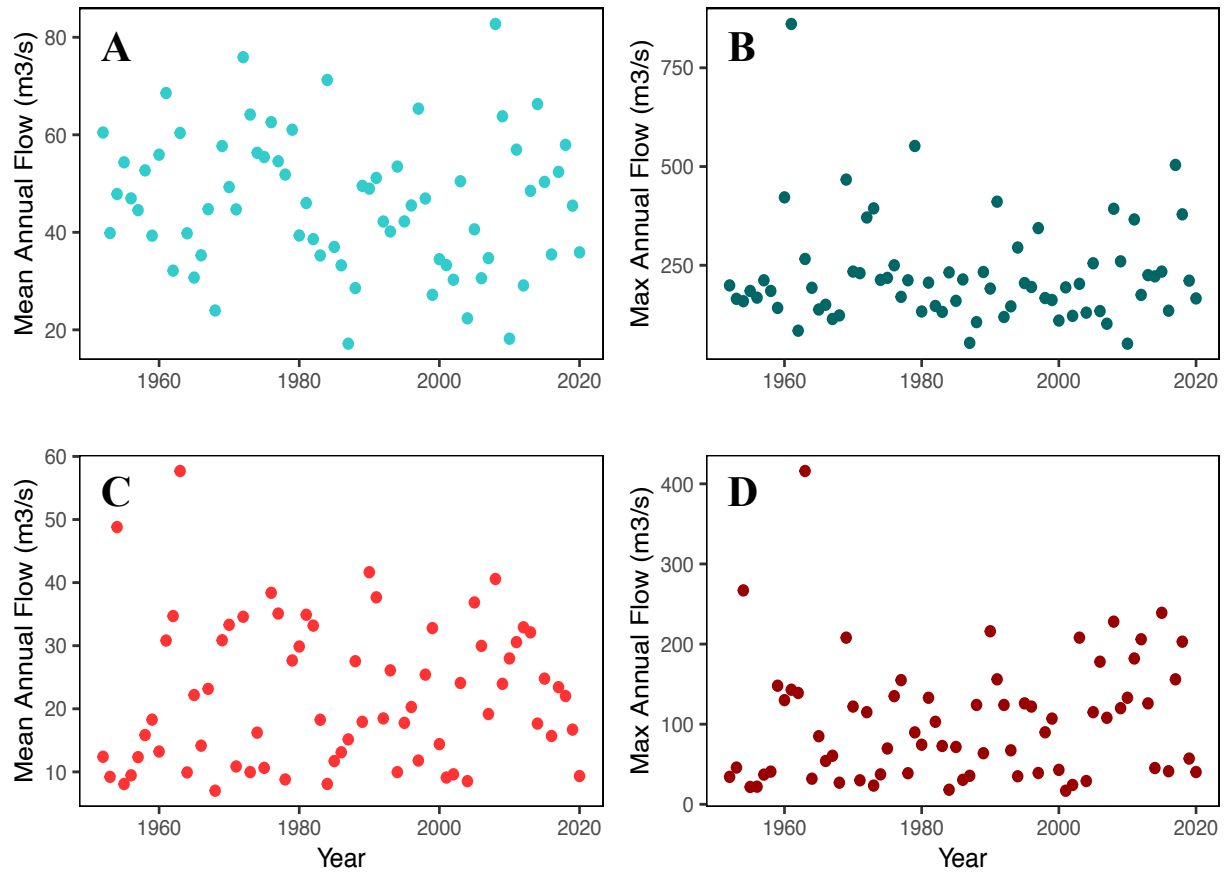
Figure 8. Mean and maximum annual flow in m^3/s during the early (A/B), and late (C/D) runs in the northwest branch of the Miramichi River (Station 01BP001), 1952-2020.
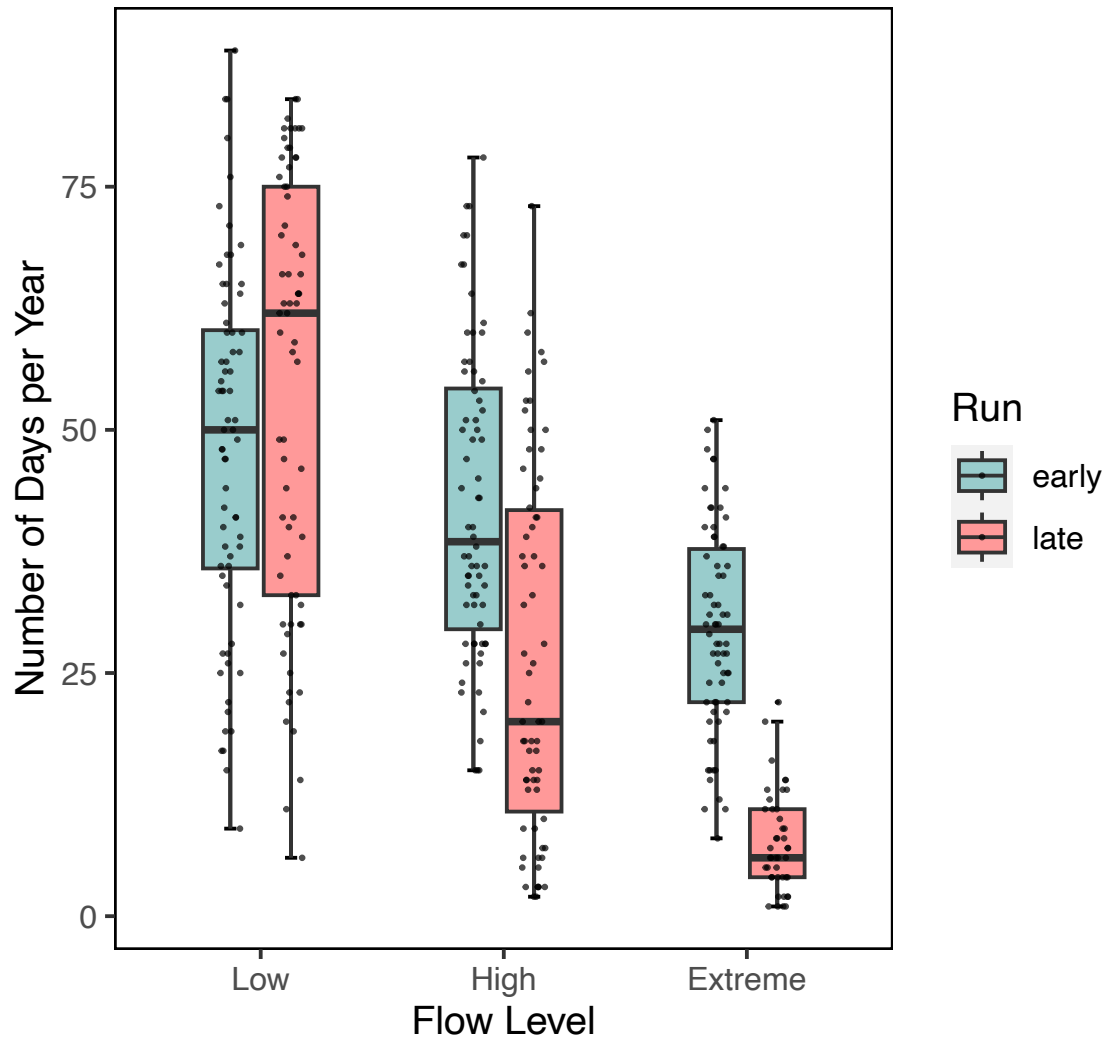
Figure 9. Number of days in each year with low (<=20m^3/s), high (20m^3/s-60m^3/s), and extreme (>60m^3/s) flow rates in the Northwest branch of the Miramichi River, 1951-2020.
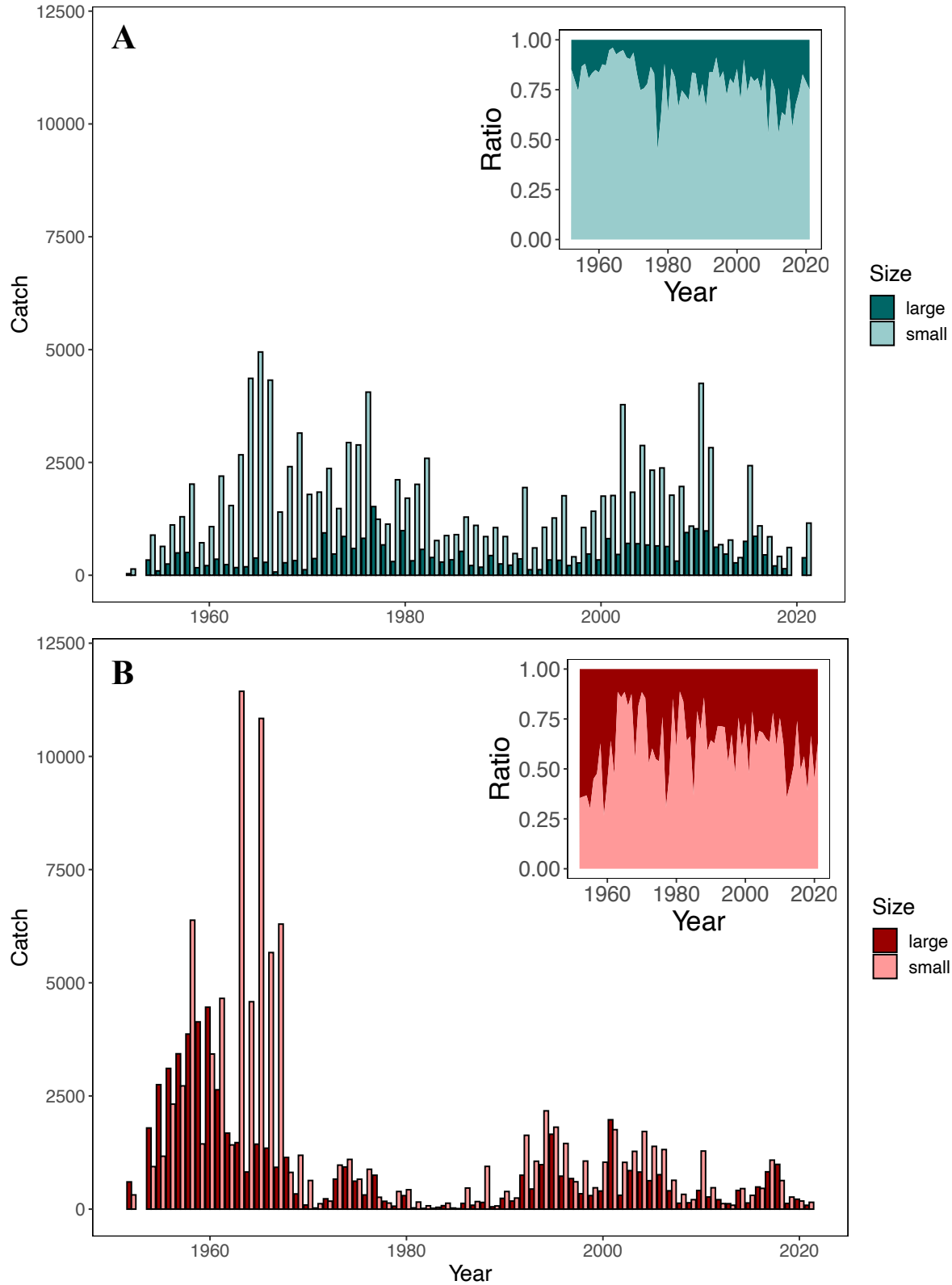
Figure 10. Number of small and large fish caught in trapnets in the Miramichi River in early (A) and late (B) runs, 1952-2021. Smaller figures show the ratio of small and large fish caught in each year.
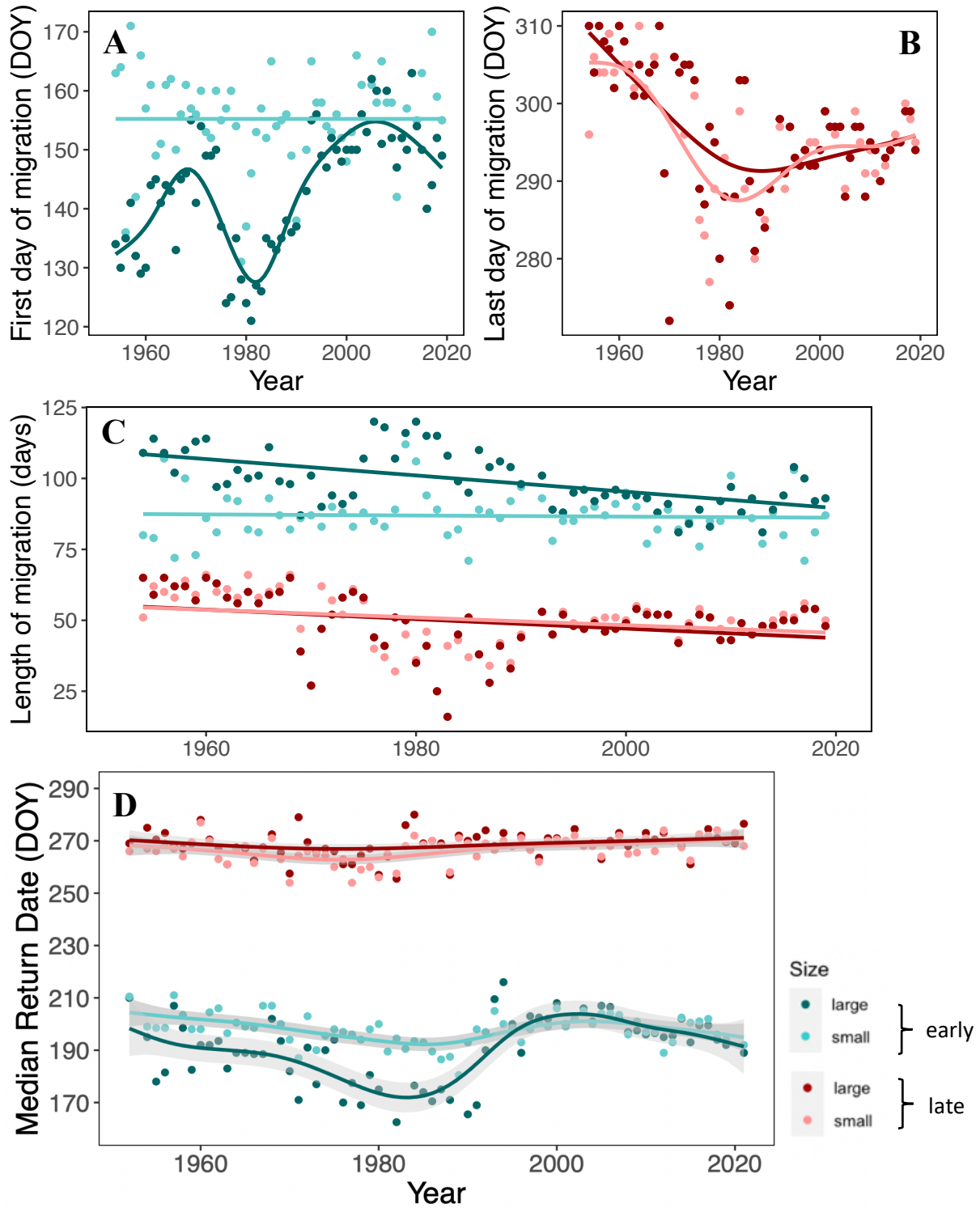
Figure 11. First (A) and last (B) day of migration for small and large salmon in the early and late runs in the Miramichi River, 1952-2021. Length of the early and late migration periods for small and large fish (C). Median return date in the early and late runs for small and large fish (D).
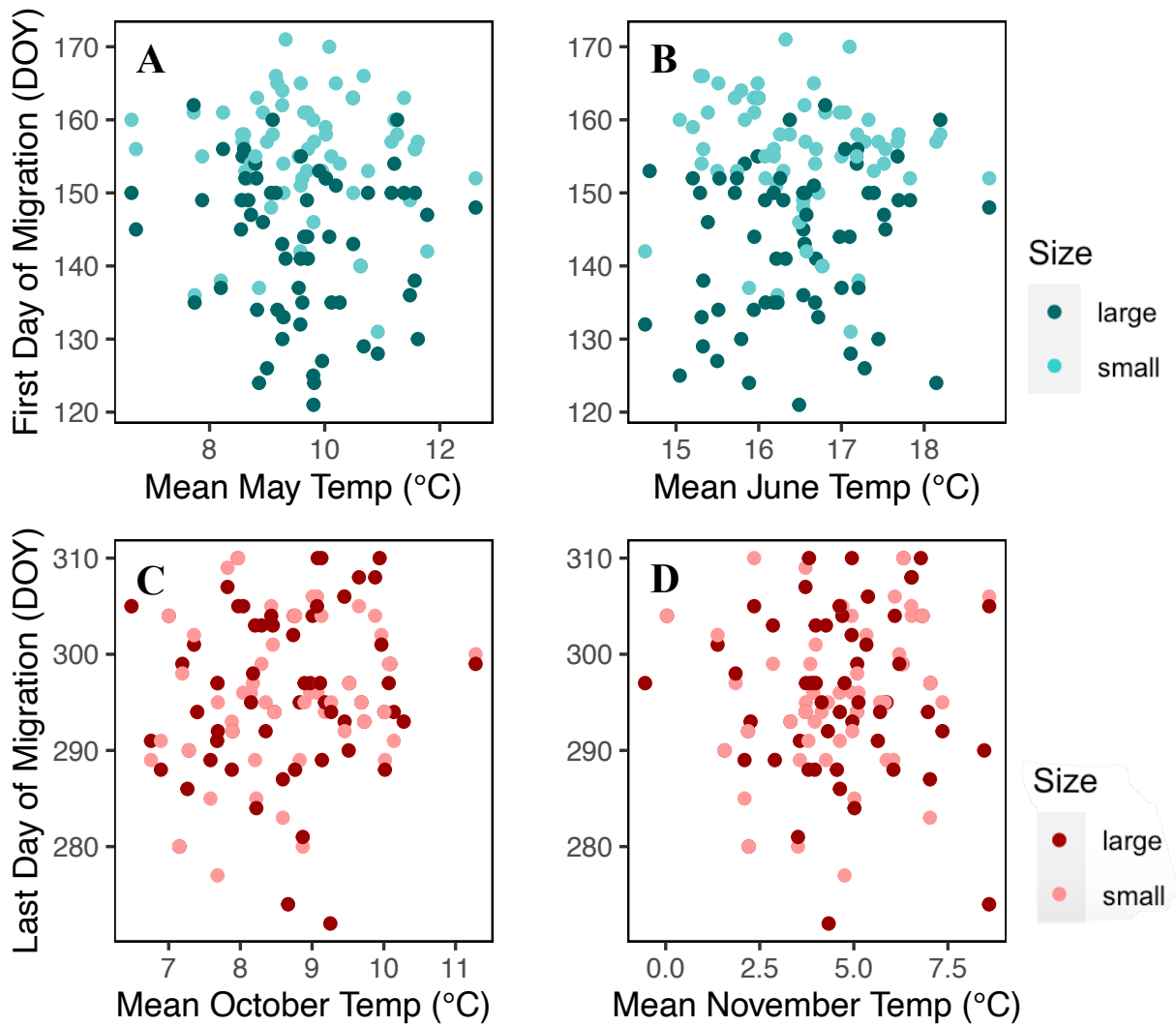
Figure 12. First day of annual salmon migration in the Miramichi River plotted against mean annual river temperature (°C) in May (A) and June (B) and last day of annual salmon migration in the Miramichi River plotted against mean annual river temperature (°C) in October (C) and November (D) for small and large salmon, 1952-2021.
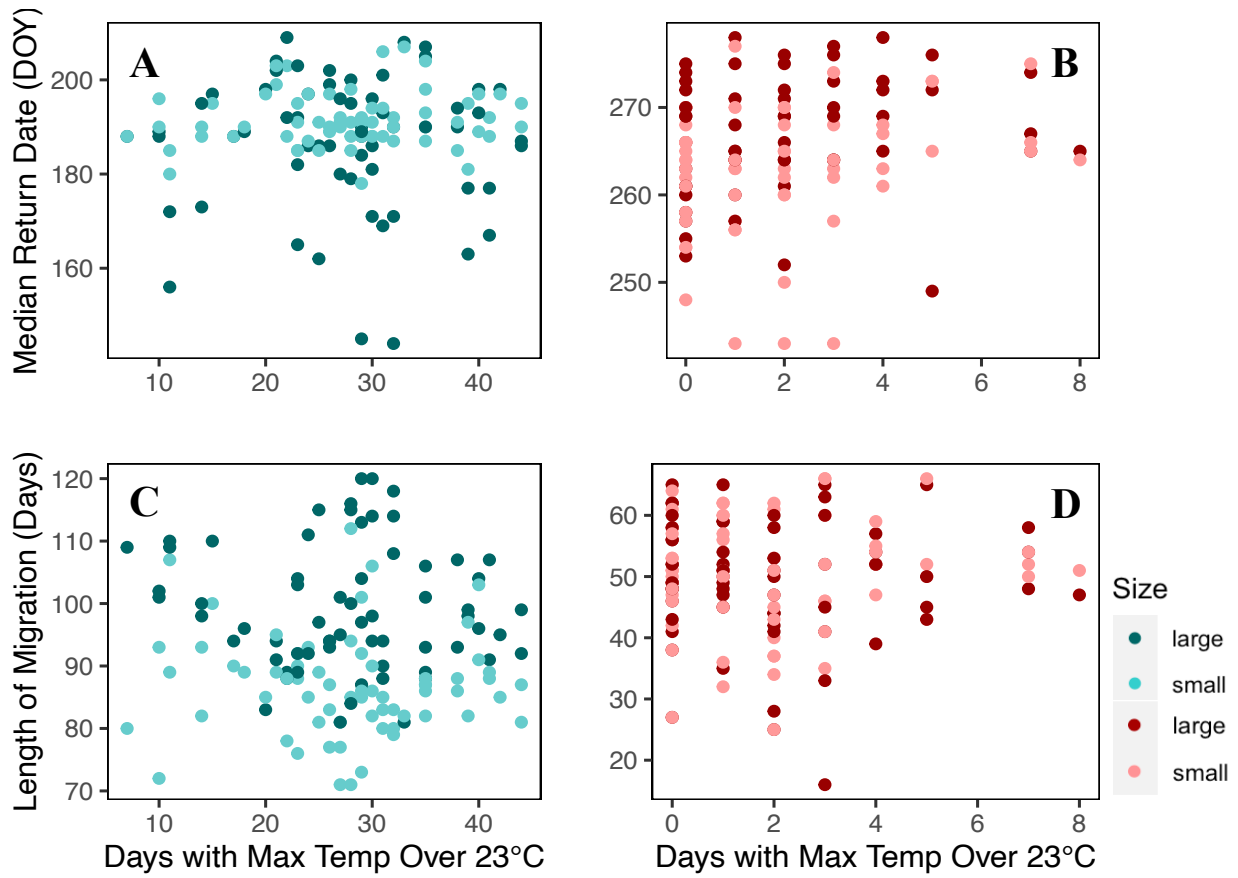
Figure 13. Annual median return date of salmon in the Miramichi River in the early (A) and late (B) runs and length of the annual migration period for early (C) and late (D) runs plotted against days with maximum temperature over 23°C, 1952-2021.
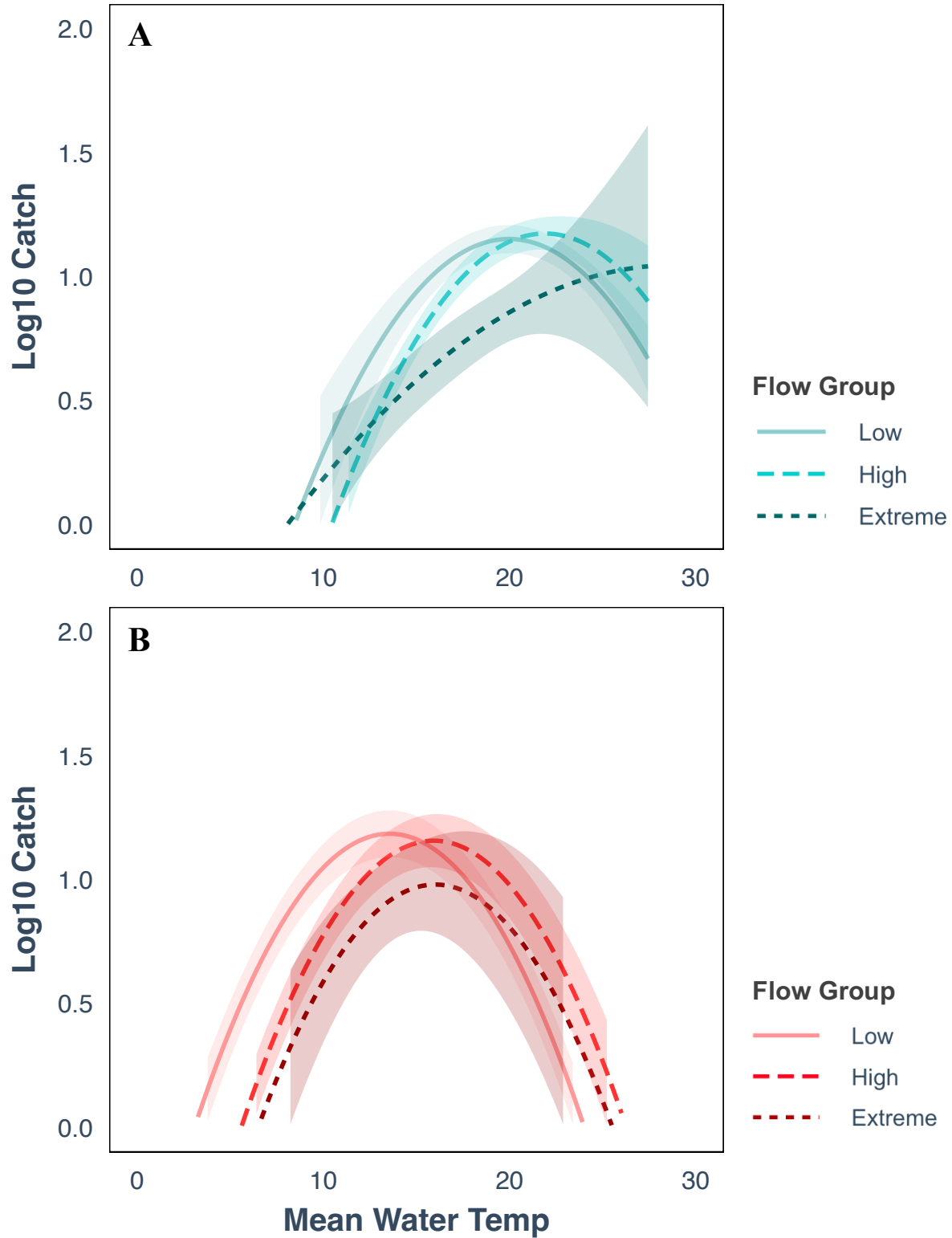
Figure 14. Interactive effects of discharge rate (low, high, extreme) and mean water temperature (°C) on trapnet catch of small fish in the Miramichi River for early (A) and late (B) runs, 1952-2020.
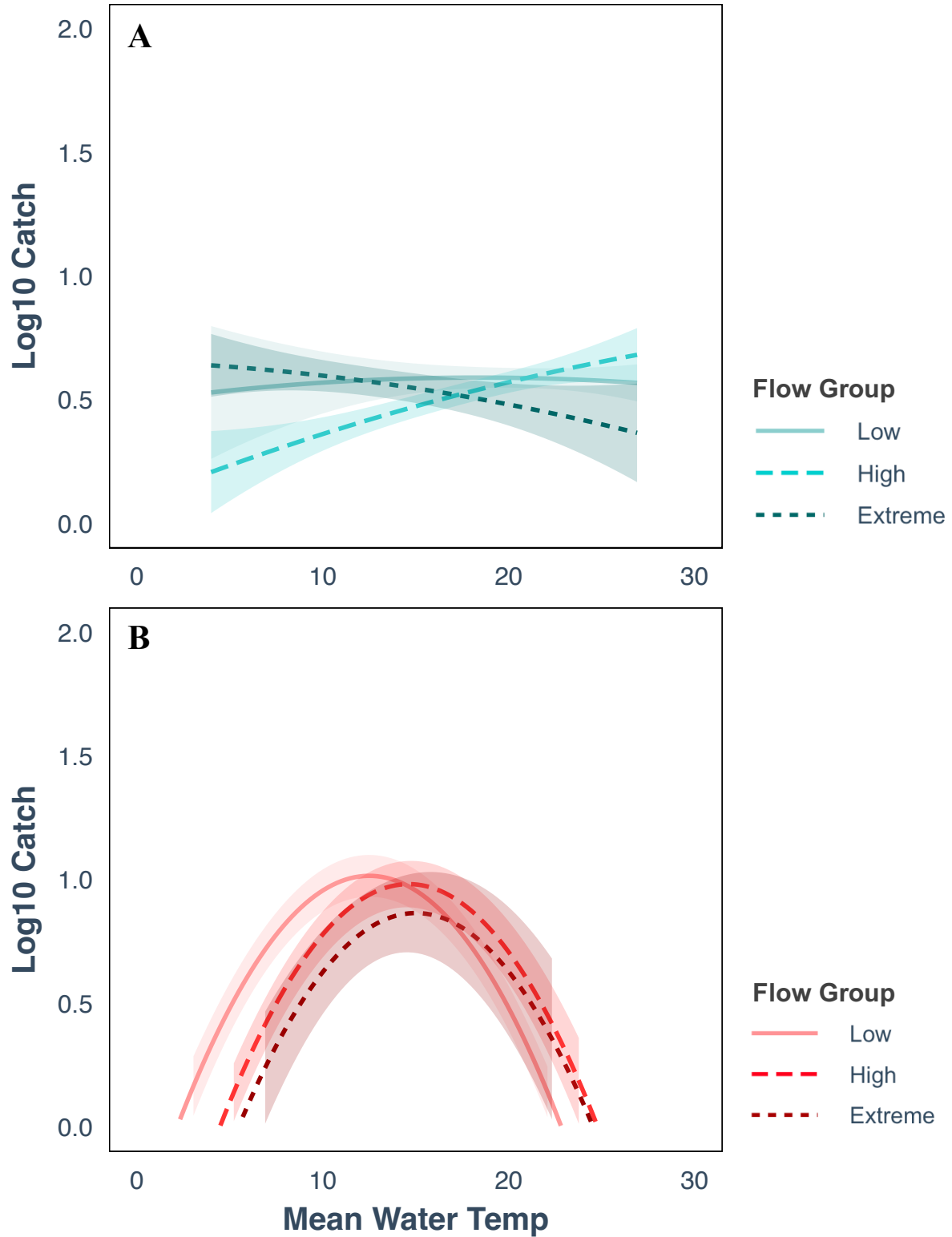
Figure 15. Interactive effects of discharge rate (low, high, extreme) and mean water temperature (°C) on trapnet catch of large fish in the Miramichi River for early (A) and late (B) runs, 1952-2020.

DISCUSSION

Characterization of run timing and effects of temperature

Median return date of Atlantic salmon in the Miramichi River was found to vary significantly across years in the early and late runs. This variation was most pronounced for large salmon in the early run, where median return date occurred later in the season at present than in previous years and occurred much earlier in the 80s and 90s than any other point in the time series. The first and last days of the year that salmon were caught in the trapnet changed across the time series, resulting in a significantly shorter run in recent decades. Arevalo *et al.* (2021) note that populations with shorter migration windows may have more difficulty adapting to changes in local climate when migrating into tributaries. Significant decreases in the length of the early salmon run could prove to be problematic, as increased activity during high temperature events may be associated with increased mortality (Wilkie *et al.*, 1997; Brander, 2007) or increased migratory costs that may result in decreased energy stores remaining for reproduction in surviving fish (Glebe & Leggett, 1981; Lennox *et al.*, 2018; Snyder *et al.*, 2022). This decrease in run length in the main branches of the river does not appear to be driven by river temperature.

Unlike the study conducted by Valiente *et al.* (2011), which found delays in the first day of catch related to increases in river temperature at the southern edge of the European distribution, there was no relationship between the first day of salmon catch in the Miramichi trapnets and average water temperatures in May or June, which are the months that the fish begin to be caught in the Miramichi estuary trapnet. Similarly, the last day of migration was not related to average temperatures in September, October, or November.

Sex

A population of Atlantic salmon studied by Dahl *et al.* in Sweden (2004) exhibited a sex-dependent relationship, where female salmon returned earlier than males and had stronger responses to temperature. Salmon in that study were kept for captive breeding; therefore, reliable sex determination was possible. In the Miramichi, data collected for sex was done visually and considered reliable from September onward. Chaput *et al.* (2016) showed that large salmon in the Miramichi are typically mainly female in both the early and late runs (~80%), while small salmon are typically mostly made up of male fish. Large fish in the early run experienced the most variation in median return date, so this could indicate a similar pattern of stronger responses in female fish; however, due to the difficulty of identifying sex in the early run and the weak relationships found with temperature, it is not possible to discern any pattern at present.

Fish size and interactions between river temperature and flow

Small salmon ascending earlier than large salmon is consistent with what is seen in some other systems (e.g. Jonsson *et al.*, 1990a, Norway; Bacon *et al.*, 2009, Scotland). It was found in this study that small and large salmon from the Miramichi react differently to environmental factors, so analyses were run separately for the two size groups. Large salmon typically respond more strongly to increased river discharge than small salmon, with increased migration at higher flow, especially in small rivers where high water levels are necessary for movement (Jonsson *et al.*, 1991). Jonsson *et al.* (1991) found that in rivers with discharge rates between 40-300m^3/s this relationship was lost. Discharge rates in the Miramichi can exceed 1000m^3/s, so it is likely that flow is not a limiting factor for small or large salmon downstream. Low R^2 values for the interactive models for temperature and flow indicate that these freshwater covariates are not

strong predictors of estuary entry in the Miramichi, even when considering their combined effects. At most river temperature and flow explain 16% of the variability in daily catch, with higher explanatory power in the late than early run for both size groups.

The use of single environmental monitoring stations is a limiting factor in this study, as the conditions in the river are not homogenous. The location of the trapnets changed throughout the time series, which could influence the observed results. This work provides a general description of the conditions in the river and their relationship to timing over seven decades.

Other factors that could influence run timing & future directions for research
The use of thermal refugia could be a factor that allows salmon to migrate into the estuary during periods with temperatures outside of their optimal range. Juvenile salmon, who have a higher thermal tolerance than adults (Elliot & Elliot, 2010), have been shown to use thermal refugia extensively in freshwater in the Miramichi River during high temperature events (e.g. Cunjak *et al.*, 2005; Breau *et al.*, 2007; Corey *et al.*, 2020; Corey *et al.*, 2023). Adult Pacific salmon make use of thermal refugia in river systems in British Colombia, suggesting that this behaviour is not specific to one life stage (e.g. Berman & Quinn, 1991; Tanaka *et al.*, 2000; Snyder *et al.*, 2022). Berman & Quinn (1991) report that chinook salmon using cool water refuges are able to maintain a lower body temperature than the ambient temperature in their system. Additionally, chum salmon in the marine environment were able to take advantage of temperature gradients in the water column to avoid high surface temperatures (Tanaka *et al.*, 2000). Although fish in that study dove to cooler waters when temperatures were high, they returned to the surface frequently and remained at the surface when temperatures were cool. This study indicates that behavioural

thermoregulation is not limited to freshwater. The water in estuary sites in the Miramichi River is deeper than headwater sites, and salmon may be able to take advantage of temperature gradients across the water column before moving further upstream. Behavioural thermoregulation is frequently studied in the freshwater environment, and further work examining how salmon respond to temperature in the estuary would contribute to our understanding of their migratory behaviour.

Recent work in Quebec (Frechette *et al.*, 2018) and in smaller tributaries in the Miramichi (Carrow, 2021) report that adult Atlantic salmon in Canadian systems do make use of thermal refugia, with fish in the Miramichi seeking refuge at higher ambient temperatures (19-22°C) than those in Quebec (17-19°C). This difference could indicate a level of adaptation to local temperature at different latitudes. Antilla *et al.*, (2014) found that juvenile salmon reared in warmer water exhibit improved cardiovascular performance at increased temperature, which agrees with the potential for some adaptation to temperature based on freshwater conditions, however, it is not known whether these effects would persist in adult fish. Despite refuge use in freshwater, high temperature events were significantly correlated with mortality in the Miramichi (Carrow, 2021); thus, the presence of refugia may influence salmon behaviour but may not improve condition or decrease mortality. Studies of refuge use further downstream in the Miramichi, where low flow is less likely to threaten connectivity between cool water sites and deeper water may provide a temperature gradient, may provide more insight on movement through the estuary/main branches in this system.

Unlike smaller tributaries, where low flow conditions could result in obstacles, heightened predation, or water levels that are physically too low for some fish to swim in (e.g. Smith *et al.*, 1994), the estuary retains a relatively high water level, which may lead to decreased reliance on discharge for movement. Additionally, the head of tide is several kilometers above the convergence point of the two main branches (Cunjak & Newbury, 2005), meaning that tides bring an influx of water twice daily that is independent from discharge. Influxes of water into these branches from tidal activity could be an influential factor for migration, and could relate to why discharge rate is a poor predictor of catch in the lower portion of the Miramichi River.

Studies in the Miramichi using tagged fish (Chaput *et al.*, 2016) and radio telemetry (Carrow, 2021) have found that fish may not immediately move upstream into tributaries upon entry to the system, and that fish may reside in the estuary for several weeks prior to freshwater migration (Carrow, 2021). Other populations of salmon exhibit holding behaviour in estuaries prior to freshwater migration, which has been correlated with freshwater variables, but as with most characteristics the response varies by system (Potter, 1988; Milner *et al.*, 2012). Although estuary entrance is not strongly correlated with temperature and discharge, holding behaviour prior to upstream migration could be related to environmental variables in fresh water. Real or perceived threats in the marine environment could influence movement out of the estuary, while poor upstream conditions or low migratory motivation could deter fish from immediately migrating to spawning sites. Investigating movement between the traps used in this project and traps in the headwaters could provide insight on movement in relation to river temperature and discharge rates through smaller tributaries. Additionally, further observation of the movement of tagged fish could allow us to determine whether refuge use downstream is associated with

delayed entry to tributaries, particularly if water temperature is locally monitored on a smaller scale.

Movement into the main branches from the ocean could be more heavily influenced by a need to move out of the ocean than motivation to migrate to spawning sites. Dahl *et al.* (2004) reported that in the Baltic Sea, sea surface temperatures (SST) were significantly correlated with the 50% return date of Atlantic salmon, where warmer ocean temperatures were related to earlier returns to freshwater. Hodgson *et al.* (2006) found strong positive correlations between migration timing of sockeye salmon in the Pacific and sea surface temperature. The effect of SST varied by population, but for all populations this relationship persisted even at upstream counting facilities. Condition as a result of productivity in the marine environment could also influence run timing. In some rivers in Norway, condition factor was the primary influence on migration timing, with stronger negative correlation and explanatory power than flow at those sites (Todd *et al*., 2012). There is a trend in some European salmon populations where physical condition worsens in 1SW fish as the migration season progresses, while it improves in 2SW fish through the season (Bacon *et al*., 2009; Utne *et al.*, 2021), which could relate to differences in return timing of small and large fish. 1SW fish and multi-sea winter fish from the Miramichi migrate to different regions of the North Atlantic Ocean to feed. 1SW salmon typically stay in the Labrador Sea, while MSW fish may migrate as far as Greenland (Chaput & Benoit, 2012). Since these fish face different conditions in the marine environment, their physical condition on their return could vary between the two groups in North America as well. Atlantic salmon population declines appear to be primarily driven by poor marine survival, and reduced marine condition factor as a result of decreasing prey availability is hypothesized to be a driver for mortality at sea (Friedland *et al.*,

1993; COSEWIC, 2010; Utne *et al.*, 2021). Processes occurring in the marine environment, particularly in the different regions to which North American salmon migrate, could influence their return to the river system when freshwater variables are non-limiting.

There is evidence that run timing within a season (spring vs. fall run) has a genetic component for Atlantic salmon across rivers and tributaries (e.g. Hansen & Jonsson, 1991; Stewart *et al.*, 2002; Vähä *et al.*, 2011). This could account for some differences in seasonal timing, but likely not changes in date within a season. Early life conditions may also influence later life stages - there is evidence that climate during incubation can affect biological characteristics later in life, such as water temperature and water flow during incubation influencing growth and smolt age of hatched fish (Handeland *et al.*, 2004; Jonsson *et al.*, 2005). Jonsson *et al.*, (1990b) report differences in run timing of wild fish that experienced a downstream migration as smolt versus hatchery-reared fish that did not, indicating that juvenile learning may impact adult behaviour.

Further analyses in the Miramichi River are required to understand Atlantic salmon behaviour and factors influencing run timing. This project did have limitations with respect to data availability across the time series. Only one station was used for each environmental variable, which does not account for heterogeneity throughout the system. Looking at movement within the river system (e.g. between estuary trapnets and headwater traps or via tagging) with monitoring of temperature and discharge at a more local scale could provide more insight on how these variables influence movement further upstream. There is extensive work being done on salmon in freshwater, and the estuary environment is understudied in comparison. Further work on behavioural thermoregulation by adult salmon in the estuary will contribute to a

comprehensive understanding of salmon movement through river systems after exiting the marine environment. This is particularly important since salmon may hold in the estuary while waiting for optimal conditions in fresh water. Looking at marine factors, such as SST, coastal temperatures, productivity in feeding zones, and salmon condition upon return would provide more insight on the influence of the marine life stage on behaviour of returning fish. Finally, further work looking at conditions experienced by juveniles and their relationship to behaviour as adults could provide insight on how juvenile learning and acclimation may influence later behaviour. Since temperature in freshwater and river discharge rates are not strong predictors of estuary entry in the Miramichi, more work must be done in this area to understand what influences the run timing and return behaviours of Atlantic salmon.

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APPENDIX

Table A9. Annual correlation coefficients with significance and low/high confidence intervals for mean river discharge patterns between site 01BP001 (NW) and site 01BO001 (SW), 1962-2020

Year	Estimate	Statistic	P value	Low conf interval	High conf interval
1962	0.80555632589426	25.9028049346268	1.60669121911652e-84	0.766269177415798	0.838842340022465
1963	0.935019639080568	50.2389202902085	1.59972947712521e-165	0.920742177780563	0.946796407494224
1964	0.763329452236498	22.543631282715	4.61817691281157e-71	0.716917416884332	0.803005207256136
1965	0.835856369965269	29.0103923111719	1.40906351173656e-96	0.80202002487421	0.864345148562029
1966	0.800008783421063	25.404186620023	1.52669715289252e-82	0.759749904970555	0.834157230927985
1967	0.851193072705022	30.8989669828981	1.16090434133008e-103	0.820208599960958	0.877198064818767
1968	0.960517848022216	65.8673699884103	2.48267751364715e-204	0.951716392111812	0.967741434053091
1969	0.811948918320733	26.5015409573374	7.01617254462941e-87	0.773791566978586	0.844235017710457
1970	0.903910231612608	40.2639898277141	5.98456151182339e-136	0.88320997677112	0.921095230959704
1971	0.891129043246422	37.4177189638974	1.24699758072368e-126	0.867866474691838	0.910492408394275
1972	0.853944149122938	31.3092277796498	2.6623329929478e-105	0.823523579993995	0.879467505454907
1973	0.900494285447205	39.4527225414829	2.4582603074625e-133	0.87910487369126	0.918263976345631
1974	0.841620610286786	29.6906878364252	3.76028421363695e-99	0.80884877788335	0.869180236634722
1975	0.890516720137844	37.2933356161813	3.25631212045878e-126	0.86713250817187	0.909983806885283
1976	0.869130924691086	33.5272178493047	2.42321644119102e-113	0.841603214319091	0.8921547611149714
1977	0.883654738644305	35.9634148057969	1.05001883822866e-121	0.858914273478663	0.90428016922966
1978	0.849890580799936	30.7283567129831	4.97641737260605e-103	0.818661470617724	0.876107958444399
1979	0.948830256494907	57.246403954499	8.39951024379454e-184	0.937489230745688	0.958158169528557
1980	0.905943273841075	40.8227053497462	6.31975346337115e-138	0.885685297238347	0.922758339399432
1981	0.863573864746233	32.6310244816343	5.45510984986254e-110	0.834937450237329	0.887546664242607
1982	0.876259923974159	34.6485106689275	3.73258140572201e-117	0.850072134574743	0.898125390941547
1983	0.910212547087121	41.8742901386431	4.86706315754238e-141	0.890792099723935	0.926314042841753
1984	0.951091774063036	58.7412675155348	8.72553740612798e-188	0.940253071918934	0.96000475624091
1985	0.871115449391914	33.7970119666722	3.70635582447728e-114	0.843929471059361	0.893838534236707
1986	0.939677636588831	52.3393409823364	3.37509824243784e-171	0.926384692850558	0.950631747059903
1987	0.923585469476723	45.8972521900124	3.30122850012445e-153	0.906916550463315	0.937367443471202
1988	0.847369986056674	30.445762507644	4.24453246024826e-102	0.815716254315487	0.873964080653197
1989	0.919600221232402	44.5984286218863	2.31412212481631e-149	0.90210620938588	0.934076333545485
1990	0.869572114893503	33.5507768133048	2.77299779056817e-113	0.842088070490338	0.892551673255167
1991	0.903168276395375	40.0843237418946	2.25406409065305e-135	0.882318064556581	0.920480427228031
1992	0.868835070531755	33.4806346646444	3.5523331007434e-113	0.84125041406292	0.891907946662359
1993	0.945580923602518	55.3671006116384	4.43744256808365e-179	0.933544288631226	0.955487639792071
1994	0.948796710591416	57.2261175977344	9.43129322531229e-184	0.937448488522526	0.95813060744489
1995	0.952862815966917	59.8364757977069	4.12056207456768e-190	0.94238912701961	0.961470153180552
1996	0.866612479848496	33.1353032003504	6.10517092007584e-112	0.838600769416088	0.890053324614336
1997	0.956686113060616	62.6107090067928	1.25813831980615e-196	0.947038906275101	0.96460796165627
1998	0.928329174029235	47.576612959627	4.55853251865761e-158	0.912648047101563	0.941281699335307
1999	0.89643399184108	38.5384412197769	2.37960970978267e-130	0.874229552192131	0.914896299186987
2000	0.923490296314057	45.9282363076154	1.57123381939262e-153	0.90682685212467	0.937271623392729
2001	0.941279756673177	53.1170619620276	2.95668436802874e-173	0.928326818661503	0.951950140607754
2002	0.894822123339636	38.189467482529	3.36982068631367e-129	0.87229537215896	0.913558674873353
2003	0.953170328257131	60.0472622396344	1.29214414763016e-190	0.94276296463465	0.961722613778359
2004	0.897686666043225	38.8684386030627	1.29481603775134e-131	0.875766292222158	0.915912690718975
2005	0.941378576886554	53.1660417761201	2.19789422217909e-173	0.92844663388847	0.95203144736471
2006	0.901288124176644	39.6376858145086	6.19151330770027e-134	0.880058584052191	0.918922099507494
2007	0.942208627686732	53.5822499631589	1.78331530570694e-174	0.929453140752875	0.952714332665859
2008	0.875320013189804	34.5367512039399	6.5056639953108e-117	0.848988970309065	0.897314819898551
2009	0.928582074834813	47.670634338393	2.45702397816907e-158	0.912953783238433	0.941490282079439
2010	0.937147876548781	51.1705486081979	4.62200237727935e-168	0.923319500253555	0.948549187952164
2011	0.866254455976837	33.034953853971	1.92555010929826e-111	0.838131836024566	0.889784079973034

Year	Estimate	Statistic	P value	Low conf interval	High conf interval
2012	0.916772141613372	43.7917696276901	3.7613231641091e-147	0.898722556590347	0.931720621749883
2013	0.917807975665176	44.0441001188475	1.07011186108503e-147	0.899944319549565	0.932595453614081
2014	0.913854996942255	42.8806186917734	3.72671572465386e-144	0.895179156226207	0.929327462207425
2015	0.898987127033659	39.1072622246835	3.26418120770796e-132	0.877294658951984	0.917014213245525
2016	0.907528552283057	41.2260416072775	3.32737074651599e-139	0.887591876388404	0.924071498829492
2017	0.944186539752373	54.6100629673228	3.85069295730988e-177	0.931852292077321	0.954341139308338
2018	0.931911075824681	48.9548792397008	5.78332200711707e-162	0.916979906102688	0.944234991180835
2019	0.929900791726868	48.1688060181363	9.43180293586877e-160	0.914548287119688	0.942577748286486
2020	0.916891574516109	43.8275680004309	2.92888480379685e-147	0.898866524231039	0.931819366449489