

Evidence for reproductive senescence in a broadly distributed harvested marine fish

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ABSTRACT: Senescence is the physiological deterioration of adult organisms leading to an age-specific decline in fitness principally associated with an increase in mortality rate (actuarial senescence) and decline in fecundity (reproductive senescence). Senescence is common in natural populations of many taxa; however, there are few examples among fishes, even though they are the most speciose vertebrates and comprise a disproportionate number of long-lived animal species. A notable example in fish is Norwegian spring-spawning Atlantic herring *Clupea harengus*, which experiences actuarial senescence. Given expected associations between actuarial and reproductive senescence, Atlantic herring likely also experience reproductive senescence. We examined biological data obtained over 4 decades for 15 Canadian Atlantic herring stocks for evidence of reproductive senescence. Age- and length-specific increases in the relative frequency of morphologically non-reproductive herring and age-related decreases in reproductive investment were consistent with reproductive senescence in both sexes, combined with a post-reproductive increase in growth rate. Available evidence was not consistent with 2 alternative hypotheses: delayed maturation combined with higher survival for late-maturing fish, or an increasing frequency of skipped spawning with age. Although the incidence of post-reproductive herring was generally low, this was likely because very few individuals survive to older ages due to fishing. The present study presents the first strong example of reproductive senescence in a marine fish, notably one that is both ecologically important and a target of large fisheries throughout its range.

KEY WORDS: Atlantic herring · *Clupea harengus* · Senescence · Post-reproductive · Life history · Lifetime reproductive value

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INTRODUCTION

Senescence, or 'ageing', is the physiological deterioration of adult organisms leading to an age-specific decline in fitness principally associated with an increase in mortality rate (hereafter, actuarial senescence) and decline in fecundity (reproductive senescence). In the past, there has been widespread belief that animals in nature did not experience

senescence because external factors would kill them before ageing can take its toll and be subject to natural selection (Medawar 1952, Comfort 1956, Kirkwood & Austad 2000). Evidence collected in recent decades has revealed the contrary (Nussey et al. 2013, Roach & Carey 2014). A recent review identified 175 animal species, mostly mammals and birds, that display evidence of senescence in the wild (Nussey et al. 2013).

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The review by Nussey et al. (2013) identified a number of gaps in our understanding of senescence in nature. Notably, there are very few concrete instances of senescence in wild fishes (Gerking 1957, Carlson et al. 2007, Nussey et al. 2013; but see Uriarte et al. 2016), even though fish are the most speciose vertebrates (Chapman 2009) and comprise a disproportionate number of long-lived animal species (Carey & Judge 2000, Cailliet et al. 2001). It has been argued that fish have evolved delayed senescence owing to indeterminate growth in most species and the ensuing increase in fecundity with age (Williams 1957, Hamilton 1966, Reznick et al. 2002). Contemporary sampling of natural populations is unlikely to include senescing individuals if senescence occurs only at extreme ages at which abundance is low. Furthermore, because population monitoring in fish is largely focussed on commercially harvested species, fishing mortality may prevent individuals from reaching the advanced ages at which senescence becomes important, and it is typically very difficult to tease apart fishing and non-fishing mortality. Nonetheless, some of the most compelling evidence for actuarial senescence in fish comes from a commercially harvested species, Norwegian spring-spawning (NSS) Atlantic herring *Clupea harengus* (Beverton et al. 2004). Using data from a prolonged period of low fishing mortality during the mid-twentieth century (see Toresen & Østvedt 2000), Beverton et al. (2014) documented significant increases in mortality rates occurring 6 to 12 yr (average 9 yr) after maturation, a pattern consistent with senescence, both within and among cohorts, suggesting a somewhat constrained non-senescent adult lifespan.

The pronounced actuarial senescence in NSS herring is expected to also be associated with reproductive senescence because the progression of actuarial and reproductive senescence is almost certainly linked (Jones et al. 2008, Kirkwood & Shanley 2010), though they may not proceed synchronously, contrary to what was proposed by Williams (1957) (reviewed by Nussey et al. 2013). Declines in the function of somatic cells that contribute to increased mortality at age are also likely to contribute to declines in fertility. Furthermore, from an evolutionary perspective, there is little adaptive value to maintaining reproductive viability when the progression of actuarial senescence and the breakdown of somatic function hinder successful reproduction (Kirkwood & Shanley 2010).

Atlantic herring is a prime candidate species for studying reproductive senescence in a marine fish, given the expected occurrence of actuarial senescence

and the considerable amount of existing biological data for the species. To our knowledge, there are no other convincing examples for marine fish, let alone a broadly distributed species that is both ecologically important and a target of large fisheries throughout its range (Trenkel et al. 2014).

In this paper we consider the evidence for reproductive senescence in Canadian Atlantic herring stocks. The data are from scientific and commercial fishery sampling programmes and are cross-sectional in nature, including individual ages, lengths and maturity stages at the time of sampling. In this case, the strongest evidence for reproductive senescence is an age-specific decrease in reproductive investment and an age-specific increase in the relative incidence of macroscopically non-reproductive individuals at advanced ages, which would be consistent with a post-reproductive period. We also consider arguments and evidence against 2 other mechanisms that could underlie the age-specific pattern in non-reproductive individuals: delayed maturation combined with higher survival of late-maturing fish, and an increasing frequency of skipped spawning with age. While the latter would arguably be symptomatic of reproductive senescence in and of itself, we nonetheless consider evidence for a permanent cessation of spawning activity in these older fish.

MATERIALS AND METHODS

Data

The data cover all major Canadian Atlantic herring stocks or stock complexes (hereafter, stocks; Fig. 1), which comprise most major stocks in the northwest Atlantic, with the exception of those on Georges Bank and in the Gulf of Maine (Colette & Klein-MacPhee 2002, Stephenson et al. 2009). The stocks in the southern Gulf of St. Lawrence (sGSL) and around Newfoundland have distinct spring and fall spawning components, which themselves are considered separate stocks, whereas spawning occurs almost exclusively in the fall in the other southern stocks (Melvin et al. 2009, Stephenson et al. 2009).

The demographic composition of catches from commercial fisheries and scientific monitoring is inferred from routine sampling in all of these stocks. The sampling procedure differs between areas. Samples from Newfoundland stocks consist of 50 randomly chosen herring, from entire catches in the commercial fishery and haul-specific catches in scientific surveys, and from each net panel in multiple-

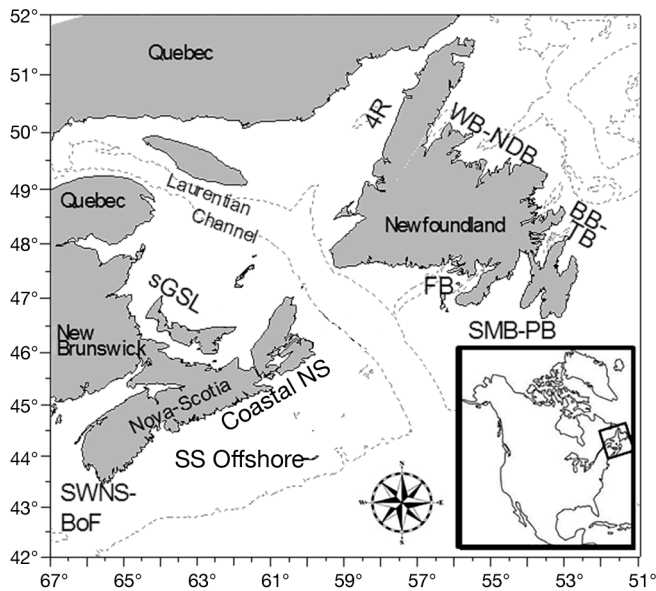


Fig. 1. Locations for the Canadian herring stocks considered in the present study: southwest Nova Scotia and Bay of Fundy (SWNS-BoF), Scotian Shelf Offshore Banks (SS Offshore), Coastal Nova Scotia (Coastal NS), southern Gulf of St. Lawrence (sGSL), Northwest Atlantic Fisheries Organization (NAFO) 4R, White Bay and Notre Dame Bay (WB-NDB), Bonavista Bay and Trinity Bay (BB-TB), Saint-Mary's Bay and Placentia Bay (SMB-PB) and Fortune Bay (FB). The dashed line indicates the 300 m contour. The inset indicates the study area with respect to North America

mesh gillnet index fisheries. Sampling is stratified for stocks from south of the Laurentian Channel (SWNS-BoF, SS Offshore, Coastal NS, sGSL Spring and sGSL Fall; hereafter, Laurentian south stocks; Fig.1) such that a length-frequency is obtained from a random sample of typically up to 200 fish, from which up to 2 fish per 0.5 cm interval are retained for detailed bio-

logical sampling. Normally the data for the latter stocks should be analysed while accounting for sampling weights. However, preliminary analyses suggested that results were very similar whether sampling weights were applied or not (see Supplement 1 at www.int-res.com/articles/suppl/m592p207_supp.pdf). Consequently, to maintain consistency in the analysis across stocks and to simplify analyses for the 5 Laurentian south stocks, the sampling weights were disregarded.

The biological sampling for all stocks consists of measurements of total length (mm), wet weight to the nearest 0.1 g and gonad weight to the nearest 0.01 g, as well as the macroscopic determination of maturity stage and the collection of otoliths for age determination. Maturity determination follows a common 8-category scheme based on the size, shape and colour of the gonads (Table 1). This scheme has been in use since at least 1970 (Messieh 1975). Gonad weights are occasionally not obtained for immature fish given the small size and fragility of the gonads. Herring sampled in Newfoundland are typically aged up to 11 yr old only, and all older fish are attributed an age of 11 (Fig. 2). For stocks with both spring and fall spawning components, spawning group attribution is based on the date of capture, maturity stage and characteristics of the otoliths (Parsons & Hodder 1975, McQuinn 1989).

For the purposes of the present study, individual herring associated with a maturity code of 1 or 2 (Table 1) were considered functionally non-reproductive, or immature, regardless of their age or size. All other fish were considered to be reproductive. (Maturity code was revised to a value of 1 based on relative gonad weights for 7 individuals from the 4R Fall stock

Table 1. Maturity staging scheme for Atlantic herring based on recommendations by the International Council for the Exploration of the Sea (ICES 1963). For details on the application of the scheme, see Parrish & Saville (1965), Landry & McQuinn (1988) and Bucholtz et al. (2008)

Code	Maturity stage	Coarse description
1	Immature (early)	Gonads are very small and thread-like. Sex cannot reliably be distinguished macroscopically.
2	Immature (late)	Gonads are small, thin and ribbon-like. Sex can be distinguished macroscopically.
3	Resting	Gonads are approximately 1–2 cm wide and two-thirds the length of the body cavity. Gamete cells are present but small. Herring enter this stage after completing stages 2 or 8.
4	Developing	Gonads are the length of the body cavity and occupy around half of its volume. Testes are white or greyish. Eggs are visible in the ovaries.
5	Ripening	Large eggs or sperm are present, but do not flow easily. The gonads occupy the volume of the body cavity, compressing the other organs.
6	Ripe/Spawning	Gonads are large and soft, and the membrane is thick. Gametes flow easily.
7	Spent	Gonads are bloodshot and flaccid, though the membrane remains thick. Residual quantities of gametes may be present.
8	Recovering	Gonads are flaccid and their membrane is thin. Gametes are not visible macroscopically.

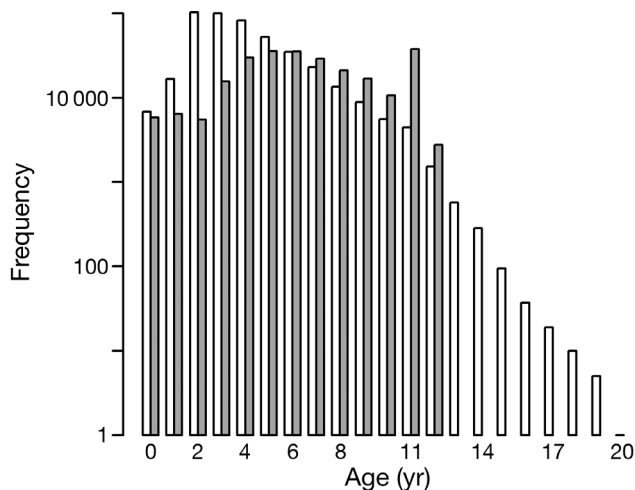


Fig. 2. Number of individual herring in the present study as a function of age for stocks from Newfoundland (grey bars) and the Laurentian south stocks (white bars)

that had previously been attributed, by default, a code of 8). Given the objective of characterizing the relative frequency of senescent traits in the respective populations, only data obtained from samples captured using fishing gear that is the least size (or age) selective were retained in most instances. Most of the data were therefore from catches in purse seines, trawls and multiple-mesh (index) gillnets fished on feeding aggregations. To fill data gaps for the Coastal NS stock, some data were obtained from targeted scientific fishing using commercial gillnet gear. The data cover the periods from 1982–2014 for the NAFO 4R stock, 1980–2011 for the other Newfoundland stocks and 1970–2014 for the remaining stocks.

Analysis

Reproductive senescence was inferred by an age-specific increase in the relative occurrence of macroscopically non-reproductive individuals and by age-specific decreases in reproductive investment. However, there was an *a priori* expectation that these patterns may be variable and that the magnitude of age-dependent change could be small. First, there can be considerable individual level or environmentally driven variability in the age of onset and the progression rate of senescence (Walker & Herndorn 2010, Roach & Carey 2014). Second, if reproductive and actuarial senescence are tightly linked, then many reproductively senescent individuals may die before being sampled. Furthermore, senescence should be most evident in the oldest fish in the population which typically will not be very numerous,

resulting in high sampling variability. Notably, there were very few old herring in the data for the Canadian stocks (Fig. 2). The analyses described below were selected taking these factors into consideration. In addition to age-specific patterns in reproductive senescence, patterns in the data also suggested length-specific increases in the relative occurrence of macroscopically non-reproductive herring. Similar methods were used in analyses of both the age-specific and length-specific patterns.

Beverton et al. (2004) observed a positive correlation between maturation age and the age at which actuarial senescence began in NSS herring cohorts. A similar correlation between maturation age and the onset of reproductive senescence in Canadian herring was therefore anticipated. Unlike NSS herring, for which maturation age and patterns in size at age of individual fish were inferred from otoliths, the available data for the Canadian stocks are cross-sectional in nature such that the maturity stage, length and age of fish is only known for the date of capture. Consequently, to adjust for temporal changes in maturation age within stocks, as observed for the Newfoundland stocks (Wheeler et al. 2009), and for differences between stocks, the age at which 20 % of individuals in a cohort and stock were mature (A_{20}) was estimated as a proxy for the age of maturation onset for that cohort. The estimates for each cohort were obtained using individual logistic regression analyses, with maturity status (mature/immature) as the dependent variable and cohort age as the independent variable. The value of A_{20} for cohort c in stock j , A_{20cj} , was estimated as:

$$A_{20cj} = -\log(1/0.2 - 1) - \beta_{0cj} / \beta_{1cj} \quad (1)$$

where β_{0cj} and β_{1cj} are, respectively, the estimated intercept and slope of the logistic regression for cohort c of stock j . To compensate for low samples sizes for certain ages and years that resulted in high frequency variability in estimates of A_{20cj} , data for cohorts born in adjacent years were included in the analysis for a particular cohort using a moving window of 5 cohort years for Laurentian south stocks and 9 cohort years for the others. The wider window for the other stocks was used due to greater sparseness of observations for young immature fish. The estimated A_{20cj} for a cohort and stock was subtracted from the observed age of individuals to produce a standardized age, the number of years following maturity onset.

Length at age has also changed over time in the Canadian herring stocks (e.g. Wheeler et al. 2009, Benoît et al. 2016). To adjust for these changes and

for differences between stocks, lengths at age were adjusted to the same average value in each stock and year using the following equation:

$$zL_{ajit} = \frac{\bar{L}_a \cdot L_{ajit}}{s(\bar{L}_{ajt})} \quad (2)$$

where zL_{ajit} is the standardized length (mm) at age a for individual herring i in stock j in year t , \bar{L}_a is the mean length at age a across all stocks and years, L_{ajit} is the observed length of herring i , and $s(\bar{L}_{ajt})$ is a local polynomial regression (loess) smooth for the mean length of herring age a in stock j and year t , with a span of 0.75 and degree of 2. The calculation was made by age for ages 0 to 10 and as a group for ages 11 and older, which occur in the asymptotic portion of the growth curve for the Canadian herring. The loess smoother was used to borrow information from adjoining years to reduce estimation uncertainty for years and ages associated with low sample sizes.

Changes in the relative occurrence of macroscopically non-reproductive individuals as a function of either standardized age or standardized length, consistent with a post-reproductive period, was modelled using the Firth method for logistic regression (Firth 1993). This penalized likelihood approach reduces the small-sample bias that is otherwise inherent in maximum likelihood estimation for rare events (King & Zeng 2001) and was chosen because the expected incidence of post-reproductive herring was small. The data for all stocks were analysed jointly in a model that included the covariate (standardized age or length), a factor for stock and an interaction between them. The models were fit to individual maturity status, reproductive or non-reproductive. Statistical significance for the factor and for the interaction was evaluated using likelihood ratio tests. Models for standardized age were not fit to the data for the Newfoundland stocks because ages were censored at 11 yr.

Across all standardized ages and lengths, the incidence of non-reproductive individuals is expected to first decrease from 100% to or near 0%, reflecting the typical maturation process, before increasing again as the prevalence of reproductive senescence increases. The interest here was in modelling only this latter ascending trend. This required choosing minimum standardized ages and lengths for the data included in the analyses. The choice of minimum values was somewhat arbitrary within certain ranges of values chosen based on patterns in the data. Sensitivity to these choices was evaluated by undertaking the Firth logistic regression analyses for different minimum values (described in Supplement 2).

We also looked for evidence of reproductive senescence in the form of an age-dependent decrease in reproductive investment in ripe or spawning fish (maturity code 6). The analysis was based on the gonadosomatic index (GSI), which was calculated as

$$GSI_i = 100 \cdot \frac{G_i}{W_i} \quad (3)$$

where G_i and W_i are respectively the gonad weight (g) and total weight (g) for individual i . Under reproductive senescence, the frequency of relatively small values of GSI is expected to increase with age. To test whether this was the case, we first estimated the tenth-percentile of GSI values for herring with maturity code 6 for each stock and sex, which we used as a threshold for small values. We then evaluated for each stock the relative incidence of GSI values that were at or below these thresholds as a function of standardized age using logistic regression. Similar to the analyses of non-reproductive herring, the data for all stocks were analysed jointly in a model that also included a factor for stock and an interaction between stock and standardized age. Furthermore, the analyses were also limited to ages that were after the descending portion of the age-dependent relationship. However, unlike the analysis of non-reproductive herring as a function of standardized age, this analysis included all stocks with sufficient data because the standardized age ranges were very similar between stocks. The stocks that were excluded due to insufficient data were SS Offshore, FB Fall and SMB-PB Fall.

Data were pooled across sexes for all analyses for a number of reasons. First, it is generally not possible to tell apart the sexes for immature herring at maturity stage 1 (Table 1). Second, the number of purported post-reproductive individuals in this study was considered too low to support separate analyses for males and females. Third, and most notably, sex-dependent differences in the age-dependent progression of senescence are expected if there are differences in reproductive investment between males and females (Lemaître & Gaillard 2017). This was examined by comparing sex-specific GSI values for ripe/spawning (maturity stage 6) and for resting stage (stage 8) herring. The difference in values between these 2 stages reflects reproductive investment as measured by the change in relative gonad weight from seasonal low to peak values. The comparison was made using beanplots, which are density trace estimates of the distribution of univariate data and are an alternative to traditional boxplots (Kampstra 2008). This comparison revealed little evidence for sex-dependent differences in investment (see 'Results').

Alternative hypotheses for age-specific increases in non-reproductive individuals

There are 2 other mechanisms that could underlie age-specific increases in non-reproductive individuals at older ages: (1) an increasing frequency of skipped spawning with age, and (2) delayed maturation combined with differential survival for early- and late-maturing fish. The rationale underlying these hypotheses and the analyses undertaken to evaluate the evidence for them are provided below.

Skipped spawning

Skipped spawning appears to be a common feature of the life history of numerous fish species (Rideout et al. 2005, Rideout & Tomkiewicz 2011), including Atlantic herring to some degree (Kennedy et al. 2011, Bucholtz et al. 2013). Skipped spawning is typically associated with poor physiological condition (Rideout et al. 2005, Kennedy et al. 2010, Skjæraasen et al. 2012), and is expected when an individual's remaining lifetime reproductive value (a product of survival and fecundity at age) is significantly enhanced by foregoing reproduction in a given year (Jørgensen et al. 2006). If age-specific increases in skipped spawning underlie an increased relative frequency of non-reproductive individuals, then condition values in those individuals should be lower relative to reproductive individuals of the same age or size. This may be particularly true seasonally during gonad development prior to spawning (Kennedy et al. 2010). The condition of similarly aged and sized individuals for the data as a whole, and on a monthly basis, was therefore compared using Fulton's condition factor K (Nash et al. 2006), defined as:

$$K_i = 100 \cdot \frac{W_i}{L_i^3} \quad (4)$$

where W_i and L_i are, respectively, the total weight (g) and total length (cm) for individual i . Beanplots were used to compare the distribution of condition values for immature individuals (stages 1 and 2) and for mature individuals that were neither spawning nor spent (stages 3–5 and 8). Individuals that were in the process of releasing gametes or had just spawned (stages 6 and 7) were not included to avoid introducing a possible negative bias in K values for mature fish.

Skipped spawners often have gonads that resemble those of spent fish and have similar GSI values (Rideout et al. 2005). By definition, the gonads of immature fish in the present study were macroscopi-

cally different from those of spent fish (Table 1), although similarities at the cellular level may still have existed. Consequently, the distribution of GSI values for immature fish was compared to that for spent and resting fish (stages 7 and 8) using beanplots to evaluate whether the values would be consistent with skipped spawning.

Delayed maturation

It is possible that some fish could experience unusually long delays in maturation. Theory predicts that this strategy should result in a lower mortality rate at age relative to individuals that matured earlier as part of a 'typical' life-history (Roff 2002). This in turn could result in an increase with age in the relative frequency of immature individuals amongst older fish. However, while survival may be enhanced by significantly delaying maturation, considerable forgone reproductive opportunities should result in selection against this strategy. To evaluate whether unusually long delays in maturation are a plausible mechanism, the average expected lifetime reproductive value (LRV) was calculated for typical herring and for theoretically unusually late-maturing herring.

If the mortality rate of late-maturing fish is proportional to that of typical individuals across all ages and if age-specific catchability of the 2 types is equal, then the relative frequency of immature individuals at age observed in sampling (p_a) should vary as:

$$p_a = \frac{N_{L,a}}{N_{T,a}} = \frac{N_{L,a_0}}{N_{T,a_0}} \cdot \frac{\exp(-r_L \sum_{y=a_0}^a Z_y)}{\exp(-\sum_{y=a_0}^a Z_y)} \quad (5)$$

where $N_{L,a}$ and $N_{T,a}$ are, respectively, the abundance of late-maturing and typical herring at age, a_0 is the initial age in the analysis, Z_y is the total instantaneous mortality rate at age for a typical herring, and r_L is relative survival premium for an unusually late-maturing fish under this hypothesis. By rearranging Eq. (5), r_L can be estimated using linear regression based on estimates of p_a from the biological samples and estimates Z_y from stock assessments:

$$\left(\log(p_a) - \sum_{y=a_0}^a Z_y \right) = \log\left(\frac{N_{L,a_0}}{N_{T,a_0}}\right) - r_L \sum_{y=a_0}^a Z_y \quad (6)$$

The LRV for herring of type X , either typical or late maturing, can then be calculated as

$$\text{LRV}_X = \sum_{a=2}^{a_{\max}} \text{Mat}_{X,a} \cdot \text{Fec}_{X,a} \cdot \exp\left(-\sum_{y=2}^a r_X Z_y\right) \quad (7)$$

where $\text{Mat}_{X,a}$ and $\text{Fec}_{X,a}$ are, respectively, the probability of being mature at age and the fecundity at age (in 1000s eggs female⁻¹) for herring of type X ; $r_X = 1$ for typical individuals and for late-maturing herring once they have matured and $r_X = r_L$ for late-maturing individuals prior to maturation. Other age-dependent maternal effects on fish reproductive success, such as enhanced hatching rates (Green 2008), were not included as these appear to contribute considerably less to LRV compared to Fec_a (e.g. Le Bris et al. 2015).

For illustrative purposes, the calculations were based on the information available for cohorts of the sGSL fall spawning stock born in 1990–1994 (see Supplement 3 for details in addition to those below). The total mortalities at age for the cohorts, Z_{yr} , were taken from the most recent assessment for the stock (Swain 2016). $\text{Mat}_{T,a}$ was estimated using logistic regression of the available maturity data for ages 0–8 for these cohorts, while $\text{Mat}_{L,a}$ was set to 0 for ages 0–14, and 1 for subsequent ages, reflecting the minimum age at maturity for these fish based on the hypothesis at hand and the observation of increases in the proportion of immature fish at least up to 14 yr of age (see Results). Fecundity was estimated using the empirical relationship for the stock published in Messieh (1976),

$$\text{Fec}_{T,a} = 102.28 \cdot W_{T,a}^{1.26} \quad (8)$$

where $W_{T,a}$ is the weight at age (g) for a typical herring and was estimated from the available data. As is shown below, old immature fish in the present study were also found to be longer at age. The weight at age for late-maturing herring was therefore increased accordingly to calculate $\text{Fec}_{L,a}$ (see Supplement 3).

RESULTS

A_{20} has decreased over time in the SS Offshore stock and in all Newfoundland stocks except for the 4R Fall and WB-NBD Fall stocks (Fig. 3). In contrast, A_{20} increased by about 1 yr in the 2 sGSL stocks, and varied without trend in the 4 remaining stocks. Estimates of A_{20} typically varied between 2 and 3.5 yr old but were as low as 1 yr in some stocks and years.

These results underscored the need to standardize age for the subsequent analyses. Mean length at age declined continuously over the 1970–2014 period for all Laurentian south stocks (Fig. 4). Similar declines were observed for the remaining stocks up to the early 1990s, following which length at age varied with little or perhaps a slight positive trend. Mean lengths at young ages (e.g. 4 yr) in a given year were lowest in the most southerly distributed stocks and typically greatest in the more northerly Newfoundland stocks (Fig. 4). For some stocks there were sufficient data to examine patterns in the incidence of non-reproductive individuals as a function of length and by decade. Although the patterns were variable, there was an indication that the increase in incidence occurred at longer lengths in the 1980s, when mean length at age was larger, compared to the later decades (see example in Fig. S6 in Supplement 4). In contrast, patterns in the incidence were comparable across decades when expressed as a function of standardized length (Fig. S6 in Supplement 4). Given these results, standardized length values were used for the subsequent analyses. Although the temporal and cross-stock patterns in A_{20} and length at age are compelling and exploration of the

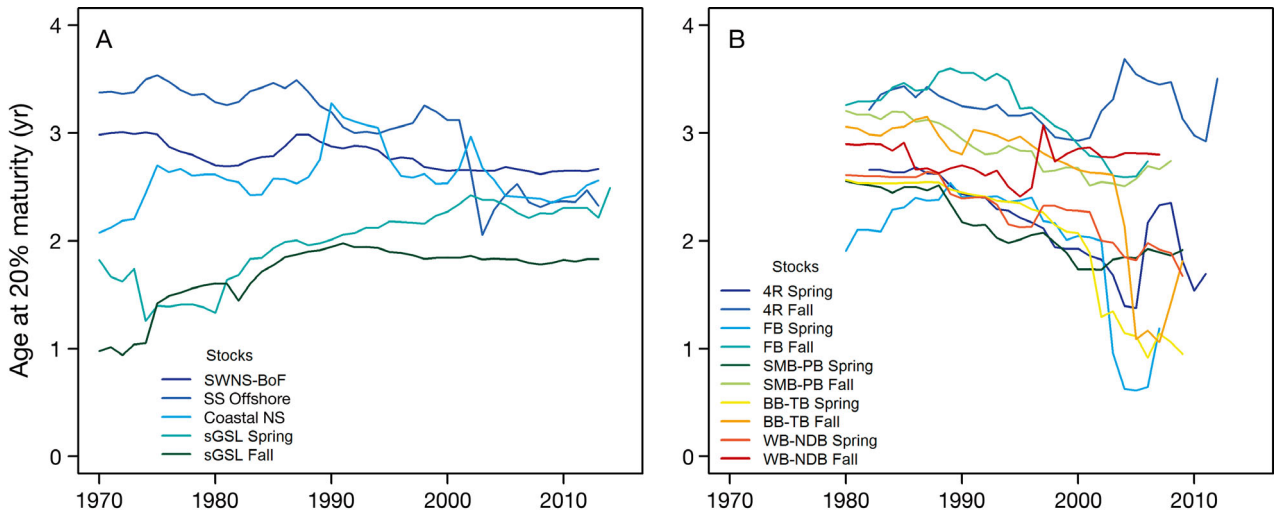


Fig. 3. Trends in the predicted age at which 20% of herring are mature by year class for each stock (colours; see Fig. 1 for locations): (A) Laurentian south stocks, (B) Newfoundland stocks

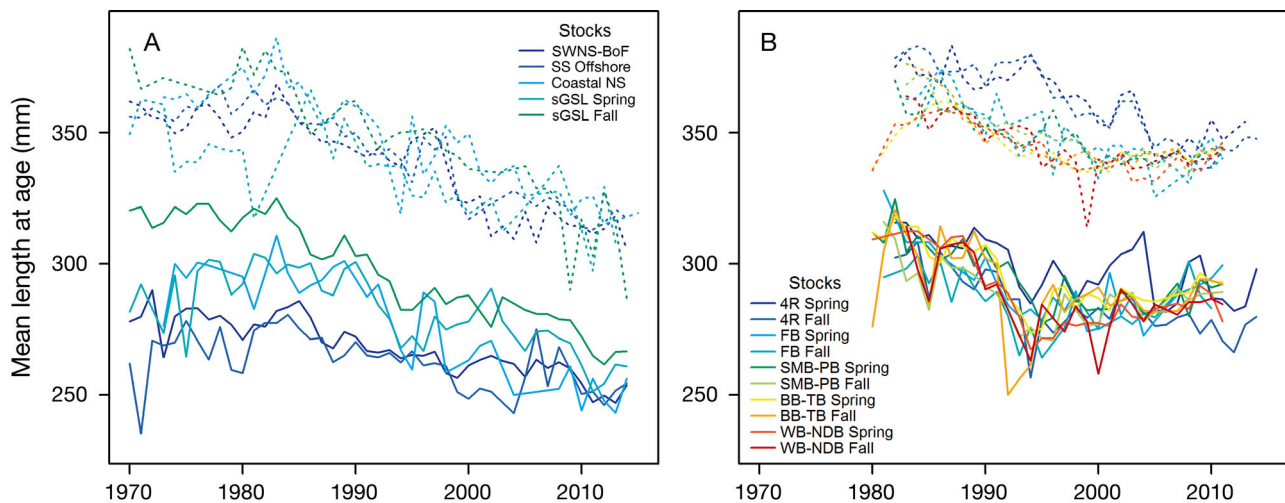


Fig. 4. Interannual trends in the mean length of herring at age 4 (solid line) and age 10 (dotted line) for each stock (colours; see Fig. 1 for locations): (A) Laurentian south stocks, (B) Newfoundland stocks. Mean lengths for stocks from south of the Laurentian Channel were calculated accounting for the stratified sampling employed for those stocks

drivers of these patterns is worthy of study, this is not pursued here as it is beyond the scope of this paper.

Reproductive investments appeared similar between male and female herring based on GSI for the data overall (Fig. 5) and for individual stocks (Fig. S7 in Supplement 4). Furthermore, amongst herring with standardized ages ≥ 5 yr and classified as maturity stage 2 (macroscopically non-reproductive but sexes distinguishable), 60 were female and 73 were male. These results suggest respectively that differences in senescence rates between sexes in Atlantic herring are neither expected nor supported by observations.

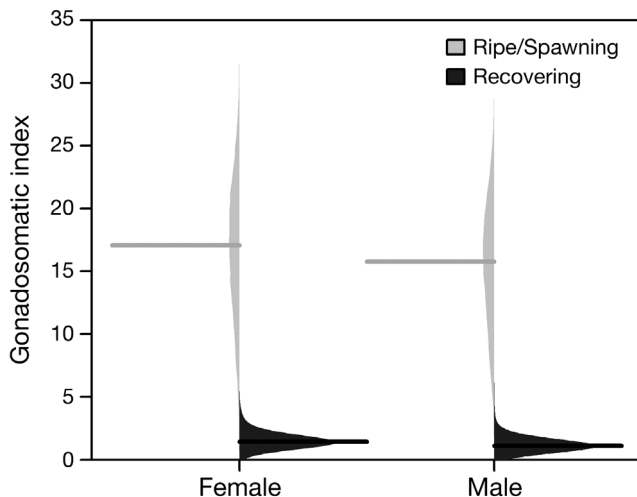


Fig. 5. Density trace of gonadosomatic index values for ripe/spawning (maturity code 6) and recovering (maturity code 8) herring, by sex. The horizontal lines indicate the median values for each group

Increases at older ages in the relative incidence of non-reproductive herring as a function of standardized age were most evident in the Coastal NS, SS Offshore and both sGSL stocks, with some evidence for small increases in the SWNS-BoF, FB Fall, SMB-PB Spring and Fall, and BB-TB Fall stocks (Fig. 6). A minimum standardized age of 5 yr was chosen for the Firth logistic regression analysis based on the sensitivity analyses (details in Supplement 2). The interaction between stock and standardized age was not significant ($\chi^2_4 = 3.42$; $p = 0.489$; Table S1 in Supplement 2) but the additive effects of standardized age (coefficient = -0.173 ± 0.050 SE, $p = 0.0011$) and stock ($\chi^2_4 = 38.29$, $p < 0.0001$) were. The model predicted statistically significant increases in the relative incidence of non-reproductive herring in SS Offshore, Coastal NS and sGSL Fall stocks that reached approximately 1 to 2 % of herring 11 yr after maturation onset (Fig. 6). The predicted rate of increase for the sGSL Spring stock was greater but considerably more uncertain because the increase appeared to begin at lower standardized ages than in other stocks and because of the absence of fish older than 8 yr following maturity onset.

The data suggested increases in the relative incidence of non-reproductive herring as a function of standardized length in the majority of stocks beyond standardized lengths of around 330–350 mm (Fig. 7). A minimum standardized length of 350 mm was chosen for the Firth logistic regression analysis based on the sensitivity analyses (details in Supplement 2). The interaction between stock and standardized length was not significant ($\chi^2_{14} = 15.51$; $p =$

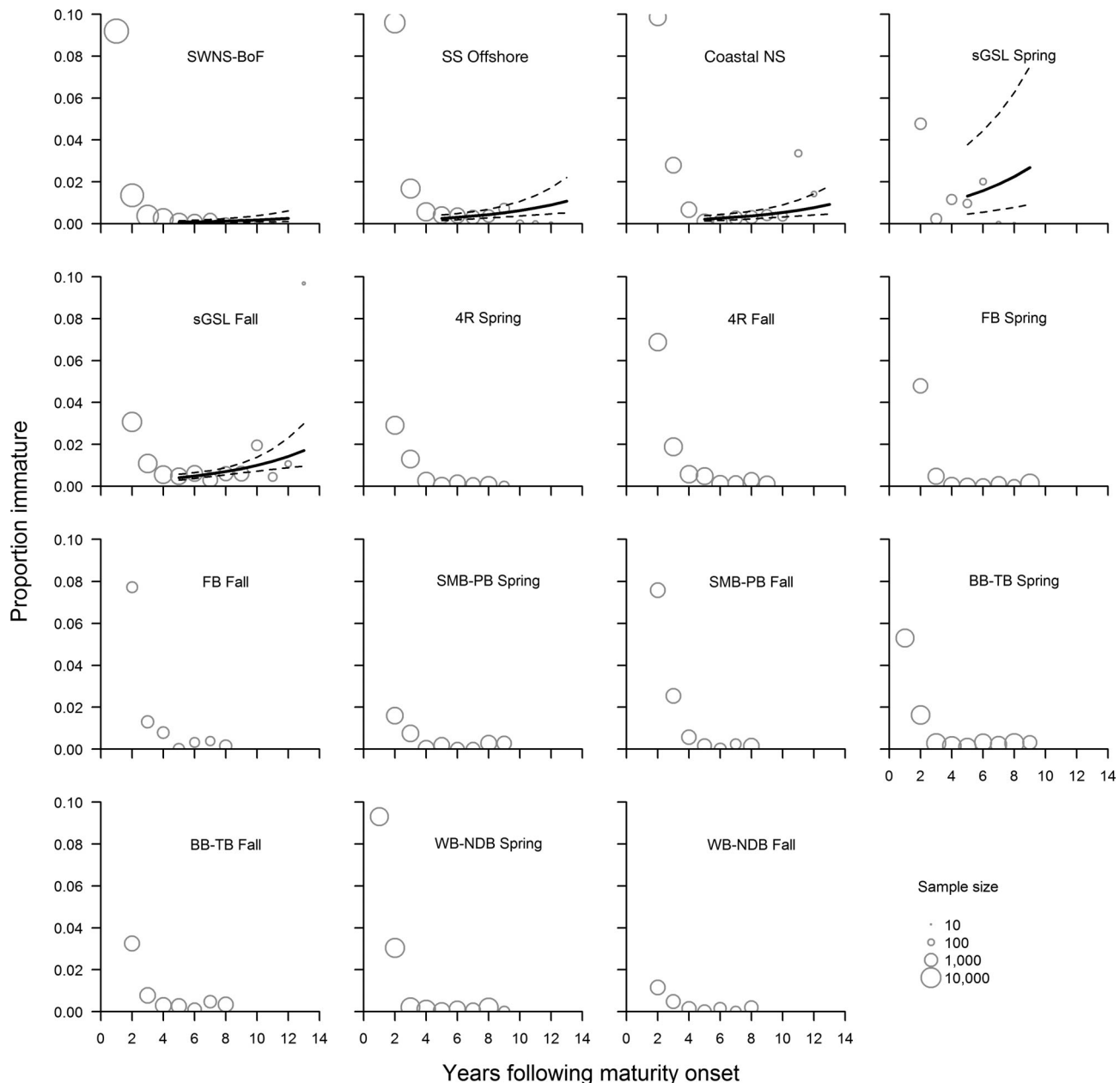


Fig. 6. Observed proportion of macroscopically immature herring (circles) as a function of standardized age (number of years following maturity onset) in the cohorts for each stock (panels; see Fig. 1 for locations). Predicted proportions based on the Firth logistic regression (solid lines) with 95% confidence intervals (dashed lines) are indicated for the 5 Laurentian south stocks. Predictions were drawn to 1 yr beyond the oldest observed standardized age for a stock to avoid extrapolation far outside the range of the data. Standardized age was rounded to the nearest integer prior to calculating the observed proportions. Circle diameter reflects the number of fish used to calculate the proportions

0.344; Table S1 in Supplement 2); however, the additive effects of standardized length (coefficient = -0.060 ± 0.005 SE, $p < 0.0001$) and stock ($\chi^2_4 = 124.64$, $p < 0.0001$) were. At the largest standardized lengths observed for each stock, the predicted percentage of non-reproductive herring was around 9 and 12% in the sGSL Spring and Fall stocks,

respectively, and between 3 and 4% for the SWNS-BoF, SS Offshore, Coastal NS, 4R Fall, SMB-PB Spring and both BB-TB stocks (Fig. 7). For the remaining stocks, the lower confidence interval on the prediction at the largest standardized length was $<1\%$ which we interpreted as indicating a non-significant predicted increase.

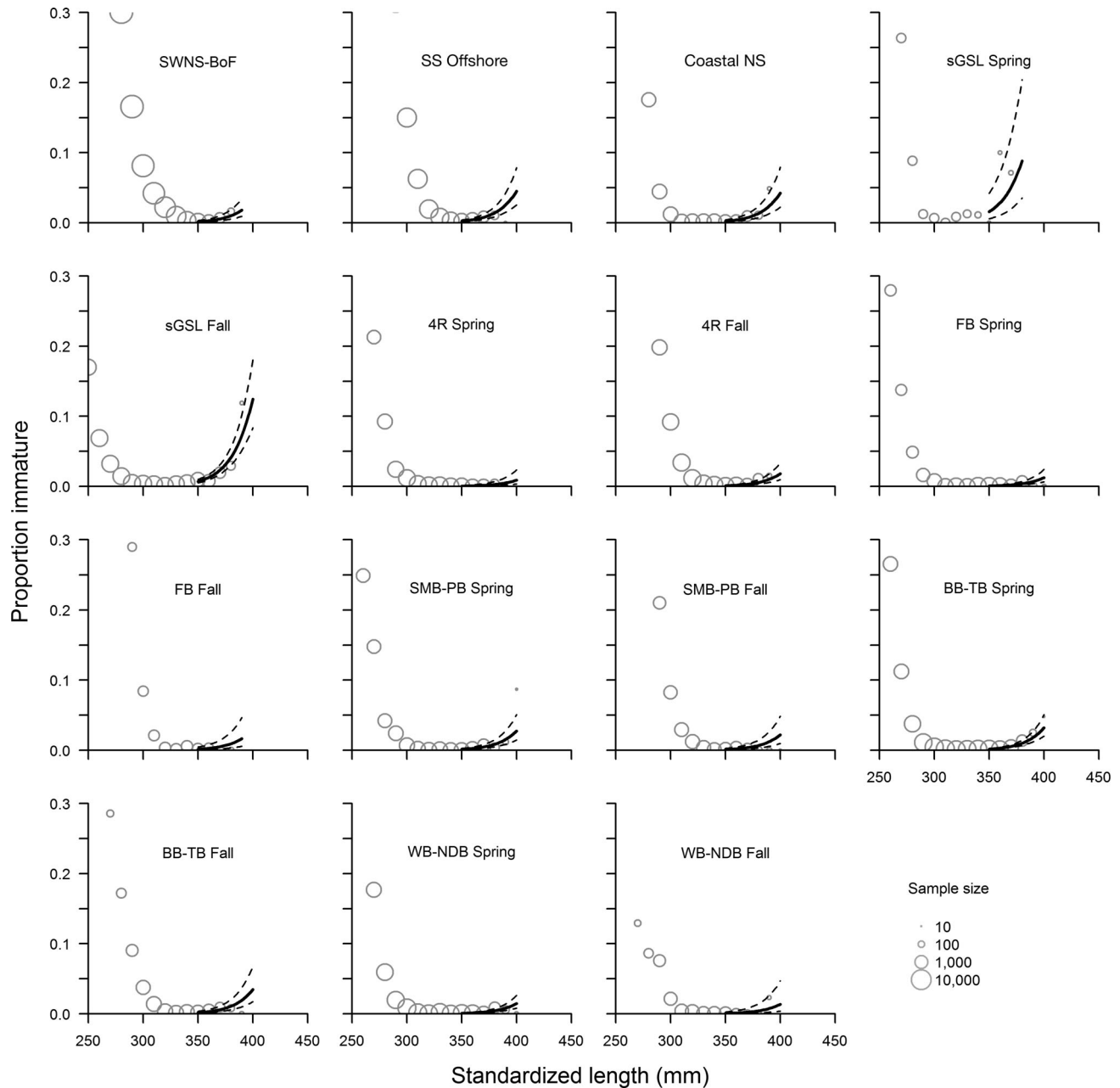


Fig. 7. Observed (circles) and predicted (solid line with 95% confidence interval indicated by dashes) proportion of macroscopically immature herring as a function of standardized length for each stock (panels; see Fig. 1 for locations). Predictions were drawn to 10 mm beyond the largest observed standardized length for a stock to avoid extrapolation far outside the range of the data. Standardized lengths were rounded to the nearest 10 mm prior to calculating the proportions. Circle diameter reflects the number of fish used to calculate the proportions

The proportion of spawning herring with GSI values below the low-value thresholds (i.e. sex- and stock-specific tenth-percentile values) decreased from the onset of maturity to around a standardized age of 5 in all stocks with sufficient data, except 4R Fall (Fig. 8). From that age onwards, the proportion increased in the majority of stocks. Following on

these results and those for analyses of non-reproductive herring, a minimum standardized age of 5 yr was chosen for the logistic regression analysis of GSI. The interaction between stock and standardized age was significant ($\chi^2_{11} = 24.67$; $p = 0.010$), but the marginal effects of stock ($\chi^2_{11} = 17.89$; $p = 0.084$) and standardized age ($\chi^2_1 = 1.28$; $p = 0.257$) were not.

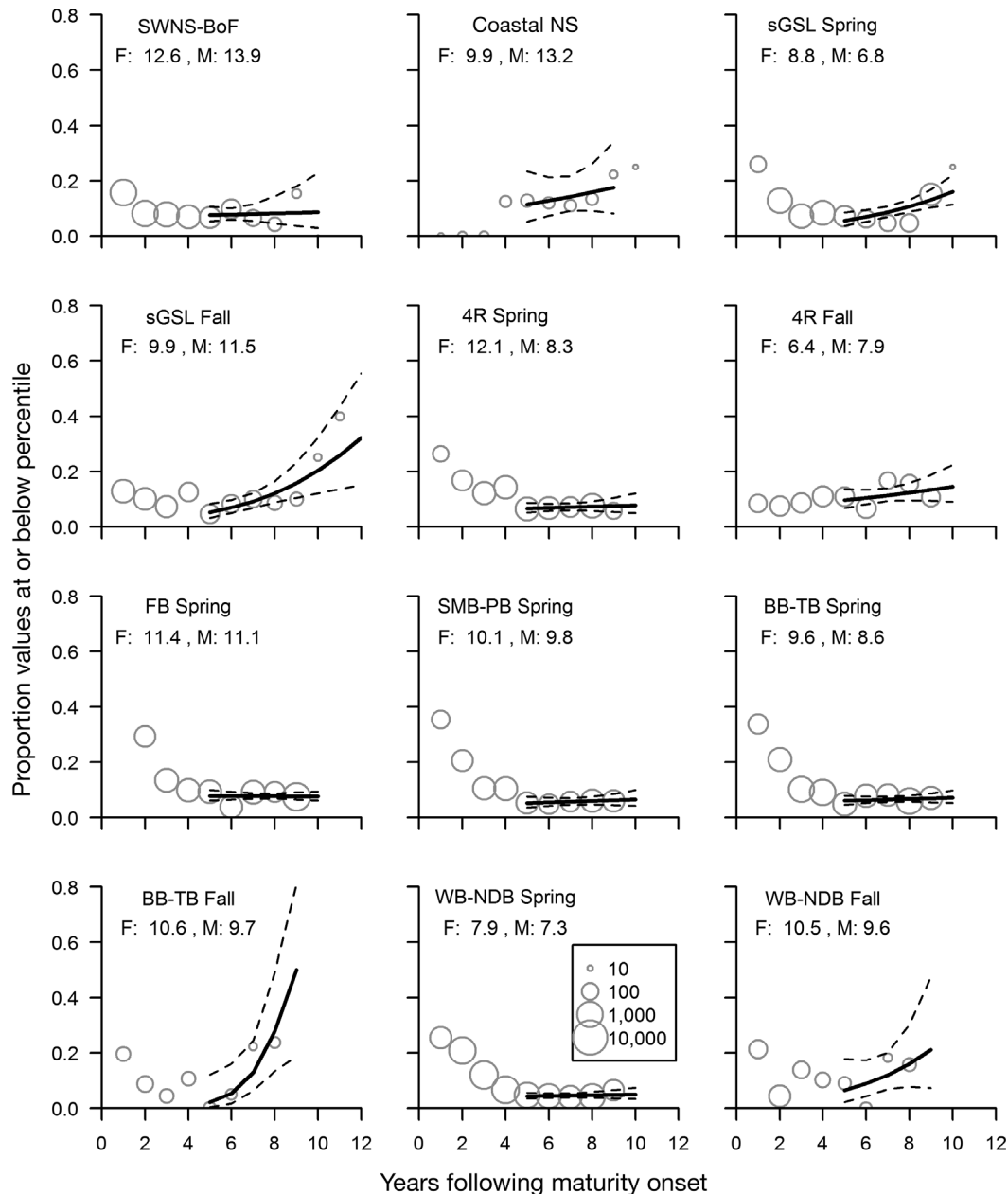


Fig. 8. Observed (circles) and predicted (solid line with 95 % confidence interval indicated by dashes) proportion of adult herring with gonadosomatic index (GSI) values that were at or below the tenth percentile of sex- and stock-specific GSI values, as a function of standardized age. All data were limited to herring that were ripe or spawning (maturity code 6). Circle diameter reflects the number of fish used to calculate the proportions, and the numbers in the plots are the values for the tenth percentile for females (F) and males (M). Plots are not shown due to low sample sizes for 3 stocks: SS Offshore, FB Fall and SMB-PB Fall (see Fig. 1 for locations)

The increase, as a function of standardized age, in the relative incidence of GSI values falling below the threshold was significant for the sGSL Spring, sGSL Fall and BB-TB Fall stocks based on the confidence intervals for the predictions (Fig. 8). The slopes for the relationship were positive for all other stocks even though the increases were not signifi-

cant. The 3 stocks with significant relationships are also ones that displayed some of the strongest trends in the incidence of non-reproductive individuals as a function of standardized age or length (Figs. 6 & 7). The result for sGSL herring is consistent with previous observations of age-dependent fecundity patterns (Messieh 1976).

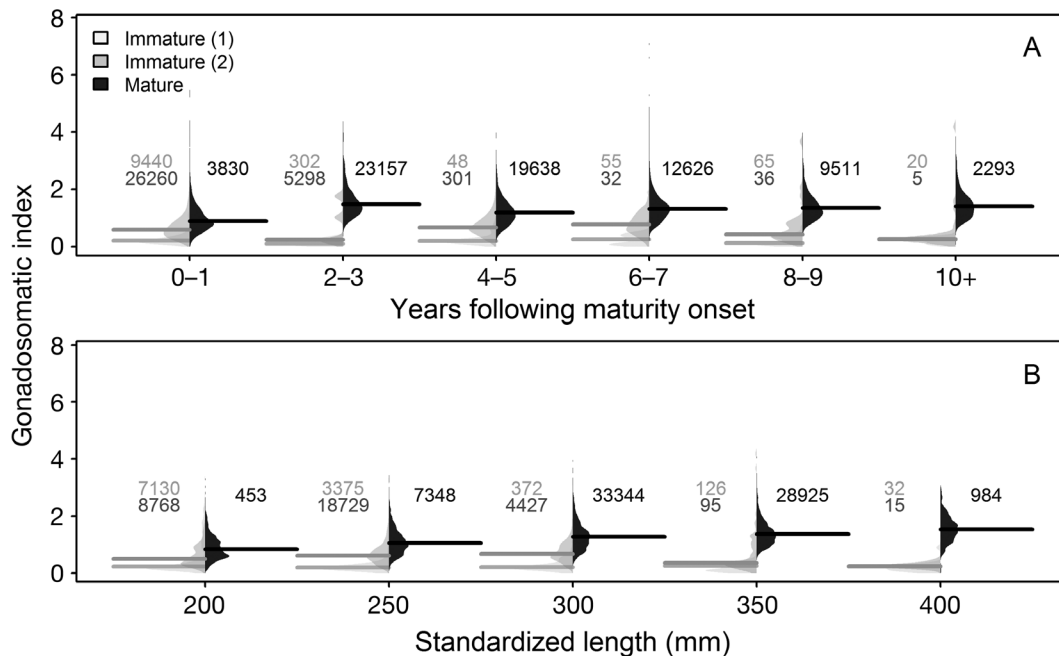


Fig. 9. Density trace of gonadosomatic index (GSI) values for macroscopically immature herring (stages 1 and 2; plotted separately using shading) and mature (spent and resting; stages 7 and 8) as a function of (A) standardized age, rounded to the nearest integer, and (B) standardized length. The horizontal lines indicate the median values for each group and the numbers indicate the sample sizes

Alternative hypotheses for age-specific increases in non-reproductive individuals

Skipped spawning

The relative weights of gonads for non-mature fish were similar to those of spent and resting herring at standardized ages of 0 and 1 yr and at small standardized lengths (Fig. 9). With increasing standardized ages and lengths, the distributions of GSI values for these 2 groups diverged. For standardized ages greater than 8 and lengths greater than around 330, there was very little overlap in these distributions. At these ages and lengths, the GSI values for non-mature herring were much smaller and of comparable magnitude or smaller than values for standardized ages of 0 to 1, which would represent herring that had not matured. This result suggests that the gonads of the oldest and largest non-mature and presumed senescent herring were likely non-functional at the time of sampling.

The distributions of condition factor values were very similar for non-mature and mature (though not spawning) herring at all standardized lengths for all data combined (Fig. 10A). The distribution of condition factor values for large non-mature herring (≥ 330 mm standardized length), which were presumed senescent, was shifted to larger values relative to

those for large mature fish in all months except May to July and November (Fig. 10B). From July to October, the distribution of condition values shifted progressively to larger values in those non-mature herring, consistent with weight gain during the summer and early autumn feeding season. These results for condition factor, either overall or prior to spawning in either the spring (April–May) or autumn (August–September), are inconsistent with expectations under the skipped spawning hypothesis.

Delayed maturation

The average LRV for a typical herring was approximately 132 000 eggs (Table S2 in Supplement 3). In contrast, the LRV was 235 eggs for a herring that delayed maturation to 14 yr (approximately 11–12 years following maturity onset in the cohort). From this result it is clear that this latter strategy would have very little adaptive value and should rapidly disappear from a population if it occurred and had a heritable basis.

If the increase in the relative occurrence of non-mature herring at larger standardized lengths (Fig. 7) reflected a better survival of fast-growing herring that never matured, the stocks should include immature individuals that are larger than same-age mature

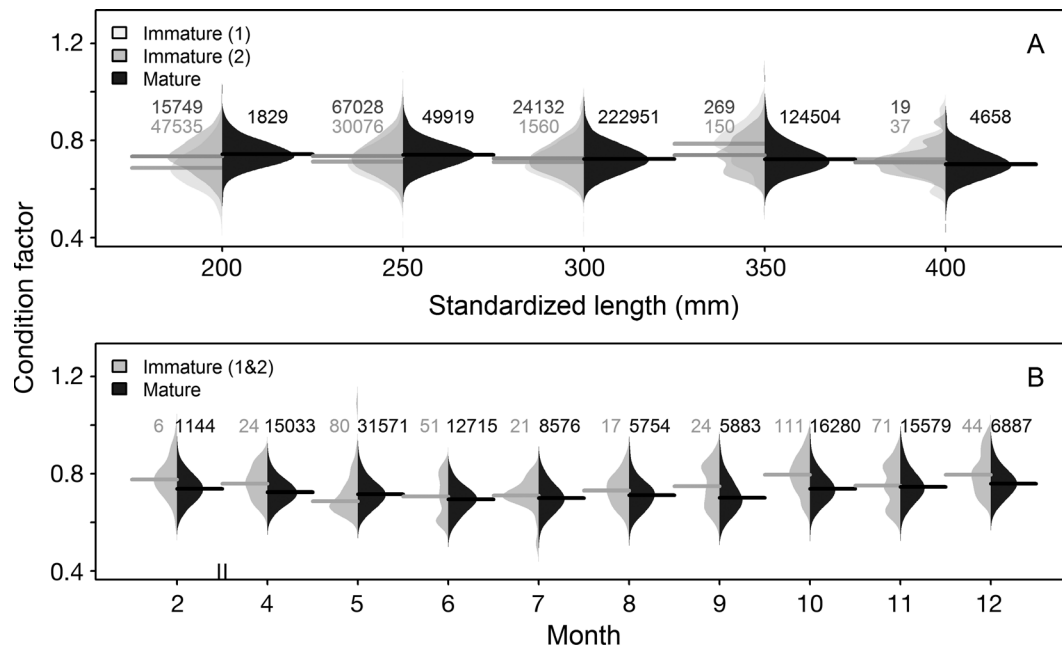


Fig. 10. Density trace of Fulton's *K* condition values for macroscopically immature herring (stages 1 and 2) and mature herring that were neither spawning nor spent (stages 3–5 and 8) as a function of (A) standardized length and (B) month for herring 330 mm and larger. The horizontal lines indicate the median values for each group and the numbers indicate the sample sizes. Note that the distributions for immature herring are plotted for each stage in (A), but combined in (B) due to the lower sample sizes. Note the axis break in (B) due to lack of information for month 3, March

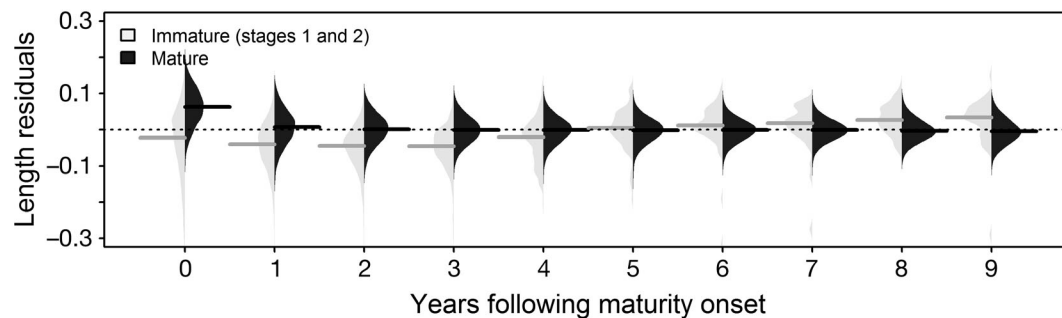


Fig. 11. Density trace of length residuals for macroscopically immature herring (stages 1 and 2) and mature herring (stages 3–8) as a function of standardized age, rounded to the nearest integer. Residuals were calculated relative to the mean length at age and year predicted from the stock-specific loess analyses: $\log(\text{observed}) - \log(\text{predicted})$. The thick horizontal lines indicate the median values for each group and the dashed horizontal line indicates a residual value of 0

fish across all ages. Instead, residual length values from Eq. (2) indicate that at standardized ages below 4 yr, non-mature individuals are smaller than mature ones, and there are no individuals that reach the largest relative lengths achieved by some mature fish (Fig. 11). Beginning at a standardized age of 3, the distribution of length residuals for non-mature fish shifted progressively to more positive values with increasing age such that by age 6, the majority of values were positive and there was a large density of non-mature herring with residual values above those observed in the largest mature fish.

DISCUSSION

Beverton et al. (2004) found that adulthood in NSS Atlantic herring comprised 2 phases, a pre-senescent phase followed by a senescent phase characterized by a large increase in mortality. Among cohorts and across years, the ages at maturation and senescence onset co-varied, resulting in a somewhat constrained non-senescent adult period with a mean duration of 9 yr. This resulted in a positive relationship between cohort maturation age and inferred maximum age (in light of little fishing mortality). Such a relationship

was also observed in an earlier cross-stock comparison that included the 2 sGSL stocks and NSS herring (Jennings & Beverton 1991). Those results, combined with very low levels of genetic differentiation between herring stocks across the Atlantic (Lamichhane et al. 2017), suggest that actuarial senescence is likely for Canadian herring stocks. However, moderate to high levels of fishing mortality in the Canadian stocks likely prevent many herring from reaching the ages at which actuarial senescence becomes important, and make it difficult to tease apart the 2 causes of mortality.

Nonetheless, given anticipated links between actuarial and reproductive senescence (Jones et al. 2008, Kirkwood & Shanley 2010), reproductive senescence was also expected in the Canadian stocks. Increases in the frequency of small GSI values with age in a number of Canadian stocks is consistent with reproductive senescence in Atlantic herring in the Northwest Atlantic. Furthermore, statistically significant increases in non-reproductive individuals with standardized age in 4 of 5 stocks south of the Laurentian channel, and evidence of increases in a number of Newfoundland stocks, are consistent with a post-reproductive senescent period. Although the relative incidence of post-reproductive fish was low (approximately 1–2%) at the observed ages in the Laurentian south stocks, it is important to note that, historically, maximum observed age was elevated in at least 2 of the stocks: sGSL Spring (23 yr) and sGSL Fall (25 yr; Jennings & Beverton 1991). In the absence of fishing, these stocks would likely live to much older ages, with a greater incidence of reproductive senescence, than at present.

Reproductive investment as measured by GSI was similar for both sexes. This might be explained by the fact that there is no parental care in herring and fertilization is external, with females and males releasing masses of adhesive eggs and milt simultaneously in large spawning shoals. Similar reproductive investment, growth rates and ages at maturity between sexes suggest that the timing of onset and rate of progression of reproductive senescence should also be similar (Lemaître & Gaillard 2017). Although the data were limited, they were consistent with this theory.

The evidence for a post-reproductive senescent period presented here is admittedly indirect as a consequence of the available data. Histological analysis of the gonad tissues would confirm whether herring have previously spawned or are apt to spawn again, thereby definitively distinguishing between the 3 hypotheses examined here. It has not been possible to undertake histological analysis of the gonads of

purported senesced herring because samples have always been frozen prior to detailed biological sampling, resulting in damage to the structure of reproductive tissues. Although the incidence of old and large non-reproductive herring is low in the stocks considered here, and considerable effort may be required to sample fresh individuals for histological analysis, this should be a research priority.

Despite the absence of direct confirmation of senescence via histological analysis, the available evidence suggests that the alternative hypotheses were unlikely. Patterns in individual condition across sizes and across months for larger herring do not indicate a lower condition for non-reproductive individuals that would be consistent with skipped spawning (Rideout et al. 2005, Kennedy et al. 2010, Skjæraasen et al. 2012). In fact, the condition factor values for these individuals were typically greater than those of reproductive individuals in most months. Furthermore, GSI values for older and larger non-reproductive herring were sufficiently small as to suggest that cessation of reproduction was more than temporary. Nonetheless, even if reproduction could resume, an age-related increase in the frequency of skipped spawning would arguably be a manifestation of reproductive senescence, which is defined as a decline in the contribution of reproduction to fitness that is not limited to the permanent cessation of reproduction (Maynard Smith 1962). The available evidence also suggests that the late maturity hypothesis is highly unlikely. The inferred survival and growth advantages under this hypothesis of delaying maturation to much older ages than is typical are greatly outweighed by the foregone opportunities to reproduce, resulting in a very low estimated average lifetime reproductive value. To the extent that age at maturity is heritable in fish (Allendorf & Hard 2009, Audzijonyte et al. 2013), there would be considerable selection against a strategy that involved delaying maturation to the degree that this hypothesis implies from the present data.

After standardizing for the age at maturity onset, patterns of increase in the relative incidence of non-reproductive herring were reasonably similar among stocks. The same was true and perhaps more evident for patterns as a function of standardized length. This relative consistency among stocks occurred despite important differences in their environments with respect to water temperatures (Melvin et al. 2009), predators (e.g. Guenette & Stephenson 2012, Benoit & Rail 2016) and fishing intensities (e.g. elevated in sGSL stocks, but low for Coastal NS and many Newfoundland stocks; DFO 2013, 2015, 2016). This sug-

gests that there may be a genetic basis underlying the patterns, as would be expected with senescence, given that these stocks are geographically isolated (with the notable exception of common-area spring and fall spawning stocks). Furthermore, given that herring are likely to experience different mortality rates in their respective areas, one would not expect this much consistency under the alternative delayed maturity hypothesis.

Maturation in most Canadian stocks was largely completed within 3 to 4 yr following onset in cohorts (Fig. 6). Over that period, immature herring were shorter than same-age counterparts. This is consistent with Beverton et al. (2004), who found a similar result across all maturation ages in NSS herring. In that study, later-maturing fish grew more slowly and matured at longer lengths, although their lengths at age were always smaller or comparable to those of earlier-maturing fish. The patterns in standardized length residuals reported here differ markedly from those results. Non-mature herring at purported senescent ages (standardized ages ≥ 6 yr), were progressively larger with age relative to mature counterparts, leading to an increase in the incidence of non-reproductive herring as a function of standardized length. To the extent that the detailed maturation and growth patterns reported for NSS herring are typical for non-senescent individuals of the species, the patterns in length residuals in Canadian herring are inconsistent with the delayed maturation hypothesis.

The results of the present study suggest that patterns in growth for senescent individuals may differ from existing models of fish growth. These models typically assume that size at age reflects a balance between energy intake and expenditures associated with growth, reproduction and maintenance, resulting in a relatively rapid pre-maturation phase, followed by a largely asymptotic post-maturation growth phase (Quince et al. 2008; reviewed briefly by Olsson & Gislason 2016). During a third, yet to be considered, post-reproductive phase, growth could accelerate provided that energy intake remains greater than the likely accelerating costs of somatic maintenance with age. While the data presented here are consistent with this mechanism, the evidence is only indirect given the cross-sectional nature of the data. Much stronger evidence would be obtained from a growth back-calculation study (Campana 1990), which would allow for the characterization of individual growth trajectories for senescent and non-senescent individuals.

Senescence in Atlantic herring and other commercially harvested fish may have consequences for our

understanding of how stocks respond to fishing. First, it is generally assumed that fecundity scales positively, even exponentially, with body size (e.g. Le Bris et al. 2015; for herring see e.g. Messieh 1976) and that the reproductive period spans to the end of life (for herring see Jennings & Beverton 1991). Old large fish are thought to contribute disproportionately to stock recruitment (e.g. Marshall et al. 1998, Hixon et al. 2014), and predicted resilience of stocks to exploitation appears to be particularly sensitive to the assumed fecundity–size relationship (Le Bris et al. 2015). However, with both actuarial and reproductive senescence, the projected benefits of conserving the oldest and largest individuals in a stock by reducing fishing mortality may be overestimated. For example, although the relative incidence of purported post-reproductive senescence was small ($\sim 2\%$) in the sGSL Fall stock at a standardized age of 13 (approximate total age 15), it could conceivably be projected to be much greater at the maximum observed age for this stock of 25 yr (Jennings & Beverton 1991). Furthermore, decreases in GSI at older ages suggest that reproductive output will diminish leading up to the complete cessation of reproduction.

As a second consequence, senescence may have implications for fishing-induced phenotypic and genetic changes in maturation age. The prevailing theories for the evolution of senescence—antagonistic pleiotropy (Williams 1957) and disposable soma (Kirkwood 1977)—make similar predictions about a life-history trade-off for which an increased allocation to reproduction in early life leads to an increased rate of ageing later (Kirkwood & Rose 1991). These theories and the apparent constraint on the duration of the reproductive period in herring due to actuarial (Beverton et al. 2004) and reproductive senescence (present study) suggest that fishing-induced declines in maturation age (e.g. Law 2000, Olsen et al. 2004) could be linked to an earlier onset of senescence. Traits related to maturation, and particularly age at maturation, appear to evolve the most rapidly in response to fishing (Allendorf & Hard 2009, Audzijonyte et al. 2013). Earlier maturation in turn is expected to negatively influence stock productivity and resilience to environmental change (Hutchings 2005, Jørgensen et al. 2007), which could be compounded by a concurrent earlier onset or enhanced progression of senescence.

A number of theories attempt to explain the evolution of a post-reproductive period (PRP). Many are based on inclusive fitness via parental care after reproduction or other forms of kin selection, such as benefits of grouping or serving as targets for predators

(Bourke 2007, Croft et al. 2015). Others have argued that PRPs may have evolved in some species as insurance to minimize the likelihood of dying before the cessation of reproduction (Tully & Lambert 2011). Alternatively, the duration of the PRP may not be an adaptive trait itself, reflecting a pleiotropic effect via selection on another trait or simply reflecting non-adaptive differences in ageing rates of reproductive and somatic tissues (e.g. Reznick et al. 2006). It is clearly premature to properly evaluate causal mechanisms for herring because, amongst other reasons, the mean and variability in the duration of PRPs is not known. Small groups of older herring are known to be important leaders in the formation of schools and in migrations to overwintering, feeding and spawning grounds (Corten 2002, Makris et al. 2009). However, the available data do not indicate whether those herring tend to be non-reproductive nor whether there is an advantage to being non-reproductive to fulfill such leadership roles. Furthermore, because herring spawn in large shoals where eggs and sperm are mixed and effective population sizes are likely to be large (Lamichhaney et al. 2012), it appears unlikely that any benefits obtained via kin selection would outweigh losses from foregone reproduction.

In summary, the present study provides evidence for reproductive senescence in numerous Canadian Atlantic herring stocks, consistent with predictions based on observed actuarial senescence in NSS herring and expectations from theory. Although our results are based on cross-sectional data and the evidence is therefore not fully conclusive in and of itself, additional available evidence appears to rule out 2 alternative hypotheses that could explain increases as a function of age in the relative incidence of non-reproductive individuals in older fish. Evidence of reproductive senescence was heretofore very limited for fish in general (e.g. platyfish *Xiphophorus* sp. and guppies *Poecilia reticulata*; Reznick et al. 2006), and essentially absent for marine fish (Nussey et al. 2013), with perhaps the exception of weak evidence in fertility rates in orange roughy *Hoplostethus atlanticus* (Koslow et al. 1995). However, the intensity of monitoring on herring, their known actuarial senescence (Beverton et al. 2004) and expected earlier and more pronounced senescence due to their comparatively rapid life history (Jones et al. 2008, Lemaître et al. 2015, Lemaître & Gaillard 2017) all contributed to increasing the likelihood of detecting reproductive senescence in this species. Given the pervasiveness of senescence in other well studied vertebrates, such as mammals and birds (Nussey et al. 2013), it is reasonable to expect that senescence exists for numer-

ous fish species, though it may be delayed relative to other taxa (Reznick et al. 2002) and not expressed or detected because of fishing mortality.

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