



**Reviews in Fisheries Science & Aquaculture** 

ISSN: (Print) (Online) Journal homepage: www.tandfonline.com/journals/brfs21

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To cite this article: J. Brian Dempson, Travis E. Van Leeuwen, Jan R. Bradbury, Sarah J. Lehnert, David Coté, Frédéric Cyr, Christina Pretty & Nicholas I. Kelly (18 Apr 2024): A Review of Factors Potentially Contributing to the Long-Term Decline of Atlantic Salmon in the Conne River, Newfoundland, Canada, Reviews in Fisheries Science & Aquaculture, DOI: 10.1080/23308249.2024.2341023

To link to this article: <u>https://doi.org/10.1080/23308249.2024.2341023</u>



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Published online: 18 Apr 2024.



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### A Review of Factors Potentially Contributing to the Long-Term Decline of Atlantic Salmon in the Conne River, Newfoundland, Canada

J. Brian Dempson (), Travis E. Van Leeuwen (), Ian R. Bradbury (), Sarah J. Lehnert (), David Coté (), Frédéric Cyr (), Christina Pretty and Nicholas I. Kelly

Fisheries and Oceans Canada, Northwest Atlantic Fisheries Centre, Newfoundland and LabradorA1C5X1, Canada

#### ABSTRACT

Species extinction and population extirpation are now widespread across aquatic ecosystems with many diadromous species, including Atlantic salmon (Salmo salar), in decline throughout much of the North Atlantic. Declines can occur simultaneously at both large and small regional scales rendering factors driving the decreases more elusive. On the south coast of Newfoundland abundance of Atlantic salmon at Conne River fell by 92% over a period of almost four decades in contrast with most other populations in the region suggesting local factors may be contributing to the decline. Here factors potentially contributing to the long-term decline of salmon are reviewed by (1) examining long-term trends in abundance and survival at different life stages, (2) presenting a synopsis on the presence and absence of factors impacting survival and productivity of this population, (3) using a semi-quantitative two dimensional classification system, based on expert opinion, to rank factors potentially contributing to the decline, and (4) utilizing a quantitative Random Forest analysis to complement the expert opinion approach in identifying factors possibly affecting salmon abundance in this south coast Newfoundland population. Results from both qualitative and quantitative analyses identified factors associated with salmon aquaculture as a possible driver of the decline. Additional factors include the influence of both climate change and predation in freshwater and marine habitats. As various Atlantic salmon populations across the native range approach extirpation, the results further highlight the necessity of river-specific analyses in addition to long-term monitoring and fine-scale demographic and threat information in the prioritization of research necessary for conserving or restoring endangered populations.

#### Introduction

Among the various species discussed in a narrative on recreational fishing in Britain in the mid-to late 1600s, it was Atlantic salmon (Salmo salar, Linnaeus, 1758) that Sir Izzak Walton deemed to be the king of freshwater fish (Walton 1808). If Sir Walton were alive today there is little doubt that he would be disappointed with the degree to which salmon has lost its regal status. It is now common for researchers to acknowledge the depressed state of anadromous Atlantic salmon in various regions of the North Atlantic (e.g. Jenkins 2003; Todd et al. 2008; Mills et al. 2013; Dadswell et al. 2022; Kocik et al. 2022). Many of the extreme declines or extirpations have occurred in southern, more populated areas, where Atlantic salmon are on the southern edge of their natural distribution (Parrish et al. 1998; Kocik and

**KEYWORDS** 

Local extirpation; aquaculture; habitat; exploitation; predation; Newfoundland

Brown 2002; Gibson et al. 2011; Dadswell et al. 2022). Various Atlantic salmon populations in the eastern United States were extirpated by the mid-to-late 1800s (MacCrimmon and Gots 1979; Kocik and Brown 2002). Remaining populations in Maine, USA were listed as Endangered in 2000 (Clegg et al. 2004; Legault 2005). In Eastern Canada, Inner Bay of Fundy Atlantic salmon were evaluated by the Committee on the Status of Endangered Wildlife in Canada (COSEWIC) and designated Endangered in 2001 and again in 2006 (COSEWIC, 2006). Additionally, among the 16 unique geographic areas (i.e. designatable units; DUs) in Eastern Canada, COSEWIC concluded that Atlantic salmon were now Endangered in five DUs and Threatened in one (COSEWIC, 2010). Declines and extirpations have also been reported for Atlantic salmon in Europe (e.g. MacCrimmon and Gots 1979; Parrish et al. 1998; Nicola et al. 2018) with evidence

**CONTACT** J. Brian Dempson brian.dempson@dfo-mpo.gc.ca Fisheries and Oceans Canada, Northwest Atlantic Fisheries Centre, 80 East White Hills Rd, St. John's, Newfoundland and Labrador A1C5X1, Canada.

Supplemental data for this article can be accessed online at https://doi.org/10.1080/23308249.2024.2341023.

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showing that some European populations were in decline as far back as the Middle Ages (Lenders et al. 2016).

In eastern North America measures taken to reverse declining population trends included the use of fish culture facilities (Dunfield 1985) and regulations to reduce exploitation including the eventual moratorium on domestic commercial ocean salmon fishing along with various restrictions in recreational fisheries (O'Connell, Dempson, & Reddin, 1992a; Lear 1993; Kocik and Brown 2002). Additional measures have also significantly reduced the harvest of Atlantic salmon at West Greenland (Bradbury et al. 2016b). Despite the numerous measures introduced over the past several decades, however, Atlantic salmon populations continued to decline.

Various researchers (e.g. Mills et al. 2013; Friedland et al. 2014; Olmos et al. 2020) have associated wide-spread synchronous changes in abundance or survival among populations of Atlantic salmon to large scale climate-driven changes in the North Atlantic. Some (e.g. Dadswell et al. 2022) however, have questioned this premise while others (Soto et al. 2018; Cote et al. 2021; Pardo et al. 2021; Tirronen et al. 2022) have indicated that at times survival at sea may be more impacted by regional or local factors and advocated for more attention to smaller-scale regional correlates of survival as anomalies were consistently noted for some salmon populations.

In Newfoundland, Canada one of the greatest declines in Atlantic salmon abundance is occurring at Conne River (Robertson et al. 2013; DFO 2022b), located on the South Coast of Newfoundland in a region where Atlantic salmon are presently designated as Threatened (COSEWIC. 2010). In contrast to other rivers in Atlantic Canada that were in decline during the 1970s and 1980s, Conne River had an abundance of salmon with adult returns averaging 7700 fish (Dempson et al. 2011). This changed rapidly in the early 1990s coincident with widespread declines that resulted in the closure of the Newfoundland commercial Atlantic salmon fishery in 1992 (Lear 1993). Immediately following the commercial fishery closure salmon abundance increased in many Newfoundland rivers, but Conne River failed to respond (Dempson et al. 2004a). Abundance continues to decline with successive record lows of less than 300 Atlantic salmon annually returning to Conne River from 2020 to 2022 (DFO 2023). Thus, the question is why does the Conne River salmon population consistently exhibit trends that are anomalous from those observed in many other Newfoundland rivers?

Herein, factors potentially contributing to the long-term decline of Atlantic salmon in Conne River are reviewed by (1) examining long-term trends in abundance and survival at different life stages, (2) presenting a synopsis on the presence and absence of factors impacting survival and productivity of this population, (3) using a semi-quantitative two dimensional classification system, based on expert opinion, to rank factors potentially contributing to the decline, and (4) utilizing a quantitative Random Forest analysis to complement the expert opinion approach in identifying factors possibly affecting salmon abundance in Conne River. As various Atlantic salmon populations across the native range approach extirpation, identifying river-specific threats for prioritizing targeted research necessary for conserving or restoring endangered populations will become increasingly relevant.

## Population characteristics and trends in abundance and survival

#### **Conne River**

Conne River (47°54′N, 55°41′W) has a drainage area of 602 km<sup>2</sup>, an axial length of 45 km, and a total length including tributaries of 905 km, that flow into Bay d'Espoir, an estuarine fjord 230 km<sup>2</sup> in area located on the South Coast of Newfoundland (Figure 1B,C). Besides the main stem, there are two major tributaries, Twillick Brook and Bernard Brook, along with a vast network of small ponds and lakes throughout the watershed (Figure 1A). Despite the relatively small size of the Conne River watershed, genetic differences have been identified between the main stem population and the tributaries (Beacham and Dempson 1998; DFO 2022b).

The Bay d'Espoir fjord consists of two main arms and extends inland from Hermitage Bay for approximately 53 km (Figure 1B). Water temperatures range from <0 °C in winter, when much of the fjord can freeze over, to 20 °C in surface waters during the summer (Pepper et al. 2003a; Anderson et al. 2005; Donnet et al. 2018). Salinities are highly variable and generally <25 psu in the inner fjord and upper water column (<5m) and 25–31 psu in the middle and outer fjord (Pepper et al. 2003a; Anderson et al. 2005; Tlusty et al. 2005).

Atlantic salmon have been a primary food source for the Mi'kmaq who have been present in this region for several centuries (Martijn 2003), with the traditional rights to harvesting salmon for food from the Conne River salmon population formalized in 1986

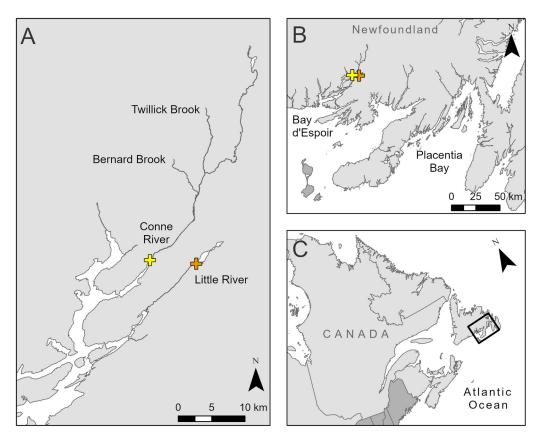


Figure 1. (A) Locations of the fish counting fence for Conne River (yellow cross) and nearby Little River (orange cross) and the two main tributaries to Conne River (Twillick Brook and Bernard Brook), in relation to (B) southern Newfoundland, and (C) eastern North America.

when the Miawpukek First Nation entered into an agreement with Government of Canada (Hinks 2012). Accordingly, returns of adult Atlantic salmon have been monitored at Conne River since 1986 using a fish counting fence while smolt runs have been surveyed since 1987 in order to inform conservation and management of this resource.

#### Life history

In Newfoundland and Labrador, Atlantic salmon are classified into small (<63 cm) and large ( $\geq$ 63 cm) size classes (O'Connell et al. 2006). At Conne River, Atlantic salmon were sampled either from fish captured in the recreational fishery, or directly from the fish counting fence trap. Small salmon represent 95% of the returning run of adult fish of which 94% are maiden one-sea-winter (1SW) salmon (i.e. grilse). Small salmon averaged 51.5 cm in length (N=5252) and 1.47 kg in weight (N=2328), of which 77% are female (N=2171). Within the large size category, most (89%) are a combination of consecutive and alternate spawning grilse with the remainder (11%) maiden two-sea-winter (2SW) salmon. Overall, 2SW salmon

make up less than 1% of the salmon that return to Conne River. Large salmon averaged 68.8 cm in length (N=320) and 3.2 kg in weight (N=9), with 83% of a limited sample (N=12) sexed as female. Smolt have a modal age of 3 years (range: 2–5 years), averaged 14.8 cm in length (N=7933) and 31.8 g (N=7788) in weight.

#### Movement, residence, and run timing

Movement and residence of smolt from Conne River to the outer fjord was determined from a three year acoustic telemetry study that was conducted from 2006 to 2008 (Dempson et al. 2011), whereas a more recent acoustic telemetry study (Martha Robertson, DFO, unpublished data) was used to determine movement of smolt from the outer fjord to overwintering areas in the Northwest Atlantic. Overwintering areas of south coast Newfoundland Atlantic salmon were also inferred from Bradbury et al. (2021), who used genetic reassignment of archived individual samples collected over a half century (1968–2018) throughout the North Atlantic. Return date and movement from overwintering areas back to Conne River, was inferred using logbooks of historic catches (Ash 1984) from the commercial fishery and the Food, Social and Ceremonial fishery (FSC), and return date to the Conne River counting fence. Lastly, the run timing date for smolt (1987–2022) and adult (1986–2022) Atlantic salmon was determined using counts from the Conne River fish counting fence program. Run timing was assessed as the date in which half (50%) of the run (smolt and adult) for a given year moved through the counting fence.

Juvenile Atlantic salmon in Conne River make extensive use of lacustrine habitat for rearing (O'Connell and Dempson 1996) with 75% of juveniles utilizing these areas (Dempson et al. 1996). Average run timing date for smolt leaving Conne River was May 14 (min=May 3 in 1996, max=May 26 in 1997). Once through the counting fence, smolt enter the Conne estuary where they spend anywhere from 6 to 10d (Dempson et al. 2011), before migrating via one of three routes (Main channel, Little passage, and Lampidoes passage) to reach the outer area of the Bay d'Espoir fjord and Hermitage Bay (Dempson et al. 2011). Total residence from release (27 April to May 13) at the fish counting fence through to Hermitage Bay was approximately 40 days, although some smolt remained in the nearshore coastal area for a combined period of two months (Dempson et al. 2011). This suggests that some smolt have an extended period of residency within the fjord and are likely present from late May to early July (Dempson et al. 2011). Beyond Hermitage Bay, the majority of smolt from Conne River migrate east of the island of Newfoundland and then north through the Grand Banks toward overwintering areas in the Labrador Sea, although some smolt migrated west and entered the Labrador Sea through the Strait of Belle Isle (Martha Robertson, DFO, unpublished data). While specific movements of Atlantic salmon on the Grand Banks and Labrador Sea areas remain limited, genetic reassignment of archived samples from Bradbury et al. (2021), further support the preliminary finding of (Martha Robertson, DFO, unpublished data) that South Coast salmon, including those from Conne River, overwinter in the Labrador sea (Bradbury et al. 2021) and likely present from late June to February. Catches of Atlantic salmon in the former South Coast commercial fishery in Fortune Bay and Bay d'Espoir occurred from mid-May to early August, whereas catches in the FSC fishery in the upper Bay d'Espoir fjord using trap nets, occurred in early June (Ash 1984). This suggests that returning South Coast adult Atlantic salmon are likely in Fortune Bay, Hermitage Bay, and Bay d'Espoir from mid May to early August, consistent with a mean run timing of

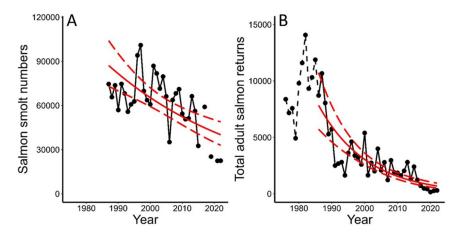
returning adult salmon for Conne River of June 26 (min=June 18 in 1999, max=July 7 in 1991).

#### Abundance

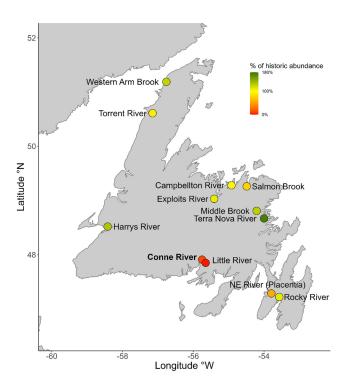
From 1987 to 2018, Atlantic salmon smolt abundance was estimated annually by mark-recapture (Dempson and Stansbury 1991; Schwarz and Dempson 1994). Owing to high spring water levels in 2016 and 2018, and the pandemic in 2020, no estimates were obtained while a fish counting fence has been used to obtain a full count of smolt since 2019. The abundance trend for smolt was determined using a generalized linear model (GLM) with a negative binomial error distribution. Results showed that smolt abundance has significantly declined by 51% since 1987 (GLM,  $Z_{32,31} = -4.68$ , p < .001; Figure 2A) and has fallen from more than 90,000 smolts in 1996–97 to less than 30,000 smolts in recent years (Figure 2A).

Adult salmon abundance was derived from salmon returns to the fish counting fence at Conne River (1986-2022) located on the lower section of the river approximately two kilometers from the mouth and estimated for the ten-year period preceding the counting fence operation (1976-1985; Figure 2B). The abundance reconstruction for 1976-1985 was done for illustrative purposes so as to place the initial return data from the fish counting fence in the context of what local knowledge suggested returns could have been in earlier years prior to monitoring (Figure 2B). Procedures to estimate returns prior to the operation of the counting fence followed those used by the International Council for the Exploration of the Sea (ICES) Working Group on North Atlantic Salmon (WGNAS) to infer pre-fishery abundance of salmon for various regions in the North Atlantic (e.g. Reddin and Veinott 2010; Chaput 2012; ICES 2021). Angling exploitation rates were used to expand recreational catch into total returns. At Conne River, exploitation rates were available from the reported catch, and the returns of salmon to the fish counting fence from 1986 to 1990. During these years angling catch averaged 1401 small salmon (range: 767-2060) while returns averaged 7284 (range: 4968-10,155) yielding a mean angling exploitation rate of 0.19 (range: 0.14-0.25). These rates were applied to the 1976-1985 angling catch to estimate salmon returns (Figure 2B). For the abundance reconstructions, exploitation rates were randomly selected from a uniform distribution within the observed range. One thousand realizations were run.

The abundance trend for total adult Atlantic salmon (small+large fish), over the time series of counting



**Figure 2.** The annual number of (A) emigrating Atlantic salmon smolt and (B) total returning adult Atlantic salmon for Conne River, Newfoundland, Canada. Solid black lines represent numbers from the counting fence program. Dashed black lines represent median values of reconstructed returns estimated from angling catches (see text for details). Solid red lines represent the regression trend (solid line)  $\pm$  95% confidence intervals (dotted red line) for the time series.



**Figure 3.** Percent change in total salmon returns to monitored rivers in Newfoundland, Canada relative to the 1992 commercial salmon fishery moratorium. Estimated percent change in abundance was calculated as the difference between average total returns over six years (one generation; DFO 2022b) from 1992 to 1997 (one generation following the commercial salmon fishery moratorium; i.e. historic abundance) relative to the average returns from 2017 to 2022 (current abundance). Red circles represent declining populations, yellow circles represent those with no changes, and green circles represent increasing populations.

fence observations (N=37 years, 1986–2022; Figure 2B), was determined using a generalized linear model with a negative binomial error distribution (DFO 2013). Since 1986, adult Atlantic salmon abundance

has declined by 92% (GLM,  $Z_{36,35} = -8.805$ , p < .001) and for the period 2017–2022, abundance is now 13% of the average during the initial years following the commercial salmon fishery moratorium (1992–1997; Figures 2B and 3).

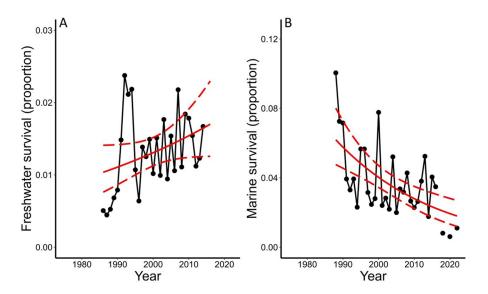
#### Survival

Trend in egg-to-smolt (freshwater) survival, derived using estimates of fecundity and percent female salmon from annual stock assessment status reviews (DFO 2020) (1986–2015; Figure 4A), was modeled using a generalized linear model and a quasi-binomial error distribution for proportional data. Egg-to-smolt (freshwater) survival averaged 1.29% (range: 0.45– 2.38%), and despite increasing in an irregular fashion since 1996 there was no significant relationship across years (GLM,  $t_{30.29} = 1.142$ , p=0.26; Figure 4A).

Trend in survival from smolt to returning adult 1SW salmon (marine), modeled using a generalized linear model and a quasi-binomial error distribution, averaged 3.73% across all years (range: 0.61–10.05%; Figure 4B), but has significantly decreased (GLM,  $t_{30,29} = -4.146$ , p < 0.001) by 70% since 1987 with record low survivals of less than 1% occurring in recent years (Figure 4B).

# Synopsis of factors impacting survival and productivity of salmon

More than two decades ago, when describing the status of Atlantic salmon in the North Atlantic, Parrish et al. (1998) posed the question: "Why aren't there more Atlantic salmon?" Similarly, Dadswell et al. (2022) asked: "Where have all the salmon gone?"



**Figure 4.** Temporal trends of (A) freshwater (egg to smolt) survival and (B) marine (smolt to adult) survival of Atlantic salmon for Conne River, Newfoundland, Canada. Solid black lines represent numbers from the counting fence program. Red lines represent the regression trend (solid line)  $\pm$  95% confidence intervals (red dashed lines) for the time series.

Many of the declines, or extirpations, were attributed to habitat alteration or destruction, pollution, overfishing and more recently ocean climate conditions and intensive aquaculture with many of these threats previously associated with other species extinctions (Limburg and Waldman 2009; Sodhi et al. 2009). Additional threats such as introductions, pathogens and disease, and predation were also discussed in the context of contributing to declines but not necessarily extirpations (Parrish et al. 1998). Impacts associated with hatcheries or other stocking programs have also been recognized as potential threats (Frankham 2008; Gibson et al. 2011; McMillan et al. 2023). What is clear is that human activities, such as those listed above, have been negatively impacting not only Atlantic and various Pacific salmon populations, but many other species for a long time (Lichatowich et al. 1999; Ruckelshaus et al. 2002; Dulvy et al. 2003; Waldman and Quinn 2022) with consequences likely only to worsen when coupled with the reality of changing climate (Kocik et al. 2022; Henderson et al. 2023).

One of the more comprehensive reviews dealing with threats to Atlantic salmon was by Forseth et al. (2017). These authors examined a suite of anthropogenic factors to determine the most important expanding threats to wild Norwegian Atlantic salmon. Here, those threats that have been frequently associated with major declines or extirpations, namely exploitation, habitat issues, and pollution followed by a synopsis of other factors potentially affecting Atlantic salmon are evaluated. In total sixteen factors (Table S1) were examined for their presence or absence in Conne River including: introductions, predation, hatcheries or other stocking programs, climate, hydropower regulation, and aquaculture. Three additional threats associated specifically with Norwegian salmon (e.g. mining, water abstraction, *Gyrodactylus salaris*, Malmberg, 1957) were also considered but determined to have no bearing here and thus were excluded from the review of potential threats.

#### Potential threat factors considered

#### Exploitation

#### Newfoundland commercial fishery

Commercial fishing for Atlantic salmon in Newfoundland began during the 1700s (Lear 1993). Peak landings occurred during the 1920s to early 1950s with more than 2000 t harvested in some years. Information on harvest by region is available since 1974 with commercial landings from the South Coast accounting for about 15% of the total catch from insular Newfoundland, by weight, up to the time the fishery closed beginning in 1992 (O'Connell et al. 1992b; Lear 1993). The specific region of the South Coast that includes Fortune Bay and Bay d'Espoir, accounted for 9% of the total Newfoundland harvest averaging 67 t annually (range: 22-190 t; equivalent to 8100-62,600 salmon by number), but decreased over the years coincident with the reduction in the number of licensed commercial salmon fishers (O'Connell et al. 1992b). The average harvest from this region for the period 1986-1990, coinciding with the first five years of abundance monitoring at Conne River, was 50% lower by comparison with the harvest from 1974 to 1985.

During the five years following the closure of the commercial salmon fishery (1992–1996), when many monitored rivers in Newfoundland experienced increased salmon returns (Dempson et al. 2004a), some increasing by a factor of two or more, average returns to Conne River declined by over 50%. As the abundance of salmon at Conne River remained high during periods when the commercial salmon fishery was operating, and actually decreased following the closure of the commercial fishery, commercial exploitation was not considered to be driving the on-going decline.

#### Other marine fisheries and oceanic distribution

Atlantic salmon from Newfoundland rivers were identified from the mixed stock fishery at West Greenland where they make up ~5% of the harvest (Bradbury et al. 2016b), with less than 1% originating from the South Coast of Newfoundland (ICES 2020). Since the West Greenland fishery primarily harvests non-maturing 1SW salmon (Bradbury et al. 2016b) that are destined to return to home rivers in a subsequent year as multi-sea-winter (MSW) fish, the number of Conne River salmon captured at West Greenland would likely be few, if any, as less than 1% of the salmon returning to Conne River are MSW.

In contrast, Atlantic salmon fisheries in the French territorial waters around the islands of Saint Pierre and Miquelon, located off the South Coast of Newfoundland, intercept 1SW and MSW salmon originating from Newfoundland (Bradbury et al. 2016a; ICES 2021). Since 1990, 1-5.3 t of salmon were harvested annually in this fishery, equivalent to 500 to 1800 salmon of which less than 20% were identified as originating from the section of the South Coast of Newfoundland where Conne River is located (ICES 2020). Accordingly, some Conne River salmon could be intercepted in this fishery, but reported catches are a small fraction of the former commercial salmon fishery that occurred in this region when salmon abundance remained high and thus the Saint Pierre and Miquelon fishery was not considered to be a major threat to the Conne River salmon population.

#### **Recreational fishing**

Angling data from the Conne River are available since 1953 (Moores et al. 1978). Angling catch increased steadily during the early 1950s to mid-1960s, with the highest reported catches from 1968 to 1988 when they averaged more than 2000 salmon per year. Removals by the recreational fishery, however, declined substantially in the early 1990s coincident with a reduction in effort when quotas were introduced in some years, followed by the closure of the recreational fishery from 1993 to 1996. The recreational fishery reopened briefly in 1997, closed again in 1998 and 1999, but was sporadic with limited two-week openings occurring before a complete closure beginning in 2015. Removals from the recreational fishery were high during the late 1960s to late 1980s, but the abundance of salmon returning to Conne River, either estimated from the retrospective analysis (1976-1985) or during the first five years of the operation of the fish counting fence (1986-1990), remained high with spawning escapements well in excess of the conservation spawning requirements and thus were not considered a significant threat.

#### Food, social and ceremonial fisheries

The Miawpukek First Nation holds a FSC communal fishing license and began fishing in June 1986 under an annual allocation of 1200 salmon (Reddin and Short 1986). The fishery occurred in the upper Bay d'Espoir area using trap nets with 522 salmon caught during the first year of operation. The highest catch occurred in 1990 when 959 salmon were captured (Dempson et al. 2004b). Fishing did not occur from 1994 to 1996, while 515 salmon were harvested in 1997. Excluding 1987 when only 18 salmon were caught, the overall annual average catch was 522 salmon with the entire catch over the years the FSC fishery operated accounting for 11% of the total returns to Conne River. Regardless, there has been no FSC fishery since 1998 as the Miawpukek First Nation has chosen not to fish owing to ongoing conservation concerns. Therefore, given the continued decline of Conne River salmon despite no FSC fishery operating, the FSC fishery was not considered a current threat to the Conne River salmon population.

#### Other exploitation (bycatch, poaching)

The extent of Atlantic salmon in Conne River lost to bycatch in other legal fisheries (e.g. Atlantic herring, *Clupea harengus*, Linnaeus, 1758, capelin, *Mallotus villosus*, Müller, 1777), or taken illegally (poaching) is largely unknown. A recent region wide analysis of enforcement records pertaining to Atlantic salmon from NL, by Van Leeuwen et al. (2024), however, showed that illegal incidents have declined by 66% between 2001 and 2020. In particular this was driven by a 67% reduction in netting and jigging-related violations, which among the examined violations is likely to impose the highest levels of mortality on adult salmon. Therefore, while the full magnitude of illegal fishing mortality remains unknown, it is likely lower than it was two decades ago. Nevertheless, it is worth noting that illegal fishing has negatively impacted some Newfoundland Atlantic salmon populations that eventually achieved recovery as a result of a community engagement process (Cote et al. 2021), but this does not seem to be the case for Conne River, which continues to have strong community engagement and presence of enforcement.

Information summarizing bycatch in capelin gear (1981–1999) found that Atlantic herring and Atlantic cod (*Gadus morhua*, Linnaeus, 1758) were the most frequent species encountered with salmon occasionally captured, most of which were usually released alive (Nakashima and Clark 2001). Annual telephone surveys with fishers involved in the herring bait net fishery similarly reported minimal bycatch of salmon over the period 2013–2020 with most reported from the Northeast Coast of Newfoundland (Christina Bourne DFO, pers. comm) and hence does not appear to have influenced salmon returns to Conne River.

#### Habitat alteration or destruction

Forestry operations occurred in the region where Conne River is located from 1942 until 1958. During this time several logging dams were present but were inactivated after logging ended in 1958 (Mercer 1961). Some remedial work was also carried out in 1962 and in the early 1970s to facilitate fish passage on several Conne River tributaries. Regardless, there have been no other habitat issues reported and currently the headwaters of the Conne River remain undeveloped and accessible to migrating salmon. Hence, habitat issues were not considered a threat to the Conne River salmon population.

#### Acidification and pollution

Rivers along the South Coast of Newfoundland are known to be sensitive to acidification (Scruton 1986) although widespread low pH values to the extent of those found in Nova Scotia, Canada, did not occur in Newfoundland (Clair et al. 2007). For Conne River, pH values were in the range of 5.0–6.8 and generally higher than other rivers in the area owing to its bedrock geology allowing more buffering capacity (Scruton 1986). While current information specific to Conne River is lacking, water quality monitoring of three watersheds located within 5 km of Conne River yield pH values averaging 6.5 (range: 5.4–7.2) based on 27 readings between May 2003 and September 2021 (Newfoundland and Labrador Water Resources Portal https://maps.gov.nl.ca/water/ accessed May 5, 2022) with no evidence of any water quality issues. Additionally, recent investigations of precipitation acidity in Atlantic Canada have found reductions in acid inputs since the late 1990s and early 2000s (Houle et al. 2022). Therefore, in the absence of any known pollution issues affecting Conne River, neither acidification nor pollution were deemed to be threats to Conne River salmon.

#### Hatchery programs and enhancement

The widespread use of hatcheries was used to maintain or restore Atlantic salmon populations in eastern North America going back to the late 1800s (Dunfield 1985; Kocik and Brown 2002). In Newfoundland these techniques were also used to colonize newly available habitat for which obstructions were bypassed with fishways (Mullins et al. 2003). These practices ended in Newfoundland in the early 1990s following recent evidence that stocking may do more harm than good by lowering fitness and reducing genetic diversity of the existing population (e.g. Meffe 1992; Östergren et al. 2021; Thorstad et al. 2021). This is particularly likely if the integrity of the genetic stock is compromised or the importance of local adaptation is not considered.

In contrast with various rivers in the Maritimes region of Canada or those in the New England area of the USA, that have been stocked for over a century (e.g. Kocik and Brown 2002; Clegg et al. 2004; Chaput et al. 2016), there has been minimal enhancement carried out at Conne River such that impacts to the wild salmon population are believed to be minimal or non-existent. The Miawpukek First Nation requested an enhancement program for Conne River in 1993. One hundred and twenty-eight thousand salmon fry derived from Conne River salmon, were stocked in 1995, and twenty-three thousand stocked in 1997 in the course of evaluating deep substrate versus trough-style incubators. In addition, a smolt-to-adult supplementation program was conducted in 1995-1996 when 5000 out migrating smolt were transferred to an aquaculture grow-out site in Bay d'Espoir and reared for a year (Dempson et al. 1999). Survivors from this experiment were released into the bay of which 286 returned to Conne River. This project was carried out to evaluate the utility of the approach for Conne River and was not intended as a directed restoration program and hence why salmon were released into Bay d'Espoir and not transferred to the river itself. Smolt-to-adult supplementation programs have also been shown to have risks to wild populations (Fraser 2008, 2016; Bordeleau et al. 2018). Given the minimal enhancement carried out at Conne River, however, it was not recognized as a threat to Conne River salmon.

#### **Introduced species**

Invasive species or introductions of non-native species can often threaten existing fish populations, including those of Atlantic salmon (Crossman 1991). Threats can include competition, predation, disease, parasites, and genetics (introgression) (Limburg and Waldman 2009; Forseth et al. 2017).

Newfoundland has a limited freshwater fish species community that is dominated by salmonids (Van Zyll de Jong et al. 2004). Introduced species include brown trout (Salmo trutta, Linnaeus, 1758), rainbow trout (Oncorhynchus mykiss, Walbaum, 1792), pink salmon (Oncorhynchus gorbushca, Walbaum, 1792), lake whitefish (Coregonus clupeaformis, Mitchill, 1818), and lake trout (Salvelinus namaycush, Walbaum 1792) (Scott and Crossman 1964; Van Zyll de Jong et al. 2004). Lake whitefish are currently found in several areas in eastern Newfoundland but pink salmon and lake trout failed to establish (Van Zyll de Jong et al. 2004). Brown trout and rainbow trout were introduced during the late 1880s with the former largely confined to eastern Newfoundland, particularly the Avalon Peninsula, with no populations known to occur on the South Coast of Newfoundland west of the Burin Peninsula (Westley and Fleming 2011).

Rainbow trout have been observed in various locations in Newfoundland with the frequency of occurrences coinciding with expansion of marine cage rearing of rainbows in eastern Canada (Porter 2000). This species was also used in the developing aquaculture industry on the South Coast of Newfoundland and is the only introduced species commonly reported from Conne River, particularly in years before most of the aquaculture production transitioned to Atlantic salmon. All-female triploid rainbow trout were often used for aquaculture purposes in the early years of the developing aquaculture industry and later an all-female (sex-reversed) diploid strain of anadromous rainbow trout were approved for commercial use (Pepper et al. 2003a). Despite this there are no established populations of rainbow trout in this region of the South Coast (Porter 2000). Thus, by comparison with other regions of Atlantic Canada where

introduced species such as smallmouth bass (*Micropterus dolomieu*, Lacépède, 1802) are of particular concern (DFO 2009), the introduction of species at Conne River has been minimal and hence not considered to be a threat.

#### Hydropower regulation

The effects of hydropower regulation on Atlantic salmon populations originate from dams directly impacting fish passage, mortalities resulting from fish going through power turbines, altered discharge, and changes in water temperatures (Johnsen et al. 2011; Forseth et al. 2017). The Bay d'Espoir hydroelectric facility has three generating stations located in this region, the first of which began operation in 1967 (604 MW), along with the Upper Salmon (1983, 84 MW) and Granite Canal (2003, 41 MW) (DFO 2013) all of which contribute to the freshwater discharge entering into an arm of the upper Bay d'Espoir fjord, but none of which directly affect the Conne River watershed. Within the Bay d'Espoir fjord, water temperature and salinity profiles are influenced by the large freshwater discharge from the hydroelectric facility located at the head of the bay (Anderson et al. 2005; Ratsimandresy et al. 2020) approximately 10 km from the Conne River estuary. Any long-term impacts on Atlantic salmon are unknown (DFO 2013) but are believed to be inconsequential as the steepest declines in salmon abundance at Conne River occurred well after the hydropower development.

#### Predation

In freshwater, Atlantic salmon are preyed upon across several life history stages (embryo, fry, parr, smolt) by various fish, birds, and mammals (Ward and Hvidsten 2011). At Conne River, smolt abundance was relatively stable for almost two decades suggesting freshwater predatory impacts were likely minor and in agreement with the overall increase in egg-to-smolt survival (Figure 4A). Since low marine survival is often noted as a contributing factor for declines in abundance (e.g. Thorstad et al. 2021) it is likely that the threat of predation is more important when salmon are migrating to sea as smolt, or while post-smolt or adults are at sea.

In a review of common predators of Atlantic salmon, marine fish species such as Atlantic cod, pollack (*Pollachius pollachius*, Linnaeus, 1758), and sea trout (*Salmo trutta*, Linnaeus, 1758) were noted (Ward and Hvidsten 2011) with incidental reports of predation by Atlantic halibut (Hippoglossus vulgaris,-Linnaeus, 1758), porbeagle (Lamna nasus, Bonnaterre, 1788) and Greenland sharks (Somniosus microcephalus, Bloch and Schneider, 1801), and bluefin tuna (Thunnus thynnus, Linnaeus, 1758) on salmon kelt (Lacroix 2014). Analysis of data from pop-up satellite archival tags attached to North American Atlantic salmon kelt (Strøm et al. 2019) suggested potential predation by deep-diving toothed whales (long-finned pilot whale (Globicephala melas, Lesson 1828)) or beluga whale (Delphinapterus leucas, Lacépède, 1804) and endothermic fish (likely bluefin tuna or porbeagle). Marine birds such as gannets (Morus bassanus, Vieillot, 1816) and mergansers (Mergus merganser, Linnaeus, 1758) as well as marine mammals particularly harbor (Phoca vitulina, Linnaeus, 1758) and grey seals (Halichoerus grypus, Nilsson, 1820) were also listed (Ward and Hvidsten 2011).

Predation by gannets on Atlantic salmon in the Northwest Atlantic increased during the early 1990s (Montevecchi et al. 2002) with evidence from some rivers on the South Coast of Newfoundland, including Conne River, of a negative association between relative consumption levels of gannets at the Funk Islands, Northeast Coast, Newfoundland, and the number of salmon returning the following year (Montevecchi and Cairns 2003). When capelin abundance was low, researchers found that gannets foraged more offshore, targeting species such as Atlantic salmon (Montevecchi et al. 2009). Salmon tags recovered at the Funk Islands indicated that gannets were preying on hatchery salmon that originate from Maine, New Brunswick, Nova Scotia, and the Northeast Coast of Newfoundland (Montevecchi et al. 1988). Therefore, it is conceivable that some Conne River salmon may be preved upon by seabirds such as gannets.

An examination of salmon – seal interactions identified specific locations in Newfoundland and Labrador where interactions were occurring and their frequency (Sjare and Reddin 2004). The perceived importance of predation by seals was considered either low or very low at 17 of 22 rivers studied, including the Conne River. Subsequent investigations reported a low incidence of seals frequenting the Conne River area (Lenky 2007). More recently, during a 2021 survey of harbor and grey seals along the Newfoundland coast, less than 15 harbor seals at three haul-out locations were observed near the mouth of Conne River, but none in the river itself (Hamilton et al. 2023).

A separate diet study focused on harbor seal (Sjare et al. 2005), that are also found along the South Coast in Placentia Bay and locations proximate to the French Islands of Saint Pierre and Miquelon, examined more than 200 stomachs, with approximately 40 prey species identified. No salmon were observed in the samples obtained from 1985 to 2003 (Sjare et al. 2005). Harbor and grey seal scats collected nearby in Placentia Bay in 2021 also did not suggest consumption of Atlantic salmon (Garry Stenson, DFO, unpublished data). Regardless, if seals had been a significant threat contributing to the extreme decline of the salmon population at Conne River, then it would be unusual why other populations outside of the Bay d'Espoir fjord are not experiencing similar declines (Figure 3).

Impacts on Atlantic salmon due to predation are more likely to be a result of cumulative effects by a variety of species along with other anthropogenic factors rather than any one individual component (Montevecchi and Cairns 2003). Thorstad et al. (2021) state that predation is a natural phenomenon and one that does not necessarily imply that it is a particular driver of the current population declines of salmon. Dadswell et al. (2022) have similarly noted that predation impacts on Atlantic salmon are not likely to be the primary cause for population declines in the North Atlantic but as others have noted (Falkegård et al. 2023) predation may act to keep already depressed populations from recovering.

#### Climate change

The climate of the Northwest Atlantic Ocean undergoes large fluctuations at decadal time scales (Cyr and Galbraith 2021). With respect to Atlantic salmon, the periodic occurrence and later high abundance of salmon at West Greenland was attributed to variability and subsequent warming of waters in the North Atlantic (Dunbar and Thomson 1979). More recent studies have noted that the distribution, abundance, and size of Atlantic salmon were linked to changes in the climate of the North Atlantic that may have contributed to decreased productivity (Beaugrand and Reid 2012; Rikardsen et al. 2021; Utne et al. 2021), often with the greatest impacts observed on southern populations as life history leaves them among the most exposed and vulnerable (Todd et al. 2011; Nicola et al. 2018). Simply by nature of their life history Atlantic salmon are susceptible to climate influences and impacts both in fresh as well as marine waters (Hare et al. 2016).

Potential climate-related impacts have been thoroughly reviewed in the context of their potential consequences for Atlantic salmon both in freshwater and marine environments (e.g. Jonsson and Jonsson 2009; Todd et al. 2011; Mills et al. 2013). Besides direct effects, climate shifts can influence prey availability, predator abundance, and alter other traits such as sea age at maturity, age at smolification, run timing, disease resistance, and growth (Cote et al. 2015; Olmos et al. 2020; Thorstad et al. 2021). These pathways of effects can be partitioned into those manifested in the local freshwater environments of the Conne River, or those in the marine environment of the Northwest Atlantic.

#### Fresh water

Mean monthly water temperatures recorded at the Conne River fish counting fence monitoring facility (May-August) are variable with July (1986–2019;  $r^2$ = 0.21, p = 0.01) and August (1987–2019;  $r^2 = 0.19$ , p = 0.02) temperatures increasing significantly over time. Water levels have also been variable with severe drought conditions periodically affecting many Newfoundland rivers, including Conne River, particularly in 1987 (O'Connell et al. 1991). Nevertheless, no definitive association between the 1987 drought conditions and abundance or subsequent river age distributions of out-migrating smolt that could have been suggestive of differential impacts on the survival of specific age classes of parr were found (Dempson and Reddin 1995). Juvenile salmon at Conne River make extensive use of lacustrine habitat (O'Connell and Dempson 1996) which may provide refugia from the warmer conditions more likely to occur in fluvial areas when water levels are low and water temperatures are high.

#### Marine

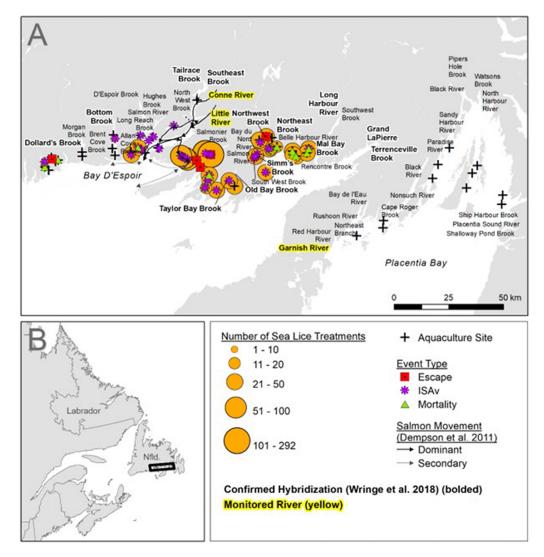
Investigations examining linkages between ocean climate conditions with growth, survival and abundance of salmon in the North Atlantic have been ongoing for several decades (Friedland et al. 1993; Todd et al. 2008; Almodóvar et al. 2019). As ocean temperatures increase, as a result of anthropogenic climate change, the size or condition of Atlantic salmon decreased in some populations with subsequent impacts on survival (Todd et al. 2021). Other studies from the Northwest Atlantic have noted a positive association between growth and temperature although with differences among sea-age groups (Friedland et al. 2005).

In the Northwest Atlantic, anomalous cold water conditions in the early 1990s (Cyr and Galbraith 2021) were linked to lower salmon productivity across a broad geographic range (Chaput et al. 2005; Mills et al. 2013). This coincided with the collapse of capelin and various groundfish stocks (Pedersen et al. 2017; Murphy et al. 2021) and changes to the pelagic food web in the Northwest Atlantic shelf (Buren et al. 2014). These unusually cold years were followed by a period of warming that peaked around 2010–2011, cool conditions during 2014–2017, and warming during the past several years (2018–2021) (Cyr et al. 2022). Over this time period mean lengths of small salmon returning to Conne River have varied, initially increasing before trending downward beginning in the late 1990s – early 2000s.

Atlantic salmon returns to Conne River were abundant during the mid-1970s to late 1980s averaging about 7700 salmon from 1986 to 1990 before falling to 2500 salmon in 1991. The decrease coincided with major declines in salmon in other regions of eastern North America and was attributed to broad scale environmental and ecosystem conditions occurring in the Northwest Atlantic (Mills et al. 2013). The closure of the commercial Atlantic salmon fishery in Newfoundland that began in 1992 resulted in an immediate increase in salmon returns to many Newfoundland rivers (Dempson et al. 2004a), but this was not the case at Conne River which has continued to decline (Figure 2, DFO 2023). At nearby Little River (Figure 1A), salmon abundance has also declined by over 90% since the mid-1990s (Figure 3), although Little River was enhanced with unfred fry from 1989 to 2000 with the exception of 1995 and 1998, and later from 2005 to 2011, when adult salmon returning to Little River were transported above a series of impassable falls. The locally divergent trend in abundance of Bay d'Espoir rivers like Conne and Little River, from other monitored rivers in Newfoundland, six of which have experienced record high returns since 2010 (DFO 2023), is inconsistent with the hypothesis of wide-spread synchronous declines driven by changes in marine climate (e.g. Mills et al. 2013; Olmos et al. 2020). Rather, as noted by Tirronen et al. (2022), declines occurring at Bay d'Espoir may very well depend on smaller scale regional or local factors. This is evident in Newfoundland where salmon stocks on the Northeast Coast of Newfoundland are doing relatively well by comparison with those on the South Coast, with Conne and Little River experiencing the most severe declines (DFO 2023; Figure 3).

#### Aquaculture

Concerns regarding the impacts of cultured salmon on wild stocks fall largely into two broad categories: ecological and genetic, and for many years concerns have been expressed not only in Europe (e.g. Hindar et al. 1991; Fleming et al. 2000; McGinnity et al. 2003) but also in Atlantic Canada (Carr et al. 1997; Lacroix 1998; Morris et al. 2008). In Newfoundland, the marine cage culture of salmonids started in the mid-1980s at Bay d'Espoir and later expanded east into Fortune Bay (Pepper et al. 2003b; Anderson et al. 2005; Figure 5) and more recently expanding into Placentia Bay, Newfoundland, using an all-female strain of European triploid (sterile) Atlantic salmon (origin: Norwegian salmon, Icelandic hatchery, DFO 2022a). Growth of the industry was initially slow with rainbow trout accounting for most of the production during the first decade. By 2001 more than 1000 t of Atlantic salmon were being produced annually with a greater proportion of the total yield represented by Atlantic salmon in subsequent years. Despite aquaculture operations occurring in a limited geographic area of the south coast of Newfoundland, production peaked in 2016 at over 25,000 t declining to approximately 15,000 t in 2019 falling again to less than 8000 t in 2020 with the latter attributed to a mass mortality event associated with a prolonged increase in water temperatures and reduced dissolved oxygen levels that led to asphyxiation (Burke et al. 2020; Singh et al. 2024; Figure 5A). Some researchers, however, do not fully support the rationale for this mortality event (Gamperl et al. 2021).



**Figure 5.** (A) Wild Atlantic salmon populations and the three south coast rivers, including Conne River, monitored by Fisheries and Oceans Canada (yellow highlight) in relation to aquaculture lease site areas (crosses). Aquaculture lease site areas in Placentia Bay are new with smolt stocked in 2022. Bolded river names are those including Conne River, with confirmed hybridization between wild and farmed salmon (Wringe et al. 2018). Orange circles represent available data for location and number of sea lice treatments (defined as the number of times an active chemical ingredient was administered at a cage site) between 2016 and 2021. Red squares represent location of reported escape events most notably those in 2013, 2018, 2019, 2020, and 2021. Purple asterisks represent locations of confirmed ISAv events between 2008 and April 2022. Green triangles represent locations of reported mass mortality events (>10% mortality at a cage site), most notably those that occurred in 2019 and 2021. Curved directional arrows show movements of Conne River salmon that were tagged with acoustic transmitters. (B) Location of Panel A (rectangle) in relation to the rest of Newfoundland. Note that aquaculture activities only occur on the south coast of Newfoundland.

The first known Atlantic salmon escapees appeared at Conne River in 1994 with sporadic but low numbers occurring in subsequent years (Morris et al. 2008), at least during times when the fish counting fence was in operation (usually mid-May to late August). As production of farmed salmonids expanded, so too did scrutiny and concern regarding the scale of impacts on the declining wild populations of Atlantic salmon (Ford and Myers 2008; Glover et al. 2017; Nylund et al. 2019), including Conne River (Hinks 2012).

Research in southern Newfoundland identified extensive hybridization between escaped farmed fish that originate from Saint John River, New Brunswick (Keyser et al. 2018) and wild salmon in various rivers including Conne River (Keyser et al. 2018; Sylvester et al. 2018; Wringe et al. 2018; Figure 5A). Subsequent sampling of South Coast rivers shows that first generation hybrids are present in most years, even in years without reported escape events indicating that trickle losses from salmon farm sites are a regular occurrence. There is also evidence of recent European introgression in farmed salmon in Newfoundland, with the potential for farm escapees to introduce European alleles into wild populations (Bradbury et al. 2022). Recently, evidence of high levels (>10%) of European ancestry was found in juvenile salmon sampled in a number of South Coast systems including Conne River (Bradbury et al. 2022). This phenomenon, previously reported from New Brunswick (O'Reilly et al. 2006), increases the potential for negative consequences resulting from hybridization with the remaining natural population as acknowledged by Cote et al. (2015) and Verspoor et al. (2015) for the South Coast region of Newfoundland. Additional modeling and empirical studies, both of which have included Conne River, suggest reduced survival of the resulting offspring and predictions of negative genetic and demographic impacts due to interbreeding with escapees (Sylvester et al. 2019; Bradbury et al. 2020; DFO 2024). Thus, current evidence suggests hybridization is impacting the wild salmon population at Conne River. Predictions of escapees currently exceed the threshold for demographic and genetic impacts (Bradbury et al. 2020) such that further expansion of the industry will likely intensify and affect the full life cycle of salmon as shown from recent studies in Norway (Bolstad et al. 2021).

There is also a substantial body of information pertaining to the amplification and spillover of naturally-occurring pathogens from other provinces and countries with the potential for negative impacts on wild salmon (Garseth et al. 2013; Madhun et al. 2015, 2018; Nylund et al. 2019). In southern Newfoundland disease outbreaks on salmon farms occur (Figure 5A), particularly infectious salmon anemia (ISAv) (https://inspection.canada.ca) with the virulent form able to result in significant mortality (Rigby et al. 2017). The risk to wild Atlantic salmon populations from spillover of ISAv from farms, however, remains unknown, although pathological screening (2018, 2019 and 2023) of wild Conne River smolt at the counting fence, in fresh water and prior to their migration to sea, for background presence of ISAv has been negative. In Newfoundland, information on ISAv over the period 2008 to April 2022 shows an increase from 2017 to 2020, with a record high 13 outbreaks in 2020. Outbreaks have occurred in every month of the year except February with peaks occurring in March, July, October, and December.

Salmon lice (Lepeophtheirus salmonis, Krøyer, 1837) have been identified as one of the greatest threats to wild Norwegian salmon (Forseth et al. 2017) although other parasite species (e.g. Caligus spp., Ergasilus labracis, Krøyer, 1863) could also be important (Murray and Ang 2018; Hemmingsen et al. 2020) and hence for simplicity, we use the generic term sea lice throughout. Extensive research over the last decade in Norway, Scotland, and Ireland has demonstrated significant demographic impacts to wild Atlantic salmon, as well as to sea trout (Salmo trutta) populations (Fiske et al. 2024) due to the amplification of sea lice associated with salmon aquaculture (e.g. Thorstad et al. 2015; Shephard and Gargan 2017; Dempster et al. 2021; Johnsen et al. 2021; Vollset et al. 2022). The magnitude of wild population decline in years of sea lice outbreaks in salmon farms has been reported to be between 12 and 50% (Shephard and Gargan 2017; Thorstad et al. 2015). Moreover, prophylactically treating out-migrating smolts for sea lice has been shown to improve survival by 50 times (Bøhn et al. 2020).

Long-term data on sea lice abundance in southern Newfoundland is lacking, although as of January 2021, public reporting of monthly averages of sea lice per fish across all sites/company has become a requirement for periods in which water temperatures are above 5 °C (Aquaculture Policy 17; www.gov.nl.ca/ffa/ files/licensing-pdf-aquaculture-polic y-procedures-manual.pdf). Drug and pesticide use reporting, however, has been a requirement since 2016. As a result, drug and pesticide use reporting is the only information currently available for inferring sea lice infestation potential on Conne River salmon. Sea lice treatments included: bath pesticides Salmosan<sup>\*</sup> (azamethiphos) and Interox Paramove 50<sup>°</sup> (hydrogen peroxide), and the in-feed drugs: SLICE<sup>\*</sup> (emamectin benzoate) and IVOMEC<sup>\*</sup> (ivermectin). While some cage sites reported low or no chemical usage for controlling sea lice (Figure 5), sea lice treatments (defined as the number of times an active chemical ingredient was administered at a cage site) in Newfoundland over the period 2016-2021 peaked in 2017, declined in 2020 and increased again in 2021 (unpublished data DFO NL Region; Hamoutene et al. 2022; Figure 5A). The high number of treatments in 2017 coincided with warmer surface temperature in the fall, a higher freshwater input in spring, and stronger wind conditions (Hamoutene et al. 2022). It is unknown, however, whether the decline from 2017 to 2021 is a result of decreased salmon aquaculture production over this period, increased use of innovations (i.e. non-chemical methods) using biological and mechanical treatment methods (e.g. use of cleaner fish, thermolicers), a change in how the numbers are reported (i.e. a chemical bath treatment of a single net-pen, a series of chemical bath treatments on multiple net-pens, one feeding or a sequence of feeding events using medicated feed; Hamoutene et al. 2022), or a natural reduction in sea lice in the marine environment due to unfavorable environmental conditions. Nevertheless, sea lice treatments appear to peak in July but have occurred from June to December and thus outbreaks can coincide with the period wild salmon are either migrating from, or returning to local rivers. Similar to viral outbreaks, no data exist on sea lice impacts on wild salmon in southern Newfoundland, but ongoing needs for cleaner fish or chemical treatments to control for sea lice (Figure 5A), in combination or as successive treatments, not only suggest there is a substantive problem (Hamoutene et al. 2022), but also the potential for impacts on wild Atlantic salmon populations in the region.

#### Scoring of potential threat factors

The approach of using expert opinion has been broadly accepted as a means by which various threats, judgements or perceived status of populations are used to inform on conservation and rebuilding of at-risk or endangered fish populations (e.g. Forseth et al. 2017; Lennox et al. 2021; Stokes et al. 2021; Gillson et al. 2022; Marine Scotland and Fisheries Management Scotland 2023; Fiske et al. 2024), as well as being incorporated into the annual status review of Norwegian salmon populations (e.g. Norwegian Scientific Advisory Committee for Atlantic Salmon Management 2022).

Characteristics and scoring for each potential threat discussed in the synopsis above were used to describe each factor along a Severity and Projected magnitude axis (Table S1). For the Severity axis, three characteristics were considered for each potential decline factor and scored as follows: pervasiveness of potential factor (1: widespread in Newfoundland and Labrador Region, 2: scattered in Newfoundland and Labrador Region, 3: specific to Conne River area); potential to cause reductions in salmon abundance due to reduced production capacity, or reduced freshwater or marine survival from 1986 to 2021 (1: small reduction <10%, 2: moderate reduction 10-25%, 3: large reduction 25-75%, 4: very large reduction >75%) and; have mitigation measures addressed the factor for Conne River? (1: factor has little or no remaining effect, 2: some factor effect removed, 3: no factor effect removed).

For the Projected magnitude axis, two characteristics were considered for each potential decline factor (Table S1) and scored as follows: additional or continuation of existing mitigation measures planned to address the factor (1: very effective mitigations planned, 2: moderately effective mitigations planned, 3: few/no effective mitigations planned), and; likelihood of factor to cause further losses to the Conne River salmon population under existing conditions (1: low, 2: medium, 3: high).

Scoring was conducted independently by thirteen Biologists/Research Scientists who ranged in experience from 4 to 30+ years (mean = 16 years) either working with Atlantic salmon in Newfoundland and Labrador (n=9), or who regularly participate in the stock assessment review process for salmon as well as other marine fish species (n=4). All participants were associated with Fisheries and Oceans Canada. In addition, all authors of the manuscript, except two (C. Pretty and F. Cyr), were among those who participated in the scoring. This is because both authors expertise is not related to Atlantic salmon and voluntarily removed themselves from the scoring.

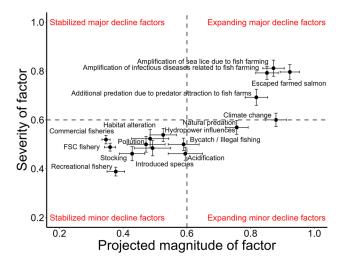
As an alternative to trying to achieve consensus among experts (e.g. Forseth et al. 2017; Gillson et al. 2022), cumulative scores and standard errors were estimated for each decline factor to incorporate the variability among scoring participants. These scores were then expressed as a proportion of the potential maximum score for each axis (Table S1) and graphed to rank and highlight the most likely threats for Conne River that warrant further targeted research efforts (Figure 6).

Of the nineteen factors originally identified in this study, and commonly associated with Atlantic salmon

declines elsewhere, three were ruled-out entirely (mining, water abstraction, and Gyrodactylus salaris; Table S1; Figure 6). Of the remaining sixteen threats, ten were considered stabilized risk factors (recreational fishery, FSC fishery, commercial fishery, stocking, pollution, habitat alteration, introduced species, hydropower influences, bycatch/illegal fishing, acidification; Table S1; Figure 6), one was considered an expanding minor decline factor (natural predation), and five identified as expanding major decline factors that may have potentially contributed to declines observed at Conne River, specifically, aquaculture related factors unique to this area of the south coast (escaped farm salmon, amplification of sea lice due to fish farming, amplification of infectious diseases related to fish farming, additional predation due to predator attraction to fish farms), and climate change (Table S1; Figure 6). Based on the pattern of standard errors among participants, there was strong agreement among scores in relation to the severity axis, with more variability associated with the projected magnitude axis (Table S1; Figure 6).

#### **Random forest analysis**

In addition to expert opinion, factors based on available data were quantitatively and independently



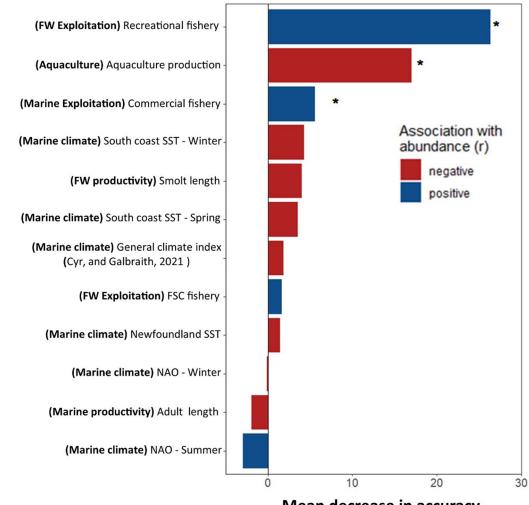
**Figure 6.** Ranking of potential decline factors to the Conne River Atlantic salmon population as scored by expert survey respondents. Solid circles represent the mean score±standard error for each factor. Plot quadrats (separated by dashed lines) represent the four categories of potential threats. In order of increasing research priority these include: stabilized minor decline factors, stabilized major decline factors, expanding minor decline factors and expanding major decline factors. Scoring was conducted independently by thirteen Biologists/ Research Scientists who ranged in experience from 4 to 30+years (mean = 16 years).

assessed, to determine which were potentially most relevant for explaining salmon declines for Conne River. Here, random forest (RF) regression (Breiman 2001) with available data was used to identify top variables associated with trends in salmon abundance at Conne River. First, correlations among 19 variables spanning a time series from 1987 to 2021, with 1987 being the first year of smolt abundance was assessed. All variables were scaled using the scale() function in R prior to running analyses. Only variables that were not highly correlated with each other (|r|<0.75)and had complete observations for all years were included in the subsequent RF analysis. Thus, a total of 12 predictors were subsequently used in the RF model with salmon abundance as the response. Predictors included catch statistics from the recreational fishery, commercial fishery, and FSC fishery, aquaculture production, smolt length, adult length, a common climate related index that characterizes the Newfoundland and Labrador shelf (Cyr and Galbraith 2021), and five additional climate related variables: summer NAO, Winter NAO, Spring (April-June) and the Winter (January-April) sea surface temperature (SST) for the South Coast of Newfoundland west of the Burin peninsula from the NOAA OI-SST product (https://www.ncei.noaa.gov/products/ optimum-interpolation-sst). In the final iteration, the metric of abundance based on returns of small salmon was used as this size class accounts for the majority (95%) of returns at Conne River, although the addition of using small and large salmon (i.e. total returns) returns did not alter any of the conclusions. Data spanned 35 years from 1987 to 2021. RF was run using the R packages randomForest (Liaw and Wiener 2002) and rfPermute (Archer and Archer 2016). Following the methods described in Brieuc et al. (2018), the best parameter values were selected from mtry (number of predictors randomly sampled) and ntree (number of trees) based on maximizing the proportion of variance explained in the RF model. Here, mtry was 8 and ntree was 1000 using the randomForest() function. The importance() function was used to identify the top ranked predictors based on mean decrease in accuracy (MDA), which represents how the accuracy of RF decreases when the variable is excluded, where higher values indicate greater importance, with negative values indicating that inclusion of the variable reduced model accuracy. In addition, using the rfPermute package in R (Archer and Archer 2016), statistical significance of the importance metrics was determined by permutating the response variable, where a *p*-value was generated for each predictor to determine their significance in the model. For this

rfPermute() with 1000 permutations using the same parameters as the RF model above was used.

The RF model explained 62% of variance in small salmon returns. The top three variables associated with small salmon returns to Conne River with significant importance were numbers of salmon harvested in the recreational fishery (p=0.001), aquaculture production (p=0.001), and commercial fishery landings (p=0.01) (Figure 7). No other predictors were significant. Fishery indices (commercial and recreational) were correlated with each other, but had a positive relationship with abundance, suggesting more fishing occurred when there was greater opportunity (i.e. higher abundance) which also translated into higher returns back to Conne

River. Conversely, there was a negative association between salmon abundance and aquaculture production (Figure 7). Consistent with the expanding major decline factors identified by expert opinion, the results of the RF analysis support that aquaculture production is potentially an important factor for explaining declines in salmon returns at Conne River. The RF analyses, however, did not rank climate indices as significantly important for explaining the decline, and thus the effects of climate may be more limited or not yet realized. In addition, due to limited data, the influence of natural predation, which was identified as an expanding minor decline factor by experts, was unable to be quantitatively assessed.





**Figure 7.** Mean decrease in accuracy (MDA) for 12 predictors in the random forest regression with small salmon returns (< 63 cm) as the response. Data spanned 35 years from 1987 to 2021, and predictor variables included fisheries indices (recreational, FSC, and commercial), aquaculture production, salmon length (as smolts and returning adults), and climate indices. Predictors are ordered by MDA values, which represent how the accuracy of random forest decreases when the variable is excluded, with higher values indicating greater importance. Predictors of significant importance (p < .05) are indicated by asterisks (\*). Variables are colored by their positive (blue) or negative (red) correlation (r) with abundance (small returns).

#### Discussion

Multiple factors often contribute to the decline of Atlantic salmon populations (Parrish et al. 1998; Dadswell et al. 2022) and Conne River is undoubtedly no exception. The synopsis and subsequent scoring of threats derived from expert opinion identified aquaculture, predation and climate change as expanding major decline factors. The importance of aquaculture for explaining declines at Conne River was also quantitatively reinforced by random forest analysis, whereas various climate indices were not significant. This finding further supports the position by Tirronen et al. (2022), that the continued declines at Conne River depend on smaller scale regional, or local factors.

Regarding aquaculture, over two decades of research has demonstrated that hybridization and introgression between wild and escaped farmed salmon results in wild salmon population decline and the genetic alteration of wild salmon populations (DFO 2024). These studies include both empirical estimates of reduced hybrid survival and population decline (Fleming et al. 2000; McGinnity et al. 2003; Skaala et al. 2012; Sylvester et al. 2019), and model-based predictions of population responses to introgression (Castellani et al. 2018; Sylvester et al. 2019; Bradbury et al. 2020). For example, Fleming et al. (2000) reported reductions of >30% in productivity of wild salmon due to hybridization in an experimental population, where sexually mature farm and wild salmon were genetically screened, radio tagged and released into the River Imsa, Norway where no other salmon had been allowed to ascend. Others have reported decreased homing in hybrids between wild and farmed salmon (Jonsson and Jonsson 2017). Following a two-generation experiment, McGinnity et al. (2003) concluded that introgression with escapees reduces wild population productivity, potentially leading to the extinction of vulnerable populations. Skaala et al. (2019) conducted a common garden experiment with wild, farm, and hybrid salmon and demonstrated that hybridization reduces wild smolt output and subsequent adult returns, as well as alters key life history traits. These field observations are further supported by the modeling efforts of Castellani et al. (2018) and Bradbury et al. (2020), both of whom modeled the response of wild populations to hybridization with escapees and report significant decreases in population size and genetic changes when the proportion of escapees exceeds ~10% of the wild population, which is a highly plausible scenario for Conne River. Regardless, the consensus of these studies is clear; genetic impacts

of escaped farmed salmon scale with the proportion of escapees present within a population (Heino et al. 2015, Sylvester et al. 2018; Wringe et al. 2018) such that in areas where the potential exists for reproductively viable salmon to escape, wild populations will be at risk (Diserud et al. 2022). Accordingly, the ultimate impact on wild populations exposed to escapees will be significantly greater in small or depressed populations, such as Conne River, and these impacts will likely increase as populations decline toward local extirpation.

Various studies have shown that farmed salmon can influence the abundance of sea lice (Dempster et al. 2021) ultimately causing negative consequences to wild fish (Costello 2009; Johnsen et al. 2021; Shephard and Gargan 2021) with the expectation that this will only worsen as water temperatures increase (Godwin et al. 2020). Outbreaks, particularly those associated with sea lice and infectious salmon anemia, have been problematic for the aquaculture industry in Newfoundland (Hamoutene et al. 2022). While the severity of these impacts on wild Conne River salmon are unknown, the potential threat from sea lice or disease transmission cannot be dismissed despite varying opinions (Rigby et al. 2017).

Climate change was also highlighted as an expanding major factor potentially contributing to the decline of the Conne River salmon population in the synopsis and subsequent expert opinion scoring of threats analysis. In contrast, marine climate was not identified as important in the random forest analysis, despite including a common climate related index (Cyr and Galbraith 2021) that has been used to examine its influence on other species in the Northwest Atlantic (e.g. Murphy et al. 2021) along with information specific to the South Coast of Newfoundland. Chaput et al. (2005) provided substantive evidence for a phase shift in Atlantic salmon productivity in the North Atlantic during the early 1990s, and argues that this change was coincident with an environmental/ecosystem regime shift. Supportive evidence was also provided by Mills et al. (2013) for major declines of Atlantic salmon in other regions of eastern North America that also coincided with 1991 being one of the lowest years on record for salmon stocks in insular Newfoundland (Dempson et al. 2004a). This was consistent with the environmental evidence that showed for the Newfoundland and Labrador shelf area that 1991 was one of the coldest years on record (Cyr and Galbraith 2021). While this wider phenomenon may have contributed to the initial decline at Conne River, it doesn't explain why since 2000, there has been a continued decline of adult Atlantic salmon with less

than 300 Atlantic salmon annually returning from 2020 to 2022 despite successive cycles of warmer (~2001–2011; 2018–2021) and cooler (2014–2017) periods of the Northwest Atlantic climate (Cyr and Galbraith 2021). Further, the random forest approach did not identify any of the six climate indices included in the final analyses as significantly important for explaining declines at Conne River; although, future changes in climate may still represent a threat to salmon, including Conne River.

Debate for the role of predation on wild fish stocks including Atlantic salmon, persists such that natural predation was identified by the expert panel as an expanding minor decline factor, whereas additional predation due to predator attraction to fish farms was identified as an expanding major decline factor. While predation is a common process that can potentially impact Atlantic salmon across various life-history stages, the context or conditions that contribute where and when predation occurs is important to consider (Mather 1998). With respect to Conne River, it is difficult to rationalize how one population would be differentially impacted to the extent that Conne River salmon have declined unless conditions were such that the predatory influence was highly concentrated in the local area. For example, predation by striped bass (Morone saxatilis, Walbaum, 1792) is believed to be a factor contributing to the decline of Atlantic salmon at the Miramichi River, New Brunswick, Canada (Daniels et al. 2018; Andrews et al. 2019). If a similar phenomenon of concentrated predators was occurring at Conne River, it is surprising that this would not have been observed given the extent of studies carried out over the past several decades. Salmon farms, however, are known to attract various fish assemblages including large predatory fish (Dempster et al. 2009; Callier et al. 2018). As part of an experimental release of tagged aquaculture salmon in Fortune Bay, Newfoundland, natural mortality of some of the tagged fish was indicative of predation events by bluefin tuna (Hamoutene et al. 2018). Therefore, given this result and the projected magnitude of proposed aquaculture expansion (DFO 2022a), additional predation due to predator attraction to fish farms was scored higher than natural predation and could not be dismissed as a potential factor contributing to the ongoing declines. This result, however, is not supported by English et al. (2024), who used acoustic telemetry in combination with predation event tags to quantify predation events by seals and porpoises attracted to cage sites, in New Brunswick, Canada, and concluded that the current low return of adult Atlantic salmon observed in their area in

recent years was not heavily influenced by endothermic predation on post-smolt in the first weeks at sea. Unfortunately, due to a lack of time series, estimates of predation or predator abundance could not be included as a variable in the random forest model used in our analysis.

Overexploitation of Atlantic salmon, particularly by ocean fisheries, is often considered a primary threat to the conservation of wild populations (e.g. Parrish et al. 1998). As a result of various closures or dramatic reductions in many of these fisheries (Lear 1993; Kocik and Brown 2002), however, results of the semi-quantitative 2D classification system ranked exploitation as a stabilized minor decline factor of Conne River salmon. While fisheries exploitation (commercial and recreational) were ranked as important factors in the random forest analysis, these variables had a positive association with abundance at Conne River, consistent with more fishing occurring when there was greater opportunity, and thus did not explain the declining abundance of salmon. These results are contrary to an alternative explanation for the continued decline of salmon in the North Atlantic recently provided by Dadswell et al. (2022). Rather than associating widespread declines to factors such as predation, changing climate, aquaculture, competition, or changes in prey abundance, they argue that the most likely explanation is related to illegal, unreported, and unregulated high seas fisheries. This premise, however, raises the question as to why other monitored Newfoundland populations have not collapsed like Conne River, since salmon from other rivers in this region are also commonly found on the Grand Banks and Labrador Sea areas (Bradbury et al. 2021).

While declines in Atlantic salmon populations are widespread, local stressors, when addressed, can reverse population declines (e.g. Cote et al. 2021). Extensive information exists for the South Coast region of Newfoundland regarding the extent of hybridization and introgression with wild and escaped farmed Atlantic salmon, and expectations of reduced survival and overall population decline predicted by empirical and model-based studies. In view of plans to expand aquaculture in Newfoundland (Maxwell and Filgueira 2020), additional studies are required to investigate how threatened or endangered salmon populations will respond to the challenges of changing climate, along with focused studies to examine the impacts of sea lice and disease on those populations. Such data are critical to informing management approaches needed to reverse the decline of this population that is clearly on an extirpation

trajectory and thus should also include examining evidence for, and implications of depensation (Liermann and Hilborn 2001). Owing to the ecological and cultural significance of Conne River Atlantic salmon, as well as the importance of the aquaculture industry to communities on the South Coast of Newfoundland, it is suggested that rather than simply documenting the ongoing decline of the Conne River salmon, collaboration is required between fisheries managers, the aquaculture industry, and local First Nations to actively pursue evidence-based research along with experimental and adaptive restoration measures within this salmon population's socio-ecological landscape.

#### **Acknowledgements**

We would like to thank George Furey, Marc Bloom, Milton Shears and members of Miawpukek Mi'kamawey Mawi'omi, Conne River, in particular Ross Hinks, for their invaluable field assistance and support since 1986. In addition, we thank Chantelle Burke, Michelle Fitzsimmons, Amber Messmer, Rebecca Poole and Kristin Loughlin for their contributions to the scoring of potential threats. Bill Montevecchi, Garry Stenson, and Charmain Hamilton reviewed various sections of the manuscript with GS and CH kindly sharing preliminary results from seal surveys carried out in 2021. Thanks also to Keith Clarke, Rex Porter and Craig Purchase for providing comments on an earlier version of the manuscript. We also thank two anonymous reviewers, and also John Kocik and the Editor, Sandra Shumway for their help and assistance. Funding for the counting fence program was provided from Fisheries and Oceans Canada and the Miawpukek First Nation.

#### **Disclosure statement**

No potential conflict of interest was reported by the author(s).

#### ORCID

J. Brian Dempson b http://orcid.org/0000-0001-9817-062X Travis E. Van Leeuwen b http://orcid.org/0000-0003-0209-543X Ian R. Bradbury b http://orcid.org/0000-0002-8152-4943 Sarah J. Lehnert b http://orcid.org/0000-0002-3569-8299 David Coté b http://orcid.org/0000-0002-5805-5077 Frédéric Cyr b http://orcid.org/0000-0002-1581-7502

#### Data availability statement

The time series of smolt and adult salmon abundance information and climate data used in the Random Forest analysis are available on request. R scripts for running random forest analyses are available at: https://github. com/SarahLehnert/ConneDeclines/

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