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# Spatio-temporal trends in the importance of iteroparity across Atlantic salmon populations of the northwest Atlantic

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Iteroparity is a bet-hedging strategy where individuals spread the risk of reproductive failure over time. The occurrence of iteroparity (i.e. proportion of repeat spawners in annual returns) varies among Atlantic salmon (*Salmo salar*) populations, yet information on its ecological importance is limited. We compiled multi-decadal time series on the spawning history composition of Atlantic salmon annual returns across ten populations of the northwest Atlantic and West Greenland mixed-stock fishery landings to: (i) describe spatio-temporal patterns of iteroparity at the continental scale; (ii) quantify the reproductive contributions of repeat spawners; and (iii) test the hypothesis that iteroparity acts as a population safeguard during periods of low recruitment through repeat spawners' contributions. Despite high variability in the representation of repeat spawners among populations and years (range: 0–24.7%; average: 5.0%), we identified broad-scale spatio-temporal shifts in iteroparity, with increases in mid-latitudinal and northern populations (from 3.1% to 7.6%) and declines in southern areas (from 4.1% to 2.7%), between the 1971–1992 and 1993–2017 periods. Our findings highlight the potential for increased prevalence of iteroparity when threats are mitigated (e.g. fishing pressure), with measurable benefits to population processes manifested by the high reproductive contributions of repeat spawners, especially in years of low maiden spawner abundance.

**Keywords:** demographic changes, dynamic factor analysis, kelts, life-history strategies, previous spawners

## Introduction

One of the central assumptions of life-history theory is that reproduction is costly and involves a trade-off between reproductive effort and adult survival (Stearns, 1976). Across sexually reproducing organisms, breeding systems are classified as semelparous (i.e. single life-time reproductive event followed by death) or iteroparous (i.e. two or more life-time reproductive events) as strategies to maximize lifetime fitness (Cole, 1954; Murphy, 1968). With increasing variability in the survival of offspring, and increasing survival of adults, natural selection favours life histories that spread the risk of reproductive failure over space or time (Murphy, 1968; Stearns, 1976). Semelparity and iteroparity can exist as a continuum as manifested by intra-specific variability in the occurrence of iteroparity. Examples include populations of capelin (*Mallotus villosus*, Christiansen *et al.*, 2008) and American shad (*Alosa sapidissima*, Leggett and Carscadden, 1978). Various degrees of iteroparity have also been observed in anadromous salmonid species such as Atlantic salmon (*Salmo salar*), brown

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trout (*Salmo trutta*), Arctic char (*Salvelinus alpinus*), brook trout (*Salvelinus fontinalis*), Dolly Varden charr (*Salvelinus malma*), rainbow/steelhead trout (*Oncorhynchus mykiss*), cutthroat trout (*Oncorhynchus clarki*) (reviewed in Fleming, 1998), as well as Chinook salmon (*Oncorhynchus tshawytscha*) (Barry *et al.*, 2001).

Whether semelparous or iteroparous, most salmonids are capital breeders, fasting during their extended spawning periods and instead relying on somatic energy reserves accrued prior to breeding to power migrations to natal spawning areas, produce gametes, develop secondary sexual characteristics, and support reproductive behaviours (Fleming and Reynolds, 2004; Jager *et al.*, 2008). The evolutionary trade-off between reproductive investment and survival has received much attention in iteroparous salmonids, with spawning investment (i.e. total energy loss of 46–70%) being negatively correlated with post-spawning survival (Fleming, 1996, 1998; Jonsson *et al.*, 1997; Fleming and Reynolds, 2004), reflective of a bet hedging strategy (Slatkin, 1974). This was further corroborated by a recent study that identified a genotypic co-inheritance between sea-age at maturity and iteroparity in Atlantic salmon, with iteroparity being more likely in smaller, earlier-maturing salmon that invest proportionally less into reproduction (Aykanat *et al.*, 2019). In Atlantic salmon and iteroparous salmonids more broadly, constraints imposed by capital breeding and by environmental conditions that affect somatic reconditioning are known to affect the post-spawning survival and the potential for repeat spawning (Belding, 1934; Fleming and Reynolds, 2004; Chaput and Benoit, 2012), both of which affect population demographics. However, anthropogenic factors such as exploitation and migration challenges posed by hydroelectric dams can also affect the survival of juvenile and adult salmon, inducing demographic changes and modifying life-history traits through size-selective mortality (Dempson *et al.*, 2004; Nyqvist *et al.*, 2016; Maynard *et al.*, 2017; Erkinaro *et al.*, 2019).

Atlantic salmon returns have generally declined throughout the North Atlantic stock complex over the past 50 years (ICES, 2018). Nonetheless, broad temporal fluctuations in the degree of iteroparity have been documented in different regions of the species' global range, with increases in some populations (Dempson *et al.*, 2004; Chaput and Benoit, 2012; Erkinaro *et al.*, 2019) and declines in others (Hubley and Gibson, 2011; Maynard *et al.*, 2017). Repeat spawners in Atlantic salmon represent on average 11% of all spawners (range: 1–43%), and similarly 10% on average in steelhead trout (range: 1–31%), compared with an average of 20–41% in other anadromous iteroparous salmonids (range 5–69%) (Fleming, 1998). Atlantic salmon can mature and migrate back to freshwater to spawn after feeding at sea for one (one-sea-winter, 1SW) or more years (multi-sea-winter). Similarly to variation in sea-age at maturity, Atlantic salmon can repeat spawn in consecutive or alternate years (up to seven times in rare cases, Chaput and Jones, 2006), spending as little as a few months at sea to more than a year for reconditioning, respectively (Jonsson *et al.*, 1991; Fleming, 1996). Maiden (first-time) 1SW spawners and consecutive repeat spawners generally exhibit shorter feeding migrations (e.g. Gulf of St. Lawrence or Bay of Fundy) than maiden MSW (mostly 2SW) spawners and alternate repeat spawners that mostly migrate to distant feeding grounds (e.g. Labrador Sea and West Greenland) (Hubley *et al.*, 2008; Chaput and Benoit, 2012; Lacroix, 2013; Strøm *et al.*, 2017).

Despite their generally low occurrence (especially in Atlantic salmon and steelhead trout, Fleming 1998), repeat spawners can make considerable contributions to annual reproduction, especially females via their comparatively large body size which translates into high fecundity, thus contributing to population viability (Keefer *et al.*, 2008; Seamons and Quinn, 2010; Halttunen, 2011; Reid and Chaput, 2012; Lawrence *et al.*, 2016). In addition to a direct contribution to recruitment, repeat spawning also plays a role in maintaining genetic diversity via a genetic contribution of one year-class to several other age-classes (Saunders and Schom, 1985; Palstra *et al.*, 2009). However, in the Atlantic salmon literature, and for iteroparous salmonid fishes more broadly, information on the occurrence of iteroparity and its potential ecological importance is sparse and often speculative. Despite the volume of data collected annually on the composition of Atlantic salmon returns throughout their global range, as well as a growing number of studies assessing some aspects of the biology and ecology of post-spawners (e.g. Jonsson *et al.*, 1991; Niemelä *et al.*, 2006a; Chaput and Benoit, 2012; Halttunen *et al.*, 2013), limited attempts have been made to quantify the contributions of repeat spawners to population processes (Halttunen, 2011; Lawrence *et al.*, 2016). Moreover, no previous study has specifically assessed spatio-temporal patterns in iteroparity levels at the continental scale of the species' distribution, nor empirically tested the circumstances in which iteroparity may act as a safeguard against low recruitment periods.

Here, we compiled multi-decadal time series on the sea-age and spawning history composition of Atlantic salmon returns for ten North American populations in addition to mixed-stock fishery landings from West Greenland to: (i) assess spatio-temporal patterns of iteroparity at the continental scale; (ii) quantify the relative reproductive contributions of repeat spawners across varying population contexts (i.e. different latitude and sea-age at maturity composition); and (iii) evaluate the extent to which repeat spawners can compensate for losses in total reproductive output (i.e. increased relative importance of repeat spawners) during periods of low maiden spawner returns.

## Methods

### Data sources

To describe sea-age at maturity and spawning history composition of Atlantic salmon annual returns, we compiled published and unpublished long-term data series from a total of ten populations in Newfoundland and Labrador (3), Quebec (2), New Brunswick (3), Nova Scotia (1), and Maine (1), in addition to mixed-stock fishery landings from West Greenland to quantify the degree of iteroparity from a suite of North American populations across a latitudinal gradient (Figure 1). The data were collected by the Department of Fisheries and Oceans Canada (DFO), Quebec's Ministère des Forêts, de la Faune et des Parcs (MFFP), the Maine Department of Marine Resources (DMR; Maynard *et al.*, 2017), and ICES Working Group on North Atlantic Salmon (WGNAS; ICES, 2018), between 1971 and 2017 and ranged from 21 to 47 years (Table 1). Biological information and annual return estimates were collected at estuarine trapnets, fishways, or counting fences for all populations except for the Rivière Saint Jean (Gaspé, QC), where biological information was collected on salmon captured as part of the recreational fishery and annual returns were assessed from counts made by snorkel surveys (Cauchon and April, 2017). Data on the composition of West Greenland fisheries was assessed from biological information collected on fishery landings (available in ICES, 2018).

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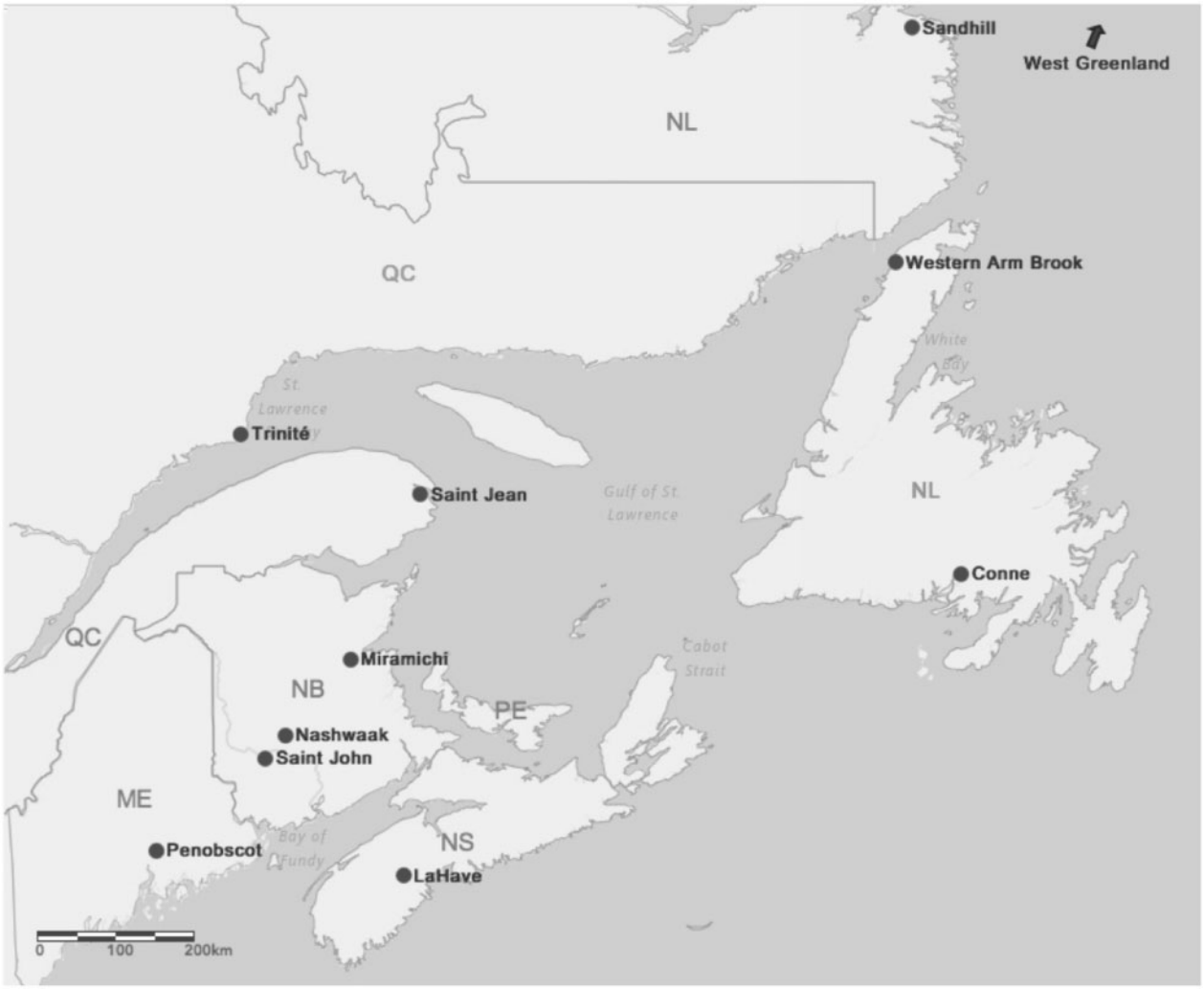


**Figure 1.** Map of the northwest Atlantic showing the location of Atlantic salmon populations with long-term monitoring programs that were included in this study (the map was produced using Esri, HERE, Garmin, NGA, USGS). Information on the extent of the time series is provided in Table 1.

We summarized spawning history groups in three categories based on scale readings (White and Medcof, 1968): maiden-1SW (salmon returning to freshwater for the first time after a single winter at sea), maiden-2SW+ (salmon returning to freshwater for the first time after two or more winters at sea), and repeat spawners (including all salmon returning to freshwater that spawned in previous years, as indicated by the presence of spawning marks on the scales). For West Greenland fishery landings, we assigned fish that had spent at least one winter at sea but still present in the area as maiden-2SW+ (as they would have not returned to freshwater as maiden-1SW salmon), and salmon with previous spawning marks as previously spawned/potential repeat spawners. These numbers exclude precocious maturation in freshwater by males as there is currently no way to empirically identify whether male spawners returning from the sea had previously matured as juveniles. For the purpose of this study, we thus defined repeat spawners as anadromous migrants that had spawned at least once in previous year(s) (based on the presence of previous spawning marks on scales; White and Medcof, 1968), excluding potential previous spawning as precocious parr.

Because only a subset of returning individuals were sampled for biological information (i.e. interpretation of scale patterns for age and previous spawning history, morphometrics, and sex) adjustment have been made to ensure that datasets are representative of the whole population. The spawning history characteristics of populations' annual return were derived by accounting for the biological data sampling design which was generally specific to the size group of salmon (small salmon $< 63$ cm fork length, large salmon $\geq 63$ cm fork length) and weighting by the estimated size group in annual return to each river:

$$p_{r,y,a} = \sum_s \left(\frac{n_{r,y,s,a}}{n_{r,y,s}} * N_{r,y,s}\right) \Big/ \sum_s N_{r,y,s} \quad (1)$$

with $p_{r,y,a}$ the proportion of the annual return in river $r$ in year $y$ of spawning history $a$; $n_{r,y,s,a}$ the number of samples aged for river $r$, year $y$, in size groups of spawning history $a$; $n_{r,y,s}$ the total number of samples processed; $N_{r,y,s}$ the total estimated return of salmon for corresponding river and year for size groups; $s$ is size group as small salmon or large salmon; and $a$ is spawning history as maiden-1SW, maiden-2SW+, or repeat spawner.

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**Table 1.** Information on the location and extent of time series included in this study, with ten populations across the northwest Atlantic range and West Greenland mixed-stock fishery landings.

| Population | Population segment (DU/DPS[a]) | Conservation status | Geographic coordinates | Time series extent | Data source |
|---|---|---|---|---|---|
| West Greenland fishery landings | – | – | N 64.161<br>W 51.819 | 1985–2017 | WGNAS[b]<br>ICES (2018) |
| Sand Hill, NL | Central Labrador | Not at risk[c] | N 53.511<br>W 56.490 | 1971–2016 | DFO[d] |
| Western Arm Brook, NL | West coast of Newfoundland | Not at risk[c] | N 51.189<br>W 56.758 | 1974–2016 | DFO |
| Trinite, QC | Quebec western north shore | Special concern[c] | N 49.411<br>W 67.337 | 1980–2017 | MFFP[e] |
| Saint Jean, QC | Gaspé—southern Gulf of St. Lawrence | Special concern[c] | N 48.771<br>W 64.431 | 1981–2017 | MFFP |
| Conne, NL | South coast of Newfoundland | Threatened[c] | N 47.915<br>W 55.688 | 1986–2016 | DFO |
| Miramichi, NB | Gaspé—southern Gulf of St. Lawrence | Special concern[c] | N 46.980<br>W 65.569 | 1971–2017 | DFO |
| Nashwaak, NB | Outer Bay of Fundy | Endangered[c] | N 45.957<br>W 66.620 | 1972–2017 | DFO |
| Saint John, NB | Outer Bay of Fundy | Endangered[c] | N 45.952<br>W 66.875 | 1978–2017 | DFO |
| LaHave, NS | Nova Scotia Southern uplands | Endangered[c] | N 44.536<br>W 64.713 | 1979–2017 | DFO |
| Penobscot, ME | Gulf of Maine | Endangered[f] | N 44.832<br>W 68.701 | 1978–2013 | DMR[g]<br>Maynard *et al.* (2017) |

[a]DU stands for Designatable Unit in Canada, the equivalent of distinct population segment (DPS) in the United States.
[b]Working Group on North Atlantic Salmon of the International Council for the Exploration of the Sea.
[c]Status assessment conducted by COSEWIC (2010).
[d]Department of Fisheries and Ocean Canada.
[e]"Ministère des Forêts, de la Faune et des Parcs du Québec".
[f]Listed on the Endangered Species Act in 2000.
[g]Maine Department of Marine Resources.

## Spatio-temporal trends in iteroparity

We conducted a dynamic factor analysis (DFA) to assess the extent of spatial coherence in the temporal trends of iteroparity across populations of Atlantic salmon in different geographic areas. DFA is a multivariate statistical technique that can be used to identify common trends shared among multiple time series (Zuur *et al.*, 2003), and more recently to assess demographic changes in life-history traits at a continental, multi-population scale (Mills *et al.*, 2013; Ohlberger *et al.*, 2018). Using the spawning history composition estimates of Atlantic salmon annual returns, we constructed population specific time series of the proportion of repeat spawners across ten populations of the northwest Atlantic and West Greenland mixed-stock fishery landings. We then transformed the proportions on the logit scale ($-\infty$, $+\infty$) and calculated z-scores for the time series to remove inter-population differences in mean and variance (Ohlberger *et al.*, 2018). DFA was then implemented in a maximum likelihood framework using a multivariate autoregressive state-space modelling approach with the "MARSS" package (Holmes *et al.*, 2012) in R v.3.5.0 (R Development Core Team, 2018). In simple terms, time series are modelled as a linear combination of "common trends" and factor loadings, plus a noise component (i.e. residual errors) (Zuur *et al.*, 2003). To allow for potential temporal patterns in iteroparity to vary across different geographic regions, we compared a suite of models based on a varying number of common trends (i.e. m = 1–3 in "MARSS" function). In addition, we tested four different structures of the variance-covariance matrix of residual errors: same or different variances and no covariances (R="diagonal and equal" or "diagonal and unequal" in "MARSS" function), same variances and same covariances ("equalvarcov"), and different variances and different covariances ("unconstrained") (Holmes *et al.*, 2012). A total of 12 models were computed and model selection was based on AICc, an adjustment of the Akaike Information Criterion developed to avoid overfitting of small sample sizes (Hurvich and Tsai, 1989). At equivalent performances (i.e. $\Delta$AICc $< 1.0$), models with a single "common" trend were preferred over more complex structures. See Zuur *et al.* (2003) or Holmes *et al.* (2012) for more information on the mathematics underlying DFA.

## Reproductive contributions of repeat spawners

To quantify the reproductive contributions of repeat spawners among varying populations (measured as eggs produced), we first quantified the adjusted spawning history composition of annual returns for females alone. From this we calculated the proportion of eggs laid by females of different spawning history groups based on the annual average length of each group and population-specific fecundity-length relationships (Table 2), which included various spawning history types (e.g. 1SW, 2SW, and repeat spawners). Due to data limitation, we restricted this analysis to four populations that had adequate sex and length data for this analysis, which were also located in different parts of the species'

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**Table 2.** Average proportion of female, fork length, and fecundity of different spawning history groups (maiden-1SW, maiden-2SW+, as well as repeat spawners [RS]), with the fecundity/length relationship utilized.

| | Prop. female | | | Fork length (cm) | | | Fecundity (eggs) | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| **Population** | **1SW** | **2SW+** | **RS** | **1SW** | **2SW+** | **RS** | **1SW** | **2SW+** | **RS** | **Fecundity-length relationship** |
| Conne, NL | 0.752 | 0.889 | 0.789 | 51.2 | 67.0 | 61.7 | 2102 | 4345 | 3476 | $F_{(eggs)} = e^{0.7945} \times L_{(cm)}^{1.8326}$ O'Connell *et al.* (2008) |
| Trinité, QC | 0.103 | 0.910 | 0.910 | 54.6 | 74.3 | 81.8 | 3349 | 6720 | 8340 | $F_{(eggs)} = e^{-0.9099} \times L_{(cm)}^{2.2566}$ Based on data provided in Cauchon and April (2017) |
| Miramichi, NB | 0.177 | 0.903 | 0.612 | 55.3 | 75.2 | 85.9 | 2583 | 5927 | 8489 | $F_{(eggs)} = 0.051 \times L_{(cm)}^{2.700}$ Reid and Chaput (2012) |
| LaHave, NS | 0.402 | 0.851 | 0.660 | 54.2 | 72.5 | 77.3 | 3180 | 6163 | 7318 | $F_{(eggs)} = 446.54 \times e^{0.0363} \times L(cm)$ Cutting *et al.* (1987) |

North American range: Conne, NL; Trinité, QC; Miramichi, NB; and LaHave, NS. While further research is needed to clarify to the effect of spawning history on the reproductive contributions of iteroparous salmonid species, we followed conclusions from a limited number of previous studies indicating that the fecundity-length relationship did not differ significantly between maiden and repeat spawners (Quinn *et al.*, 2011; Reid and Chaput, 2012).

Given the variability in available biological information among populations, we used two different approaches to quantify the composition of annual returns for females and the proportion of eggs contributed by females of different spawning history groups to estimated population total egg depositions. For the Miramichi (NB) and LaHave (NS) populations, which had adequate sampling (median of 346 and range of 23–1850 females sampled annually), the annual number of female returns by spawning history were quantified similarly to the method described [Equation (1)] using only female data. For these two populations, we then calculated the average annual fork length of each female spawning history group based on the individual biological information available and the average annual fecundity of each group based on a population-specific fecundity-length relationship (Table 2). Finally, based on the adjusted composition of annual female returns and the average fecundity of each spawning history group, we calculated the proportion of eggs deposited by each spawning history group.

For the Conne (NL) and Trinité (QC) populations, we could not directly describe the annual composition of female returns due to limited annual sampling (median of 42 and range: 1–628 females sampled annually). For these rivers, we estimated the annual composition of female returns based on the proportion of females in both small and large groups averaged over multiple years. In addition, the average annual fecundity of each spawning history group was calculated from the average annual fork length of each class from all samples available (i.e. both sexes) and using population-specific fecundity-length relationships (Table 2). The respective contributions of the different spawning history groups to total egg deposition were then calculated similarly to the method described above.

The identification of females was based on internal examination for the Conne (NL), but relied on external sex determination for the other three populations (Trinité, QC; Miramichi, NB; and LaHave, NS). While external sex determination is a standard procedure for Atlantic salmon, we recognize that current research efforts using genetic sexing could provide greater accuracy in the future. Early results from the LaHave (NS) population indicate that, for this population at least, both methods achieved similar performance for estimating total egg depositions (A. Levy, Unpubl. data).

### Safeguard against low recruitment periods

To assess the extent to which repeat spawners can compensate for losses in total reproductive output during years of low maiden spawner abundance, we assessed the relationship between brief fluctuations in the proportion of repeat spawners in annual returns against annual maiden spawner counts. More precisely, we tested the prediction that the relative importance of repeat spawners (i.e. proportion of repeat spawners in annual return) would be higher in years of low maiden spawner returns, which would not be the case if the returns of repeat and maiden spawners were similarly affected in bad years. To test this, we first detrended the data to remove large-scale temporal trends (lower frequency variability component) present in the time-series by fitting locally weighted regressions (or loess) using the "loess" function of the "stats" package in R (Cleveland and Devlin, 1988) using a relatively high common smoothing factor of "span = 0.8" (fit of individual time series can be found in Appendix 1). We then assessed potential correlations between the residuals of these loess regressions (or de-trended time series) of the proportion of repeat spawners in annual returns against that of maiden spawner annual counts at the population level by computing parametric Pearson's correlation coefficient based on meeting the assumption of normality. We performed these analyses on the same subset of populations used to describe the reproductive contributions of repeat spawners (as described above; Conne, NL; Trinite, QC; Miramichi, NB; and LaHave, NS). As for other analyses, a logit transformation was applied to proportional data on the representation of repeat spawners in annual returns. In addition, maiden spawner counts were log transformed to achieve the normality of distributions. Finally, both de-trended time series were z-score transformed and plotted on the same axes to better visualize the relationships between the proportion of repeat spawners in annual returns and maiden spawner counts in each population.

## Results

### Spatio-temporal trends in iteroparity

The proportion of repeat spawners varied greatly among populations and years, ranging from 0.0 to 24.7%, and averaging 5.0 ± 5.0% over all populations and years (Figure 2). Despite

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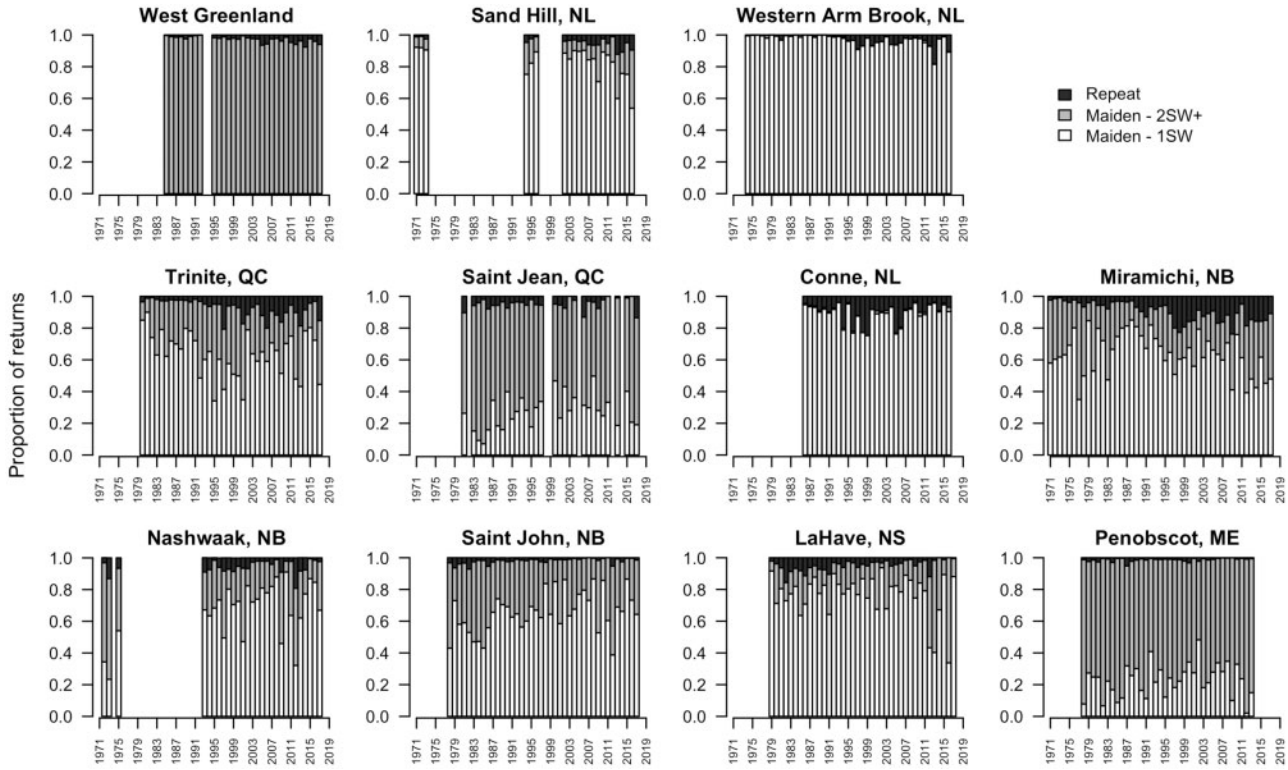


**Figure 2.** Proportional spawning history composition of Atlantic salmon annual returns (sexes combined) across populations of the northwest Atlantic from 1971 to 2017, including the West Greenland fisheries. The proportions are represented for maiden-1SW in white, maiden-2SW+ in grey, and repeat spawners in black.

large inter-annual fluctuations in the proportions of repeat spawners, broader temporal changes in iteroparity were apparent across multiple populations. DFA revealed spatial coherence in the temporal trends of iteroparity across populations of Atlantic salmon of the northwest Atlantic. The most parsimonious model (i.e. lowest AICc value) identified a single "common trend" shared among time series and correlated process errors with the same variance and covariances (R="equalvarcov," Table 3). Based on the output of the DFA (Figure 3a and b), some loadings are strongly positive and other strongly negative, indicating that populations experienced two opposite temporal tendencies, an increasing one and a decreasing one. In fact, most populations at the mid-latitudinal and northern part of the species' northwest Atlantic distribution (including West Greenland fishery landings) have shown increases in the proportion of repeat spawners through time (i.e. high positive loadings for Sand Hill, NL; Western Arm Brook, NL; Trinité QC; and Miramichi, NB), while most southern populations have shown declines (i.e. high negative loadings for Saint John, NB; LaHave, NS; and Penobscot, ME) (Figure 3b). Considering these contrasting temporal patterns, additional DFAs were computed for mid-latitudinal and northern populations combined and then separately for southern populations. Model selection was conducted as described in the Methods section and results are presented in Table 3 and Figure 3c and d. Regions' specific DFA only included a single "common trend" for both models, with different variances and no covariances (R= "diagonal and unequal") for mid-latitudinal and northern populations, and correlated process errors with different variances and different covariances (R="unconstrained") for southern populations (Table 3). The common tendency shared among mid-latitudinal and northern populations (Gulf of St. Lawrence and Labrador Sea) was divided in three distinct periods (Figure 3c). From a generally low proportion of repeat spawners in the 1971–1987 period, the proportion of repeat spawners increased after 1987 with the steepest increase from 1993 to 1997 peaking in 1998, and remaining at higher levels up to 2017

**Table 3.** Top three DFA models following model selection based on AICc for all populations combined (n = 11), then separately for mid-latitudinal and northern populations (n = 7), and southern populations (n = 4).

| Rank | Model structure | AICc | ΔAICc |
|---|---|---|---|
| | All. pop | | |
| 1 | m=1, R=equalvarcov | 957.6 | 0.0 |
| 2 | m=1, R=diagonal and equal | 973.4 | 15.8 |
| 3 | m=3, R=equalvarcov | 974.8 | 17.2 |
| | Mid-lat. and northern pop. | | |
| 1 | m=2, R=diagonal and unequal | 593.6 | 0.0 |
| 2 | m=1, R=diagonal and unequal | 594.2 | 0.6 |
| 3 | m=1, R=equalvarcov | 598.0 | 4.4 |
| | Southern pop. | | |
| 1 | m=1, R=unconstrained | 375.4 | 0.0 |
| 2 | m=1, R= equalvarcov | 377.0 | 1.6 |
| 3 | m=2, R= unconstrained | 378.9 | 3.5 |

"m" stands for the number of common trends included in the model and "R" for the structure of the variance–covariance matrix of residual errors. Dashed boxes represent preferred models as detailed in the Methods section.

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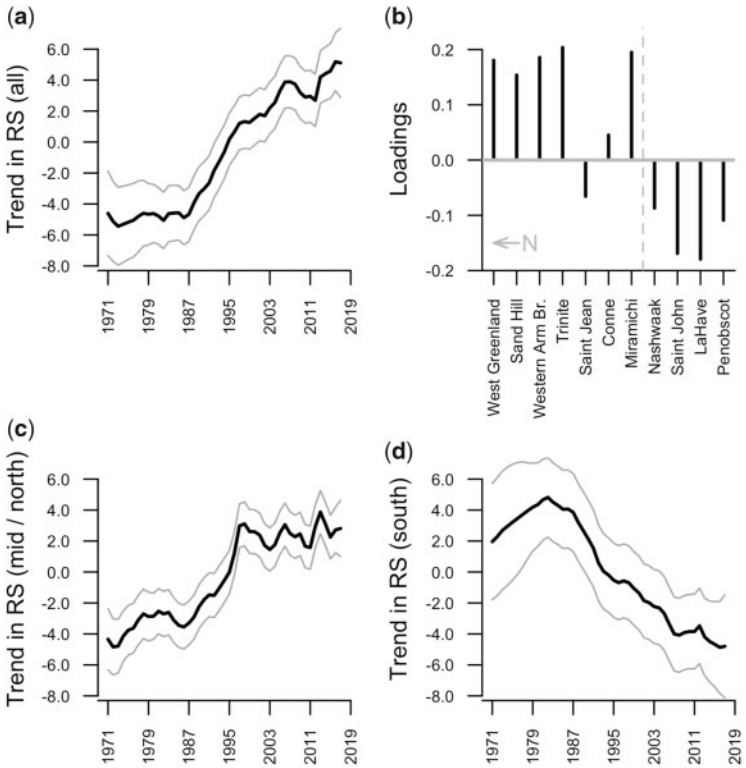


**Figure 3.** Output of the DFA for the logit proportions of repeat spawners in annual returns (z-scored): (a) the common temporal trend in repeat spawners across all ten populations of the northwest Atlantic and West Greenland fishery landings (grey lines represent ± 2 standard errors); (b) the average DFA loadings of each population on that common trend (ordered by latitude with northern most populations on the left, and southern populations right of the dotted line); (c) the common temporal trend in repeat spawners across mid-latitudinal and northern populations (n = 7); and (d) the common temporal trend in repeat spawners across southern populations (n = 4).

(with brief peaks in 1998, 2006, and 2013, Figure 3c). In contrast, the common tendency exhibited in southern populations (Scotian Shelf, Bay of Fundy, and Gulf of Maine) was a general decline in the proportion of repeat spawners beginning in the early 1980s and continuing to the present time, with a brief increase around 2012 (Figure 3d) apparent in all southern populations except the Penobscot (ME) (Figure 4).

To assess the statistical significance of broad temporal changes in the degree of iteroparity, we compared the 1971–1992 period with the 1993–2017 period, based on findings from the DFA that changes in iteroparity were steepest after 1992 (Figure 3a). Across all ten populations and the West Greenland fisheries, repeat spawners represented on average 3.5 ± 3.2% of annual returns (or of landings in West Greenland) during the 1971–1992 period with population averages ranging from 0.4 to 7.5% (Table 4). In contrast, during the 1993–2017 period, the overall occurrence of iteroparity averaged 5.8 ± 5.6% (range: 1.0–13.6%) over all populations and years (Table 4). The recent period showed not only a higher occurrence of iteroparity but also differences among broader geographical regions. In the mid-latitudinal and northern part of the species' northwest Atlantic range (Gulf of St. Lawrence and Labrador Sea), the average proportion of repeat spawners in annual returns increased from 3.1 to 7.6% (a 2.5-fold increase, p-value $\leq$ 0.001), with five out of seven individual time series showing a significant increase (Table 4; Welch two sample t-tests). During the same period, southern populations of the Scotian Shelf, Bay of Fundy, and Gulf of Maine showed the opposite trend. For these populations, the average occurrence of iteroparity decreased significantly from 4.1 to 2.7% (a 1.5-fold decrease, p-value = 0.007), with two of four individual time series showing a significant decrease (Table 4; Welch two sample t-tests). While the proportion of repeat spawners in populations of these two broader geographic regions did not statistically differ in the 1971–1992 period (4.1 vs. 3.1%, p-value = 0.079), in recent decades, southern populations exhibited lower occurrence of iteroparity than mid-latitudinal and northern populations (2.7 vs. 7.5%, p-value $\leq$ 0.001, Welch two sample t-tests).

Also worthy of interest, comparing the 1971–1992 and the 1993–2017 periods, the proportion of MSW in annual maiden spawner returns (i.e. similar to sea-age at first maturity) increased in the Sand Hill (NL; 7.0 to 15.2%, $p = 0.002$) and the Trinité (QC; 25.9 to 34.5%, $p = 0.045$), while it decreased in the Saint Jean (QC; 77.5 to 67.6%, $p = 0.022$), the Nashwaak (NB; 59.9 to 26.0%, $p = 0.056$) and the Saint John (NB; 44.9 to 29.3%, $p = 0.006$) populations (welch two sample t-tests). No statistically significant changes occurred in the other populations considered ($p > 0.125$).

## Reproductive contributions of repeat spawners

Given that a greater proportion of repeat spawners are female and that these are generally larger than their younger maiden counterparts (Table 2), the estimated egg contributions by repeat

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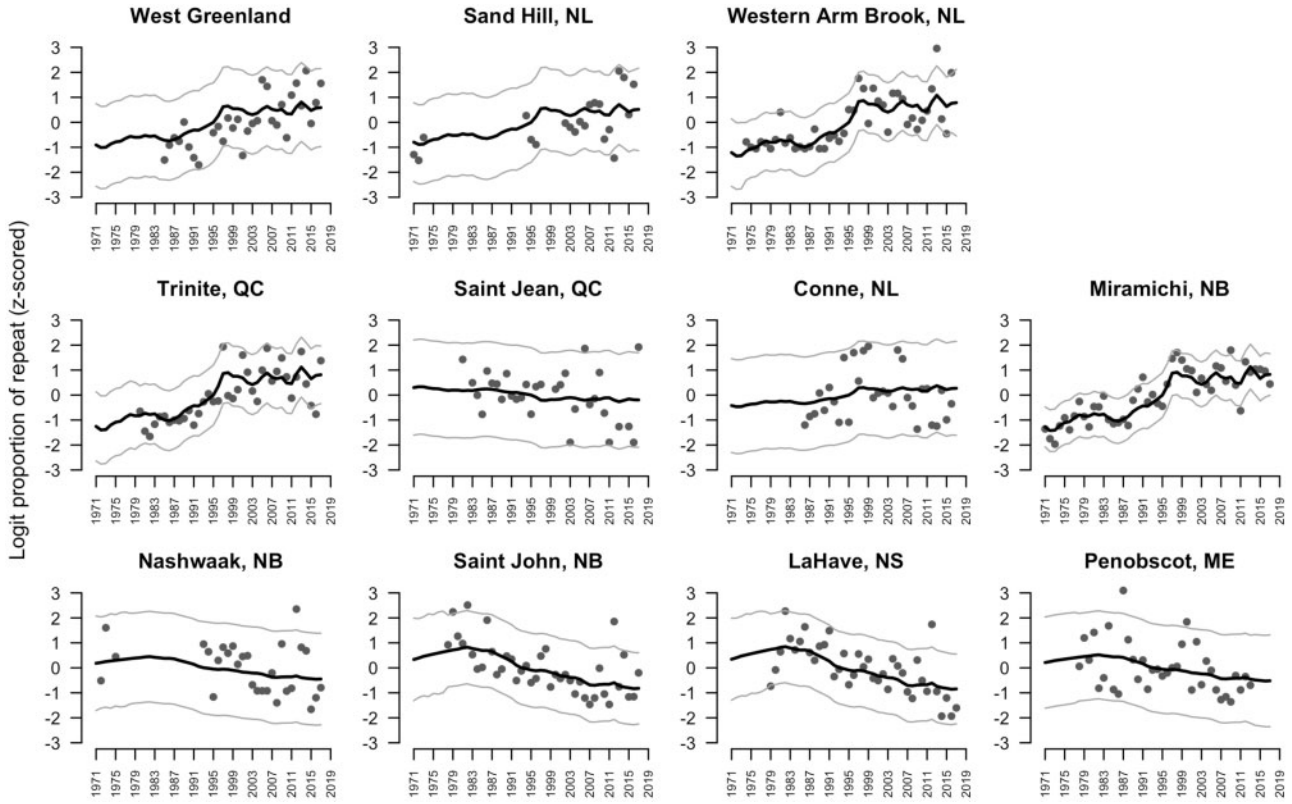


**Figure 4.** Output of the DFA showing model fit to population's specific time series of the logit proportion of repeat spawners in annual returns (z-scored) (grey lines represent ± 2 standard errors). Mid-latitudinal/northern population time series (top two rows, n = 7) and southern populations (bottom row, n = 4) were fitted with the DFA trend common to these regions, respectively, Figure 3c and d.

**Table 4.** Average proportions of repeat spawners in annual returns across Atlantic salmon populations of the northwest Atlantic Ocean, comparing the 1971–1992 and the 1993–2017 periods.

| Population | 1971–1992 average (± SD) | 1993–2017 average (± SD) | Trend | *p*-value |
|---|---|---|---|---|
| Mid-lat. and northern pop. | 0.031 (± 0.029) | 0.076 (± 0.060) | ↗ | ≤ 0.001* |
| West Greenland | 0.010 (± 0.007) | 0.033 (± 0.019) | ↗ | ≤ 0.001* |
| Sand Hill, NL | 0.015 (± 0.009) | 0.050 (± 0.032) | ↗ | 0.012* |
| Western Arm Brook, NL | 0.004 (± 0.007) | 0.046 (± 0.039) | ↗ | ≤ 0.001* |
| Trinite, QC | 0.024 (± 0.008) | 0.098 (± 0.054) | ↗ | ≤ 0.001* |
| Saint Jean, QC | 0.054 (± 0.024) | 0.043 (± 0.038) | — | 0.129 |
| Conne, NL | 0.070 (± 0.019) | 0.109 (± 0.070) | — | 0.065 |
| Miramichi, NB | 0.046 (± 0.029) | 0.136 (± 0.051) | ↗ | ≤ 0.001* |
| Southern pop. | 0.041 (± 0.035) | 0.027 (± 0.031) | ↘ | 0.007* |
| Nashwaak, NB | 0.075 (± 0.050) | 0.053 (± 0.041) | — | 0.444 |
| Saint John, NB | 0.031 (± 0.019) | 0.012 (± 0.011) | ↘ | ≤ 0.001* |
| LaHave, NS | 0.073 (± 0.036) | 0.032 (± 0.025) | ↘ | ≤ 0.001* |
| Penobscot, ME | 0.016 (± 0.013) | 0.010 (± 0.008) | — | 0.110 |
| All pop. | 0.035 (± 0.032) | 0.058 (± 0.056) | ↗ | ≤ 0.001* |

*P*-values were computed using Welch two sample t-tests after the application of a logit transformation for proportional data. Means and standard errors are back-transformed from the logit scale. Populations are ordered by latitude with northern and mid-latitude (mid-lat.) populations on top, and southern populations below, with region-specific average proportions between lines.
*$p < 0.05$.

spawners were disproportionately higher than their proportions by number (Figure 5). For the Trinité (QC) between 1993 and 2017, repeat spawners represented on average 9.8% of the annual return of both sexes combined, 20.5% of all females, and these females contributed to 27.0% of total annual egg deposition. For the same time period in the Miramichi (NB), repeat spawners composed on average 13.6% of both sexes combined, 21.8% of females, and repeat females contributed to 28.1% of eggs deposited annually. Considering their contributions to annual egg deposition, the influence of repeat spawners was 2.8-fold (i.e. 9.8%

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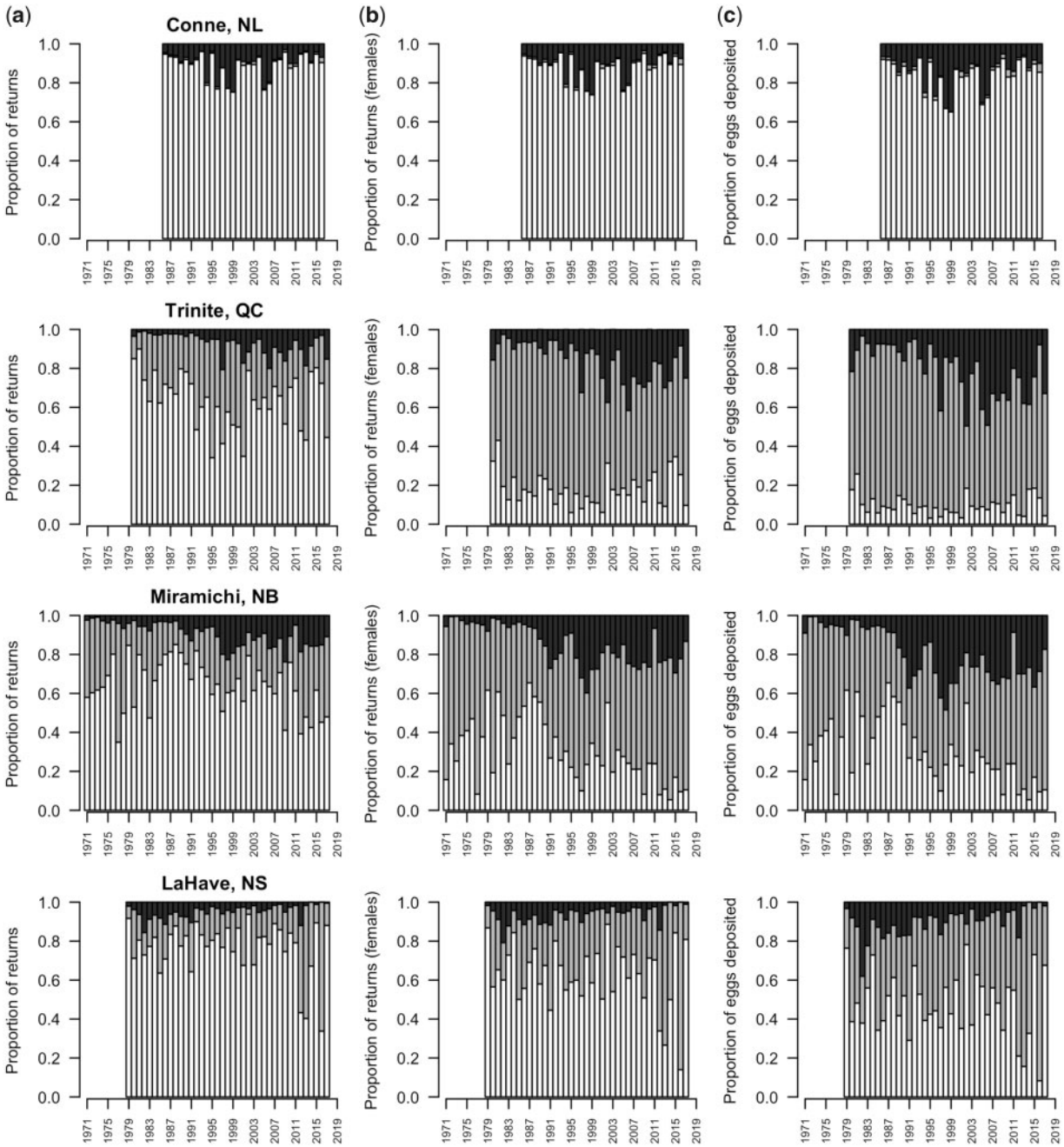


**Figure 5.** Proportions by spawning history group of Atlantic salmon annual returns across four populations of the northwest Atlantic from 1971 to 2017; (a) the proportions of all returns, sexes combined; (b) the proportions for females only; and (c) the proportions of the total annual egg deposition. The spawning history groups are maiden-1SW in white, maiden-2SW+ in grey, and repeat spawners in black.

of annual returns producing 27.0% of eggs in the Trinité, QC) and 2.1-fold greater (i.e. 13.6% of annual returns producing 28.1% of eggs in the Miramichi, NB) than assessments based solely on their relative occurrence in the annual returns of both sexes combined. Of similar magnitude (2.2-fold) but at lower occurrences, repeat spawners in the LaHave River (NS) represented 3.2% of all returning salmon, 4.5% of females, and contributed 7.1% of eggs deposited, on average. Of lower magnitude for Conne (NL) (1.4-fold), an average of 10.9% of repeat spawners in the total annual return, represented 11.6% of females, and contributed 15.3% of annual eggs deposited. The smaller difference between the proportion of repeat spawners in annual returns and the proportion of eggs contributed by female repeat spawners for the Conne (NL) (i.e. 1.4-fold) is mainly due to maiden spawners being mostly comprised of females in a 1SW dominated river, and by female repeat spawners being dominated by 1SW-consecutive spawners of similar sizes (Figure 5 and Table 2). However, in other populations with a higher proportion of males in maiden spawners, and more variability in sea-age at maturity and reconditioning strategy, such as the Trinite (QC), Miramichi (NB), and LaHave (NS) (Table 2), our findings indicate that the proportion of repeat spawners by number in the

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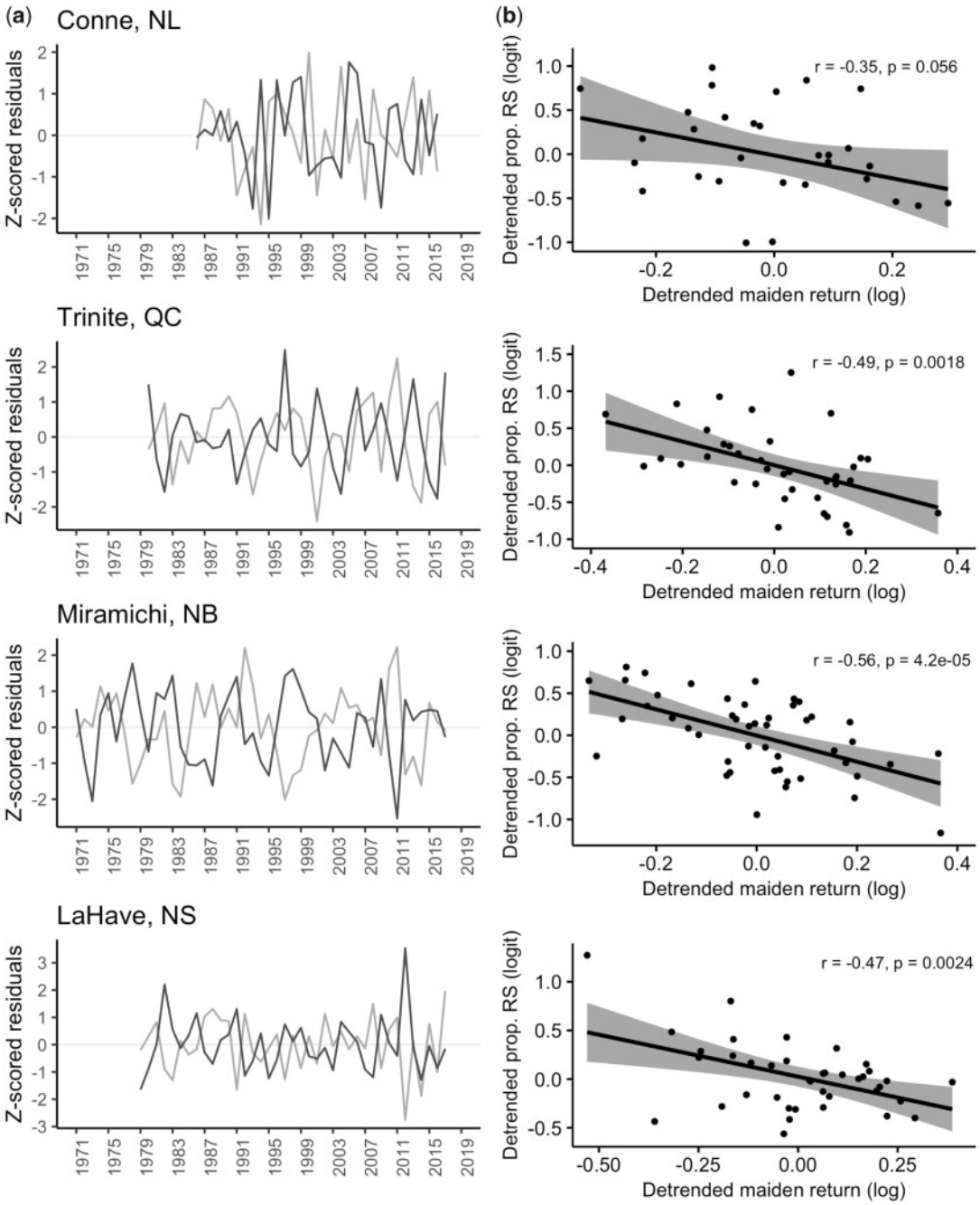


**Figure 6.** Relationships between the de-trended proportion of repeat spawners (RS) in annual returns (logit transformed) and de-trended annual maiden salmon counts (log transformed): (a) de-trended time series of the proportion of repeat spawner (black) and maiden salmon abundance (grey), z-score transformed and (b) correlation between the two de-trended time series with the Pearson correlation coefficient value and the p-value of the linear regression as inset text. The shaded area encompasses the 95% CI of the slope.

annual return underestimated their relative contribution to annual egg deposition (Figure 5).

## Safeguard against low recruitment periods

Brief temporal fluctuations (higher frequency variation component) in the proportion of repeat spawners in annual returns were negatively correlated with estimated abundances of maiden spawners across populations (Figure 6). Pearson's correlation coefficients ranged from −0.35 to −0.56 and negative relationships were statistically significant for all (p-values $\leq$ 0.002) but the Conne (NL) (p-value = 0.056, Figure 6b). These relationships indicate that the relative importance of iteroparity (i.e. increase in the representation of repeat spawners in annual returns) was emphasized in periods of low maiden spawner abundance, which would not have been the case if repeat spawners were equally affected in bad years.

To illustrate this point, the most recent decrease in maiden spawner returns occurred in all years of the 2012–2014 period for

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Trinité, QC and Miramichi, NB or in some of those years for LaHave, NS (2012) and Conne, NL (2014) (Figure 6; see also Appendix 1). During this period, in the Trinité (QC), Miramichi (NB), and LaHave (NS) populations, repeat spawners represented respectively 12.4, 16.3, and 11.9% of annual returns, and contributed to 33.7, 28.8, and 18.2% of the total annual egg deposition in those years. This emphasizes the importance of repeat spawners for future population recruitment. Other important declines in maiden spawner returns have occurred in the Trinité (QC) in 2001 (the lowest count of maiden salmon return recorded for the entire time series, at 237 individuals), and in the Miramichi (NB) during the 1997–1999 period (the lowest counts of maiden salmon return estimated prior to 2009, at between 26 049 to 31 268 individuals) (Figure 6). During these years of low recruitment, repeat spawners represented on average 17.2 to 20.6% of all spawners, and 26.9 to 41.8% of total annual egg deposition, respectively, for the Trinité (QC) and Miramichi (NB) populations (Figure 5). These findings provide evidence of iteroparity acting as a stabilizing force against periods of low maiden recruitment associated with higher post-smolt mortality at sea.

## Discussion

While the occurrence of iteroparity (i.e. proportion of repeat spawners in annual returns) shows considerable variability within and among Atlantic salmon populations, our findings revealed broad-scale spatio-temporal shifts in iteroparity across populations of the northwest Atlantic. Through the analysis of time series spanning approximately 50 years, we documented increases in iteroparity, starting in the late 1980s or early 1990s, for populations situated in the mid-latitudinal and northern part of their range (Gulf of St. Lawrence and Labrador Sea) as well as those spawned salmon in the mixed-stock West Greenland fisheries. This broad-scale spatio-temporal pattern is further corroborated by recently documented changes in the northeast Atlantic part of the species' range. These included a 3.8-fold increase in the proportion of previously spawned, European-origin salmon in the West Greenland fishery landings starting in the mid-2000s (1985–2004 average of 0.4 vs. 1.5% for the 2005–2017 period; ICES, 2018) and an increase in iteroparity in the River Teno system (Finland), with a 4.0-fold increase in the proportion of female repeat spawners since the early 2000s (1975–2000 average of 3.6 vs. 14.4% for the 2001–2014 period, Erkinaro *et al.*, 2018). In contrast, starting in the late 1980s, we documented declines in iteroparity in southern populations (i.e. Scotian Shelf, Bay of Fundy, and Gulf of Maine). More broadly, this latitudinal pattern is also reflected in overall annual returns and trends in marine survival, which have declined more severely in the southern most regions of the species' range (Chaput, 2012), and as exemplified by their conservation status (Table 1; COSEWIC, 2010). Many factors might have contributed to recent demographic changes across Atlantic salmon's global range. Most noticeably, important changes in oceanic conditions (e.g. marine climate regime shifts; Drinkwater, 2000) might be either directly or indirectly responsible for a substantial reduction in post-smolt marine survival and overall productivity of Atlantic salmon (Dempson *et al.*, 2004; Chaput, 2012; Friedland *et al.*, 2014). In addition, closures of commercial Atlantic salmon fisheries in different parts of Canada implemented through the 1980s and early 1990s, and large reductions in harvests in the West Greenland fishery over the same time period, have reduced size-selective fishing mortality of large salmon (i.e. particularly MSW and repeat spawners) (Moore *et al.*, 1995; Dempson *et al.*, 2004; Chaput, 2012).

While fluctuations in the abundance and relative importance of consecutive vs. alternate repeat spawning strategies would require further investigation, data on the composition of West Greenland mixed-stock fishery landings indicate increasing proportions of previously spawned salmon (potential alternate repeat spawners in this case) in the North Atlantic complex. This complements findings from Chaput and Benoit (2012) that increasing occurrence of iteroparity was dominated by consecutive repeat spawners in the Miramichi River (NB), suggesting that both repeat spawning strategies became more frequent since the early 1990s in the mid-latitudinal and northen part of the species' North Atlantic Ocean range. The seemingly improved post-spawning reconditioning prospects in the Gulf of St. Lawrence attributed to an increased biomass of forage fish species (Chaput and Benoit, 2012), and removal of size-selective fishing pressures in distant and local fisheries (Moore *et al.*, 1995; Dempson *et al.*, 2004), are believed to have favoured iteroparity and survival of MSW salmon. Interestingly, while earlier sea age at first maturity (i.e. 1SW) has recently been liked to iteroparity at the genotypic level (Aykanat *et al.*, 2019), we documented increases in iteroparity that occured along with increasing proportions of MSW in maiden spawner returns (or later sea-age at first maturity) in some mid-latitudinal and northern populations. These observations are consistent with expectations associated with the closure of commercial fisheries (Dempson *et al.*, 2004) and rules out the possibility for observed increases in iteroparity to have been driven by a reduction in sea age at first maturity.

In contrast, in some southern populations, the degree of iteroparity decreased along with the proportion of MSW in maiden spawners and overall population returns. However, despite the seemingly improved survival prospects of post-spawners in common feeding areas, the declines in iteroparity that we documented in southern populations suggest that regional factors (e.g. environmental and anthropogenic threats) may have been limiting iteroparity in southern areas. Recent studies revealed size-selective pressure exerted by both upstream and downstream fish passage facilities against large-bodied fish, which raises concerns about the effects of an artificially reduced potential for repeat spawning in regulated rivers, such as the Penobscot (Maine, US) and Saint John (NB) rivers (Nyqvist *et al.*, 2016; Maynard *et al.*, 2017). The contrast in the occurrence of iteroparity between populations of the Saint John (above Mactaquac Dam, NB; 1.2%) and the adjacent, dam-free Nashwaak tributary (NB; 5.3%), provides further evidence of these anthropogenic factors affecting post-spawning survival (Chaput and Jones, 2006). In addition, hatchery supplementation programs, where captively held wild-origin, local broodstock are subjected to the stress of captivity and artificial spawning, can compromise post-spawning survival of broodstock upon their return to the wild and reduce their potential for repeat spawning (Bordeleau *et al.*, 2018). These potential population-level impacts are likely amplified in large-scale hatchery programs (Bordeleau *et al.*, 2018), such as the Penobscot River (Maine, US), where the majority of returning salmon are spawned at the hatchery and released back to the wild after many months in captivity (Kincaid and Stanley, 1989; Maynard *et al.*, 2017). Furthermore, hatchery reared juveniles could have different life-history traits that could affect the maturity schedule (Fleming and Petersson, 2001) and potentially iteroparity of populations with hatchery supplementation programs. In addition to

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these direct anthropogenic threats, reduced post-spawning survival due to higher energy expenditure imposed by warmer river temperatures (Glebe and Leggett, 2010; Lennox *et al.*, 2018) might be of particular importance in southern areas of Atlantic salmon's range. Moreover, since repeat spawners are the survivors of maiden spawners, their abundance depends primarily on the survival of post-smolts some years before (Niemelä *et al.*, 2006a). As such, the potential for iteroparity to limit population declines is conditional on maintaining sufficient recruitment of maiden spawners. However, as survival decreases and fewer adults remain in the population, the potential for iteroparity to limit further population declines may be compromised, a situation which might be occurring in the southernmost regions examined in our study.

While the closure of commercial fisheries and increases in the occurrence of iteroparity have not prevented broad-scale declines in Atlantic salmon populations since the 1980s, our findings emphasize the importance of iteroparity as a buffer during periods of low post-smolt survival and recruitment. Female repeat spawners produced a relatively high number of eggs, particularly at times of low maiden spawner returns. In these low return periods (e.g. 2001, 2012–2014 in Trinité, QC; 1997–1999, 2012–2014 in Miramichi, NB; and 2012 in LaHave, NS), on average repeat spawners accounted for 11.9—18.5% of all spawners, and the repeat spawning females contributed 18.2–35.3% of all eggs estimated to have been produced by populations. During the period when population abundances were sharply decreasing across the North Atlantic (particularly in the 1980s; ICES, 2018), the marked increase in iteroparity starting in the early 1990s (as described here in many mid-latitudinal and northern populations) coincided with decreases and levelling off of population abundances (Appendix 1). While we cannot attribute this exclusively to the increased relative importance of repeat spawners as other important changes also occurred (e.g. commercial fisheries closure, Moore *et al.*, 1995; Dempson *et al.*, 2004; and marine climate regime shift, Drinkwater, 2000), increases in iteroparity likely contributed to the slowing of declines, with repeat spawners contributing, on average, 15.3–28.1% of annual egg deposition during the 1993–2017 period in different mid-latitudinal populations (Conne, NL; Trinite, QC; and Miramichi, NB). As Atlantic salmon post-smolts are more susceptible to marine environmental conditions during their first few months at sea due to size-mediated survival, resulting in lower survival during the first year than in additional years (Friedland *et al.*, 2000; Chaput, 2003; Chaput *et al.*, 2018), our findings reinforce the premise that larger iteroparous individuals can act as a safeguard against low recruitment periods and mitigate some of the effects of variability in the marine survival of juvenile salmon (as previously suggested by Saunders and Schom, 1985; Niemelä *et al.*, 2006a).

## Broader perspectives

Quantifying the composition of spawners in annual returns, and especially the contributions of different spawning history groups to total egg deposition, provides valuable information for estimating the importance of iteroparity to population dynamics. However, the importance of iteroparity likely goes beyond the relative proportion of eggs that are laid by female repeat spawners. Intergenerational effects passed by experienced breeders, via maternal effects, could confer currently unquantified benefits to offspring fitness (Fleming and Einum, 2011). While female size is positively associated with fecundity in salmonids as well as egg size, egg energy content, egg survival, and offspring survival in the wild (Fleming, 1996, 1998; Garant *et al.*, 2003), the nature of these relationships with respect to repeat spawning is unclear. In Atlantic salmon, recent hatchery-based work suggests that egg quality might depend on reconditioning strategies, with generally higher benefits to alternate repeat spawners versus maiden spawners, but lower for the consecutive repeat spawning strategy (Reid and Chaput, 2012). While this is a ripe area for future research, individual differences in spawning location and timing conferred by females' size and life experience could translate into higher competitive abilities and survival (and hence fitness) of repeat spawners' offspring in the wild. These behavioral maternal effects, not considered in hatchery-based studies, include higher digging capacity, deeper egg deposition, and lower susceptibility to redd superimposition (as correlated with size; reviewed in Quinn, 2005), higher competitive ability and access to preferred sites (as correlated with size; reviewed in Fleming and Einum, 2011), and optimal run timing (as correlated with previous spawning experience; Niemelä *et al.*, 2006b). Furthermore, other studies suggest a higher tolerance of repeat spawners than maiden spawners to environmental disturbances such as increased thermal resilience and lower vulnerability to thermally induced reproductive inhibition (cultured Tasmanian Atlantic salmon; Pankhurst *et al.*, 2011; Anderson *et al.*, 2012), and greater tolerance of eggs to hypoxic conditions (cultured Tasmanian Atlantic salmon; Polymeropoulos *et al.*, 2016). More recently, Lennox *et al.* (2018) showed that larger body size in Atlantic salmon resulted in less relative energy depletion and greater resilience to increases in pre-spawning temperature, an advantage which may also be attributed to repeat spawners. Predicting species' responses to climate change presents many challenges (Aas *et al.*, 2011; Comte *et al.*, 2013), yet these recent studies suggest further behavioural and physiological mechanisms by which iteroparity can positively influence Atlantic salmon population resilience. As more empirical information becomes available on the reproductive output and offspring fitness of maiden vs. repeat spawners, additional fitness consequences of iteroparity to salmon population dynamics should be examined, as well as addressing the life-history implications of consecutive and alternate repeat spawning strategies (Reid and Chaput, 2012).

Considering declines in marine survival (i.e. low probability of breeding once) and the poor post-spawning survival prospects of Atlantic salmon accentuated by the more severe anthropogenic stressors present in southern regions (i.e. low probability of survival between spawning events), there is potential for selection pressure to favour semelparity over iteroparity (Stearns, 1976). While iteroparity is a bet-hedging strategy allowing individuals to spread the risk of reproductive failure over multiple years (Slatkin, 1974), with the ongoing decrease in the incidence of iteroparity in southernmost regions and the potential for this decrease to become widespread is of particular concern for the viability and recovery potential of Atlantic salmon populations, particularly under increasing environmental variability associated with climate change (Stenseth *et al.*, 2002). As such, the importance of iteroparity should be considered in recovery actions, and mitigation measures should be envisioned to reduce post-spawning mortality as it relates to current anthropogenic threats occurring in freshwater (summarized in Keefer et al., 2008). Efforts should be directed at improving the design of dams to minimize downstream passage mortality for large post-spawners (Kraabøl *et al.*, 2009; Nyqvist *et al.*, 2016) and mitigating the

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many stressors and associated fitness consequences that wild-origin broodstock experience in current hatchery programs (Bordeleau *et al.*, 2018).

Whether iteroparity is generally occurring to a low degree in Atlantic salmon due to physiological constraints (i.e. trade-offs between current breeding investments and survival probability to future breeding), or whether it is maintained at a reduced level by anthropogenic activities, are key questions limiting our understanding of the importance of iteroparity for population viability and recovery potential. While the degree of iteroparity is likely driven by both natural and anthropogenic factors, the spatio-temporal trends presented here highlight the potential for increases in iteroparity to occur when anthropogenic threats are mitigated, with known benefits to population resilience.

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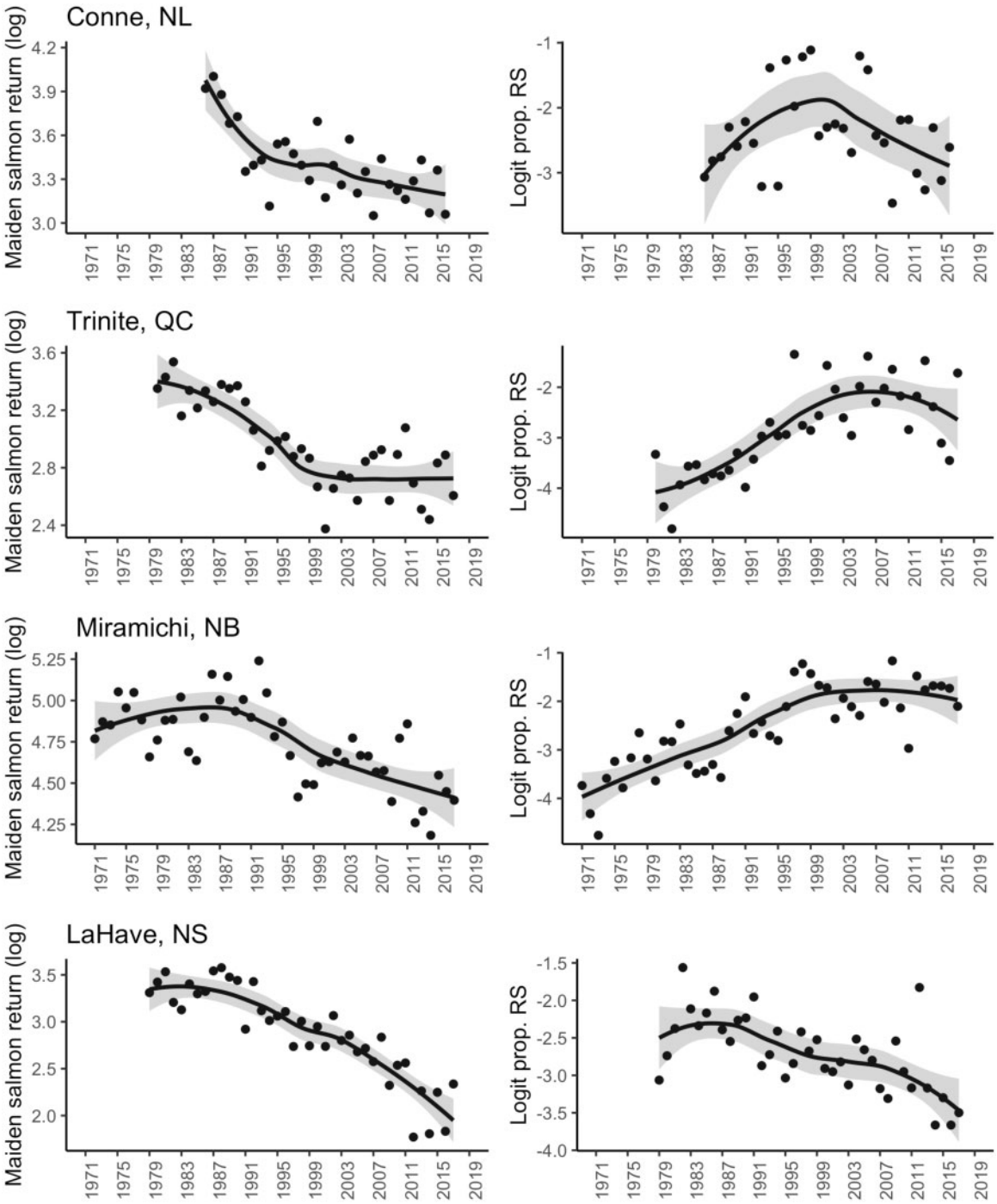
## Appendix 1

Loess regression fits to de-trend the time series (maiden salmon returns on the left and annual proportion of repeat spawners on the right) used to isolate the high frequency variation component to test the hypothesis of iteroparity acting as a safeguard against low recruitment periods.

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## Appendix 2

Table with summary information on the proportional spawning history composition (maiden-1SW, maiden-2SW+, and repeat spawners) of Atlantic salmon annual returns (sexes combined) across nine populations of the northwest Atlantic from 1971 to 2017 (Sand Hill, NL; Western Arm Brook, NL; Conne, NL; Trinité, QC; Saint Jean, QC; Miramichi, NB; Nashwaak, NB; Saint John, NB; LaHave, NS). Published data on West Greenland fisheries landings and Penobscot (ME) can be found in ICES (2018) and Maynard *et al.* (2017).

| | **Sand Hill, NL** | | | | | **Western Arm Brook, NL** | | | | | **Conne, NL** | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| **Year** | **P(1SW)** | **P(2SW+)** | **P(RS)** | **n small** | **n large** | **P(1SW)** | **P(2SW+)** | **P(RS)** | **n small** | **n large** | **P(1SW)** | **P(2SW+)** | **P(RS)** | **n small** | **n large** |
| 1971 | 0.923 | 0.065 | 0.012 | 392 | 78 | NA | NA | NA | NA | NA | NA | NA | NA | NA | NA |
| 1972 | 0.920 | 0.071 | 0.009 | 412 | 64 | NA | NA | NA | NA | NA | NA | NA | NA | NA | NA |
| 1973 | 0.906 | 0.069 | 0.025 | 951 | 227 | NA | NA | NA | NA | NA | NA | NA | NA | NA | NA |
| 1974 | NA | NA | NA | NA | NA | 0.994 | 0.001 | 0.004 | 80 | 0* | NA | NA | NA | NA | NA |
| 1975 | NA | NA | NA | NA | NA | 0.999 | 0.000 | 0.001 | 18 | 0* | NA | NA | NA | NA | NA |
| 1976 | NA | NA | NA | NA | NA | 1.000 | 0.000 | 0.000 | 6 | 0* | NA | NA | NA | NA | NA |
| 1977 | NA | NA | NA | NA | NA | 0.994 | 0.001 | 0.004 | 53 | 2* | NA | NA | NA | NA | NA |
| 1978 | NA | NA | NA | NA | NA | 0.980 | 0.016 | 0.003 | 65 | 0* | NA | NA | NA | NA | NA |
| 1979 | NA | NA | NA | NA | NA | 1.000 | 0.000 | 0.000 | 226 | 0* | NA | NA | NA | NA | NA |
| 1980 | NA | NA | NA | NA | NA | 0.992 | 0.002 | 0.006 | 58 | 2* | NA | NA | NA | NA | NA |
| 1981 | NA | NA | NA | NA | NA | 0.968 | 0.000 | 0.032 | 65 | 1* | NA | NA | NA | NA | NA |
| 1982 | NA | NA | NA | NA | NA | 0.995 | 0.001 | 0.003 | 73 | 0* | NA | NA | NA | NA | NA |
| 1983 | NA | NA | NA | NA | NA | 0.992 | 0.001 | 0.007 | 190 | 0* | NA | NA | NA | NA | NA |
| 1984 | NA | NA | NA | NA | NA | 1.000 | 0.000 | 0.000 | 117 | 0* | NA | NA | NA | NA | NA |
| 1985 | NA | NA | NA | NA | NA | 0.986 | 0.013 | 0.001 | 82 | 1* | NA | NA | NA | NA | NA |
| 1986 | NA | NA | NA | NA | NA | 1.000 | 0.000 | 0.000 | 38 | 0* | 0.947 | 0.017 | 0.035 | 360 | 1* |
| 1987 | NA | NA | NA | NA | NA | 0.998 | 0.000 | 0.001 | 80 | 1* | 0.935 | 0.018 | 0.047 | 405 | 0* |
| 1988 | NA | NA | NA | NA | NA | 0.986 | 0.000 | 0.014 | 78 | 1* | 0.931 | 0.017 | 0.051 | 808 | 3* |
| 1989 | NA | NA | NA | NA | NA | 1.000 | 0.000 | 0.000 | 140 | 0* | 0.901 | 0.008 | 0.091 | 146 | 15 |
| 1990 | NA | NA | NA | NA | NA | 1.000 | 0.000 | 0.000 | 46 | 1* | 0.919 | 0.024 | 0.057 | 177 | 0* |
| 1991 | NA | NA | NA | NA | NA | 0.993 | 0.001 | 0.007 | 224 | 1* | 0.896 | 0.000 | 0.104 | 42 | 3* |
| 1992 | NA | NA | NA | NA | NA | 0.986 | 0.005 | 0.009 | 408 | 3* | 0.918 | 0.009 | 0.073 | 293 | 13 |
| 1993 | NA | NA | NA | NA | NA | 0.990 | 0.005 | 0.005 | 251 | 4* | 0.961 | 0.000 | 0.039 | 293 | 10 |
| 1994 | 0.752 | 0.201 | 0.047 | 157 | 20 | 0.979 | 0.010 | 0.010 | 103 | 6 | 0.788 | 0.012 | 0.200 | 87 | 5 |
| 1995 | 0.823 | 0.154 | 0.023 | 149 | 26 | 0.961 | 0.003 | 0.035 | 97 | 34 | 0.952 | 0.009 | 0.039 | 113 | 7 |
| 1996 | 0.892 | 0.088 | 0.019 | 166 | 3* | 0.966 | 0.000 | 0.034 | 75 | 16 | 0.769 | 0.011 | 0.220 | 90 | 7 |
| 1997 | NA | NA | NA | NA | NA | 0.906 | 0.002 | 0.091 | 42 | 1* | 0.876 | 0.002 | 0.122 | 685 | 26 |
| 1998 | NA | NA | NA | NA | NA | 0.931 | 0.000 | 0.069 | 103 | 12 | 0.772 | 0.000 | 0.228 | 159 | 32 |
| 1999 | NA | NA | NA | NA | NA | 0.980 | 0.000 | 0.019 | 6 | 0* | 0.753 | 0.000 | 0.247 | 135 | 39 |
| 2000 | NA | NA | NA | NA | NA | 0.929 | 0.002 | 0.070 | 23 | 0* | 0.917 | 0.002 | 0.081 | 202 | 19 |
| 2001 | NA | NA | NA | NA | NA | 0.953 | 0.000 | 0.047 | 29 | 7 | 0.890 | 0.019 | 0.091 | 183 | 6 |
| 2002 | 0.886 | 0.076 | 0.039 | 63 | 6 | 0.958 | 0.000 | 0.042 | 99 | 12 | 0.898 | 0.007 | 0.095 | 227 | 26 |
| 2003 | 0.849 | 0.117 | 0.034 | 131 | 24 | 0.989 | 0.000 | 0.011 | 146 | 14 | 0.894 | 0.015 | 0.091 | 157 | 0* |
| 2004 | 0.901 | 0.069 | 0.030 | 235 | 40 | 0.940 | 0.000 | 0.060 | 69 | 12 | 0.932 | 0.004 | 0.064 | 242 | 22 |
| 2005 | 0.897 | 0.063 | 0.040 | 222 | 55 | 0.938 | 0.002 | 0.060 | 77 | 24 | 0.764 | 0.005 | 0.231 | 184 | 19 |
| 2006 | 0.903 | 0.061 | 0.036 | 299 | 42 | 0.949 | 0.000 | 0.051 | 54 | 6 | 0.796 | 0.009 | 0.195 | 171 | 20 |
| 2007 | 0.843 | 0.095 | 0.061 | 150 | 26 | 0.979 | 0.003 | 0.018 | 76 | 8 | 0.911 | 0.008 | 0.081 | 157 | 5 |
| 2008 | 0.850 | 0.086 | 0.064 | 133 | 69 | 0.975 | 0.000 | 0.025 | 56 | 3* | 0.919 | 0.016 | 0.065 | 177 | 3* |
| 2009 | 0.706 | 0.232 | 0.062 | 178 | 55 | 0.981 | 0.006 | 0.014 | 53 | 7 | 0.958 | 0.012 | 0.030 | 145 | 6 |
| 2010 | 0.892 | 0.084 | 0.024 | 155 | 16 | 0.977 | 0.000 | 0.023 | 59 | 41 | 0.875 | 0.024 | 0.101 | 126 | 6 |
| 2011 | 0.866 | 0.102 | 0.032 | 28 | 2* | 0.952 | 0.014 | 0.033 | 78 | 11 | 0.886 | 0.013 | 0.101 | 139 | 7 |
| 2012 | 0.830 | 0.160 | 0.010 | 74 | 17 | 0.929 | 0.002 | 0.069 | 30 | 30 | 0.947 | 0.017 | 0.035 | 164 | 4* |
| 2013 | 0.600 | 0.279 | 0.121 | 116 | 61 | 0.816 | 0.002 | 0.183 | 60 | 49 | 0.958 | 0.008 | 0.034 | 204 | 4* |
| 2014 | 0.758 | 0.135 | 0.108 | 149 | 27 | 0.976 | 0.000 | 0.024 | 89 | 10 | 0.903 | 0.000 | 0.097 | 124 | 2* |
| 2015 | 0.752 | 0.199 | 0.048 | 175 | 49 | 0.989 | 0.001 | 0.010 | 61 | 21 | 0.947 | 0.011 | 0.042 | 132 | 15 |
| 2016 | 0.538 | 0.367 | 0.094 | 111 | 66 | 0.892 | 0.003 | 0.105 | 58 | 51 | 0.904 | 0.027 | 0.069 | 156 | 5 |
| 2017 | NA | NA | NA | NA | NA | NA | NA | NA | NA | NA | NA | NA | NA | NA | NA |

*Continued*

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**Appendix 2.** *Continued*

| | Trinité, QC | | | | | Saint Jean, QC | | | | | Miramichi, NB | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Year | P(1SW) | P(2SW+) | P(RS) | n small | n large | P(1SW) | P(2SW+) | P(RS) | n small | n large | P(1SW) | P(2SW+) | P(RS) | n small | n large |
| 1971 | NA | NA | NA | NA | NA | NA | NA | NA | NA | NA | 0.580 | 0.397 | 0.023 | 257 | 314 |
| 1972 | NA | NA | NA | NA | NA | NA | NA | NA | NA | NA | 0.604 | 0.383 | 0.013 | 699 | 498 |
| 1973 | NA | NA | NA | NA | NA | NA | NA | NA | NA | NA | 0.617 | 0.374 | 0.008 | 744 | 724 |
| 1974 | NA | NA | NA | NA | NA | NA | NA | NA | NA | NA | 0.632 | 0.341 | 0.027 | 1378 | 569 |
| 1975 | NA | NA | NA | NA | NA | NA | NA | NA | NA | NA | 0.692 | 0.270 | 0.038 | 1020 | 338 |
| 1976 | NA | NA | NA | NA | NA | NA | NA | NA | NA | NA | 0.802 | 0.176 | 0.022 | 984 | 197 |
| 1977 | NA | NA | NA | NA | NA | NA | NA | NA | NA | NA | 0.350 | 0.610 | 0.041 | 421 | 514 |
| 1978 | NA | NA | NA | NA | NA | NA | NA | NA | NA | NA | 0.498 | 0.436 | 0.066 | 387 | 289 |
| 1979 | NA | NA | NA | NA | NA | NA | NA | NA | NA | NA | 0.847 | 0.114 | 0.040 | 743 | 97 |
| 1980 | 0.850 | 0.115 | 0.035 | NA | 39 | NA | NA | NA | NA | NA | 0.530 | 0.444 | 0.026 | 541 | 329 |
| 1981 | 0.900 | 0.088 | 0.013 | NA | 24 | 0.263 | 0.634 | 0.103 | NA | 50 | 0.799 | 0.145 | 0.056 | 607 | 52 |
| 1982 | 0.740 | 0.252 | 0.008 | NA | 64 | NA | NA | NA | NA | 4 | 0.721 | 0.223 | 0.056 | 527 | 86 |
| 1983 | 0.630 | 0.351 | 0.019 | NA | 77 | 0.152 | 0.790 | 0.058 | NA | 278 | 0.474 | 0.448 | 0.078 | 214 | 74 |
| 1984 | 0.791 | 0.181 | 0.028 | NA | 129 | 0.092 | 0.868 | 0.040 | NA | 317 | 0.666 | 0.299 | 0.035 | 237 | 96 |
| 1985 | 0.622 | 0.349 | 0.028 | NA | 253 | 0.071 | 0.909 | 0.020 | NA | 285 | 0.747 | 0.223 | 0.030 | 199 | 180 |
| 1986 | 0.719 | 0.260 | 0.021 | NA | 212 | 0.159 | 0.762 | 0.079 | NA | 214 | 0.800 | 0.169 | 0.031 | 424 | 284 |
| 1987 | 0.700 | 0.276 | 0.024 | NA | 126 | 0.345 | 0.598 | 0.057 | NA | 229 | 0.814 | 0.151 | 0.035 | 310 | 63 |
| 1988 | 0.668 | 0.309 | 0.023 | NA | 87 | 0.184 | 0.760 | 0.056 | NA | 467 | 0.851 | 0.122 | 0.027 | 326 | 249 |
| 1989 | 0.798 | 0.177 | 0.025 | NA | 111 | 0.160 | 0.805 | 0.035 | NA | 479 | 0.809 | 0.122 | 0.069 | 286 | 207 |
| 1990 | 0.782 | 0.182 | 0.036 | NA | 159 | 0.399 | 0.528 | 0.074 | NA | 245 | 0.751 | 0.153 | 0.095 | 243 | 402 |
| 1991 | 0.721 | 0.261 | 0.018 | NA | 122 | 0.227 | 0.734 | 0.039 | NA | 492 | 0.672 | 0.198 | 0.129 | 127 | 339 |
| 1992 | 0.485 | 0.483 | 0.032 | NA | 147 | 0.274 | 0.690 | 0.035 | NA | 597 | 0.819 | 0.115 | 0.065 | 662 | 1012 |
| 1993 | 0.602 | 0.349 | 0.049 | NA | 57 | 0.360 | 0.603 | 0.037 | NA | 500 | 0.734 | 0.185 | 0.081 | 275 | 524 |
| 1994 | 0.652 | 0.285 | 0.063 | NA | 33 | 0.282 | 0.663 | 0.055 | NA | 572 | 0.686 | 0.251 | 0.062 | 927 | 1002 |
| 1995 | 0.342 | 0.609 | 0.049 | NA | 107 | 0.177 | 0.803 | 0.020 | NA | 418 | 0.595 | 0.348 | 0.057 | 602 | 1708 |
| 1996 | 0.604 | 0.346 | 0.050 | NA | 63 | 0.299 | 0.649 | 0.052 | NA | 364 | 0.647 | 0.244 | 0.108 | 585 | 996 |
| 1997 | 0.414 | 0.380 | 0.206 | NA | 54 | 0.337 | 0.608 | 0.055 | NA | 204 | 0.508 | 0.292 | 0.199 | 529 | 1257 |
| 1998 | 0.576 | 0.364 | 0.060 | NA | 78 | NA | NA | NA | NA | NA | 0.604 | 0.169 | 0.227 | 1187 | 635 |
| 1999 | 0.510 | 0.436 | 0.054 | NA | 45 | NA | NA | NA | NA | NA | 0.614 | 0.193 | 0.193 | 1641 | 1081 |
| 2000 | 0.499 | 0.429 | 0.072 | NA | 14 | 0.468 | 0.484 | 0.048 | NA | 44 | 0.677 | 0.165 | 0.158 | 725 | 1047 |
| 2001 | 0.348 | 0.479 | 0.172 | NA | 34 | 0.233 | 0.712 | 0.055 | NA | 98 | 0.560 | 0.288 | 0.152 | 949 | 2193 |
| 2002 | 0.789 | 0.096 | 0.115 | NA | 22 | 0.431 | 0.495 | 0.074 | NA | 23 | 0.794 | 0.120 | 0.086 | 2200 | 771 |
| 2003 | 0.638 | 0.293 | 0.069 | NA | 84 | 0.280 | 0.720 | 0.000 | NA | 52 | 0.615 | 0.259 | 0.126 | 1395 | 1371 |
| 2004 | 0.592 | 0.358 | 0.049 | NA | 33 | 0.362 | 0.614 | 0.025 | NA | 26 | 0.718 | 0.174 | 0.108 | 1638 | 1307 |
| 2005 | 0.650 | 0.229 | 0.121 | NA | 26 | NA | NA | NA | NA | 2 | 0.662 | 0.247 | 0.092 | 1231 | 1094 |
| 2006 | 0.591 | 0.209 | 0.200 | NA | 43 | 0.313 | 0.556 | 0.131 | NA | 42 | 0.635 | 0.196 | 0.169 | 2579 | 1203 |
| 2007 | 0.707 | 0.202 | 0.091 | NA | 93 | 0.298 | 0.672 | 0.029 | NA | 48 | 0.599 | 0.240 | 0.161 | 1857 | 924 |
| 2008 | 0.659 | 0.224 | 0.117 | NA | 64 | 0.498 | 0.467 | 0.036 | NA | 14 | 0.707 | 0.176 | 0.117 | 1635 | 402 |
| 2009 | 0.515 | 0.324 | 0.162 | NA | 18 | 0.281 | 0.643 | 0.076 | NA | 57 | 0.411 | 0.351 | 0.238 | 935 | 742 |
| 2010 | 0.703 | 0.195 | 0.102 | NA | 64 | 0.247 | 0.732 | 0.021 | NA | 109 | 0.759 | 0.135 | 0.106 | 2487 | 1070 |
| 2011 | 0.750 | 0.195 | 0.055 | NA | 68 | 0.333 | 0.667 | 0.000 | NA | 44 | 0.614 | 0.338 | 0.049 | 2031 | 1046 |
| 2012 | 0.479 | 0.419 | 0.102 | NA | 87 | NA | NA | NA | NA | NA | 0.393 | 0.421 | 0.186 | 676 | 691 |
| 2013 | 0.432 | 0.382 | 0.186 | NA | 64 | 0.186 | 0.804 | 0.010 | NA | 84 | 0.479 | 0.375 | 0.146 | 812 | 553 |
| 2014 | 0.783 | 0.132 | 0.084 | NA | 36 | NA | NA | NA | NA | NA | 0.425 | 0.418 | 0.157 | 0* | 609 |
| 2015 | 0.803 | 0.154 | 0.043 | NA | 46 | 0.401 | 0.589 | 0.010 | NA | 61 | 0.617 | 0.227 | 0.157 | 0* | 720 |
| 2016 | 0.723 | 0.246 | 0.031 | NA | 81 | 0.207 | 0.793 | 0.000 | NA | 74 | 0.452 | 0.397 | 0.150 | 0* | 971 |
| 2017 | 0.445 | 0.403 | 0.152 | NA | 62 | 0.191 | 0.674 | 0.135 | NA | 12 | 0.480 | 0.411 | 0.109 | 0* | 1029 |

*Continued*

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**Appendix 2.** *Continued*

| | Nashwaak, NB | | | | | Saint John, NB | | | | | LaHave, NS | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| **Year** | **P(1SW)** | **P(2SW+)** | **P(RS)** | **n small** | **n large** | **P(1SW)** | **P(2SW+)** | **P(RS)** | **n small** | **n large** | **P(1SW)** | **P(2SW+)** | **P(RS)** | **n small** | **n large** |
| 1971 | NA | NA | NA | NA | NA | NA | NA | NA | NA | NA | NA | NA | NA | NA | NA |
| 1972 | 0.344 | 0.626 | 0.031 | NA | NA | NA | NA | NA | NA | NA | NA | NA | NA | NA | NA |
| 1973 | 0.234 | 0.636 | 0.130 | NA | NA | NA | NA | NA | NA | NA | NA | NA | NA | NA | NA |
| 1974 | NA | NA | NA | NA | NA | NA | NA | NA | NA | NA | NA | NA | NA | NA | NA |
| 1975 | 0.541 | 0.394 | 0.065 | NA | NA | NA | NA | NA | NA | NA | NA | NA | NA | NA | NA |
| 1976 | NA | NA | NA | NA | NA | NA | NA | NA | NA | NA | NA | NA | NA | NA | NA |
| 1977 | NA | NA | NA | NA | NA | NA | NA | NA | NA | NA | NA | NA | NA | NA | NA |
| 1978 | NA | NA | NA | NA | NA | NA | NA | NA | NA | NA | NA | NA | NA | NA | NA |
| 1979 | NA | NA | NA | NA | NA | NA | NA | NA | NA | NA | 0.917 | 0.063 | 0.021 | 255 | 14 |
| 1980 | NA | NA | NA | NA | NA | NA | NA | NA | NA | NA | 0.712 | 0.250 | 0.038 | 141 | 113 |
| 1981 | NA | NA | NA | NA | NA | NA | NA | NA | NA | NA | 0.805 | 0.132 | 0.063 | 330 | 184 |
| 1982 | NA | NA | NA | NA | NA | NA | NA | NA | NA | NA | 0.729 | 0.115 | 0.156 | 67 | 40 |
| 1983 | NA | NA | NA | NA | NA | NA | NA | NA | NA | NA | 0.773 | 0.140 | 0.087 | 113 | 170 |
| 1984 | NA | NA | NA | NA | NA | NA | NA | NA | NA | NA | 0.820 | 0.114 | 0.066 | 33 | 137 |
| 1985 | NA | NA | NA | NA | NA | 0.430 | 0.538 | 0.032 | NA | NA | 0.636 | 0.282 | 0.082 | 218 | 429 |
| 1986 | NA | NA | NA | NA | NA | 0.730 | 0.207 | 0.063 | NA | NA | 0.708 | 0.178 | 0.113 | 264 | 487 |
| 1987 | NA | NA | NA | NA | NA | 0.581 | 0.380 | 0.039 | NA | NA | 0.834 | 0.104 | 0.062 | 661 | 416 |
| 1988 | NA | NA | NA | NA | NA | 0.590 | 0.376 | 0.033 | NA | NA | 0.878 | 0.072 | 0.050 | 849 | 362 |
| 1989 | NA | NA | NA | NA | NA | 0.529 | 0.399 | 0.071 | NA | NA | 0.775 | 0.152 | 0.073 | 939 | 456 |
| 1990 | NA | NA | NA | NA | NA | 0.470 | 0.504 | 0.025 | NA | NA | 0.827 | 0.097 | 0.075 | 783 | 405 |
| 1991 | NA | NA | NA | NA | NA | 0.473 | 0.511 | 0.016 | NA | NA | 0.643 | 0.253 | 0.104 | 246 | 291 |
| 1992 | NA | NA | NA | NA | NA | 0.430 | 0.553 | 0.017 | NA | NA | 0.900 | 0.070 | 0.030 | 1165 | 256 |
| 1993 | 0.672 | 0.239 | 0.090 | NA | NA | 0.559 | 0.388 | 0.054 | NA | NA | 0.832 | 0.129 | 0.038 | 432 | 192 |
| 1994 | 0.635 | 0.291 | 0.074 | NA | NA | 0.657 | 0.317 | 0.027 | NA | NA | 0.773 | 0.167 | 0.060 | 202 | 231 |
| 1995 | 0.684 | 0.302 | 0.015 | NA | NA | 0.741 | 0.245 | 0.013 | NA | NA | 0.804 | 0.174 | 0.022 | 285 | 212 |
| 1996 | 0.735 | 0.206 | 0.058 | NA | NA | 0.705 | 0.279 | 0.016 | NA | NA | 0.838 | 0.131 | 0.032 | 238 | 184 |
| 1997 | 0.495 | 0.422 | 0.083 | NA | NA | 0.692 | 0.284 | 0.023 | NA | NA | 0.768 | 0.173 | 0.060 | 190 | 122 |
| 1998 | 0.803 | 0.126 | 0.071 | NA | NA | 0.626 | 0.351 | 0.022 | NA | NA | 0.868 | 0.091 | 0.041 | 360 | 133 |
| 1999 | 0.706 | 0.208 | 0.085 | NA | NA | 0.646 | 0.344 | 0.010 | NA | NA | 0.746 | 0.203 | 0.052 | 185 | 131 |
| 2000 | 0.726 | 0.221 | 0.052 | NA | NA | 0.564 | 0.422 | 0.015 | NA | NA | 0.867 | 0.104 | 0.028 | 250 | 117 |
| 2001 | 0.472 | 0.463 | 0.065 | NA | NA | 0.601 | 0.381 | 0.018 | NA | NA | 0.676 | 0.298 | 0.026 | 117 | 175 |
| 2002 | 0.824 | 0.109 | 0.067 | NA | NA | 0.693 | 0.298 | 0.009 | NA | NA | 0.938 | 0.029 | 0.033 | 222 | 68 |
| 2003 | 0.722 | 0.252 | 0.026 | NA | NA | 0.670 | 0.320 | 0.011 | NA | NA | 0.679 | 0.304 | 0.018 | 119 | 198 |
| 2004 | 0.740 | 0.240 | 0.020 | NA | NA | 0.623 | 0.353 | 0.024 | NA | NA | 0.819 | 0.129 | 0.052 | 82 | 116 |
| 2005 | 0.810 | 0.170 | 0.020 | NA | NA | 0.837 | 0.134 | 0.029 | NA | NA | 0.823 | 0.134 | 0.043 | 277 | 75 |
| 2006 | 0.780 | 0.200 | 0.020 | NA | NA | 0.644 | 0.349 | 0.007 | NA | NA | 0.785 | 0.181 | 0.034 | 358 | 107 |
| 2007 | 0.820 | 0.140 | 0.040 | NA | NA | 0.849 | 0.138 | 0.013 | NA | NA | 0.890 | 0.094 | 0.016 | 327 | 41 |
| 2008 | 0.880 | 0.110 | 0.010 | NA | NA | 0.585 | 0.404 | 0.011 | NA | NA | 0.858 | 0.131 | 0.011 | 585 | 92 |
| 2009 | 0.460 | 0.450 | 0.090 | NA | NA | 0.862 | 0.125 | 0.013 | NA | NA | 0.747 | 0.203 | 0.050 | 168 | 52 |
| 2010 | 0.911 | 0.069 | 0.020 | NA | NA | 0.634 | 0.356 | 0.010 | NA | NA | 0.841 | 0.133 | 0.026 | 294 | 52 |
| 2011 | 0.637 | 0.341 | 0.022 | NA | NA | 0.676 | 0.320 | 0.004 | NA | NA | 0.792 | 0.192 | 0.016 | 289 | 76 |
| 2012 | 0.322 | 0.487 | 0.191 | NA | NA | 0.770 | 0.220 | 0.009 | NA | NA | 0.433 | 0.448 | 0.119 | 28 | 39 |
| 2013 | 0.621 | 0.297 | 0.083 | NA | NA | 0.796 | 0.201 | 0.002 | NA | NA | 0.403 | 0.581 | 0.016 | 75 | 111 |
| 2014 | 0.773 | 0.152 | 0.076 | NA | NA | 0.732 | 0.268 | 0.000 | NA | NA | 0.672 | 0.328 | 0.000 | 43 | 21 |
| 2015 | 0.869 | 0.126 | 0.005 | NA | NA | 0.867 | 0.131 | 0.002 | NA | NA | 0.894 | 0.095 | 0.011 | 160 | 19 |
| 2016 | 0.846 | 0.140 | 0.014 | NA | NA | 0.527 | 0.456 | 0.017 | NA | NA | 0.338 | 0.662 | 0.000 | 23 | 45 |
| 2017 | 0.670 | 0.307 | 0.023 | NA | NA | 0.857 | 0.139 | 0.004 | NA | NA | 0.881 | 0.115 | 0.005 | 192 | 26 |

*indicates the years during which a low number of large salmon were sampled. For these years, the composition of large salmon was calculated based on the mean composition of an extended time period (i.e. multiple years).

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