

**LIFE HISTORY CONSEQUENCES OF OCEAN WARMING AND
EXPLOITATION IN NORTHWEST ATLANTIC HERRING
(*CLUPEA HARENGUS*)**

by

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*This thesis is dedicated to the memory of Professor Jeffrey Hutchings,
whose insights and humanity have had a profound
influence on my thinking.*



Learning from you has been one of the greatest honours of my life.

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Abstract

Explaining the mechanisms that generate and maintain intraspecific variation in life histories – the manners in which organisms acquire and allocate resources to growth, reproduction, and survival – is a fundamental goal of evolutionary biology, with applied relevance to resource conservation and management. The primary objective of this thesis was to evaluate the combined influences of temperature and exploitation strategy on metrics of life history in Atlantic herring (*Clupea harengus*), a widely distributed marine fish of key ecological and socio-economic importance in the northwest Atlantic. Chapter 2 demonstrates that a relatively simple thermal optimum model coupled with a common trend in the model residuals can account for most of the variability in mean length-at-age 4 within and among populations since the early 1960s. Building upon this evidence, Chapter 3 illustrates that the distinction between fisheries that do and do not target spawners, albeit clearly relevant for age at maturity, may be of secondary importance to reproductive success compared with effects of time-varying growth and total mortality. By developing a series of comparative analyses within and among populations of the same species, the present work illustrates how both the context and spatio-temporal scale of inference can affect perceptions concerning the relative importance of fishing and the environment for stock productivity and yield. From a management perspective, these findings call for increased collaboration among regional monitoring agencies and a more integrated view of the role of trait-based management strategies in sustainability.

List of Abbreviations and Symbols Used

AICc	Akaike's Information Criterion (corrected for small sample sizes)
ANCOVA	Analysis of Covariance
A_{50}	Age at which 50% of a cohort (or stock) is mature
BB-TB	Bonavista Bay and Trinity Bay
CI95	95% Confidence Intervals
d	Rate of phenotypic change in darwins
DFA	Dynamic Factor Analysis
DFO	Department of Fisheries and Oceans of Canada
F	Fishing Mortality
FB	Fortune Bay
FIE	Fisheries-Induced Evolution
GDD	Growing Degree-Day
GOM	Gulf of Maine
GSL	Gulf of St. Lawrence [s: southern; n: northern]
ICES	International Council for the Exploration of the Sea
L_{\max}	Maximum Length
LRS	Lifetime Reproductive Success
l_x	Age-specific survival
L_{50}	Length at which 50% of a cohort (or stock) is mature
L_{p50}	Length at which the probability of an immature fish maturing is 50%
L_{∞}	Asymptotic Length

M	Natural Mortality
MVN	Multivariate Normal
m_x	Age-specific fecundity
NAFO	Northwest Atlantic Fisheries Organization
NAO	North Atlantic Oscillation
NEFSC	Northeast Fisheries Science Center
NOAA	National Oceanic and Atmospheric Administration
NST	Non-Spawner-Targeted
PMRN	Probabilistic Maturation Reaction Norm
SMB-PB	Saint-Mary's Bay and Placentia Bay
SSB	Spawning Stock Biomass
SST	Sea Surface Temperature
ST	Spawner-Targeted
SWNS-BoF	Southwest Nova Scotia and Bay of Fundy
T_{opt}	Thermal Optimum
TPC	Thermal Performance Curve
WB-NDB	White Bay and Notre Dame Bay
w_i	Akaike weight for model i
Z	Total Mortality

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Chapter 1 Introduction

Explaining the mechanisms that generate and maintain intraspecific variation in life histories – the manners in which organisms acquire and allocate resources to growth, reproduction, and survival – is a fundamental goal of evolutionary biology, with applied relevance to resource conservation and management. Over the past century, several exploited fish populations have exhibited directional trends towards earlier maturity, decreased body sizes and shortened lifespans concomitant with human alterations to ecosystems (Jørgensen, 1990; Rijnsdorp, 1993; Trippel, 1995; Ohlberger, 2013; Audzijonyte *et al.*, 2016). Given the close links that exist between these correlates of fitness and the intrinsic rate of population increase, a central objective is to identify the causes and predict the consequences of these putative adaptations to population productivity and levels of sustainable yield (Heino *et al.*, 2013; Laugen *et al.*, 2014).

The Atlantic herring (*Clupea harengus*) is a prime candidate species for the study of life-history evolution because of its long history of commercial exploitation and remarkable capacity for phenotypic change (Bekkevold *et al.*, 2005; Geffen, 2009). Temporal reductions in size-at-age have been described for all the principal stocks and stock complexes in the northwest Atlantic (*e.g.*, Wheeler *et al.*, 2009; Brunel and Dickey-Collas, 2010; Boyce *et al.*, 2019), but a comprehensive understanding of the drivers responsible is lacking. In response to the increased incidence of undersized herring in commercial landings, stakeholders in several regions have requested that fishery managers consider reducing the minimum size limit below the size at maturation. However, there is considerable uncertainty regarding the possible consequences of such a

policy for life history because current theories predict either an exacerbation (*e.g.*, Ernande *et al.*, 2004) or relaxation (*e.g.*, Law and Plank, 2018) of the selection pressures operating against older and larger individuals, while other investigations have reached mixed conclusions on the realized costs to stock productivity (*e.g.*, Halliday and Pinhorn, 2002; Vasilakopoulos *et al.*, 2011). This discrepancy highlights the need to evaluate the risks posed by fisheries-induced evolution in the broader context of ecological and environmental change. It also suggests that consequences to life history might well differ among populations.

Comparative approaches can help overcome some of these challenges by broadening the geographical range of the populations considered, and presumably the range of selection pressures to which they are exposed, thus providing the potential for contrasts in the magnitude of different putative causal factors. Since at least 1960, northwest Atlantic herring have experienced divergent thermal regimes (Melvin *et al.*, 2009) and fisheries management (Stephenson *et al.*, 2009), with generally higher temperatures and fishing intensities in the southern Gulf of St Lawrence and western Scotian Shelf (Messieh, 1989; Hebert *et al.*, 2018; Galbraith *et al.*, 2019) than in the more northerly Newfoundland areas (Day, 1970; Cyr *et al.*, 2020). Since the phenotypic changes attributed to these selective agents have potential to interact, and even amplify each other (Audzijonyte *et al.*, 2016), determining their relative contributions to population life history and demography is essential for the development of sustainable management strategies.

The present work develops a series of comparative analyses aimed at revealing the causes of life-history trait changes in all major commercially exploited stocks of Atlantic herring

in the northwest Atlantic. Building upon extensive time series of biological, fishery and sea surface temperature data collected since the early 1960s, my thesis aims to evaluate how past and ongoing responses to warming ocean temperatures associated with climate change can help to resolve the effects of concomitant environmental pressures on size-at-age (Chapter 2) and, complementarily, provide the necessary context in which to infer the consequences of fisheries-induced evolution of age and length at maturation to lifetime reproductive success (Chapter 3). The final chapter summarises the main findings and propose future avenues of research (Chapter 4).

Chapters 2 and 3 are formatted as research manuscripts and, therefore, are written in third person in acknowledgement of my co-authors (Hugues P. Benoît and Jeffrey A. Hutchings). The dominant themes of these chapters can be summarised with the following keywords:

Chapter 2: thermal performance curve, size structure, spatial synchrony, dynamic factor analysis, North Atlantic Oscillation, life history theory

Chapter 3: evolutionarily optimal harvesting strategy, maturity ogive, von Bertalanffy, minimum landing size, density-dependence, probabilistic maturation reaction norm

Chapter 2 Thermal optima reveal coherent size-at-age responses to large-scale environmental change in a broadly distributed marine fish

2.0 Abstract

A central challenge in predicting ectotherm responses to climate warming is to identify the form and spatio-temporal scale of temperature-trait associations for species whose distribution spans broad thermal and ecological gradients. Based on the analysis of size-at-age data of 16 Atlantic herring (*Clupea harengus*) populations in the northwest Atlantic, we find strong empirical evidence for a model incorporating quadratic temperature responses with population-specific thermal optima over a period of 56 years. This nonlinear function not only explained geographic differences in the strength and direction of size trends over time, but also revealed a compelling pattern of growth synchrony across all northwest Atlantic ecosystems. Thus, despite widely differing expectations about the effects of demographic and life-historical factors on size-at-age, both within and among populations, most of the variation in the model residuals could be explained by shared processes. Our findings underscore the necessity of a comparative approach within species for separating the effects of temperature from the effects of concomitant selection pressures in the wild.

2.1 Introduction

The hypothesis that organisms become smaller in warmer environments was originally proposed in descriptions of geographic clines in animal size in the mid-1800s (Bergmann, 1847; Mayr, 1956). However, it was only in recent decades that research on the effects of increasing temperature on ectotherm development, motivated by growing concern over the present and future state of biodiversity, gained an applied focus (Huey and Kingsolver, 1989; Atkinson, 1994; Brander *et al.*, 2013). It is now well established, based on studies in experimental physiology on both terrestrial and aquatic ectotherms (Brett *et al.*, 1969; Huey and Kingsolver, 1989; Lefevre *et al.*, 2021), that somatic growth responds nonlinearly to temperature, showing a progressive increase to a specific optimum (T_{opt}) followed by a rapid decline to a critical maximum. Since the properties of this physiological response are inextricably linked to ecological performance in nature, the intended primary application is to predict the impacts of climate warming on species productivity and persistence.

Despite the ubiquity of thermal performance curves (TPCs) in the literature pertaining to ectotherm growth, our capacity to predict the strength and direction of size responses to warming remains limited for species in the wild. Analyses of long-term monitoring data have identified positive, negative and, in some instances, no association between temperature and size (*e.g.*, Gardner *et al.*, 2011; Sheridan and Bickford, 2011; Verberk *et al.*, 2021, and references therein), a discrepancy that partly reflects inherent difficulties in separating the effects of multiple selection pressures acting simultaneously on size. The applicability of laboratory-derived TPCs to wild populations has also been debated given the potential for plastic and evolutionary changes in the position or shape of the function

(Angilletta *et al.*, 2003; Baumann and Conover, 2011; Ohlberger, 2013; Sinclair *et al.*, 2016; Tüzün and Stoks, 2018). Although many studies have acknowledged the role of thermal optima in defining ectotherm responses to warming (*e.g.*, Holsman *et al.*, 2019; Audzijonyte *et al.*, 2020; Oke *et al.*, 2020), their potential importance in resolving the effects of other stressors in the environment has, to our knowledge, not previously been explored among populations of marine fishes.

Size at a given age – an imperfect, but commonly measured proxy of individual fitness – not only tracks the thermal dependence of growth (Huss *et al.*, 2019), but also captures the response to a variety of selection pressures over space and time. Selective removals by fisheries and predators, and selective sampling may shift the mean value either positively or negatively, depending on the type and degree of size selection imposed (Sinclair *et al.*, 2002; Swain *et al.*, 2007). Life history theory also predicts that sufficiently high mortality, selective or not, can cause directional changes in heritable traits such as growth (Handford *et al.*, 1977; Ricker, 1981) and age at maturity (Reznick, 1982; Stearns and Koella, 1986) over relatively short time scales (*i.e.*, less than five generations). A prior expectation, therefore, is that the relative proportion of small individuals and total mortality (Sharpe and Hendry, 2009) should correlate positively with the probability and rate of size decline, with the potential to generate widely diverging patterns of variation within and among populations.

Here, using data on the 16 principal stocks and stock complexes (hereafter, populations) of Atlantic herring (*Clupea harengus*) in the northwest Atlantic (**Figure 2.1**), we explicitly evaluate the form and spatio-temporal scale of thermal dependency of size-at-age and investigate its impact on the inference of other selection pressures relevant to

size. Our data set spans the time period from 1962 to 2018 and comprises populations which differ considerably in their current and past fishery exploitation history (Stephenson *et al.*, 2009; Guénette *et al.*, 2014) and ecological contexts (Savenkoff *et al.*, 2007; Bundy *et al.*, 2009; Morissette *et al.*, 2009). For example, fishing intensities have been historically high in the southern Gulf of St Lawrence (DFO, 2020), the southwest Nova Scotia and Bay of Fundy (DFO, 2018), and in Fortune Bay (Winters and Moores, 1980), and comparatively low along the southeast coast of Nova Scotia (DFO, 2018) and in most northern bays of Newfoundland (DFO, 2019). The levels of protection afforded to juvenile fish, as well as the overall attention paid to population integrity (Stephenson *et al.*, 2009; Guénette *et al.*, 2014), also have varied among management units, resulting in populations experiencing vastly different schedules of mortality over space and time.

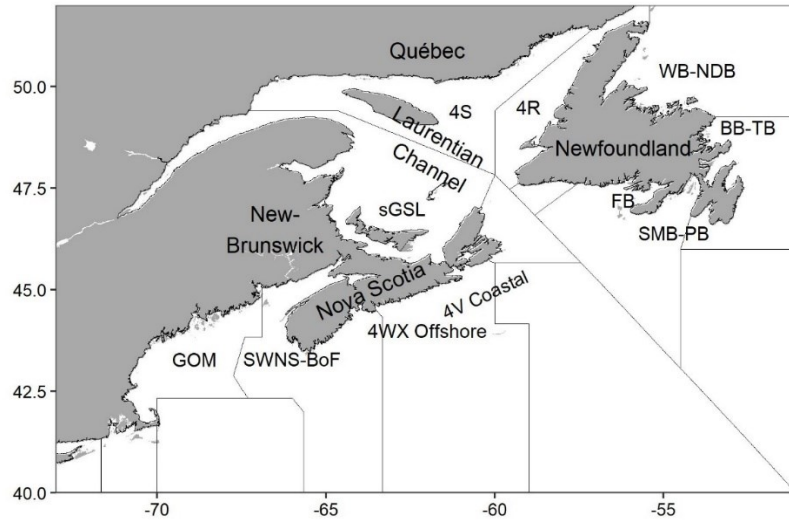


Figure 2.1 Locations for the 16 Atlantic herring populations considered in the present study: Gulf of Maine (GOM), southwest Nova Scotia and Bay of Fundy (SWNS-BoF), Scotian Shelf Offshore Banks (4WX Offshore), Coastal Nova Scotia (4V Coastal), southern Gulf of St. Lawrence (sGSL), northern Gulf of St. Lawrence (nGSL; comprising the west coast of Newfoundland, 4R, and Quebec’s North Shore, 4S), 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). Solid lines delineate divisions and subareas defined by the Northwest Atlantic Fisheries Organization (NAFO).

2.2 Methods

Our approach is threefold. First, we quantified temporal trends in size and temperature for all populations over the 1962-2014 cohorts (*trends in size and temperature*). Then, we evaluated different statistical models with shared or population-specific parameters to assess the functional form of temperature dependency of size (*thermal optimum model*). Selecting the most probable model, we contrasted trends in residuals across space and time, revealing a remarkable degree of coherence among all populations. Finally, we examined whether the temporal signal could reflect common synchronized responses to population abundance or shared climatic drivers (*coherence in model residuals*).

2.2.1 Trends in Size and Temperature

Biological data were obtained from samples collected in Fisheries and Oceans Canada (DFO) and Northeast Fisheries Science Center (NEFSC) research surveys and commercial fishery catches during the 1962-2018 period. To minimize potential effects of sampling on measured size-at-age, only fish captured using fishing gear that is the least size-selective were retained for analysis (**Table A1**; sampling methods for Canadian and Gulf of Maine populations in Benoit *et al.* (2018) and Becker *et al.* (2020), respectively). Thus, neither the absolute size nor the size trends over time differed among dominant gear types (**Figure A1**). Populations were classified into two descriptive categories to simplify the presentation of the analysis: those that occur in warm waters south of the Laurentian Channel (hereafter, warm-water populations; mean temperature range: 10.7 – 13.1°C), and those distributed along the coasts of Newfoundland, where waters are comparatively colder (hereafter, cold-water populations; mean temperature range: 5.50 – 10.0°C).

The trait examined in this study is mean length-at-age 4, a metric that integrates past and current variations in somatic growth, size-selective mortality and, when applicable, size-selective sampling within each cohort (*i.e.*, fish of the same population born in the same year). Four years is the youngest age at which herring are fully recruited to the spawning population and assumed to be representatively sampled in scientific sampling across the northwest Atlantic populations. Trends at that age closely resembled those at older ages, suggesting similar expectations for asymptotic length (Chapter 3, this document).

Individual length-at-age observations were adjusted to a common date in the year of capture prior to being averaged at the cohort level (**Table A2**). Although these

adjustments turned out not to alter the conclusions of the study (**Table A3; Figure A2**), they were nonetheless deemed necessary to account for intra-annual growth between the various dates of sampling. Estimates for the Gulf of Maine population were obtained from a recent study on growth rates in that population (Becker *et al.*, 2020).

Thermal history for each cohort was defined as the average sea surface temperature (SST) experienced from birth up to an age of four years (hereafter, lifetime SST). This metric was preferred over a simple year-specific average (*e.g.*, SST measured at different time lags) to reflect the continued influence of temperature throughout ontogeny, though we note that temperature might scale more accurately with growth increments when both are measured on annual time steps (Lorenzen, 2016). The annual means used to estimate lifetime SST were obtained by averaging monthly SST observations from the National Oceanic and Atmospheric Administration's (NOAA) Extended Reconstructed Sea Surface Temperature v5 model (Huang *et al.*, 2017; years 1962-1981) and DFO's Atlantic Zone Monitoring Program (Galbraith and Larouche, 2013; years 1982-2018) over the May-November period each year. We considered these temperatures to be physiologically representative of those experienced by herring during their growing season given that they primarily spawn and feed in the well-mixed surface layer (depth range: 0 to 150 m, depending on season and area (Hebert *et al.*, 2018; Galbraith *et al.*, 2019; Cyr *et al.*, 2020)).

2.2.2 Thermal Optimum Model

Mean lengths-at-age 4 were regressed on lifetime SST to assess how populations responded, on average, to increases in temperature (**Table 2.1**). First, we compared models with linear (models 1-2) or quadratic (models 3-6) temperature effects to test for

the presence of a thermal optimum (T_{opt}). Secondly, we contrasted the model intercepts (models 1-3) and/or temperature terms (models 2, 5-6) to evaluate whether population differences primarily occurred along the horizontal or vertical axis of the response function. The former pattern would involve a shift in the position of T_{opt} presumably consistent with a pattern of local adaptation whereas the latter would suggest spatial differences in size independent of T_{opt} . The six models were compared, using the small sample size version of Akaike's Information Criterion (AICc; Burnham and Anderson, 2002), Akaike weights (w_i) and adjusted R^2 as relative measures of parsimony and potential explanatory power.

Table 2.1 Support for models describing the functional relationship between mean length-at-age 4 and lifetime SST (β 's are model parameters; T is the mean temperature experienced up to an age of 4 years; s indicates the population; Δi is the AICc of model i minus the minimum AICc of the considered models; and w_i is the Akaike weight for model i).

Model	Covariates	Adj. R^2	Δi	w_i
1	$\beta_{0,s} + \beta_1 T$	0.53856	43.574	0
2	$\beta_{0,s} + \beta_{1,s} T$	0.57307	4.2162	0.089091
3	$\beta_0 + \beta_1 T + \beta_2 T^2$	0.34370	283.19	0
4	$\beta_{0,s} + \beta_1 T + \beta_2 T^2$	0.56271	5.8408	0.039541
5	$\beta_0 + (\beta_1 + \beta_{2,s}) \cdot T + (\beta_3 + \beta_{4,s}) \cdot T^2$	0.57623	0	0.73344
6	$\beta_{0,s} + (\beta_1 + \beta_{2,s}) \cdot T + (\beta_3 + \beta_{4,s}) \cdot T^2$	0.58471	3.3421	0.13793

2.2.3 Coherence in Model Residuals

A dynamic factor analysis (DFA), a multivariate modelling approach (Zuur *et al.*, 2003), was performed to objectively identify common trends in the residuals of the selected model and establish their association to covariates. The 16 time series of residual lengths-at-age 4 at time t (y_t) were standardized (*i.e.*, z-scored) and modeled as a linear combination of m hidden trends (x_t), q explanatory variables (d_t) and observation errors (v_t), as follows:

$$(2.1) \quad y_t = Zx_t + Dd_t + v_t, \text{ where } v_t \sim \text{MVN}(0, R)$$

$$(2.2) \quad x_t = x_{t-1} + w_t, \text{ where } w_t \sim \text{MVN}(0, Q),$$

where Z is a $16 \times m$ matrix of factor loadings on the hidden trends and D is a $16 \times q$ matrix of the regression coefficients. The observation (v_t) and process (w_t) errors are multivariate normally distributed (MVN) with mean zero and variance-covariance matrices R (*diagonal and unequal*) and Q (*identity*), respectively. Model parameters and states were estimated using the MARSS package (Holmes *et al.*, 2012) in R version 3.6.2 (R Core Team, 2019).

We examined evidence for two hypotheses that could explain the dominant trend. The first was a role of the North Atlantic Oscillation (NAO) index as a synchronizing agent among northwest Atlantic ecosystems (Hurrell, 1995). To our knowledge, the NAO is the only index of climate variability that tracks oceanographic conditions likely to impact all populations simultaneously, including primary productivity (Head and Sameoto, 2007; Nye *et al.*, 2014) and abiotic factors (Greene *et al.*, 2013). The second was a common manifestation of density-dependence, a negative association between spawning stock

biomass (SSB) and mean length-at-age 4, which we evaluate for the seven population for which SSB estimates were available for at least a third of the time period considered. These two covariates were averaged from birth up to an age of 4 years to reflect each cohort's lifetime exposure (**Table A4; Figure A3**).

We compared DFA models with one or two hidden trends (x_t) and either no covariate (models 7-8) or the NAO index (models 9-10) as a single covariate (**Table A5**), using an arbitrary cutoff level for factors loadings of 0.2 to determine whether a time series was associated with x_t or not (Zuur *et al.*, 2003). The hypothesis of density-dependence was tested by regressing the common trend of model 7 on lifetime SSB for each of the seven populations considered.

2.3 Results

2.3.1 Trends in Size and Temperature

The northwest Atlantic has warmed, on average, by 1.34 °C over the 1962-2014 cohorts (**Figure 2.2a**). Although there were statistically significant differences in the slopes of temperature trends among ecosystems, the estimated rates of warming did not vary in a systematic manner among warm and cold locations (analysis of covariance (ANCOVA): *cohort* × *ecosystem*: $F_{8,417} = 4.28$; $p < 0.0001$; **Table A6**). Locations rank from the slowest to the fastest rate of increase in lifetime SST was the following: 4V Coastal, BB-TB, GOM, WB-NDB, SMB-PB and FB, sGSL, 4WX Offshore, SWNS-BoF, and nGSL.

Over the same range of cohorts, there have been statistically significant declines in size in all populations (*cohort* effects: $p < 0.0001$). Warm-water populations experienced

sustained declines in mean length-at-age 4, ranging from 3.4 to 7.4 cm (corresponding to 11-22% reductions; **Figure 2.2b**). Estimates in colder-water populations increased until the mid 1970s, declined until the late 1980s, and then slowly increased from the mid-1990s onward, resulting in a net change that was considerably smaller than in the warm-water populations (**Figure 2.2c**).

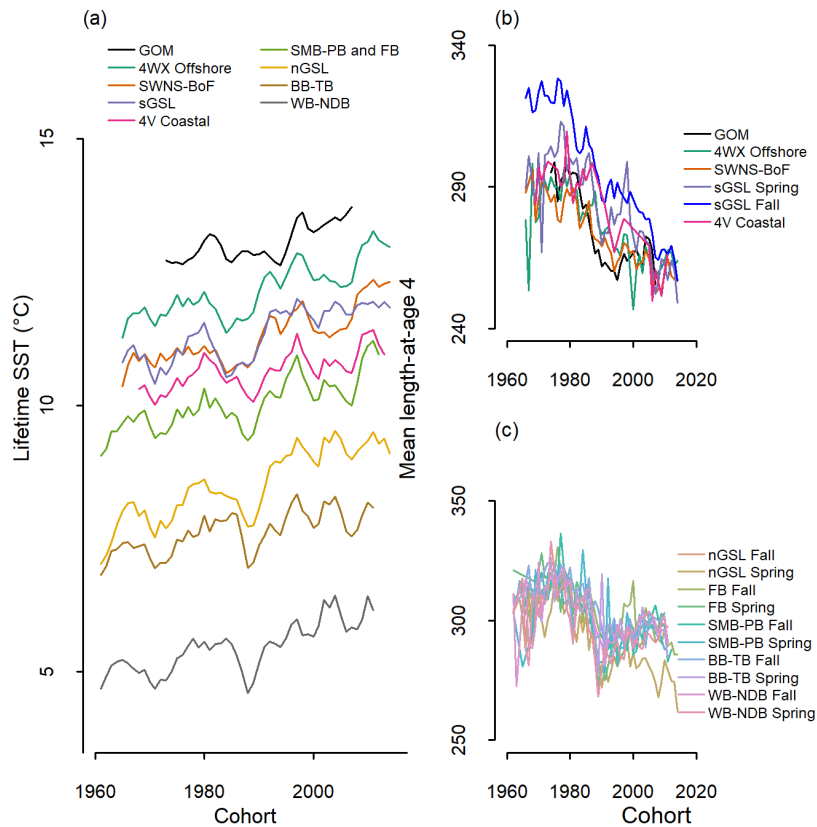


Figure 2.2 Trends across cohorts in (a) lifetime SST and in mean length-at-age 4 for (b) warm-, and (c) cold-water populations of Atlantic herring.

2.3.2 Thermal Optimum Model

The relationship between lifetime SST and mean length-at-age 4 was best captured by a quadratic term, with the strongest evidence for the model incorporating a shared intercept and population-varying T_{opt} (model 5 in **Table 2.1**; **Figure 2.3**). Despite an overall increase in T_{opt} towards warmer locations, warm-water populations were distributed farther from estimated T_{opt} (range of differences: 3.5-4.1 °C) than cold-water populations (range: 0.2-2.3 °C). There was considerably less support for a linear model with population-specific slopes (models 1-2) and essentially no support for the other models based on Akaike weights. Models with a population-specific T_{opt} (models 5 and 6) were associated with a combined Akaike weight of 0.87, indicating strong support.

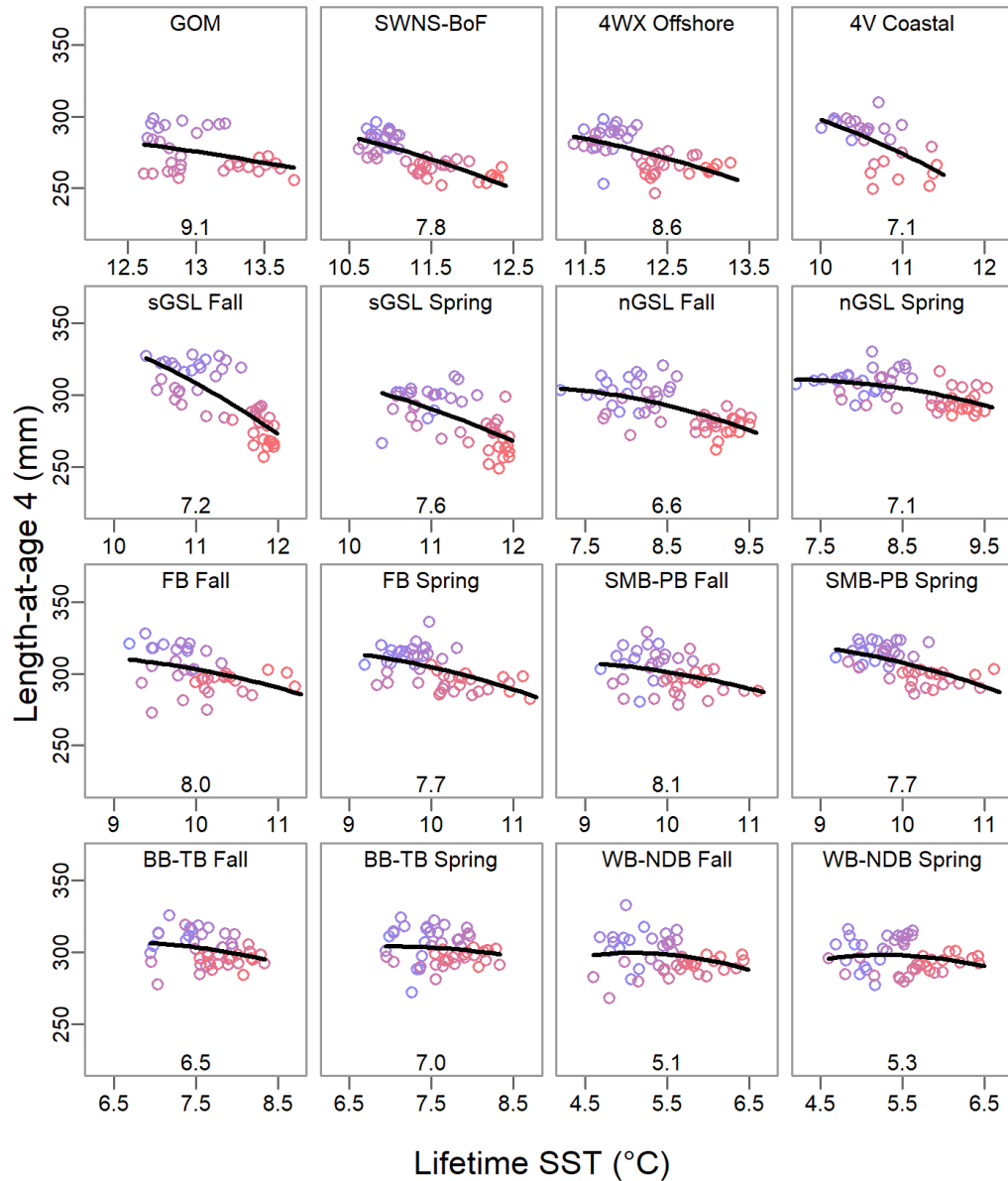


Figure 2.3 Mean length-at-age 4 as a function of lifetime SST for the 16 Atlantic herring populations, with predictions from model 5 illustrated as a black solid line and model-inferred T_{opt} indicated at the bottom of each panel. The color gradient from blue to red illustrates the temporal progression of data points for cohorts from 1962 to 2014.

2.3.3 Coherence in Model Residuals

A common temporal trend predicted very well the residual variation over time and among populations (**Figure 2.4**). Comparing the 1- and 2-trend models revealed that variability for certain populations (*e.g.*, sGSL Fall, sGSL Spring) was better captured by a second trend (models 7-8 in **Table A5**; **Figures A5-A6**). However, both models yielded similar predictions.

Neither the NAO nor the SSB covariate could adequately account for the dominant trend identified in **Figure 2.4**. Inclusion of the NAO index to the one- and two-trend models led to increases in AICc of 6.06 and 7.57, respectively, suggesting that variability explained by this covariate was low (**Figures A4** and **A7-A9**). The predicted negative association with population abundance was statistically significant in only 3 of the 7 populations examined (GOM, sGSL Fall and FB Spring; **Figure A10**), suggesting that the correlation could be spurious or that size and abundance shared common drivers in these ecosystems only.

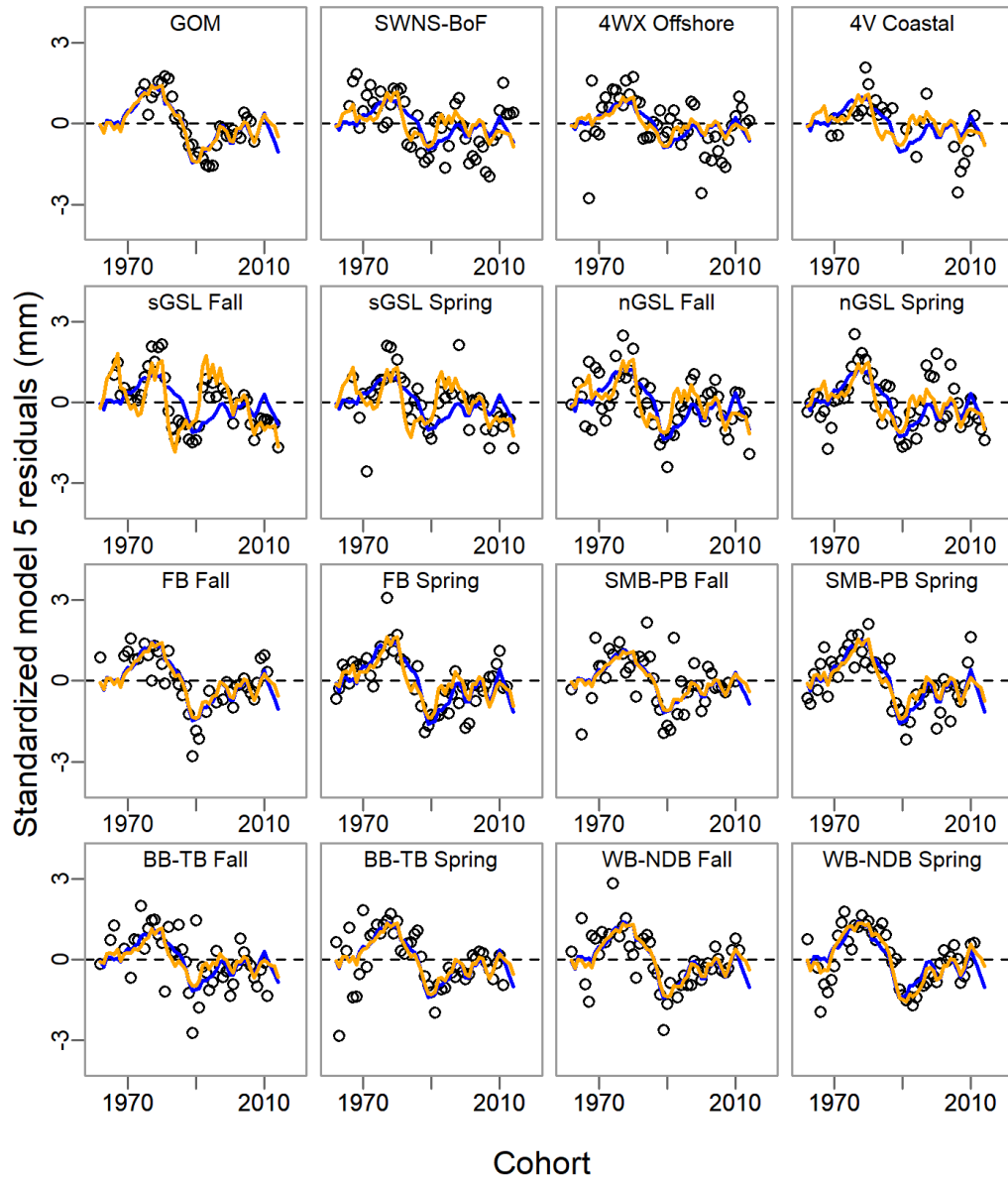


Figure 2.4 Trends across cohorts in the standardized residuals of model 5 for the 16 Atlantic herring populations. The solid lines give the predictions of a dynamic factor analysis (DFA) model with one (blue: model 7) or two (orange: model 8) common trends and no covariate.

2.4 Discussion

We find that the relationship between temperature experienced and mean length-at-age 4 followed a dome-shaped function with population-specific thermal optima over a period of 56 years. Explicitly accounting for differential effects of temperature on size, both within and among populations, revealed a compelling unanticipated pattern of synchrony across all northwest Atlantic ecosystems. The importance of thermal optima in revealing the effects of both temperature and large-scale environmental change on size-at-age underscores the necessity of a comparative approach within species for separating the effects of increasing temperature on growth from those of concomitant selection pressures in the wild.

The present study provides some of the strongest empirical evidence to date for differing size-at-age responses to temperature in a marine fish in the wild. The faster declines experienced by warm-water populations likely stem from steeper increases of metabolic costs with temperature compared to realized energy intake beyond the optimum, as routinely observed in farmed fishes fed *ad libitum* (Brett *et al.*, 1969; Volkoff and Rønnestad, 2020). Conversely, the closer proximity of cold-water populations to T_{opt} was associated with a smaller net impact of warming on size. Nonlinearity, therefore, resulted in populations with contrasting thermal histories showing different patterns of response to increases in temperature.

The apparent increase in population-specific T_{opt} towards warmer locations possibly reflects a degree of local adaptation or concurrent changes in specific ecological factors, such as per capita prey availability (Brett *et al.*, 1969; Tüzün and Stoks, 2018; Volkoff and Rønnestad, 2020) or predation risk (Lankford *et al.*, 2001). The implications of this

finding are not entirely clear, as empirically determined T_{opt} may either under- (Childress and Letcher, 2017) or over-estimate (van Denderen *et al.*, 2020) realized responses to warming depending on the strength of competing influences on the measured proxy of growth. In general, the broad range of T_{opt} inferred from our model highlights the requirement that data be collected on a sufficient number of populations, over a sufficient time period, to account for plastic and evolutionary changes in the responses to warming (Ohlberger, 2013; Sinclair *et al.*, 2016).

We predicted that geographic differences in fishery management regimes and ecological contexts would generate widely diverging patterns of size-at-age within and among populations. Yet, contrary to this expectation, neither the rate (Sharpe and Hendry, 2009) nor the direction (Stearns and Koella, 1986) of the model residuals differed between populations experiencing high (*e.g.*, sGSL Fall and SWNS-BoF; DFO, 2018, 2020) and low exploitation (*e.g.*, 4V Coastal and many Newfoundland populations; DFO, 2018, 2019). Likewise, postulated influences of growth- and size-mediated interactions on size-at-age, demonstrated to vary considerably both within and between ecosystems (Savenkoff *et al.*, 2007; Bundy *et al.*, 2009; Morissette *et al.*, 2009), appear incompatible with the observed pattern of synchrony. This discrepancy between predicted and observed coherence suggests that processes operating at the scale of the northwest Atlantic dominated the effects of ecological factors acting independently on specific populations, a finding that only became evident after accounting for nonlinear effects of temperature on size.

Importantly, our results illustrate how both the theoretical basis and spatial scale of analysis can affect inferences concerning temperature dependent and independent

processes in the wild. Single-population time-series may not have the power to detect a thermal optimum. They also risk drawing spurious conclusions, exemplified by the three populations for which abundance trends resulted in negative correlations with residuals. Viewed comparatively, the common trend appears to reflect remote climate forcing of growth, a hypothesis consistent with recent evidence of growth synchrony in biochronologies of terrestrial and aquatic ecosystems (Black, 2009; Morrongiello *et al.*, 2021). We note, however, that while our DFA models provide a statistical link between exogenous factors operating at the scale of the northwest Atlantic and more proximal correlates of growth, the empirical basis for the temporal signal remains uncertain. Nevertheless, from a practical management perspective, it is the synchrony itself that is thought to affect species productivity and persistence (Schindler *et al.*, 2010).

Given that the analyses presented here link individual-based mechanisms (*i.e.*, growth TPCs) to population-level data, the conclusions resulting therefrom must be interpreted in light of key limitations. For example, temporal trends in length-at-age almost certainly reflect a combination of explanatory factors, most of which cannot be readily partitioned from the effects of temperature because of limited covariate data at appropriate scales. Furthermore, temperature does not act uniformly on size throughout ontogeny (Sinclair *et al.*, 2016; Huss *et al.*, 2019), nor does mean size at a given age reflect instantaneous growth in thermally variable environments. Alternative approaches to better capture the thermal dependency of growth would be to relate back-calculated length increments to a proxy of selection by the environment, as developed by Swain and colleagues (Swain *et al.*, 2007), or to expand the linear growing degree-day method (Neuheimer *et al.*, 2008) to a nonlinear framework to minimize uncertainty resulting from Jensen's inequality at

thermal extremes (Jensen, 1906; Ruel and Ayres, 1999). Acknowledgement that hypotheses pertaining to size-at-age are mutually non-exclusive is an important step toward improving the biological realism of future modelling attempts.

Our conclusions regarding the effects of temperature on size-at-age are consistent with thermal performance curves traditionally applied to short-term laboratory observations (Huey and Kingsolver, 1989; Ohlberger, 2013; Sinclair *et al.*, 2016; Holsman *et al.*, 2019; Huss *et al.*, 2019) and recent comparisons of temperature-size relationships among species (Audzijonyte *et al.*, 2020; Oke *et al.*, 2020). A novel, but perhaps less intuitive finding in our study, is that nonlinearity can affect perceptions concerning a number of processes relevant to body size in nature, some of which may be operating at spatio-temporal scales that largely exceed those at which conservation strategies are typically established. Integrating observations across multiple generations and over broad spatial scales will increase the probability that thermal optima can be detected and, thus, strengthen the science advice pertaining to the effects of global warming on the productivity of marine fishes and other ectotherms.

2.5 Acknowledgements

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Chapter 3 Combined effects of exploitation and environmental change on life history: an empirical exploration on Atlantic herring

3.0 Abstract

The consequences of fisheries-induced evolution on stock productivity and yield depend, to a large extent, on the general prospects for growth and survival. Here, we compare the selection pressures imposed by two distinct patterns of exploitation – principally targeting spawning or non-spawning aggregations – on age at maturity among 15 Canadian stocks of Atlantic herring (*Clupea harengus*) that have exhibited a consistent pattern of size-at-age responses to common large scale environmental drivers since the 1960s. In accordance with expectations for maturity-dependent harvesting, the establishment of a spawner-targeted fishery in the southern Gulf of St Lawrence coincided with a shift towards delayed maturity in both resident stocks, whereas stocks elsewhere subject to fisheries that also exploited juveniles were more commonly associated with trends towards earlier maturity. Despite these differences, we find that environmentally driven changes in length at maturation, combined with total mortality, may overwhelmingly determine reproductive success and possibly fitness. By linking phenotypic changes experienced in the juvenile period to simple correlates of egg production in mature age-classes, our study highlights the importance of managing fisheries in the context of ubiquitous environmental constraints on life histories.

3.1 Introduction

Evidence is accumulating that excessively high levels of fishing mortality have potential to induce rapid evolutionary changes in key aspects of organismal life history, such as age and length at maturity, with consequences for fitness and population viability (Handford *et al.*, 1977; Ricker, 1981; Conover and Munch, 2002). Over recent decades, much empirical research in fisheries-induced evolution (FIE) has been dedicated to disentangling the demographic, phenotypic and potentially genetic components of trait changes documented in overexploited populations (Heino *et al.*, 2002; Sinclair *et al.*, 2002; Dieckmann and Heino, 2007). However, comparatively less attention has been devoted to understanding how varying intensities and patterns of exploitation might affect species that are differentially affected by the environment, or climate change, across their distributional range. This constitutes a major source of uncertainty, given that environmental variation can represent a central determinant of a stock's resilience to exploitation (Brander, 2007).

The Atlantic herring (*Clupea harengus*) is an ideal species with which to evaluate this interaction because of its long and diverse history of commercial exploitation. In some stocks, fishing takes place on the spawning grounds, where mature herring aggregate into distinct stock components to reproduce, while in others it targets feeding, overwintering or migratory aggregations of mature and immature fish or even strictly juveniles (Day, 1970; Stephenson *et al.*, 2009; Gu enette *et al.*, 2014). Although the selective pressures generated by fisheries that do and do not target spawners have been extensively discussed in the context of FIE (*e.g.*, Law, 2007; Dunlop *et al.*, 2009a; J rgensen *et al.*, 2009), there is uncertainty in the degree to which such selection might affect population life history

and demography on time scales relevant for fisheries management (Hutchings and Kuparinen, 2019, 2021; Pinsky *et al.*, 2021).

Spawner-targeted (ST) fisheries differ from non-spawner-targeted (NST) fisheries in an important way. In the former, maturity itself is the factor that inexorably increases an individual's probability of death; this is not measurably different from semelparity, wherein the act of reproduction causes death (Bell, 1980). This pattern is predicted to favor individuals that delay maturation until they are larger and/or more fecund, thereby potentially increasing maximum yield over the long term (Law and Grey, 1989). By contrast, in many NST fisheries the probability of death by fishing is more a function of an individual's size (or age), thus providing survival and fitness benefits to those capable of maturing at relatively small sizes and young ages at which fishing mortality is low or nil (Law and Grey, 1989). The dominant type of selection does not only depend on the socio-economic context of a fishery (*e.g.*, production of herring roe; Burke and Phyne, 2008), but also on the existence of, and compliance with, specific management measures such as minimum landing sizes and spatio-temporal fishery closures (Froese, 2004; Dunlop *et al.*, 2009; Jørgensen *et al.*, 2009; Vasilakopoulos *et al.*, 2011).

The most widely applied framework for the detection of FIE in field-collected data is the probabilistic maturation reaction norm (PMRN), a statistical model defining the age- and length-specific probability of an immature individual maturing during a given time interval (Heino *et al.*, 2002; Barot *et al.*, 2004). Intending to account for the effects of phenotypic plasticity associated with variation in a cohort's mean length-at-age, PMRNs have the potential to reveal changes in maturation traits that are potentially genetic in origin (Dieckmann and Heino, 2007). In studies of overexploited populations, temporal

shifts in PMRNs have been interpreted as evidence against a compensatory growth response to fishing, the process in which prolonged fishing pressure leads to a reduction in population density and a concomitant relaxation of competition for resources, thus increasing rates of individual growth and leading to earlier maturity (Heino *et al.*, 2002; Engelhard and Heino, 2004b). In a multi-stock approach, the degree to which a shift in PMRN might be indicative of FIE, as opposed to plastic influences not mediated by somatic growth, can be partly inferred by comparing rates of phenotypic change over time among populations having divergent exploitation histories (Sharpe and Hendry, 2009; Devine *et al.*, 2012; Audzijonyte *et al.*, 2013a; Kendall *et al.*, 2014).

The consequences of early or delayed maturation to individual reproductive success will depend, to a large extent, on the general prospects for growth and survival (Stearns and Koella, 1986). Most of the variability in somatic growth observed in herring in the northwest Atlantic has previously been attributed to changes in temperature and/or population density (*e.g.*, Moores and Winters, 1982; Melvin and Stephenson, 2007; Brunel and Dickey-Collas, 2010; Becker *et al.*, 2020), with recent evidence suggesting a dominant influence of environmental factors on mean length-at-age 4 across populations (Chapter 2, this document). Since fecundity scales positively with body size in Atlantic herring (Messieh, 1976; Bradford and Stephenson, 1992), as in most other fishes (Tsoukali *et al.*, 2016; Barneche *et al.*, 2018), a general expectation is that variables expected to affect growth in the juvenile period, such as temperature, will also constrain the number of eggs produced by females upon maturation and, possibly, throughout their entire reproductive lifespans (Charnov, 1993; Lambert, 2008; Lorenzen, 2016).

The present study examines the level of empirical support for several hypothesized links between exploitation, environmental change, and life history within and among the 15 principal stocks and stock complexes (hereafter, stocks) of Atlantic herring in the Canadian Atlantic (**Figure 3.1**). Building upon recent evidence of differential effects of temperature on mean lengths-at-age 4 across the northwest Atlantic (Chapter 2, this document), our analyses focus first on the causes and second on the consequences of spatio-temporal variations in age and length at maturation. The strength of a comparative approach, relative to a study on single populations, lies in the ability to test predictions across a multitude of contexts. We thereby aim to clarify the importance of exploitation pattern – the only aspect of selection, besides harvest intensity, that is amenable to direct management action – in light of presumably strong environmental constraints on body size.

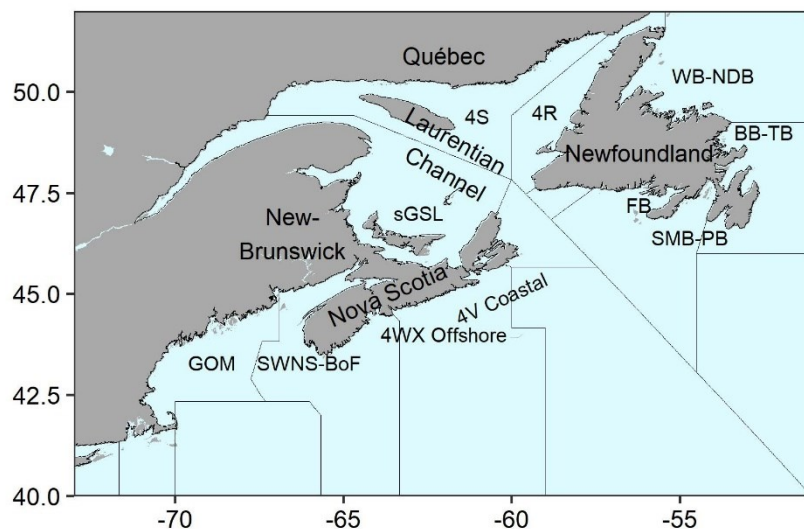


Figure 3.1 Locations of the 15 Atlantic herring populations considered in the present study: southwest Nova Scotia and Bay of Fundy (SWNS-BoF), Scotian Shelf Offshore Banks (4WX Offshore), Coastal Nova Scotia (4V Coastal), southern Gulf of St. Lawrence (sGSL), northern Gulf of St. Lawrence (nGSL; comprising the west coast of Newfoundland, 4R, and Quebec’s North Shore, 4S), 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). Solid lines delineate divisions and subareas defined by the Northwest Atlantic Fisheries Organization (NAFO).

3.2 Methods

3.2.1 Data Collection

Biological data were obtained from samples collected by Fisheries and Oceans Canada (DFO) during standardized research surveys or via sampling of commercial fishery catches. There are genetically distinct spring and fall spawning stocks in the Gulf of St. Lawrence (GSL) and along the southeast coast of Newfoundland, whereas the more southerly distributed stocks on the Scotian Shelf spawn primarily in the fall (Melvin *et al.*, 2009; Lamichhaney *et al.*, 2017). For herring that are not sampled on their spawning

grounds, spawning group attribution depends on the date of capture, maturity stage, and the morphometric characteristics of the otoliths (Messieh, 1972). Information on the distribution, biological status, and exploitation history of each stock during selected time periods is summarised in **Table 3.1**.

Sampling gear retained in this study include purse seines, trawls, and scientific gillnets (*i.e.*, gillnets comprising multiple mesh sizes) and exclude more size-selective gear such as commercial gillnets. These gear types are not expected to affect perceptions of length-related traits because they have been previously demonstrated to produce comparable estimates of mean length-at-age 4 in this study system (Chapter 2, this document).

Life-history traits were quantified by cohort, rather than cross-sectionally across cohorts by year, because it is the cohort that grows and matures (Morgan and Colbourne, 1999). Maturity status was assigned based on macroscopic characteristics of the gonads, following an 8-category scheme (ICES, 1963), wherein stages 1 and 2 refer to immature individuals (*i.e.*, juvenile) and stages 3 (resting) to 8 (recovering) to mature individuals (*i.e.*, adult). The sexes were combined because it is often impossible to distinguish males from females in young immature individuals. However, because age-specific and lifetime reproductive investment and survival are very comparable between the sexes (Bradford, 1993; Winters and Wheeler, 1996; Benoît *et al.*, 2018), combining them should not be consequential for our analyses.

Our dataset spans between 18 and 53 cohorts (1963 – 2015) for each of the 15 major Atlantic herring stocks in the Canadian Atlantic. These data were restricted to fish aged 0-10 years because older ages (≥ 11) were either right-censored (older ages being

combined, as in most Newfoundland stocks) or potentially reproductively senescent (Benoît *et al.*, 2018, 2019). They were also limited to samples collected during a common period each year, either winter, spring and/or fall, depending on total sample sizes. While differences in the timing of sampling have the potential to affect the mean value of traits such as age and size at maturity, preliminary comparisons within cohorts of the well-sampled SWNS-BoF stock indicated that such differences should not meaningfully impact the interpretation of trends over time (**Figure B1**).

Table 3.1 Location, biological status, time period investigated and dominant exploitation pattern (ST: spawner-targeted; NST: non-spawner-targeted) for the 15 Atlantic herring stocks examined. The terms ‘warm’ and ‘cold’ water refer to stocks distributed far from and near their thermal optima, respectively, according to a recent study on temperature-length relationships (Chapter 2, this document). Abbreviations for stock names are provided in the caption of **Figure 3.1**.

NAFO Divisions	Stock	Stock Status (Reference)	Cohorts (Months)	Exploitation Pattern
Warm-water stocks				
4T	sGSL Fall	Cautious (DFO, 2020)	1968-2014 (8-11)	NST (≤ 1979) ST (> 1980)
4T	sGSL Spring	Critical (DFO, 2020)	1968-2014 (8-11)	NST (≤ 1979) ST (> 1980)
4WX	SWNS-BoF	Cautious/Critical (DFO, 2018)	1966-2015 (8-11)	NST
4WX	4WX Offshore	Uncertain (DFO, 2018)	1966-2015 (1-6)	NST
4V	4V Coastal	Uncertain (DFO, 2018)	1969-1986 (11-12)	NST

NAFO Divisions	Stock	Stock Status (Reference)	Cohorts (Months)	Exploitation Pattern
Cold-water stocks				
4RS	nGSL Fall	Uncertain (DFO, 2021)	1965-2013 (8-11)	NST
4RS	nGSL Spring	Uncertain (DFO, 2021)	1969-2013 (8-11)	NST
3K	WB-NDB Fall	Uncertain (DFO, 2019)	1967-2009 (8-11)	NST
3K	WB-NDB Spring	Uncertain (DFO, 2019)	1963-2010 (8-11)	NST
3L	BB-TB Fall	Uncertain (DFO, 2019)	1966-2010 (1-6)	NST
3L	BB-TB Spring	Uncertain (DFO, 2019)	1963-2010 (1-6)	NST
3Ps	SMB-PB Fall	Uncertain (DFO, 2019)	1967-2009 (1-6)	NST
3Ps	SMB-PB Spring	Uncertain (DFO, 2019)	1963-2009 (1-6)	NST
3Ps	FB Fall	Uncertain (DFO, 2019)	1968-2008 (1-6)	NST
3Ps	FB Spring	Uncertain (DFO, 2019)	1964-2011 (1-6)	NST

3.2.2 Exploitation Patterns

A landings-based index of exploitation pattern was estimated for each year and Northwest Atlantic Fisheries Organization (NAFO) division, using publicly available landings data (**Figure 3.2**). All landings that were made during the spawning season by gillnets were assumed to be targeting spawning herring whereas all other catches (other

months, other gears) were assumed to be fishing non-spawning herring. Misattributions between spawner-targeted and non-spawner-targeted catches were deemed unlikely because spawning aggregations are always harvested with gillnets in specific times of the year whereas seines and other mobile gear are never allowed on the spawning grounds because they can damage them. A more detailed index based on observed (realized) selection history would have been preferable, given the diversity of catch regulations employed within the NST category, but could not be constructed owing to the difficulty in estimating the underlying demographic structure of each stock.

Although Law and Grey (1989) did not specify a proportion-based threshold for the distinction between ST and NST exploitation, we note that theoretical expectations for fisheries targeting both mature and immature individuals are qualitatively the same as for fisheries exploiting immature fish only (Ernande *et al.*, 2004). Thus, a relaxation of the selection pressures against late-maturing individuals might only occur in fisheries that principally harvest spawning aggregations while simultaneously minimizing the F on immature fish. While this definition was met for several combinations of stocks and years, the pattern was most consistently expressed for the sGSL (NAFO division 4T) during the 1980-2014 period. Therefore, comparisons focussed on the distinction between this time period and an earlier period of NST exploitation in this fishery (1968-1979), as well as with stocks in all other regions.

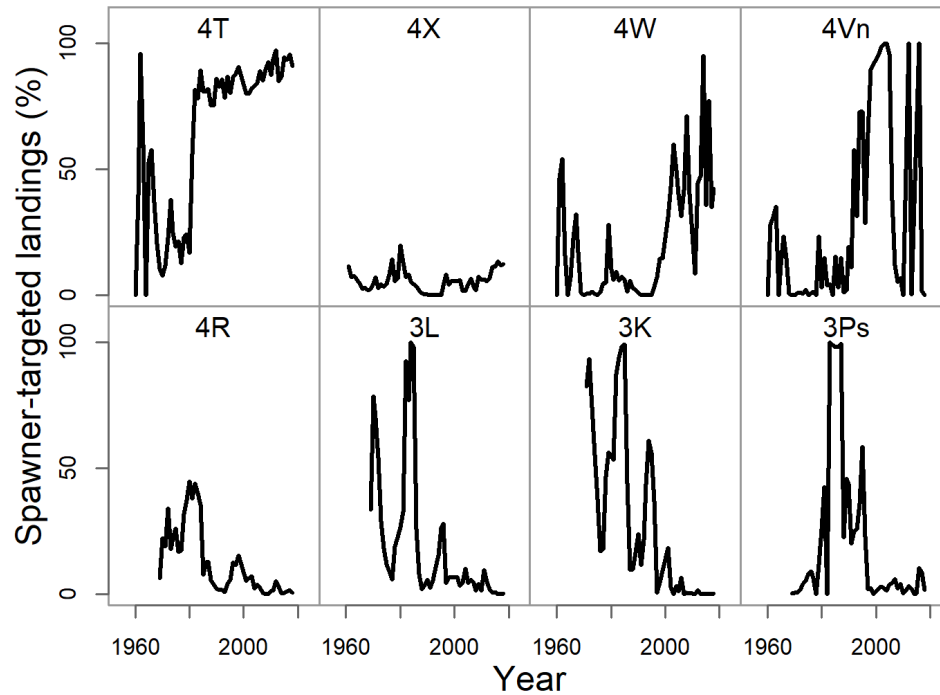


Figure 3.2 Percentage of the landings that were made while targeting spawning fish for each Northwest Atlantic Fisheries Organization (NAFO) division and year. Stocks associated with each region are specified in **Table 3.1**.

3.2.3 Analyses

Our analysis began with the estimation of trends in maturity ogives for stocks exposed to contrasting exploitation and environmental regimes (*trends in age and length at maturation*). Then, we modelled probabilistic maturation reaction norms for age and length at maturation, a commonly employed framework for detecting maturation responses to fishing and environmental factors, in a subset of five herring stocks for which sample sizes per age and cohort exceeded a pre-determined threshold (*probabilistic maturation reaction norms*). Finally, we explored the consequences of the

changes observed to reproductive success by estimating the ratio of length at maturation to maximum observed length in the 15 stocks and a simple metric of length-based lifetime egg production in the 2 sGSL stocks (*consequences to lifetime reproductive success*).

3.2.3.1 Trends in Age and Length at Maturation

Maturity ogives, a function that specifies the proportion of individuals in a cohort that are mature at a given age and/or length (Trippel, 1995; Cadigan *et al.*, 2014), were estimated separately for each stock, using the following logistic regression model involving cohort specific intercept and slope parameters,

$$(3.1) \quad \text{logit}(p_i) = \beta_0 + \beta_{1c} + \beta_2 X_i + \beta_{3c} X_i ,$$

where p_i is the probability of individual i being mature, X_i indicates the age or length, depending on the analysis, and c indexes cohort. The predicted ages and lengths at 50% mature, A_{50} and L_{50} , were calculated as $-\beta_0/\beta_2$ for the reference cohort and as $-(\beta_0 + \beta_{1ci})/(\beta_2 + \beta_{3,ci})$ for the remaining cohorts. The 95% confidence intervals (CI95) were then obtained by bootstrapping with 1000 iterations. The sign and strength of the monotonic trends over time (across cohorts) of A_{50} and L_{50} were summarised for each stock, using Spearman's rank correlation coefficient (ρ).

3.2.3.2 Probabilistic Maturation Reaction Norms

Probabilistic maturation reaction norms (PMRNs), a model intended to account for variations in survival- and growth-mediated plasticity in maturation, were quantified following the demographic estimation method developed by Barot *et al.* (2004a) because our data did not distinguish between recruit and repeat-spawners (Heino *et al.*, 2002;

Dieckmann and Heino, 2007). A minimum number of 100 individuals per cohort and age class is recommended for this model to be considered robust to its main simplifying assumptions, namely that mature and immature fish of the same cohort and age class have equal growth and survival rates (Barot *et al.*, 2004). This requirement was met for three stocks known to have collapsed in the 1960s-70s (SWNS-BoF, sGSL Fall, sGSL Spring) as well as for cohorts in two stocks believed to have experienced lower harvest intensities over the same time period (4WX Offshore and nGSL Fall).

PMRNs were estimated by first specifying the probabilities of being mature as a function of cohort, age and length,

$$(3.2) \quad \text{logit}(p_i) = \beta_0 + \beta_{1c} + \beta_2 A_i + \beta_{3c} A_i + \beta_4 L_i + \beta_{5c} L_i + \beta_6 A_i L_i ,$$

where L_i , A_i and c are defined as in equation 3.1. Because a fully factorial model (*i.e.*, age and cohorts treated as factors, with all possible interactions) failed to converge for some cohorts, we omitted the cohort \times age \times length interaction and treated age as a continuous variable. To limit collinearity between age and length caused by treating age as continuous, calculations were restricted to a narrow range of ages at which maturation is most likely to occur (≤ 6 years).

Following Barot *et al.* (2004a), average growth increments, $\Delta L_{c,A}$, were estimated as the difference in mean length between two consecutive ages,

$$(3.3) \quad \Delta L_{c,A} = L_{c,A} - L_{c,A-1},$$

with observations from adjacent cohorts being combined when direct measurements were unavailable.

The resulting reaction norms, $m(c,A,L)$, were then computed as:

$$(3.4) \quad m(c, A, L) = \frac{o(c,A,L) - o(c,A-1,L-\Delta L)}{1 - o(c,A-1,L-\Delta L)},$$

where $o(c,A,L)$ and $o(c,A-1,L-\Delta L)$ are the predicted probabilities of being mature at ages A and $A-1$, respectively. For each age and cohort group, PMRN midpoints for fish maturing at ages 2, 3 and 4 years, denoted as L_{p50} , were estimated by linear interpolation between the lengths that yield probabilities of maturing immediately below and above 50%. The CI95 of each estimate were obtained by bootstrapping with 1000 iterations.

The respective contributions of fisheries-induced evolution (FIE) and direct plasticity in maturation schedules (hereafter referred to as growth-independent phenotypic plasticity) were examined by comparing the trends in L_{p50} over time and among stocks. We note that, although various sources of information point to more intensive exploitation in the sGSL (Turcotte *et al.*, 2021) and SWNS-BoF stocks (Sinclair *et al.*, 1985) than in 4WX Offshore (absence of a directed fishery until 1996; DFO, 2018) and nGSL Fall (McQuinn *et al.*, 1999; Grégoire *et al.*, 2015), the lack of reliable estimates of F for stocks outside the sGSL generally limited the strength of comparisons based on intensity of harvest. Following the approach proposed by Sharpe and Hendry (2009), the rates of change in L_{p50} , d , were quantified in darwins, or proportional change per million years,

$$(3.5) \quad d = \frac{\ln\left(\frac{H_1}{H_0}\right)}{\Delta t \times 10^{-6}},$$

where H_0 and H_1 are the averages of the first and last three estimates of L_{p50} , respectively, of a period of Δt years. A key assumption of this approach is that the stocks

(or time series) being compared have similar generation times; this reflects the fact that darwins are expressed on absolute, rather than relative, time scales (Haldane, 1949; Gingerich, 1993). Because our purpose was to compare rates of change among stocks of the same species, this assumption should not be too consequential for the interpretation of our results.

3.2.3.3 Consequences to Lifetime Reproductive Success

The potential consequences of selection on age and length at maturation for reproductive success were investigated by (i) testing the predicted association between length at maturity and maximum observed length at the cohort level; and (ii) integrating data on length-dependent fecundity, age at maturity and total mortality into a metric of lifetime production of eggs for the two spawner-targeted stocks in the sGSL.

A positive relationship between L_{50} and asymptotic length (L_{∞}) is expected based on trade-offs between present and future growth and reproduction (Roff, 1983; Stearns, 1989) and the theory on life-history invariants (Beverton and Holt, 1959; Charnov, 1993). However, the degree to which this pattern extends to specific cohorts and stocks in the wild is uncertain given the potential for variable sampling, survival and growth rates to modify length-at-age trajectories at the population level (Hordyk *et al.*, 2015a, 2015b; Prince *et al.*, 2015). Since the data required to parameterize the von Bertalanffy (1938) growth equation were available for only 6 of the 15 herring stocks examined (sGSL Fall, sGSL Spring, SWNS-BoF, 4WX Offshore, nGSL Fall, nGSL Spring), we tested instead the association between L_{50} and the maximum observed length (L_{\max}), a trait that was found to be well correlated with L_{∞} for the above-mentioned stocks (**Figure B2**). We also

estimated the ratio of L_{50} to L_{\max} , which is used as a proxy for the proportion of theoretical maximum size that is completed at maturity for each cohort.

A more informative proxy of lifetime reproductive success (*LRS*) than the L_{50}/L_{\max} ratio in marine fish is the average number of eggs produced by an average female over its reproductive lifespan. Taking advantage of extensive fishery-dependent and independent data on the two sGSL stocks, we estimated this metric as the product of age-specific survival and fecundity within each cohort from 1976 to 2008,

$$(3.6) \quad LRS = \sum_{x=\alpha_{min}}^{x=\tau} l_x \cdot m_x,$$

where l_x and m_x denote the age-specific survival and fecundity, respectively, of a female from the minimum observed age at maturity (here, $\alpha_{min} = 2$ years) to the observed maximum age at reproduction (here, $\tau = 11$ years). This time window was chosen to encompass the range of ages at which most herring are representatively sampled by sampling gear and also to acknowledge the occurrence, albeit rare, of reproductive senescence in herring older than 11 years old (Benoît *et al.*, 2018, 2019).

Age-specific survival, l_x , was specified by converting instantaneous mortalities to cumulative probabilities of survival,

$$(3.7) \quad l_x = \sum_{x=\alpha_{min}}^{x=\tau} e^{-Z_x},$$

where the instantaneous rate of total mortality, Z_x , is the sum of fishing (F_x) and natural (M_x) mortality at age x . Estimates of F_x for the sGSL Fall and sGSL Spring stocks were obtained from Tables 21 and 45, respectively, of the most recent assessment report for these stocks (Turcotte *et al.*, 2021) whereas M_x was assumed to equal 0.2 at all ages (the

assumption used in both assessment models). The potential for time variation in M_x was explored in the assessment for the three regional sub-components (North, Middle, and South) of the sGSL Fall stock (Turcotte *et al.*, 2021) to account for a perceived increase in predation after 1990 (Benoît and Rail, 2016). However, this predation-based version was not retained because it yielded extremely low values of M_x for age-classes 2-6 years which we deemed biologically implausible (**Figure B3**).

Age-specific fecundity, m_x , was estimated as,

$$(3.8) \quad m_x = p_x \cdot (a \times L_x^b),$$

where p_x is the proportion mature at age obtained from equation 3.1 and L_x is mean length at age x . The a and b parameters were obtained from relationships published by Messieh (1976) for the sGSL Fall [$a = 1.734 \times 10^{-5}$ and $b = 3.930$] and sGSL Spring [$a = 3.067 \times 10^{-5}$ and $b = 3.750$] stocks separately.

3.3 Results

3.3.1 Trends in Age and Length at Maturation

The hypothesized influence of exploitation pattern on age at maturity was empirically well supported for most stocks (**Figure 3.3**). In accordance with predictions for spawner-targeted (ST) fisheries, A_{50} increased by 0.59 and 0.49 year in the sGSL Spring and Fall stocks, respectively, over the 1972-2014 cohorts. Conversely, A_{50} in the non-spawner-targeted (NST) SWNS-BoF and 4WX Offshore stocks decreased by 0.37 and 1.61 years over the same time period, the direction expected for fisheries exploiting both mature and immature fish. Consistent with rising and declining F in the NST fishery (McQuinn *et al.*, 1999; Grégoire *et al.*, 2015), A_{50} in the two nGSL stocks decreased from the mid 1960s until the mid 1990s and then shifted towards later maturity. While similar changes also occurred in coastal Newfoundland stocks (*e.g.*, WB-NDB Spring, BB-TB Fall), their interpretation was somewhat more uncertain given the wider confidence intervals associated with each estimate.

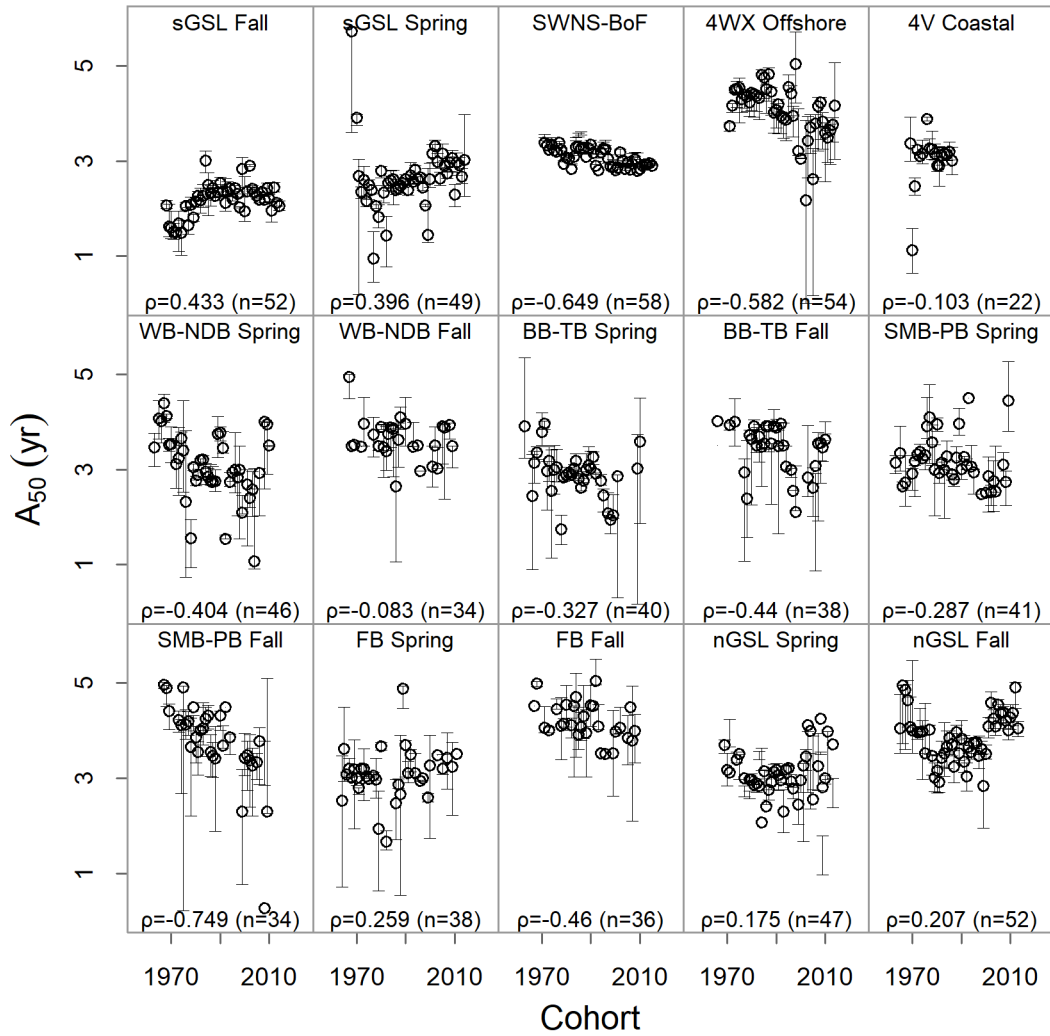


Figure 3.3 Trends in age at maturity ($A_{50} \pm CI_{95}$) for the 15 Atlantic herring stocks examined, with Spearman's rank correlation coefficients (ρ) and associated sample sizes (n). The degree of monotony and direction of trends are given by the absolute value and sign of ρ , respectively.

Length at maturity followed a strong geographic pattern over the study period investigated (**Figure 3.4**). Over a common range of cohorts (1972-2014), L_{50} declined continuously in all warm-water stocks, resulting in total reductions of 3.1-3.3 cm in the Scotian Shelf stocks and 2.4-2.8 cm in the sGSL stocks. In contrast, L_{50} in the colder-water Newfoundland stocks mostly declined between the mid 1970s and early 1990s, following which the trend partly reverted to intermediate values. This resulted in net reductions ranging from approximately 2 cm to less than 1 cm. These spatio-temporal patterns more closely resembled the mean lengths-at-age 4 reported in Chapter 2 (**Figure B4**) than the trends in A_{50} documented in the present study (**Figure B5**).

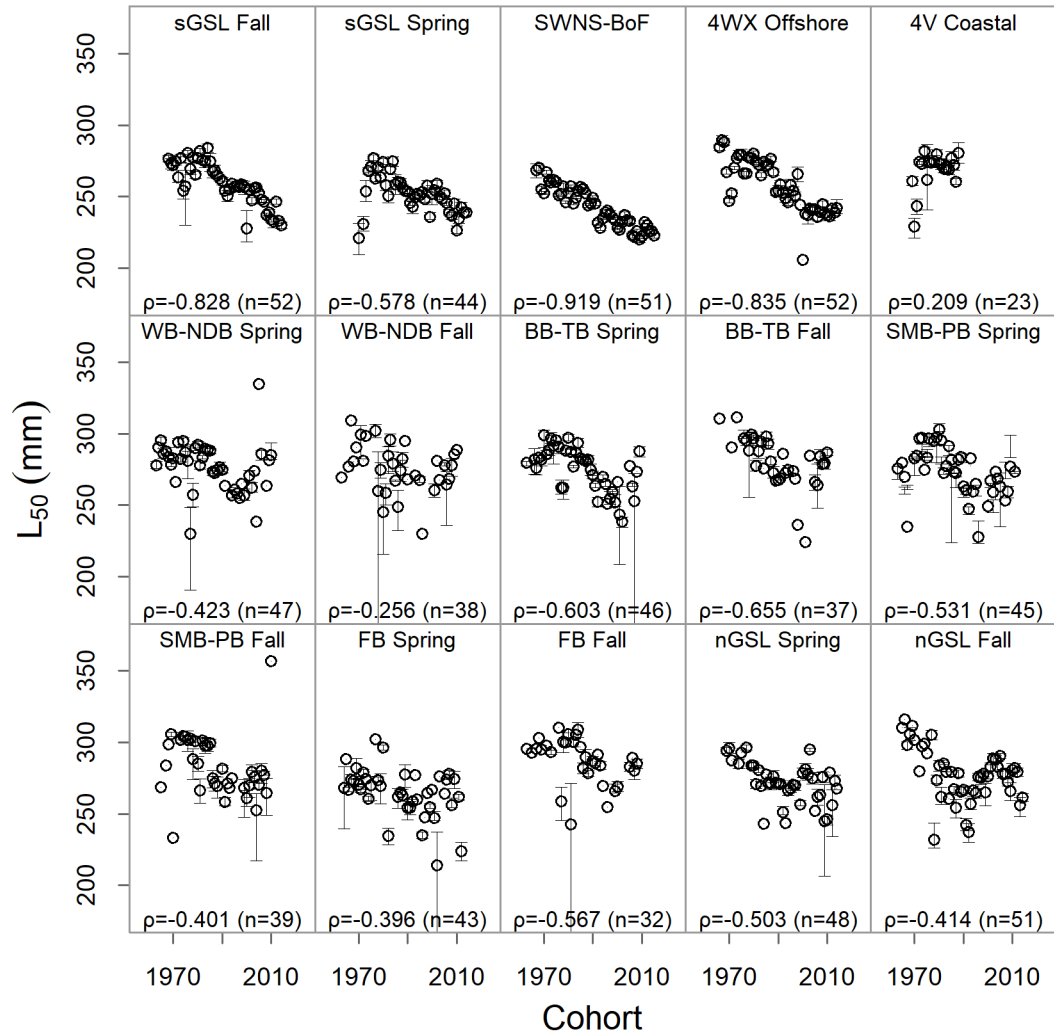


Figure 3.4 Trends in length at maturity ($L_{50} \pm CI_{95}$) for the 15 Atlantic herring stocks considered in the present study, with Spearman's rank correlation coefficients (ρ) and associated sample sizes (n). The degree of monotony and direction of trends are given by the absolute value and sign of ρ , respectively.

3.3.2 Probabilistic Maturation Reaction Norms

The predicted lengths at which the probability of an immature individual maturing is 50%, or PMRN midpoints (L_{p50}), varied between 20 and 30 cm, with estimates for a given cohort generally decreasing with age (**Figure 3.5**). Sample sizes for mature and immature fish were largest for the most highly exploited stocks (sGSL Fall, sGSL Spring, SWNS-BoF; **Tables B1-B3**) and comparatively smaller for the less intensively exploited ones (4WX Offshore and nGSL Fall; **Tables B4-B5**). For the latter two stocks, only one estimate could be produced at an age of 2 years due to the very low occurrence of mature herring in the samples at that age.

Temporal trends in L_{p50} decreased across most ages in the SWNS-BoF, sGSL Spring, sGSL Fall, and 4WX Offshore stocks, indicating a tendency for herring to mature at progressively shorter lengths in these stocks. With perhaps the exception of the SWNS-BoF stock, for which the declines encompassed the entire observation period (1968-2014), L_{p50} in these warm-water stocks varied little or increased rapidly until the late 1970s/early 1980s before declining to historically low values. By contrast, L_{p50} in the colder-water nGSL Fall stock increased from the mid 1990s until the mid to late 2000s, a pattern that resembled the trend in L_{50} (see **Figure 3.4**).

Estimated rates of change in L_{p50} varied between -6.44×10^3 (SWNS-BoF, age 4) and 3.27×10^3 (nGSL Fall, age 3) darwins. The ranking of warm-water stocks from fastest to slowest rates of decline in L_{p50} at a common age of 3 years old was the following: sGSL Fall, 4WX Offshore, SWNS-BoF, and sGSL Spring. At an age of 4 years old, this ranking changed to: SWNS-BoF, 4WX Offshore, sGSL Fall, and sGSL Spring.

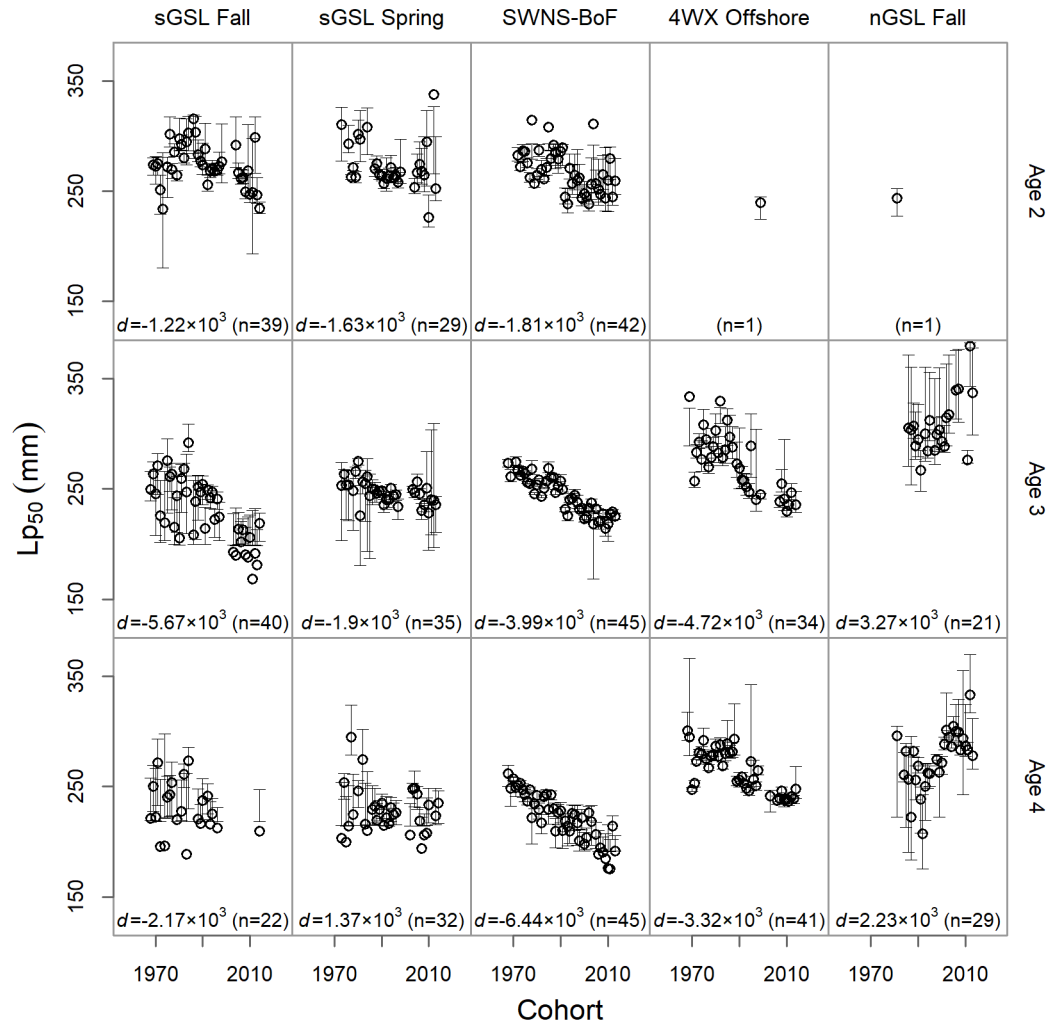


Figure 3.5 Trends in PMRN midpoints ($L_{p50} \pm CI95$) estimated at ages of 2, 3 and 4 years for 5 Atlantic herring stocks, with rates of phenotypic change in darwins (d) and associated sample sizes (n).

3.3.3 Consequences to Lifetime Reproductive Success

All stocks exhibited a positive association between L_{50} and L_{\max} , indicating a general propensity for small- and large-maturing cohorts to remain small and large, respectively, throughout their observable lifespan (**Figure 3.6**). The slope of this relationship differed significantly between stocks (analysis of covariance (ANCOVA), $L_{50} \times \text{stock}$: $F_{14,473} = 11.02$, $p < 0.0001$), which suggests that the biological and/or sampling-related processes affecting body length in mature age-classes might not have not been uniform across locations. The average ratios of L_{50} to L_{\max} varied between 0.65 and 0.73, corresponding to maturation occurring at approximately two thirds of the maximum observed length. This narrow range of estimates is largely consistent with theory and empirical findings which point to a typical or optimal value of 0.66 for the more widely applied L_{50}/L_{∞} ratio (Jensen, 1997; Hordyk *et al.*, 2015a).

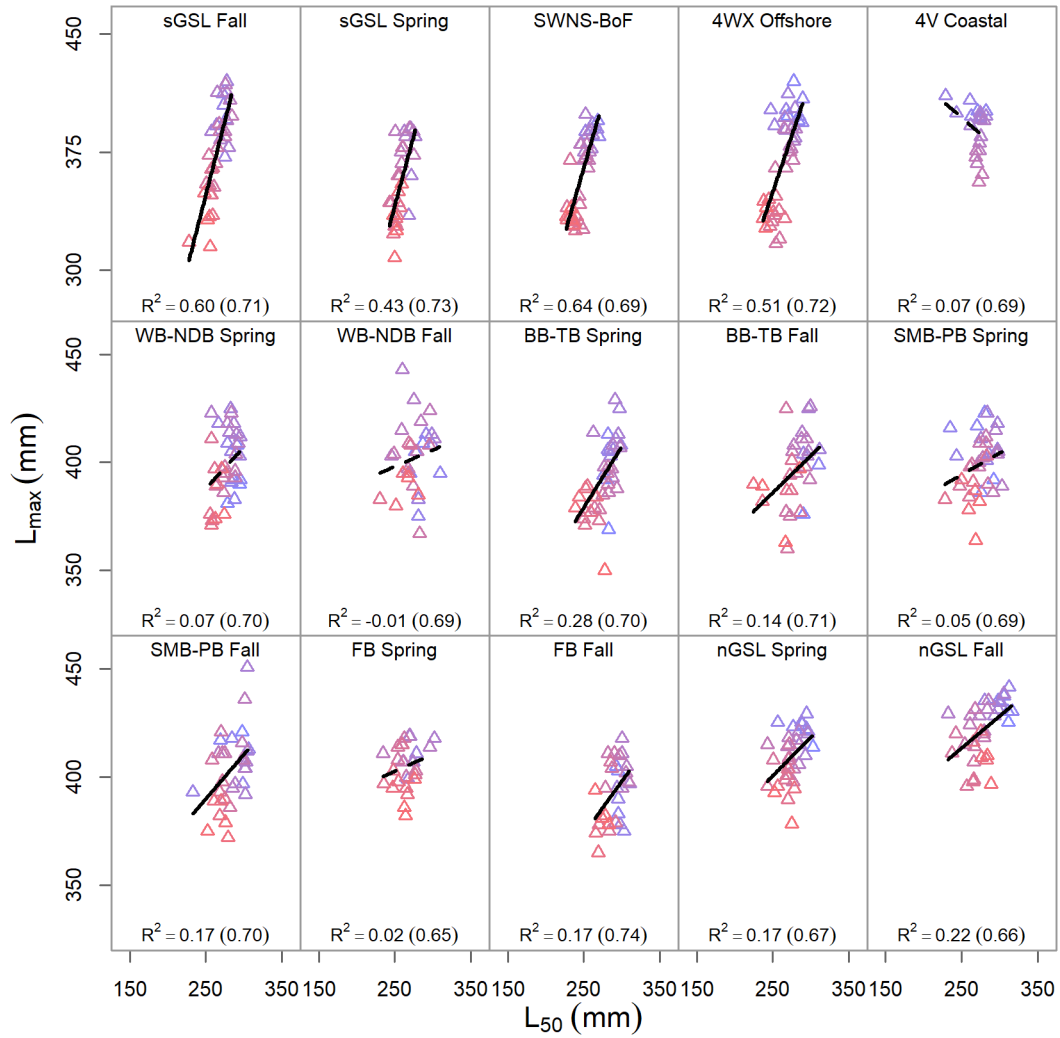


Figure 3.6 Linear associations between length at maturity (L_{50}) and maximum observed length (L_{max}) for the 15 Atlantic herring stocks examined, with predictions from statistically significant ($p \leq 0.05$) model fits illustrated as black solid lines. Adjusted R^2 are indicated at the bottom of each panel, with the average L_{50}/L_{max} ratio for each stock specified in parentheses.

Age-specific probabilities of survival and fecundity have decreased in both the sGSL Fall and sGSL Spring stocks over the time period investigated (**Figure 3.7, a-d**). Cumulative survival to age 11 years decreased until the late 1990s and then steadily increased for the remainder of the time period. In contrast, estimated fecundity declined in a nearly continuous manner throughout the time period. In any given cohort, the mean estimates of l_x and m_x were greater in fall than in spring spawners.

Changes in age-specific survival and fecundity have resulted in net reductions in lifetime reproductive success (*LRS*) for both the sGSL Fall and sGSL Spring stocks (**Figure 3.7, e-f**). In the former, *LRS* for an average female decreased from over 425,000 eggs in the late 1970s to less than 200,000 eggs in the early 2000s, corresponding to a relative decline of 56% over the 1976-2008 period. Over the same range of cohorts, *LRS* in the latter stock is estimated to have decreased from more than 155,000 eggs to approximately 110,000 eggs, representing a historical reduction of 30%. Thus, despite having both experienced a shift towards delayed maturity consistent with spawner-targeted exploitation, neither of the two stocks are perceived to have experienced meaningful increases in egg production over the time period investigated.

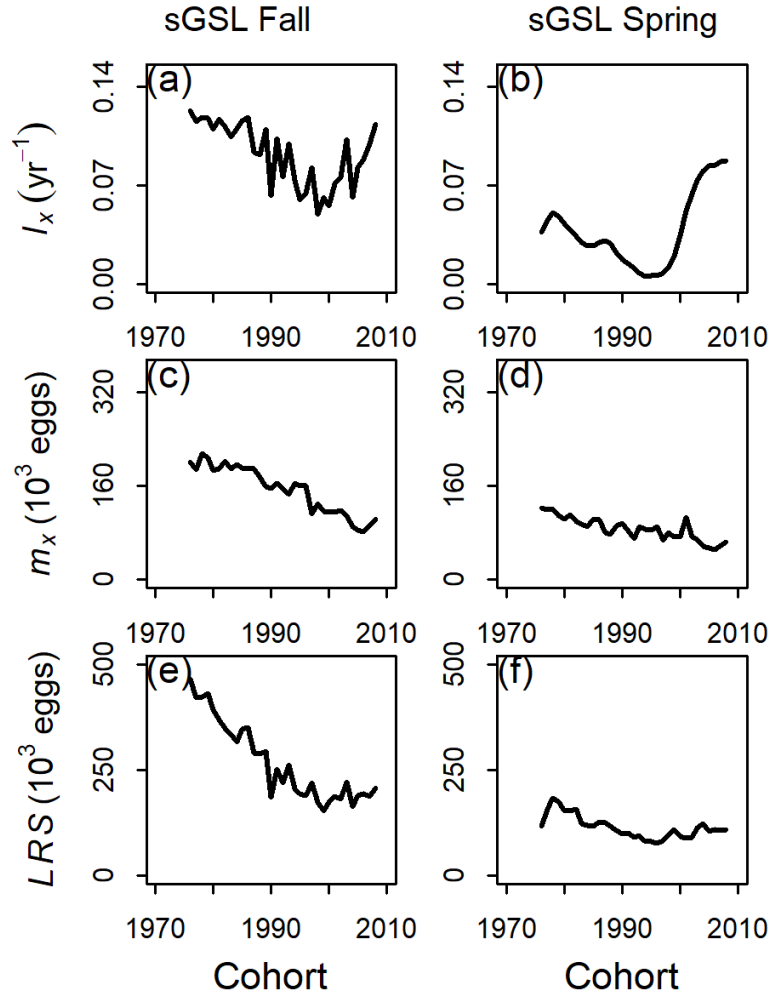


Figure 3.7 Temporal trends in (a,b) age-specific survival (l_x), (c,d) age-specific fecundity (m_x), and (e,f) lifetime reproductive success (LRS) at a maximum observed age of 11 years for the (a,c,e) sGSL Fall and (b,d,f) sGSL Spring stocks.

3.4 Discussion

The present study investigates the combined influence of fishing and the environment on life history in the Atlantic herring, a broadly distributed marine fish in the northwest Atlantic. Our analysis of trends in age at maturation (A_{50}) generally supports the hypothesis that putative FIE towards earlier maturity has a lower probability of occurring when fishing intensity is low and/or mainly targets mature fish on their spawning grounds (Law and Grey, 1989). However, the observation that all stocks examined exhibited temporally and spatially consistent patterns in length at maturation (L_{50}), PMRN midpoints (L_{p50}), and maximum observed length (L_{max}), all of which closely followed the mean lengths-at-age 4 reported in a previous study (Chapter 2, this document), suggests a comparatively stronger influence of environmental factors on the metric of lifetime reproductive success defined here. Together, our findings indicate that the pattern or strategy of exploitation can have reasonably predictable consequences on traits that affect individual fitness and population viability, such as age at maturity, length at maturity, and lifetime production of eggs.

3.4.1 Trends in Age and Length at Maturation

Consistent with theoretical expectations for maturity-dependent harvesting (Law and Grey, 1989; Ernande *et al.*, 2004), age at maturity for stocks exposed to ST and NST exploitation generally changed in opposite directions. The distinction between the two patterns was particularly evident in the sGSL stocks, for which observed increases in A_{50} coincided with a transition from a whole-fish, winter fishery by purse-seiners to a roe-driven fishery by gillnets on the spawning grounds (Messieh, 1989; Burke and Phyne, 2008). By contrast, the predominant shifts toward earlier maturity in the Scotian Shelf,

nGSL and Newfoundland regions, where ST fisheries have accounted for comparatively lower proportions of total annual catch, were more consistent with observations on other stocks that have been historically exploited on their feeding and/or overwintering grounds (e.g., Northeast Atlantic cod, *Gadus morhua*; Jørgensen, 1990; North Sea plaice, *Pleuronectes platessa*; Grift *et al.*, 2003). While the observed changes in A_{50} could not be unequivocally attributed to fishing, the present study is the first, to our knowledge, to provide comparative evidence in support of Law and Grey's (1989) seminal hypotheses among stocks of the same species.

The potential for exploitation to cause directional changes in life history may not substantially differ from naturally occurring agents of selection in the wild. In contrast with observations on A_{50} , spatio-temporal changes in L_{50} were more closely related to mean lengths-at-age 4, for which variations are strongly associated with ocean warming and broad scale environmental forcing (Chapter 2, this document), than to the dominant pattern of exploitation. Although we did not test for a common signal in these data, we note that two previously overexploited species in Newfoundland waters, northern Atlantic cod (Olsen *et al.*, 2004, 2005) and American plaice (*Hippoglossoides platessoides*; Morgan and Colbourne, 1999; Barot *et al.*, 2005; Zheng *et al.*, 2020), have exhibited some degree of recovery in their maturation schedules in the late 1990s/early 2000s. This coincidence, coupled with low to moderate F in many herring stocks in the region (Wheeler and Winters, 1995; McQuinn *et al.*, 1999; Grégoire *et al.*, 2015), has led Wheeler *et al.* (2009) to propose that these three species have responded to a common driver in the environment in addition to the main effect of fishing.

Clearly, there are multiple means in which exploitation pattern and environmental change can combine to affect life history. In many NST fisheries, for example, probability of retention by fishing gear is a logistic function of size (either length or girth), implying that temporal changes in somatic growth may progressively shift the demographic composition of the catch towards higher or lower proportions mature (Millar and Fryer, 1999; Kuparinen *et al.*, 2009; Enberg *et al.*, 2012). Fishing also has the potential to affect the manner in which individuals respond to specific changes in the environment, for example, by direct or indirect (correlational) selection on traits pertaining to physiology (Hollins *et al.*, 2018), behavior (Uusi-Heikkilä *et al.*, 2008; Claireaux *et al.*, 2018) or reproductive phenology (Wright and Trippel, 2009). These possible interactions can have unpredictable consequences on perceptions of the respective roles of ST or NST exploitation for individual fitness.

3.4.2 Probabilistic Maturation Reaction Norms

The analysis of trends in L_{p50} revealed that variations in A_{50} and L_{50} not only reflected changes in age-specific survival and growth, but also a change in the propensity to mature *per se*. For stocks that collapsed before 1980 (SWNS-BoF, sGSL Fall, sGSL Spring), the declines in L_{p50} imply that a compensatory (density-dependent) growth response to fishing is unlikely to be the sole mechanism for changed maturation schedules (Heino *et al.*, 2002; Barot *et al.*, 2004). In contrast, the shift towards delayed maturation experienced by the more lightly exploited nGSL Fall stock in the second part of the time series seems more in line with observations on Norwegian spring-spawning, for which the relative stability in L_{p50} ($d = 0.314 \times 10^3$ darwins at 5 years old; estimated by Sharpe and Hendry, 2009) has been previously attributed to growth-mediated plasticity in

maturation (Engelhard and Heino, 2004b, 2004a). While a temporal shift in PMRNs can reflect a degree of genetic change in maturation, we note that the demographic and phenotypic components of the response are mutually non-exclusive and, therefore, cannot be directly estimated from this modelling framework (reviewed in Dieckmann and Heino, 2007).

The PMRN framework proved to be somewhat less informative in the evaluation of fishing as a selective agent, perhaps owing to the lower number of stocks employed in the comparison (N=5) or concurrent differences in data quality (**Tables B1-B5**). Although the trends in L_{p50} were in the direction expected for FIE, the observation that the 4WX Offshore stock experienced continued declines in L_{p50} at both the ages of 3 and 4 years old, despite little exploitation prior to 1996 (DFO, 2018), raises questions concerning the degree to which this method could reliably distinguish the effects of fishing from other agents of phenotypic change in our study system. More generally, the apparent geographic pattern in the direction of trends observed, wherein all warm-water stocks experienced a decline in their L_{p50} concomitant with a trend of increasing temperature (Hebert *et al.*, 2018; Galbraith *et al.*, 2019), could provide equally strong or stronger support for a growth-independent effect of temperature on maturation (Kuparinen *et al.*, 2011; Tobin and Wright, 2011), a mechanism of earlier maturation that has been previously demonstrated to result in erroneous inferences of FIE in single populations (Kraak, 2007; Marshall and McAdam, 2007). Given these caveats, and considering the lack of PMRN estimates for formerly highly exploited stocks in the colder Newfoundland region (*e.g.*, FB Spring; Winters and Moores, 1980), we remain cautious in the interpretation of our results as evidence for evolutionary responses to fishing and instead

encourage further investigations on the relative importance of growth-dependent and independent plasticity in the maturation trends of lightly exploited species.

3.4.3 Consequences to Lifetime Reproductive Success

Our evaluation of the L_{50}/L_{\max} ratio among cohorts, a metric analogous to the more widely reported L_{50}/L_{∞} ratio across fish taxa (Beverton and Holt, 1959; Charnov, 1993), was primarily intended to overcome a paucity of data on older, but more poorly represented age categories. By linking variations in length at maturity – a trait that depends on age at maturity, juvenile growth and survival – to a known correlate of fecundity in the adult stage (Messieh, 1976; Bradford and Stephenson, 1992), this life-history ratio provides empirical support to the hypothesis that phenotypic changes in the juvenile stage may overwhelmingly determine lifetime egg production in the wild (Hordyk *et al.*, 2015a, 2015b). Of course, this simple generalization does not account for the multitude of factors that are believed to determine the strength of this relationship within and among stocks, such as size-selective mortality (Sinclair *et al.*, 2002; Vincenzi *et al.*, 2014), reproductive investment (Claireaux *et al.*, 2020; dos Santos Schmidt *et al.*, 2020), and adult growth (Swain *et al.*, 2007; Enberg *et al.*, 2012), thus limiting its potential applicability to other contexts. Still, the consistency of our estimates with the optimal value of 0.66 reported among species (Jensen, 1997) implies that phenotypic variations in the early-adult period can have reasonably predictable consequences on reproductive capacity in our study system.

The management implications of a dominant influence of environmental factors on L_{50} , and thus L_{\max} , are not entirely clear. In line with the expected effect of fishing on cohorts, our exploratory analysis of the two sGSL stocks indicates that elevated F on mature age-

classes has largely prevented females from realizing the survival and reproductive benefits associated with ST exploitation over the 1976-2000 period (Law and Grey, 1989). However, concurrent declines in fecundity suggest that our metric of reproductive success (lifetime production of eggs) would likely have decreased even in the absence of a directed fishery in that ecosystem. This evidence, combined with a reversal of the trend following the relaxation of F in the late 1990s, supports the importance of combining trait-based regulations with more direct forms of harvest control, such as those encompassed by biological reference points or fishing moratoria (*e.g.*, Law and Grey, 1989; Andersen *et al.*, 2007; Dunlop *et al.*, 2009; Hutchings, 2009; Jørgensen *et al.*, 2009; Heino *et al.*, 2013).

Since our proxy of reproductive success – the average number of eggs produced over the lifetime of an average female – did not account for the potentially large impact of early-life survival on population growth, we recommend that generalizations based on our findings be performed with caution. Even if ST exploitation may only benefit fitness under specific circumstances, there might still be merit in protecting juvenile fish (Froese, 2004), particularly when the contribution of numerically dominant recruit spawners to productivity can be conclusively demonstrated to exceed that of older, but less abundant spawners (*e.g.*, Lavin *et al.*, 2021). The potential effects of reducing the minimum landing size below the L_{50} -based threshold, as requested by the fishing industry in several regions, must also be viewed in light of overarching environmental influences given the potential for favorable growth to combine with, and thus compensate for, earlier maturation in some contexts (*e.g.*, Neuheimer and Grønkjær, 2012). Clarifying the role of spawner life history in recruitment, a process that strongly depends on environmental

forcing in the Gulf of St Lawrence (Brosset *et al.*, 2019), will strengthen the basis for evaluating the implications of our findings for conservation and fisheries management.

3.4.4 Conclusion

The acknowledgement that the forcing of and consequences of fishing on life history can vary across contexts raises a number of challenges for fisheries management. Here, we demonstrate that the prevailing strategy of exploitation (ST or NST) and environmental regime (warm or cold) have potential to shift A_{50} and L_{50} in directions consistent with theory. Our analysis of PMRNs on a subset of well-sampled stocks expands this interpretation by revealing that such changes may not exclusively result from variability in growth and survival, but also could involve phenotypic plasticity or a degree of genetic change in the propensity to mature. Our exploration of the L_{50}/L_{\max} ratio within individual cohorts, coupled with simple lifetime reproduction calculations, point to a dominant effect of length at maturation and total mortality on individual reproductive success. Based on this evidence, we conclude that avoidance of overfishing remains the most reliable approach for preserving stock productivity and yield, particularly given the uncertainty in the impacts of climate change on exploited species and marine ecosystems.

3.5 Acknowledgements

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Chapter 4 Conclusion

The primary objective of this thesis was to evaluate the combined influence of environmental change and exploitation on life history in the Atlantic herring, a widely distributed marine fish of key ecological and socio-economic importance in the northwest Atlantic. The analyses revealed that the effects of temperature on mean length-at-age 4 can vary both within and across populations, with the potential to affect the consequences of specific exploitation strategies for individual reproductive success. The comparative approach employed in both chapters also illustrated how inferences based on single-population time series can differ from those obtained by testing hypotheses over a wider range of spatial and temporal scales. In this final chapter, I briefly summarise the main findings of the thesis and comment on future research avenues.

4.1 Summary

Chapter 2 examined the form and spatio-temporal scale of the association between average temperature experienced and mean length-at-age 4 across all 16 Atlantic herring populations in the northwest Atlantic. This analysis illustrated how a simple model incorporating quadratic temperature effects with population-specific thermal optima can account for most of the variability in size-at-age observed within and among populations since the early 1960s. Explicitly accounting for nonlinearity and the potential for variation in the strength of responses uncovered a compelling unanticipated pattern of synchrony in model residuals, a finding that contrasted strongly with causal inferences made at the population level. This chapter demonstrated the value of integrating life-history data across multiple generations and spatial scales for resolving the impact of multiple selection pressures acting simultaneously on size.

Chapter 3 expanded on the latter analysis by estimating trends in maturity ogives and probabilistic maturation reaction norms and exploring their possible consequences for individual reproductive success. Consistent with hypotheses on fisheries-induced evolution, populations exposed to spawner-targeted and non-spawner-targeted exploitation experienced opposing trends in age at maturation, with some populations also showing a propensity to mature at progressively shorter lengths. Importantly, however, the analyses revealed that environmental factors may overwhelmingly determine age-specific and lifetime reproductive success in this species, in a manner consistent with the patterns described in Chapter 2. This chapter argued for a more integrated perspective of the role of trait-based regulations in fisheries management, particularly in light of ongoing climate change.

4.2 Perspectives

The potential for size-at-age to respond nonlinearly to temperature has been extensively discussed by thermal physiologists aiming to predict species responses to climate change (Huey and Kingsolver, 1989; Angilletta *et al.*, 2003; Sinclair *et al.*, 2016). In fisheries science, however, this idea has received comparatively little attention, possibly owing to the more recent interest in temperature-induced evolution in life-history traits (Waples and Audzijonyte, 2016; Hollins *et al.*, 2018) or a greater emphasis on the debate whether a reduction in body size does (*e.g.*, Daufresne *et al.*, 2009; Cheung *et al.*, 2013; Baudron *et al.*, 2014; Ikpewe *et al.*, 2021) or does not (Brander *et al.*, 2013; Teplitsky and Millien, 2014; Lefevre *et al.*, 2017, 2021; Siepielski *et al.*, 2019) represent a universal response to climate change.

A possible next step to Chapter 2 would be to identify the conditions in which differential responses to warming are most likely to be detected in field-collected data, for example, by examining temperature-trait associations in both commercial and non-commercial species. It would also be helpful, and perhaps even necessary, to further investigate the occurrence of large-scale synchrony in life-history traits and clarify the implications of such patterns for fisheries management (*e.g.*, definition of stock boundaries) and conservation (*e.g.*, Portfolio effect; Schindler *et al.*, 2010; Thorson and Minte-Vera, 2016).

A primary reason for the limited integration of fisheries-induced evolution into policy is the inability to conclusively demonstrate that changes in life-history traits that have previously been attributed to fishing can have negative socio-economic and conservation consequences over timescales deemed relevant to fishery managers (Andersen and Brander, 2009; Laugen *et al.*, 2014; Kuparinen and Festa-Bianchet, 2017; Hutchings and Kuparinen, 2019, 2021). This recognition is particularly relevant in the debate on whether or not to maintain minimum size regulations, as it reflects an inherent difficulty in linking specific changes in life history – and, thus, specific trait-based regulations – to their short-term outcomes on population growth.

Based on Chapter 3, I believe that the field will benefit from continued or increased attention to how past and ongoing changes in life history traits, irrespective of the reasons for them, might impact ecosystem processes across a variety of contexts, scales of observation and timeframes (*e.g.*, Audzijonyte *et al.*, 2013b; Jusufovski and Kuparinen, 2020). Another important research avenue will be to characterize the process of growth-independent phenotypic plasticity in maturation schedules in a more comprehensive

manner, for example, by estimating the rate at which temperature might affect probabilistic maturation reaction norms in the absence of fishing (this is analogous to the more commonly addressed question of *How fast is fisheries-induced evolution?*; e.g., Sharpe and Hendry, 2009; Devine *et al.*, 2012; Audzijonyte *et al.*, 2013a). Addressing these questions will help to more accurately quantify the relative contributions of fishing and environmental change to life history, for which the qualitative expectations can be very similar.

4.3 Concluding Remark

The common trend in the residuals of the thermal optimum model is the result in this thesis which has surprised us the most given the vast amount of resources and publication effort that have been previously invested to detect the effects of local agents of selection – especially, temperature and population density – on individual populations in the past five decades (e.g., Moores and Winters, 1982; Sinclair *et al.*, 1982; Anthony and Fogarty, 1985; Brunel and Dickey-Collas, 2010; Becker *et al.*, 2020). In this regard, I believe that the DFO Science branch, and the research community as a whole, would benefit immensely from the creation of a Data Centre for biological research, wherein all data relevant to the assessment of marine fish stocks would be compiled in a common location and standardized format. Whether this takes the form of a publicly accessible database, such as the Database of Trawl Surveys (DATRAS) developed by the International Council for the Exploration of the Sea (ICES), or a DFO-level repository combining data from multiple regions, matters less than ensuring open access. In my view, developing this type of infrastructure is the most significant step that can be taken to advance our understanding of the dominant themes presented in this thesis.

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Appendix A. Supplementary Material for Chapter 2

A1. Statistical Independence

The data used in the present study originated from a very large number of relatively small samples, indicating that individual length observations were largely independent from one another (**Table A1**). Statistical non-independence would have emerged, or have been more problematic if, for example, the data had been dominated by a small number of samples each containing a large number of similar-sized fish; in such an instance, inclusion of random effects (for individual-level analysis) or exclusion of large samples (for cohort-level analysis) would have been necessary to remove the confounding influence of sampling on the dependent variable. This was not necessary for our analysis given that individual data points were averaged by cohort.

It is also important to note that scientific gillnets – the main source of fishery-independent data in the Newfoundland region – comprise multiple panels of different mesh sizes. Samples captured using this gear type usually consist of 50 randomly chosen herring from each net panel, thereby considerably reducing the size-selectivity otherwise associated with gillnets. Notably, this is in contrast to commercial gillnets, which tend to be highly selective with respect to girth and other commercially desirable traits (these have been excluded from the analysis).

Table A1 Number of fish (n) and samples (S) per population and gear type. Sample sizes are provided with the mean and standard deviation (s.d.), range and median of the distribution.

Gear type	Number of fish	Number of samples	Mean n per S (s.d.)	Range of n per S (median)
SWNS-BoF				
Purse seine	32371	3673	8.81 (7.86)	1 – 95 (7)
Trawl-bottom	625	220	2.84 (2.26)	1 – 17 (2)
Trawl-Midwater	245	37	6.62 (5.78)	1 – 24 (5)
Weir	15191	2148	7.07 (6.96)	1 – 87 (5)
4WX Offshore				
Purse seine	12810	1111	11.53 (9.26)	1 – 105 (10)
Trawl-bottom	2073	645	3.21 (3.24)	1 – 46 (2)
Trawl-Midwater	1171	114	10.27 (9.02)	1 – 67 (11)
Weir	2	1	2 (NA)	2 – 2 (2)
4V Coastal				
Purse seine	3067	318	9.64 (4.65)	1 – 32 (9)
Trawl-bottom	197	67	2.94 (3.25)	1 – 19 (2)
Trawl-Midwater	79	7	11.29 (9.48)	1 – 31 (9)
sGSL Fall				
Purse seine	4982	870	5.73 (6.21)	1 – 45 (4)
Trawl-bottom	1225	328	3.73 (2.94)	1 – 22 (3)
Trawl-Midwater	2279	447	5.1 (4.08)	1 – 29 (4)
Weir	61	15	4.07 (3.2)	1 – 13 (4)
Handline	4	1	4 (NA)	4 – 4 (4)
Pound net	181	44	4.11 (3.95)	1 – 19 (3)
sGSL Spring				
Purse seine	3025	668	4.53 (6.56)	1 – 60 (3)
Trawl-bottom	614	252	2.44 (2.48)	1 – 21 (1.5)
Trawl-Midwater	1613	390	4.14 (4.19)	1 – 23 (3)
Weir	63	14	4.5 (4.54)	1 – 19 (4)
Pound net	1380	107	12.9 (12.52)	1 – 51 (8)
nGSL Fall				
Purse seine	2941	818	3.6 (4.34)	1 – 42 (2)
Trawl-bottom	1013	283	3.58 (4.59)	1 – 39 (2)
Trap	194	43	4.51 (4.63)	1 – 21 (3)
Tuck seine	92	18	5.11 (4.2)	1 – 13 (4.5)
nGSL Spring				
Purse seine	5630	944	5.96 (8.13)	1 – 48 (3)
Trawl-bottom	738	254	2.91 (3.3)	1 – 24 (2)
Trap	66	20	3.3 (3.16)	1 – 13 (2.5)
Tuck seine	9	6	1.5 (1.22)	1 – 4 (1)
FB Fall				
Purse seine	36	24	1.5 (1.14)	1 – 5 (1)
Trawl-bottom	2	2	1 (0)	1 – 1 (1)
Trap	6	6	1 (0)	1 – 1 (1)

Gear type	Number of fish	Number of samples	Mean n per S (s.d.)	Range of n per S (median)
Bar seine	23	20	1.15 (0.37)	1 – 2 (1)
Miscellaneous	4	4	1 (0)	1 – 1 (1)
Ring net	9	4	2.25 (1.26)	1 – 4 (2)
Scientific gillnet	325	164	1.98 (1.67)	1 – 13 (1)
FB Spring				
Purse seine	3087	163	18.94 (17.88)	1 – 50 (11)
Trawl-Midwater	4	3	1.33 (0.58)	1 – 2 (1)
Trap	93	8	11.62 (15.55)	1 – 40 (2.5)
Bar seine	1043	72	14.49 (14.97)	1 – 50 (7)
Miscellaneous	26	5	5.2 (3.42)	2 – 11 (4)
Ring net	54	3	18 (14.93)	1 – 29 (24)
Scientific gillnet*	2153	326	6.6 (8.46)	1 – 44 (3)
SMB-PB Fall				
Purse seine	158	79	2 (1.93)	1 – 13 (1)
Trawl-bottom	4	1	4 (NA)	4 – 4 (4)
Trawl-Midwater	4	3	1.33 (0.58)	1 – 2 (1)
Trap	55	3	18.33 (18.01)	6 – 39 (10)
Bar seine	6	5	1.2 (0.45)	1 – 2 (1)
Ring net	123	48	2.56 (2.44)	1 – 11 (1)
Scientific gillnet	700	267	2.62 (2.69)	1 – 20 (2)
SMB-PB Spring				
Purse seine	1218	143	8.52 (11.64)	1 – 43 (2)
Trawl-bottom	16	2	8 (9.9)	1 – 15 (8)
Trawl-Midwater	20	5	4 (2.74)	1 – 8 (4)
Trap	3	2	1.5 (0.71)	1 – 2 (1.5)
Bar seine	152	17	8.94 (9.95)	1 – 30 (3)
Ring net	1184	112	10.57 (11.21)	1 – 39 (3.5)
Scientific gillnet	1910	342	5.58 (7.93)	1 – 89 (3)
BB-TB Fall				
Purse seine	451	123	3.67 (4.38)	1 - 29(2)
Trap	225	34	6.62 (6.92)	1 - 27(4.5)
Tuck seine	247	43	5.74 (7.05)	1 - 31(3)
Bar seine	53	17	3.12 (1.96)	1 - 7(4)
Ring net	61	45	1.36 (0.98)	1 - 5(1)
Scientific gillnet	1382	573	2.41 (3.93)	1 - 81(1)
BB-TB Spring				
Purse seine	1891	218	8.67 (11.31)	1 – 49 (3)
Trawl-bottom	1	1	1 (NA)	1 – 1 (1)
Trawl-Midwater	9	7	1.29 (0.49)	1 – 2 (1)
Trap	488	36	13.56 (14.98)	1 – 47 (7)
Tuck seine	160	32	5 (6.81)	1 – 28 (2)
Bar seine	450	56	8.04 (10.15)	1 – 43 (3.5)
Miscellaneous	138	6	23 (23.41)	1 – 46 (22)
Ring net	816	165	4.95 (9.8)	1 – 48 (1)
Scientific gillnet	9869	1474	6.7 (8.76)	1 – 89 (3)
Hook and line	1	1	1 (NA)	1 – 1 (1)

WB-NDB Fall				
Purse seine	205	71	2.89 (4.03)	1 – 25 (1)
Trap	174	24	7.25 (7.27)	1 – 27 (5)
Tuck seine	33	8	4.12 (1.73)	1 – 7 (4)
Bar seine	17	6	2.83 (2.56)	1 - 7(1.5)
Miscellaneous	29	14	2.07 (1.14)	1 - 5(2)
Ring net	12	10	1.2 (0.42)	1 - 2(1)
Scientific gillnet	1001	389	2.57 (4.75)	1 - 46(1)
WB-NDB Spring				
Purse seine	1193	135	8.84 (9.64)	1 - 40(4)
Trap	276	38	7.26 (9.08)	1 - 39(5)
Tuck seine	18	8	2.25 (1.49)	1 - 4(1.5)
Bar seine	127	21	6.05 (9.53)	1 - 39(2)
Miscellaneous	754	79	9.54 (11.11)	1 - 48(5)
Ring net	475	50	9.5 (11.27)	1 - 37(3)
Scientific gillnet	8704	1159	7.51 (8.37)	1 - 47(4)
Hook and line	1	1	1 (NA)	1 - 1(1)

A2. Effect of Gear Type

The proportion of fish sampled by each gear type generally differed among populations (**Table A1**). In particular, we note that sampling programs for warm- and cold-water populations have been dominated by purse seines and scientific gillnets, respectively, since at least 1980. We investigated whether these differences could have confounded the main analysis by estimating trends in mean length-at-age 4 for both gear types, and a third category combining all other gear types ('Other'), separately. Because several factors unrelated to sampling are expected to cause differences in size-at-age between warm and cold-water populations (*e.g.*, temperature), we focused the comparisons on the subset of 8 populations that have been consistently sampled by all gear types over the majority of the time period investigated.

The trends in mean length-at-age 4 were very comparable among gear types for the 8 populations considered (**Figure A1**). Higher variability for the purse seine observations likely reflected the lower sample sizes associated with this category; this suggests that repeating the analysis using purse seine-only data would likely result in similar outcomes. The similar trends observed for the 'Other' category also validate the assumption that most gear types were non selective with respect to size.

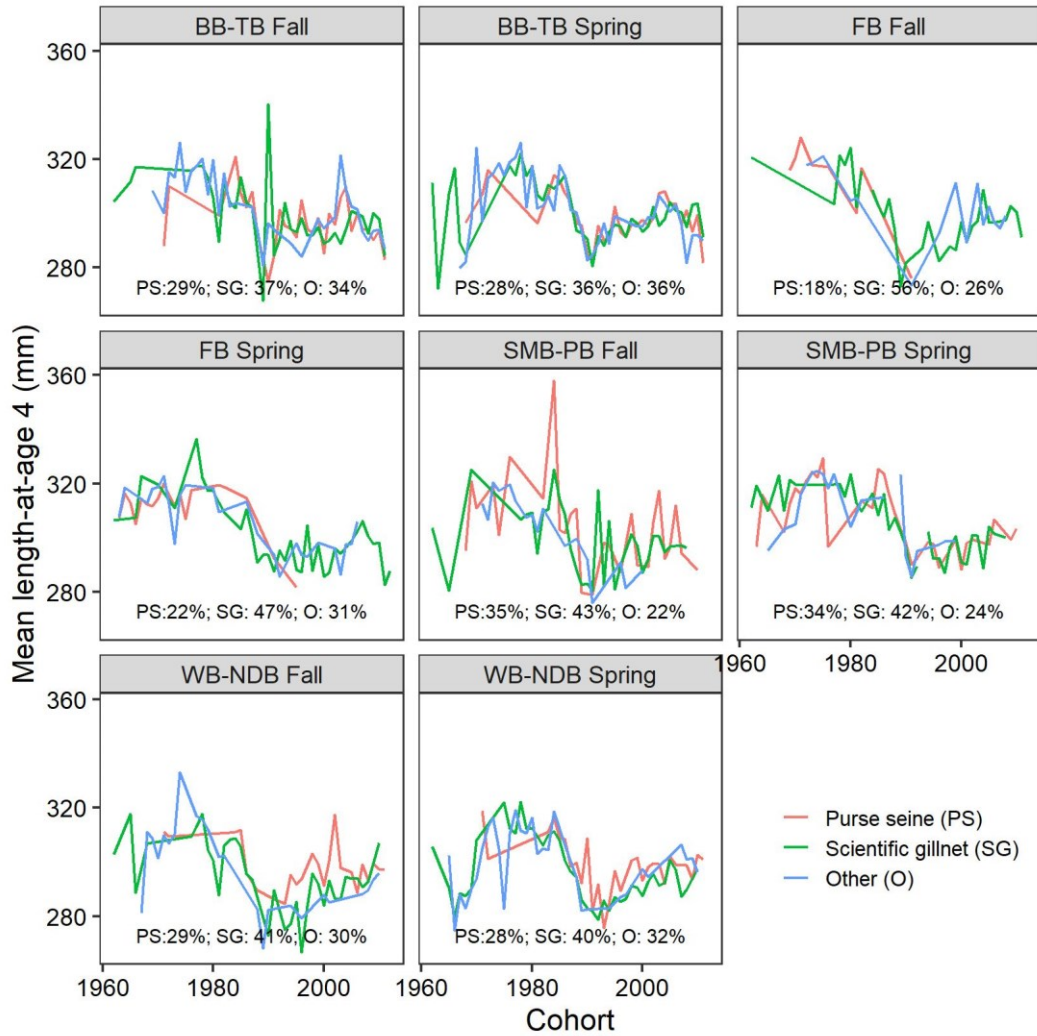


Figure A1 Comparison of trends in mean length-at-age 4 estimated from samples captured using purse seines, and scientific gillnets and other types of fishing gear combined, for 8 populations in Newfoundland. The percentages at the bottom of each panel indicate the proportions of total sample sizes (number of fish n in **Table A1**) that were captured by each gear class.

A3. Sample Sizes

Sample sizes by population and cohort are summarised in **Table A2**. Each value represents the number of fish used to estimate seasonally adjusted mean lengths-at-age 4 (*i.e.*, each cell is one datum in **Figures 2.3-2.4** in the main text; the total number of data points is 722).

Table A2 Sample sizes for the seasonally adjusted mean lengths-at-age 4 for the 15 Canadian herring populations examined in the present study, over the cohorts 1962-2014. Detailed sample size information for the GOM population was not available, but a description of the methods is provided in Becker *et al.* (2020).

Cohort	SWNS- BoF	4WX Offshore	4V Coastal	sGSL Fall	sGSL Spring	nGSL Fall	nGSL Spring	FB Fall	FB Spring	SMB- PB Fall	SMB- PB Spring	BB- TB Fall	BB- TB Spring	WB- NDB Fall	WB- NDB Spring
1962	0	0	0	0	0	14	6	1	5	3	4	13	5	26	3
1963	0	0	0	0	0	0	30	0	2007	0	38	0	36	0	0
1964	0	0	0	0	0	4	9	0	16	0	1	0	0	0	0
1965	0	0	0	0	0	26	102	0	2	2	14	1	4	5	16
1966	892	404	0	294	48	10	31	0	134	0	170	1	5	2	11
1967	335	147	0	271	73	1	11	4	46	0	4	0	104	1	86
1968	547	216	0	138	0	19	1025	0	757	5	801	0	823	4	522
1969	640	155	232	103	4	41	34	8	11	21	16	1	7	2	218
1970	3507	1710	864	73	61	18	17	2	88	1	32	0	1	6	37
1971	708	460	181	73	202	9	18	4	163	1	38	17	16	5	17
1972	2748	1581	605	175	221	28	65	4	122	1	211	7	142	11	84
1973	3657	1390	216	28	88	3	29	11	9	22	58	7	15	4	11
1974	437	136	0	254	956	6	251	0	631	12	1027	3	39	1	80
1975	1250	79	0	562	437	7	11	1	31	0	35	1	31	0	2
1976	4129	614	381	479	283	32	14	1	2	30	21	21	129	4	400
1977	2159	794	132	40	58	62	294	8	1	30	6	43	25	13	21
1978	557	332	96	181	75	32	27	6	15	6	10	25	96	65	72
1979	2112	815	36	64	124	181	288	58	48	129	17	262	473	307	516
1980	1050	662	113	139	189	87	1211	7	112	51	56	42	135	45	118
1981	1777	197	32	31	60	75	97	20	4	86	22	96	200	65	93
1982	1937	554	66	51	112	103	552	28	839	83	542	119	3226	45	1172
1983	3059	548	52	13	49	18	98	2	0	22	0	29	217	38	396
1984	1147	287	74	71	68	23	30	4	0	8	6	13	84	38	77
1985	997	163	25	115	130	41	61	1	6	19	28	10	931	18	273
1986	1567	374	0	49	106	48	32	12	16	23	102	52	379	70	215

Cohort	SWNS- BoF	4WX Offshore	4V Coastal	sGSL Fall	sGSL Spring	nGSL Fall	nGSL Spring	FB Fall	FB Spring	SMB- PB Fall	SMB- PB Spring	BB- TB Fall	BB- TB Spring	WB- NDB Fall	WB- NDB Spring
1987	1449	372	106	95	90	82	225	7	130	32	131	89	1887	34	2055
1988	761	201	0	352	528	143	79	7	22	11	3	22	46	89	155
1989	668	234	0	189	208	61	180	1	1	10	9	31	112	6	104
1990	332	148	0	107	225	213	294	13	138	55	123	40	358	4	948
1991	552	170	5	354	424	190	75	9	99	13	109	31	1142	3	83
1992	1015	748	0	190	109	36	28	0	52	2	108	7	34	0	3
1993	397	281	0	435	255	106	11	10	4	8	1	12	11	7	5
1994	1040	326	11	193	491	84	118	2	2	15	6	31	104	19	809
1995	96	38	0	246	139	352	114	0	38	1	14	33	405	8	394
1996	337	71	6	374	168	96	126	4	84	10	99	8	38	16	73
1997	211	90	6	0	0	24	98	0	36	2	4	7	55	6	239
1998	167	40	0	18	4	227	10	8	2	8	2	23	131	31	61
1999	176	0	0	128	60	134	173	2	68	5	189	34	637	28	930
2000	237	1	0	0	0	237	67	25	14	25	15	83	94	40	180
2001	259	3	0	700	64	71	63	37	6	68	12	148	124	62	199
2002	144	44	0	279	42	30	85	4	222	23	227	14	419	14	290
2003	68	23	0	153	43	64	11	22	8	29	10	5	56	12	32
2004	67	2	0	77	24	60	3	4	2	18	3	29	35	12	20
2005	845	268	16	238	31	268	11	16	5	67	18	44	66	83	66
2006	285	207	12	281	127	41	11	2	20	34	92	44	51	27	90
2007	595	149	10	176	93	115	12	3	2	21	24	25	26	23	54
2008	521	284	5	148	59	196	21	37	21	31	40	400	55	109	261
2009	229	78	10	99	39	127	31	4	18	0	2	106	679	13	39
2010	391	139	12	195	23	26	3	1	9	7	3	194	74	45	16
2011	530	161	12	89	30	105	12	1	5	0	0	196	61	5	2
2012	496	133	0	85	40	119	36	4	387	0	0	0	0	0	0
2013	850	164	27	244	25	84	145	0	0	0	0	0	0	0	0
2014	502	63	0	83	10	61	58	0	0	0	0	0	0	0	0
Total	48432	16056	3343	8732	6695	4240	6443	405	6460	1050	4503	2419	13823	1471	11548

A4. Seasonal Adjustments of Lengths-At-Age

An initial requirement of the analysis was to produce seasonally consistent estimates of mean lengths-at-age 4 that could be compared among all populations and over time. We accounted for intra-annual variations in lengths-at-age caused by differences in the timing of sampling using the growing degree-day (GDD) metric, the time-based integral of heat available for growth during ontogeny. Although the application of a linear approach conflicts with the main premise of the article (that body size responds to temperature nonlinearly), adjustments were intended for seasonal variation in temperature calibrated to individual cohorts, not interannual variation in temperatures. Furthermore, these adjustments were small (average range: 0.124 – 1.76 cm) and had a negligible impact on the models when compared to the analyses performed on unadjusted data (**Table A3, Figure A2**).

Air temperature data at a daily temporal resolution were obtained from Environment Canada's National Climate Data and Information Archive, using the *weathercan* R package (LaZerte and Albers, 2018). On the rare occasions when measurements were unavailable, missing values (fewer than 20) were imputed by linear interpolation. Following the methodology presented by Neuheimer and Taggart (Neuheimer *et al.*, 2008), the GDD at day n ($^{\circ}\text{C} \times \text{d}$) was calculated as,

$$(A4.1) \quad GDD(n) = \sum_{i=1}^n (T_i - T_{th}) \times \Delta d, \quad T_i \geq T_{th},$$

where T_i is the mean temperature at day i , T_{th} is a predetermined threshold temperature below which growth is effectively zero, and Δd is the sampling frequency (here, 1 day). The thermal history of each individual fish was described from its presumed date of birth

($i=1$; representing the midpoint of the spawning peak; around 30 April for spring spawners and 30 September for fall spawners; *e.g.*, DFO, 2020, 2021) to its recorded date of capture ($i=n$). We used a temperature-based threshold of 5.0 °C because most of the herring populations included in the analysis overwinter in deeper waters at temperatures of 4 to 5°C (HPB, unpublished result), a period during which growth does not occur.

For each population and cohort, length-at-day (LaD) was regressed on GDD ,

$$(A4.2) \quad LaD = \alpha_0 + \alpha_1 \times GDD + \varepsilon,$$

where α_0 and α_1 are the intercept (mm) and slope (mm (°C · d)⁻¹), respectively, of the LaD-at-GDD relation, and ε is a normally distributed error term. Equation A4.2 was parameterized for mature and immature individuals separately to avoid the discontinuities in energy allocation patterns that occur upon maturation (Stearns and Koella, 1986).

For each given year of capture, length was adjusted to length in the fall, as follows:

$$(A4.3) \quad L_{adj}(y) = L_{capture}(y) + (\alpha_1(c) \times \Delta GDD),$$

where $L_{adj}(y)$ is the predicted length of individual i for a pre-defined day and month in year y (here, 30 September), $L_{capture}(y)$ is the observed length of this individual on the recorded date of capture in year y , $\alpha_1(c)$ is the slope of the LaD-at-GDD relation for the individual's cohort c , and ΔGDD corresponds to the difference in GDDs between the date of capture and the pre-defined date in year y (for individuals captured before 30 September, $\Delta GDD > 0$; for individuals captured on 30 September, $\Delta GDD = 0$; and for individuals captured after 30 September, $\Delta GDD < 0$). This common date was chosen

because cohort-specific sample sizes were generally maximized over the August-November period, thus minimizing the recourse to this adjustment.

Analyses performed on unadjusted data

Analyses performed on original (*i.e.*, seasonally unadjusted) mean length-at-age 4 estimates provided the strongest evidence for model 5, indicating that the small corrections applied to individual lengths had a negligible impact on the model comparisons or inferences (**Table A3**; **Figure A2**). Population-specific T_{opt} based on unadjusted data were similar to those estimated using seasonally adjusted data (**Figure 2.3** in the main text) (**Figure A3**).

Table A3 Support for models describing the functional relationship between unadjusted mean lengths-at-age 4 and lifetime SST (β 's are model parameters; T is the mean temperature experienced up to an age of 4 years; s indicates the population; Δ_i is the AICc of model i minus the minimum AICc of the considered models; and w_i is the Akaike weight for model i).

Model	Covariates	Adj. R ²	Δ_i	w_i
1	$\beta_{0,s} + \beta_1 T$	0.52087	44.335	0
2	$\beta_{0,s} + \beta_{1,s} T$	0.55565	6.3010	0.04101
3	$\beta_0 + \beta_1 T + \beta_2 T^2$	0.32322	280.71	0
4	$\beta_{0,s} + \beta_1 T + \beta_2 T^2$	0.53670	20.991	0
5	$\beta_0 + (\beta_1 + \beta_{2,s}) \cdot T + (\beta_3 + \beta_{4,s}) \cdot T^2$	0.56018	0	0.95753
6	$\beta_{0,s} + (\beta_1 + \beta_{2,s}) \cdot T + (\beta_3 + \beta_{4,s}) \cdot T^2$	0.56314	13.015	0.0014286

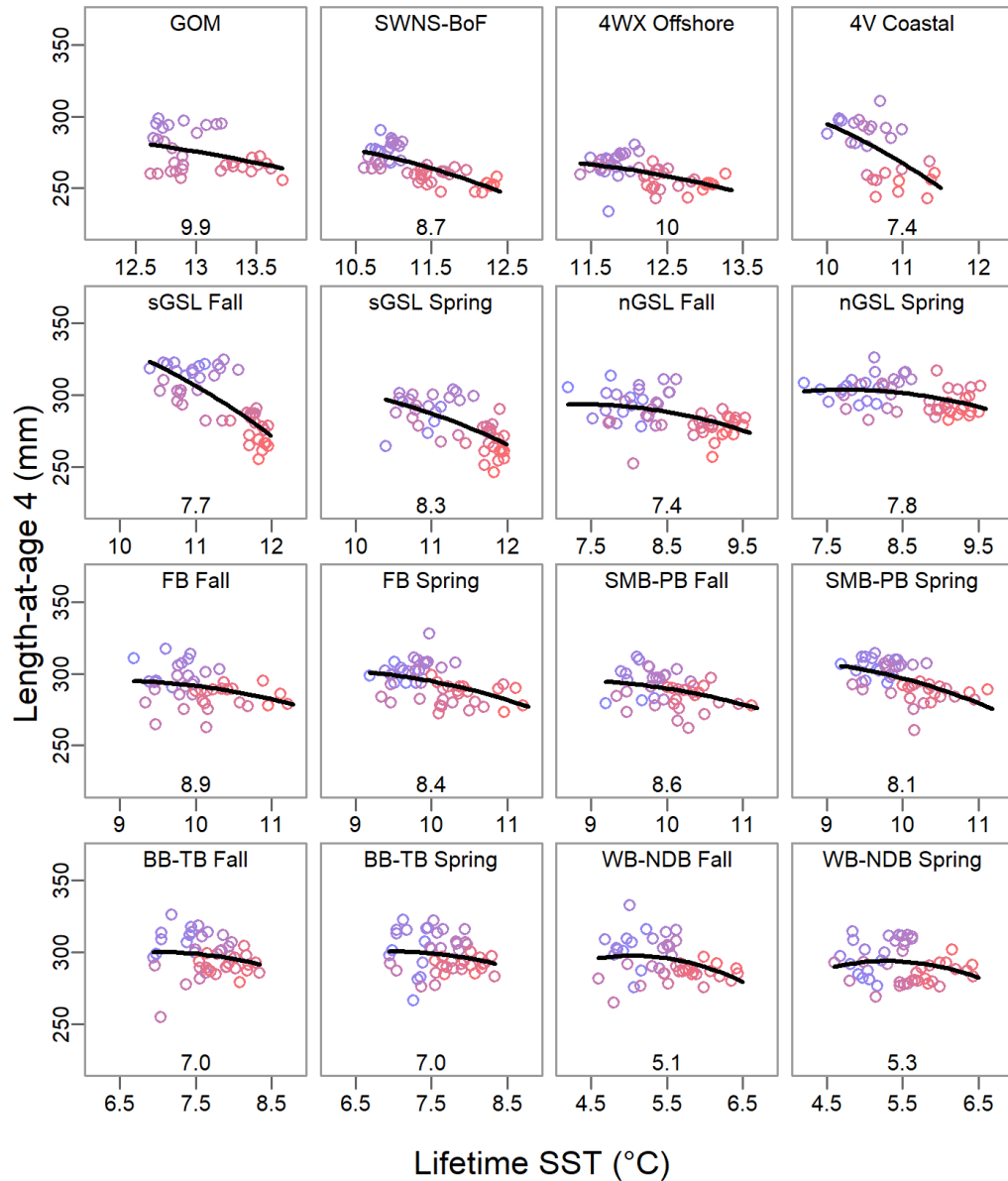


Figure A2 Seasonally unadjusted mean length-at-age 4 as a function of lifetime SST for the 16 Atlantic herring populations, with predictions from model 5 illustrated as a black solid line and model-inferred T_{opt} indicated at the bottom of each panel. The color gradient from blue to red illustrates the temporal progression of data points for cohorts from 1962 to 2014.

A5. Covariate Data

Monthly estimates of the North Atlantic Oscillation index (NAO) were extracted from the NOAA Climate Prediction Center online database (<https://www.cpc.ncep.noaa.gov/data/teledoc/nao.shtml>) and averaged over the May-November period each year.

Spawning stock biomass (SSB) estimates were obtained from publicly available reports by Fisheries and Oceans Canada (DFO) and the Northeast Fisheries Science Center (NEFSC), as well as from fishery-independent sources (**Table A4; Figure A3**). With the exceptions of sGSL Fall/Spring and GOM, assessment models have either been discontinued or never used in most populations. We also note that abundance data for the 4R populations were taken to be representative of the entire nGSL given that they dominated the area in terms of sample sizes (4R Fall and 4R Spring accounted for 81.1 and 93.7% of the data points, respectively).

Table A4 Original sources and locations within those sources (F: Figure; T: Table) of SSB data for 7 populations for which we tested the density-dependence hypothesis.

Population	Ages	Period (years)	Source	Location
sGSL Fall	≥ 2	1969-1977	Cleary (1981)	T9
		1978-2016	McDermid <i>et al.</i> (2018)	T30
sGSL Spring	≥ 2	1969-1977	Cleary (1981)	T9
		1978-2018	McDermid <i>et al.</i> (2018)	T20
SWNS-BoF	≥ 1	1965-2000	Stephenson <i>et al.</i> (2000)	T10
	Total	1999-2014	Singh <i>et al.</i> (2016)	T13
GOM	Total	1965-2017	NEFSC (2018)	FB1 (upper)
4R Fall (nGSL Fall)	≥ 2	1965-1998	McQuinn <i>et al.</i> (1999)	T16
4R Spring (nGSL Spring)	≥ 2	1965-1999	McQuinn <i>et al.</i> (1999)	T13
FB Spring	≥ 2	1966-1981	Winters and Moores (1980)	T5

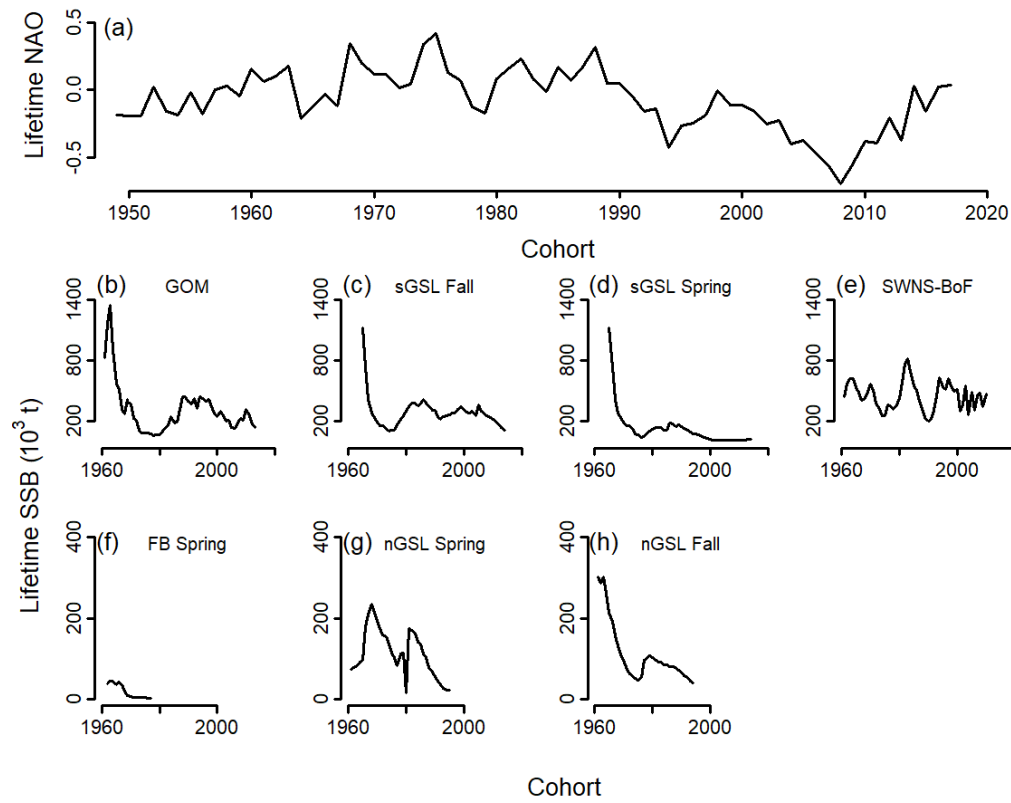


Figure A3 Trends across cohorts in (a) lifetime NAO index (4-year average, May-November period), and (b-h) available estimates of spawning stock biomass (SSB) for 7 populations for which we tested the density-dependence hypothesis.

A6. Dynamic Factor Analysis: Model Comparisons

Table A5 Comparison of dynamic factor analysis (DFA) models incorporating one or two common trends (m) and either no or one covariate (D) (Δ_i is the AICc of model i minus the minimum AICc of the considered models and w_i is the Akaike weight for model i).

Model	Trends (m)	Covariates (D)	Log-likelihood	Δ_i	w_i
7	1	None	-797.6	90.66	0
8	2	None	-735.5	0	0.9777
9	1	NAO	-782.7	96.72	0
10	2	NAO	-720.5	7.567	0.02241

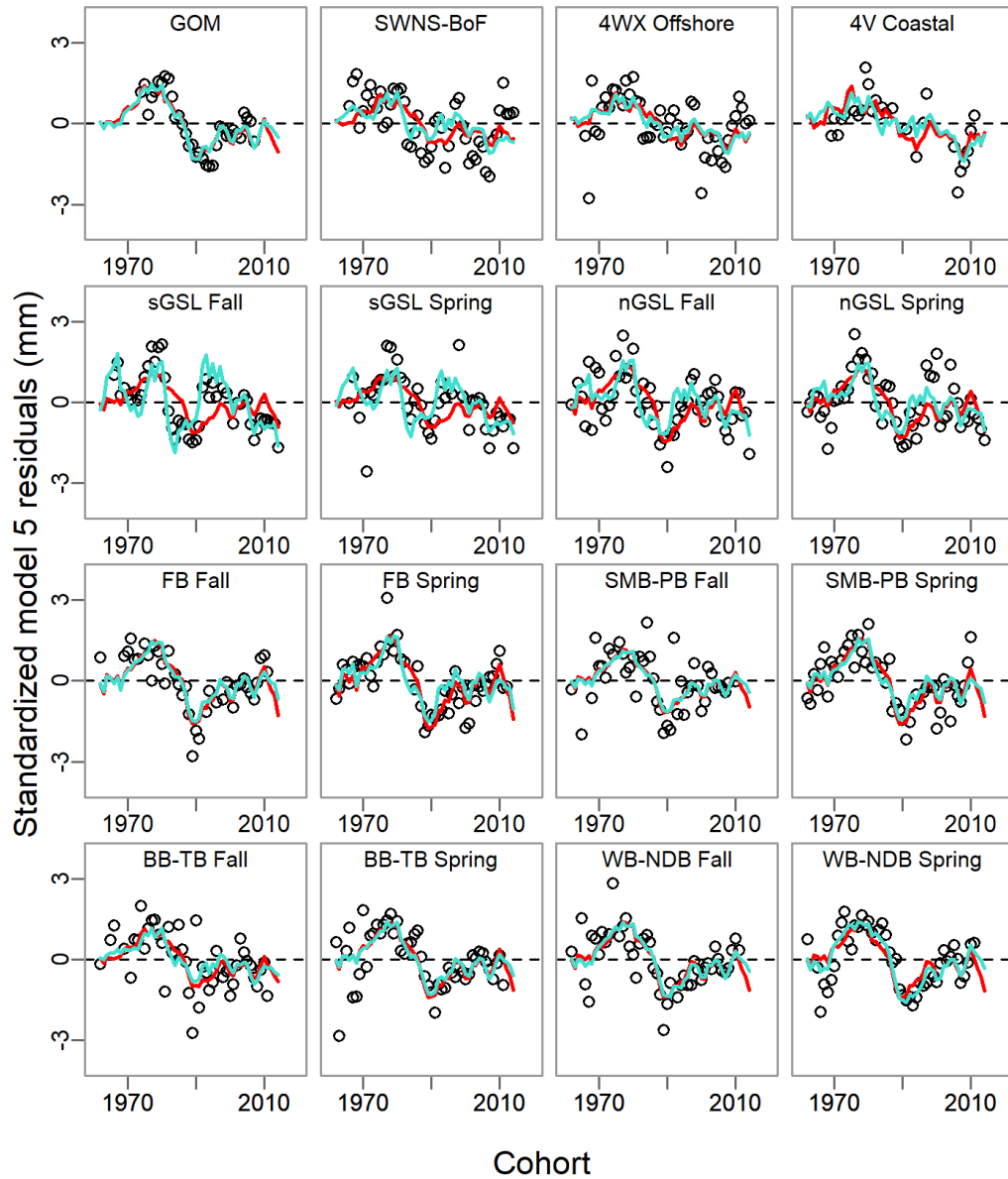


Figure A4 Trends across cohorts in the standardized residuals of model 5 for the 16 Atlantic herring populations. The solid lines provide the predictions of a dynamic factor analysis (DFA) model with the NAO index as a covariate and either one (red: model 9) or two (turquoise: model 10) common trends.

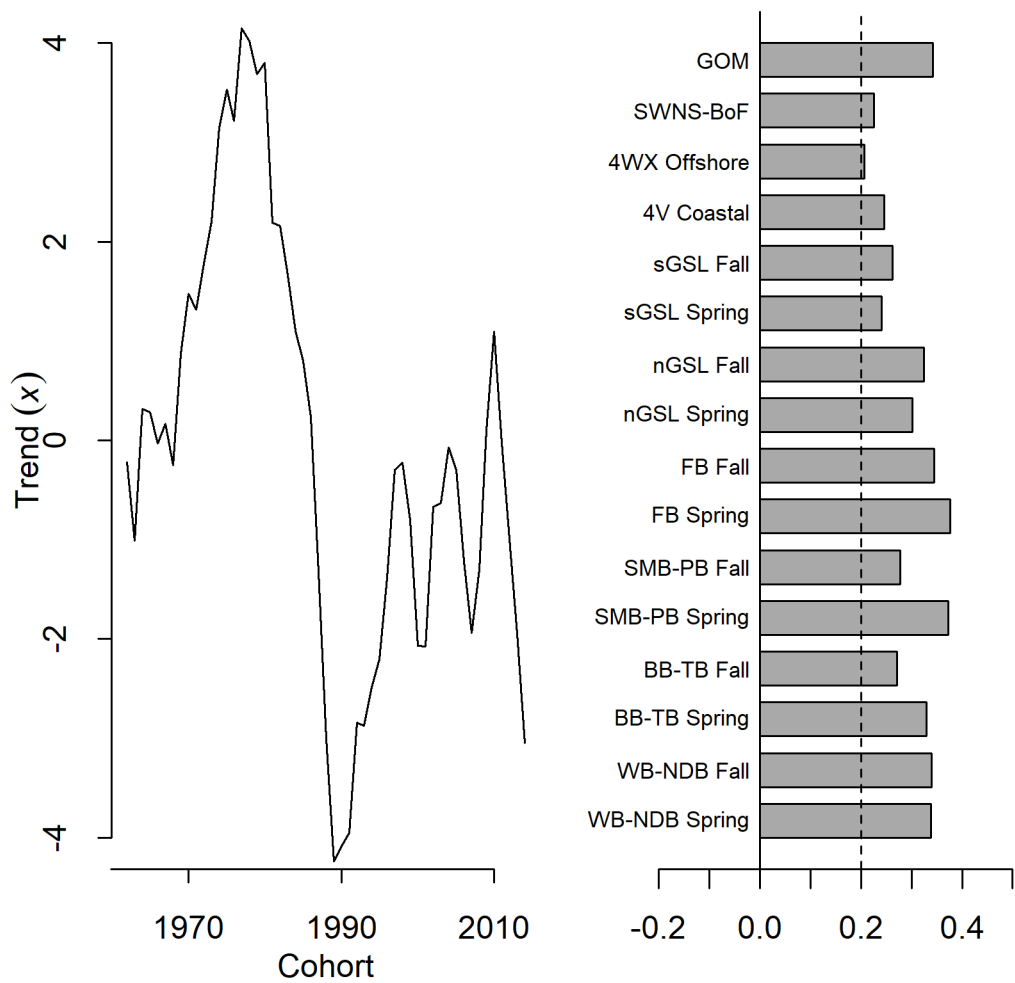


Figure A5 Population-specific loadings on the dominant common trend of DFA model 7. The vertical line shows an arbitrary cutoff level of 0.2 for determining whether a time series was associated with x_t or not (Zuur *et al.*, 2003).

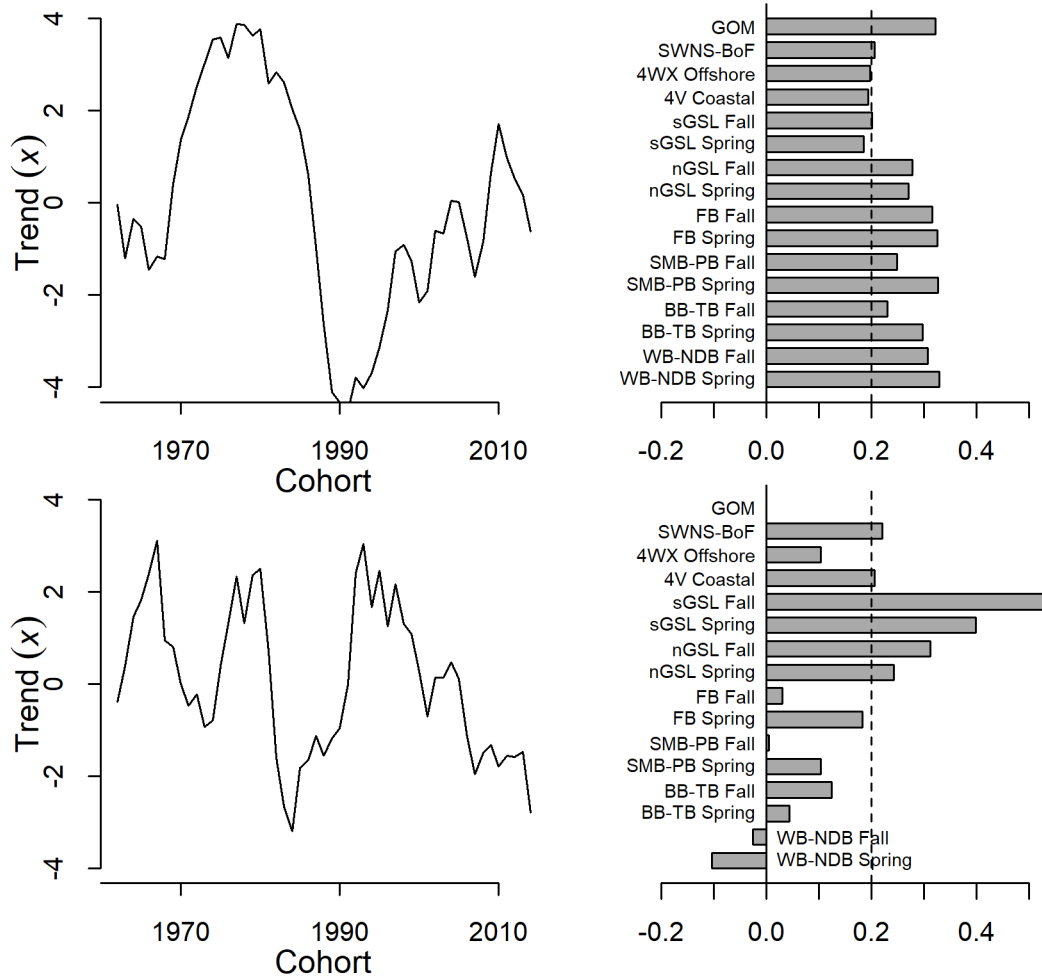


Figure A6 Population-specific loadings on the dominant common trends of DFA model 8. The vertical line shows an arbitrary cutoff level of 0.2 for determining whether a time series was associated with x_t or not (Zuur et al., 2003).

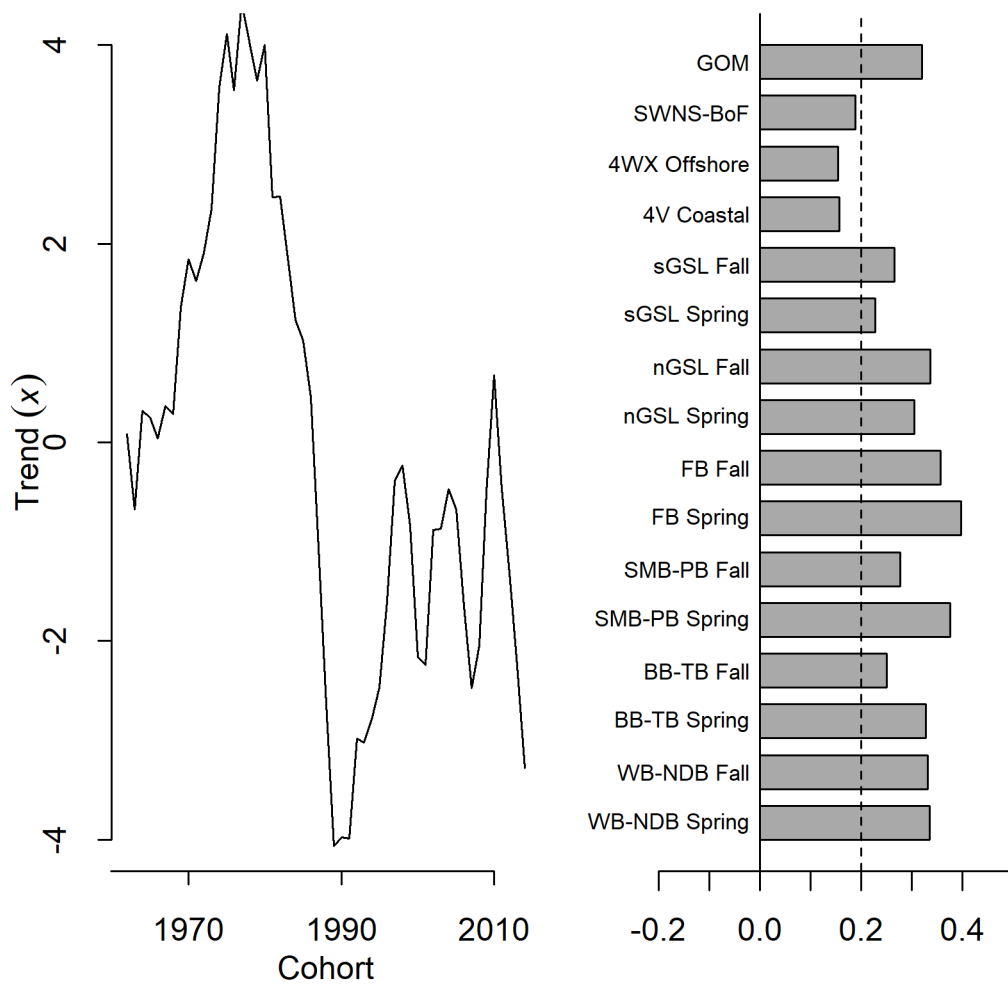


Figure A7 Population-specific loadings on the dominant common trend of DFA model 9. The vertical line shows an arbitrary cutoff level of 0.2 for determining whether a time series was associated with x_t or not (Zuur *et al.*, 2003).

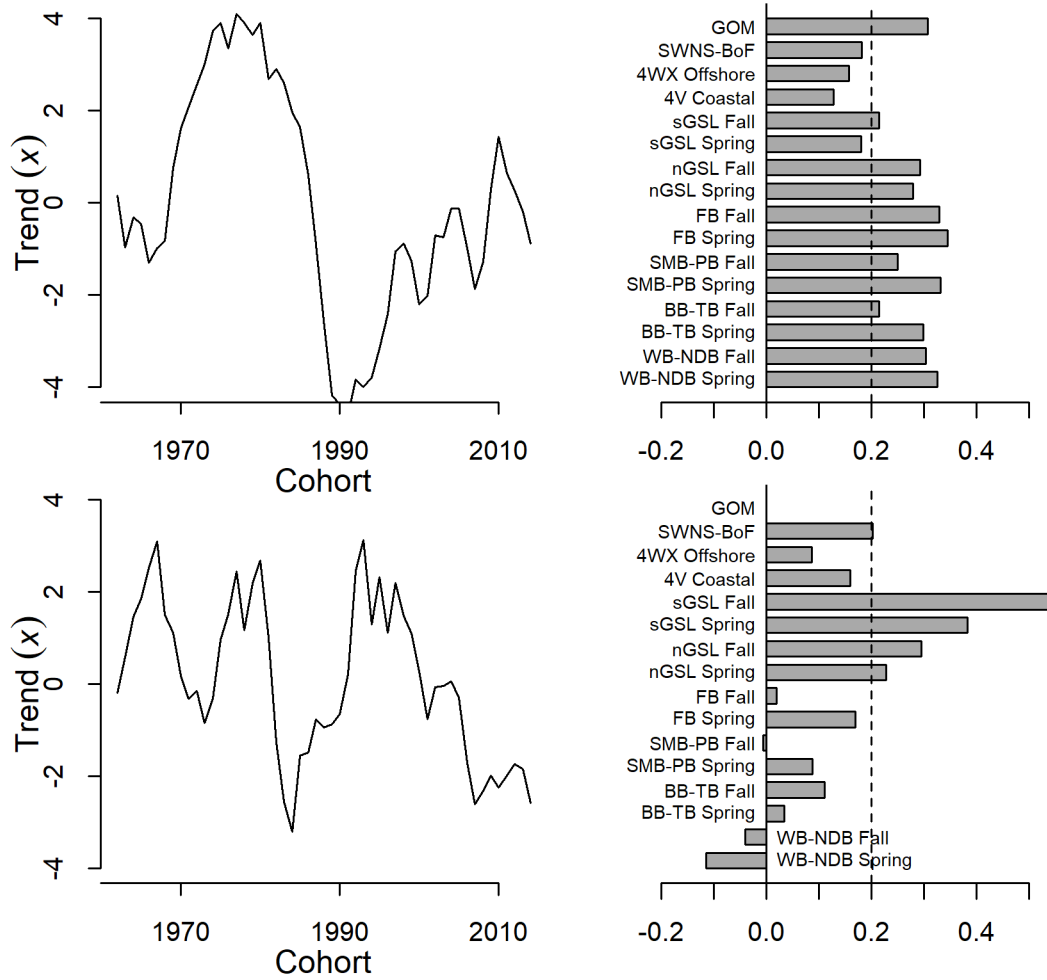


Figure A8 Population-specific loadings on the dominant common trends of DFA model 10. The vertical line shows an arbitrary cutoff level of 0.2 for determining whether a time series was associated with x_t or not (Zuur *et al.*, 2003).

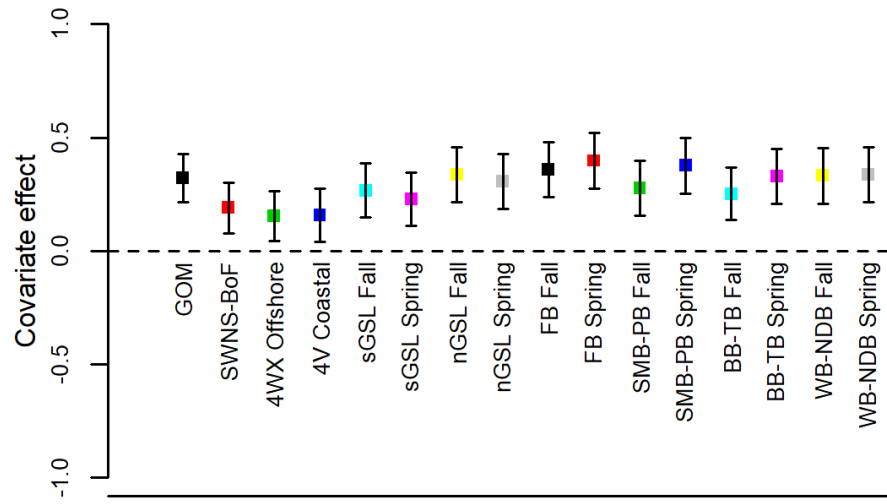


Figure A9 Maximum likelihood estimates and 95% confidence intervals for the NAO effect of the DFA model 9.

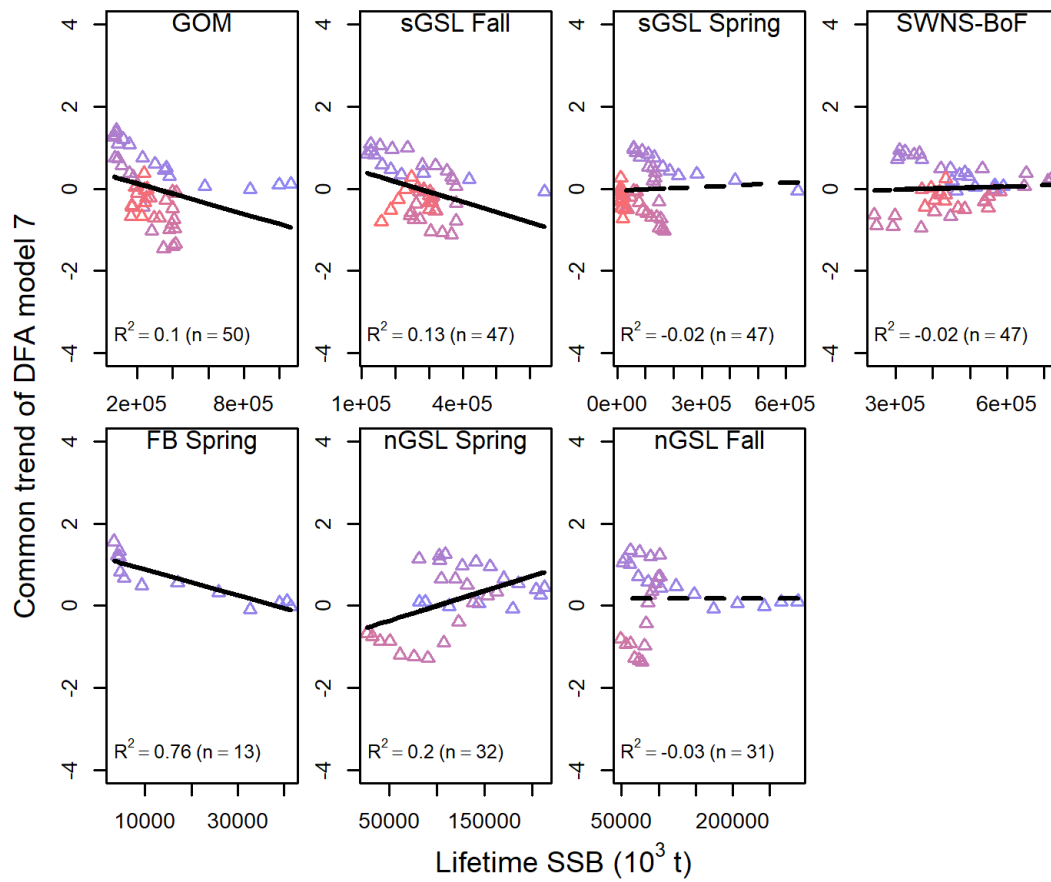


Figure A10 Common trend of DFA model 7 as a function of lifetime SSB for each cohort (age groups specified in **Table A4**). The color gradient from blue to red illustrates the temporal progression of data points for cohorts from 1962 to 2014. The black solid and dashed lines show statistically significant and non-significant model fits, respectively.

A7. Supporting Information for Figure 2.2a

Table A6 Supporting information for the trends in temperature reported in the main text (**Figure 2.2a**). Coefficients of variation were calculated as the standard deviation of all monthly observations divided by the mean (these were restricted to the NOAA temperature dataset).

Location	Baseline lifetime SST °C	Rate of increase in lifetime SST °C · cohort ⁻¹ ± S.E.	Coefficient of variation (<i>n</i>)
4V Coastal	10.1	0.0184 (0.00284)	36.3 (343)
BB-TB	7.19	0.0185 (0.00263)	57.4 (378)
GOM	12.3	0.0249 (0.00370)	25.4 (266)
WB-NDB	4.86	0.00251 (0.00271)	48.2 (378)
SMB-PB and FB	9.42	0.00255 (0.00281)	40.4 (385)
sGSL	10.6	0.0274 (0.00292)	43.9 (371)
4WX Offshore	11.3	0.0295 (0.00283)	32.8 (371)
SWNS-BoF	10.5	0.0300 (0.00278)	31.8 (371)
nGSL	7.60	0.0371 (0.00277)	48.4 (399)

Appendix B. Supplementary Material for Chapter 3

B1. Effect of Seasonality on Maturity Ogives

Since the early 1960s, sampling programs for Atlantic herring have been primarily conducted in the fall (August-November). However, due to differing logistical constraints and assessment resources over time and among regions, sample sizes for some stocks were comparatively greater in the winter and spring seasons (January-June). The potential impact of such differences on the interpretation of trends in maturity ogives was investigated in the well-sampled SWNS-BoF stock, for which sufficient sample sizes were available throughout the year. Following equation 3.1 in the main text, maturity ogives for age and for length were estimated separately in each of the four quarters of the year (Q1: Jan.-Mar.; Q2: Apr.-Jun.; Q3: Jul.-Sept.; Q4: Oct.-Dec.) over the cohorts from 1968 to 2014.

Quarterly estimates of age and length at maturity, denoted as X_{50} , generally differed in mean value, but not in temporal trend (**Figure B1**), noting that higher variability in the January-March period (Q1) was likely a function of the smaller sample sizes available for this time period. This pattern indicates that comparisons of X_{50} values may only be appropriate, or meaningful, among stocks that have been collected at the same point in their seasonal cycle. However, because comparisons in this study primarily focussed on trends over time, and given that each time series focussed on one time of the year only (see **Table 3.1** in the main text), such mean differences should not be consequential for the interpretation of our results.

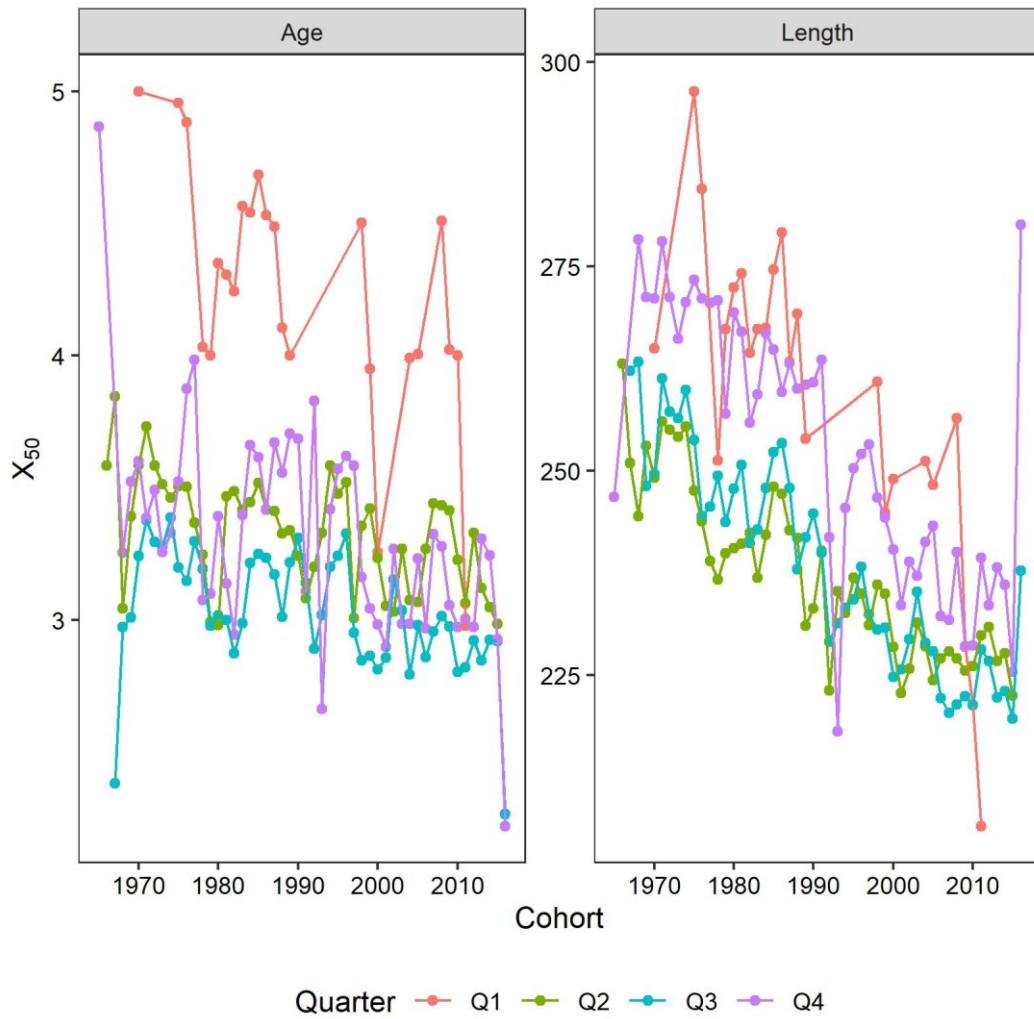


Figure B1 Comparison of trends in age and length at 50% maturity (X_{50}) among samples of the SWNS-BoF stock collected in each quarter of the year (Q1: Jan.-Mar.; Q2: Apr.-Jun.; Q3: Jul.-Sept.; Q4: Oct.-Dec.).

B2. Substitution of L_∞ for L_{\max}

The substitution of asymptotic length (L_∞) for maximum observed length (L_{\max}) requires that both metrics be correlated in the original data (Froese and Binohlan, 2000; Binohlan and Froese, 2009). We tested this requirement for the six herring stocks for which sample sizes at age were sufficient to estimate L_∞ , by parameterizing the von Bertalanffy (1938) growth equation,

$$(B2.1) L(A) = L_\infty \cdot (1 - e^{-k \cdot (A - A_0)}),$$

where L_∞ , k and A_0 are the asymptotic length (mm), Brody growth coefficient (year^{-1}), and theoretical age when the average length was zero (year), respectively. Parameterization of this curve for the two nGSL stocks was complicated by the occurrence of the asymptotic portion of the growth curve in the censored age category (11 years and older). Consequently, calculations for L_∞ were limited to ages 0-10 years and to cohorts with sufficient data at older ages (1970-2005).

Albeit not entirely linear, all stocks exhibited the expected association between L_∞ and L_{\max} among cohorts (**Figure B2**). This evidence was deemed sufficient for the purpose of our study.

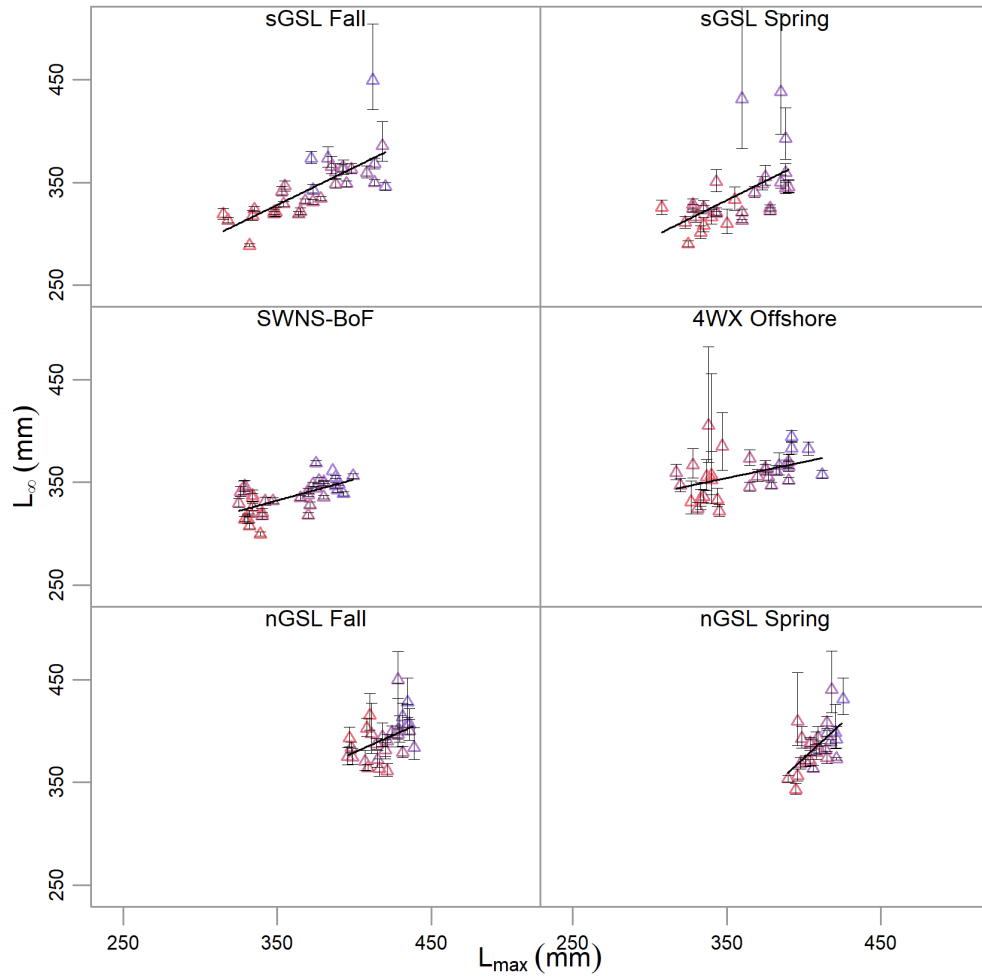


Figure B2 Association between asymptotic length ($L_{\infty} \pm \text{CI95}$) and maximum observed length (L_{\max}) for 6 stocks with sufficient sample sizes to parameterize the von Bertalanffy growth equation. The color gradient from blue to red illustrates the temporal progression of data points for cohorts from 1970 to 2005.

B3. Comparison of the qSCA and qmSCA assessment models for sGSL Fall

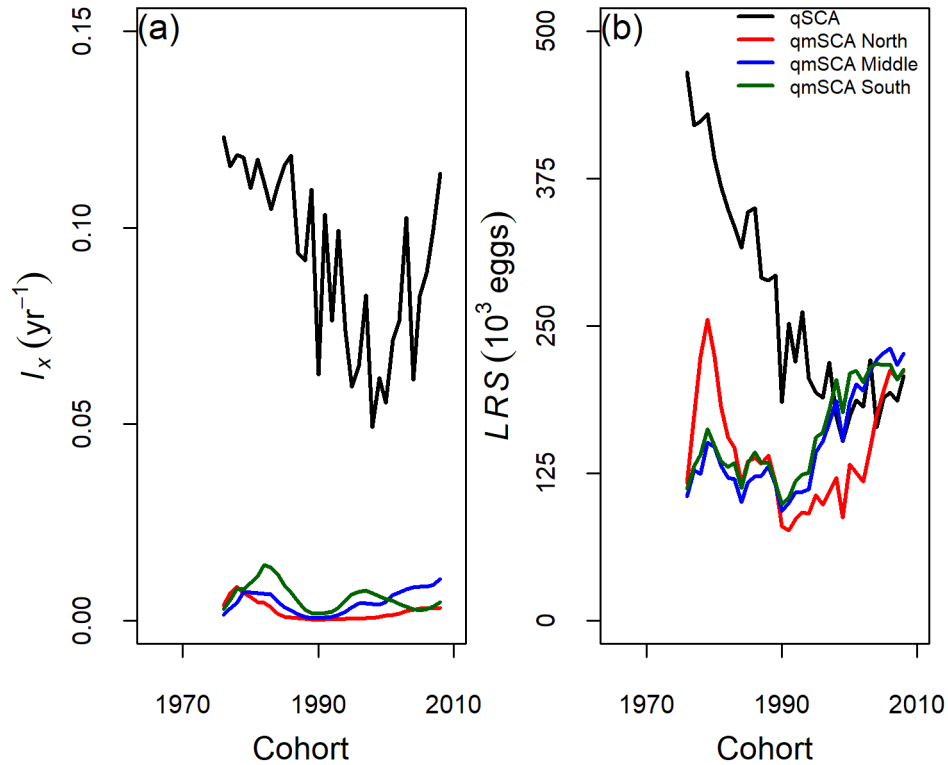


Figure B3 Comparison of trends in (a) survival to age 11 years and (b) lifetime reproductive success (LRS) between the qSCA (statistical catch-at-age model with time-varying catchability and constant $M_x = 0.2$ across all ages) and qmSCA (statistical catch-at-age model with time-varying catchability and time-varying M_x) models, for cohorts of the sGSL Fall stock born between 1976 and 2008. Estimates of F_x and M_x from the qSCA model apply to the entire sGSL whereas those from the qmSCA model are reported by subregion (Turcotte *et al.*, 2021).

B4. Associations Between L_{50} and Mean Length-At-Age 4

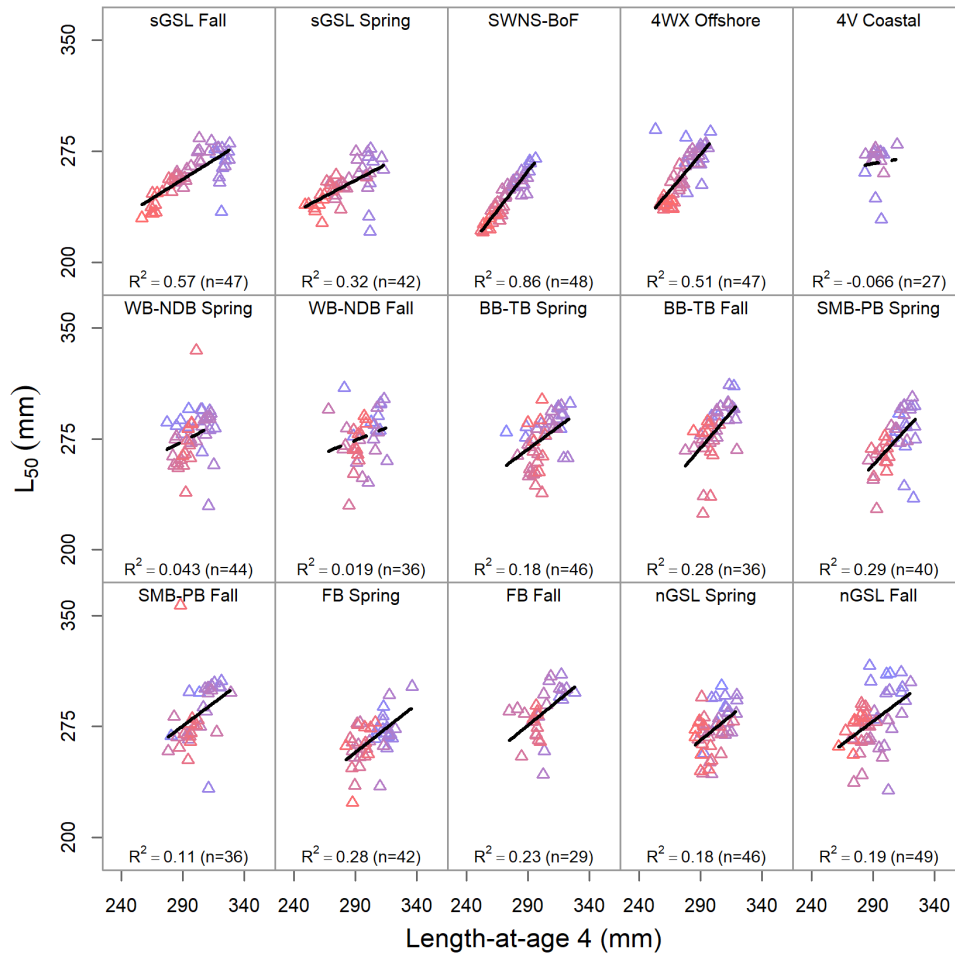


Figure B4 Linear associations between length at maturity (L_{50}) and mean length-at-age 4 for the 15 Atlantic herring stocks examined, with predictions from statistically significant ($p \leq 0.05$) model fits illustrated as black solid lines. The color gradient from blue to red illustrates the temporal progression of data points for cohorts from 1963 to 2015. Adjusted R^2 and associated sample sizes (n) are indicated at the bottom of each panel.

B5. Associations Between L_{50} and A_{50}

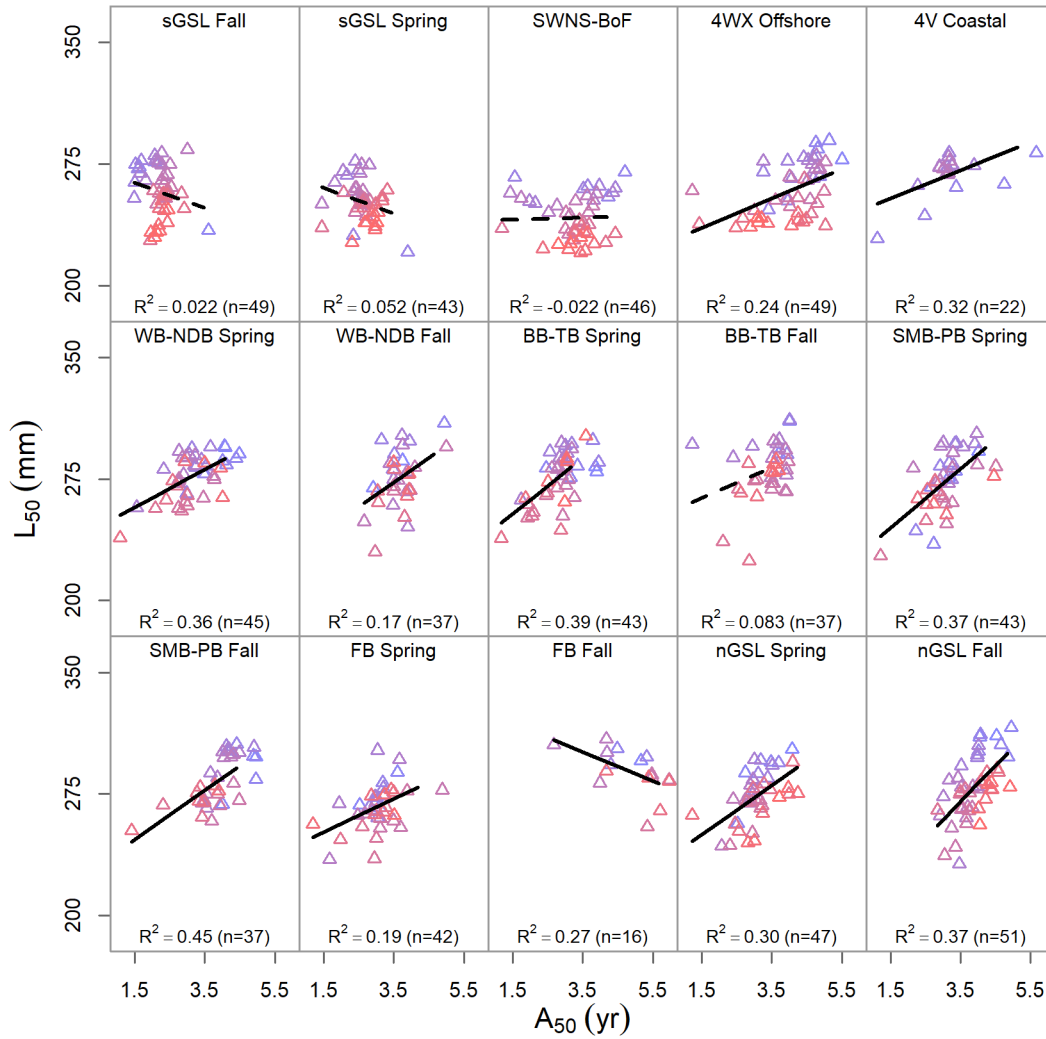


Figure B5 Linear associations between length at maturity (L_{50}) and age at maturity (A_{50}) for the 15 Atlantic herring stocks examined, with predictions from statistically significant ($p \leq 0.05$) model fits illustrated as black solid lines. The color gradient from blue to red illustrates the temporal progression of data points for cohorts from 1963 to 2015. Adjusted R^2 and associated sample sizes (n) are indicated at the bottom of each panel.

B6. Sample Sizes for the Estimation of PMRNs

Table B1 Number of immature and mature fish available for the estimation of PMRNs in the sGSL Fall stock.

Cohort	Age 2		Age 3		Age 4	
	Immat.	Mat.	Immat.	Mat.	Immat.	Mat.
1968	203	150	1	77	0	73
1969	24	62	8	140	0	98
1970	26	42	2	78	1	67
1971	4	20	4	93	0	7
1972	38	232	0	44	0	174
1973	0	3	0	35	0	28
1974	1	9	0	39	2	141
1975	3	102	11	465	0	240
1976	232	127	1	286	1	71
1977	40	94	11	89	0	19
1978	277	204	8	223	0	167
1979	68	148	7	162	1	53
1980	196	134	16	141	0	112
1981	199	89	9	116	1	30
1982	45	22	2	15	1	50
1983	22	10	2	26	0	12
1984	29	3	15	14	3	30
1985	28	3	11	34	0	115
1986	47	12	11	108	1	29
1987	65	28	11	36	2	91
1988	77	29	9	220	6	297
1989	108	37	25	191	0	180
1990	65	11	9	65	3	59
1991	111	26	15	211	2	272
1992	17	11	7	92	3	109
1993	141	40	36	317	2	346
1994	198	47	32	236	3	169
1995	341	162	16	446	0	166
1996	397	127	45	250	3	362
1997	218	73	23	308	0	0
1998	232	153	0	0	0	0
1999	0	0	0	0	5	104
2000	0	0	7	142	0	0
2001	221	88	0	0	10	684
2002	0	0	155	663	0	279
2003	378	95	29	230	0	153

Cohort	Age 2		Age 3		Age 4	
	Immat.	Mat.	Immat.	Mat.	Immat.	Mat.
2004	213	77	15	186	2	72
2005	350	174	20	298	4	234
2006	208	131	22	334	0	193
2007	355	131	13	256	0	161
2008	159	106	19	236	0	105
2009	125	46	7	85	2	86
2010	148	93	15	219	2	150
2011	43	38	0	56	1	79
2012	149	34	8	110	1	80
2013	190	142	13	251	6	238
2014	92	86	20	167	3	73

Table B2 Number of immature and mature fish available for the estimation of PMRNs in the sGSL Spring stock.

Cohor	Age 2		Age 3		Age 4	
	Immat.	Mat.	Immat.	Mat.	Immat.	Mat.
1968	0	0	0	0	0	0
1969	0	0	0	0	0	0
1970	0	0	0	0	0	0
1971	0	0	0	0	0	0
1972	67	21	10	107	3	113
1973	9	3	18	33	2	71
1974	99	50	91	856	8	494
1975	62	14	22	100	1	55
1976	165	43	10	128	4	52
1977	209	493	62	173	0	18
1978	214	196	3	24	0	9
1979	4	20	3	52	11	113
1980	59	14	153	204	1	180
1981	44	4	6	175	2	58
1982	28	60	13	61	2	105
1983	42	7	14	66	0	33
1984	51	15	9	23	1	35
1985	18	3	16	49	2	112
1986	93	26	29	213	5	73
1987	148	56	20	85	0	69
1988	297	69	21	205	17	461
1989	151	53	81	261	2	134
1990	245	34	23	90	4	128
1991	190	47	28	314	10	349
1992	24	6	20	43	4	49
1993	236	29	56	288	2	189
1994	241	16	72	148	18	425
1995	250	29	55	228	5	115
1996	611	65	49	165	3	129
1997	234	43	21	171	0	0
1998	124	44	0	0	0	0
1999	0	0	0	0	0	60
2000	0	0	27	60	0	0
2001	334	22	0	0	7	57
2002	0	0	163	40	2	40
2003	238	28	50	51	2	41
2004	114	19	14	43	1	18

Cohor	Age 2		Age 3		Age 4	
	Immat.	Mat.	Immat.	Mat.	Immat.	Mat.
2005	160	18	40	27	5	26
2006	145	23	57	56	1	106
2007	127	12	28	69	2	77
2008	76	7	68	77	2	40
2009	73	5	28	20	1	24
2010	6	5	6	39	0	16
2011	8	0	7	8	0	28
2012	56	3	24	39	4	36
2013	84	13	14	48	0	25
2014	4	1	3	2	1	7

Table B3 Number of immature and mature fish available for the estimation of PMRNs in the SWNS-BoF stock.

Cohor	Age 2		Age 3		Age 4	
	Immat.	Mat.	Immat.	Mat.	Immat.	Mat.
1968	93	0	197	158	37	271
1969	97	0	27	39	17	146
1970	0	0	1071	608	161	991
1971	569	4	771	183	24	212
1972	4023	5	705	167	49	1064
1973	2985	1	869	476	111	1076
1974	642	1	320	98	19	184
1975	1105	0	558	235	25	511
1976	1803	0	1292	702	88	1403
1977	1334	3	810	252	122	843
1978	169	1	268	95	7	275
1979	1472	6	1076	1474	29	1121
1980	2449	4	993	782	32	752
1981	2552	3	804	671	13	1194
1982	1784	1	574	1428	13	1410
1983	1804	12	1391	1206	107	1513
1984	1626	1	843	341	38	326
1985	1488	1	343	93	20	476
1986	735	0	587	256	55	612
1987	1321	1	489	188	34	618
1988	891	1	414	301	7	403
1989	968	1	295	131	20	389
1990	422	1	355	81	12	195
1991	446	0	404	172	4	276
1992	702	0	109	232	9	400
1993	244	4	38	118	8	254
1994	626	0	418	172	8	568
1995	789	2	196	87	9	52
1996	825	1	176	68	6	165
1997	268	0	30	53	9	114
1998	564	3	198	382	5	90
1999	345	6	66	129	5	121
2000	645	6	89	279	1	187
2001	1067	4	200	485	3	181
2002	441	7	259	131	3	90
2003	304	2	117	113	0	49
2004	260	1	23	71	0	37

Cohor	Age 2		Age 3		Age 4	
	Immat.	Mat.	Immat.	Mat.	Immat.	Mat.
2005	449	3	59	97	13	429
2006	219	1	71	193	4	176
2007	462	0	105	164	9	314
2008	454	0	235	209	2	269
2009	277	0	16	75	1	71
2010	106	0	39	115	1	229
2011	475	0	133	279	1	170
2012	588	0	84	148	3	287
2013	378	0	174	280	16	489
2014	0	0	0	0	0	0

Table B4 Number of immature and mature fish available for the estimation of PMRNs in the 4WX Offshore stock.

Cohort	Age 2		Age 3		Age 4	
	Immat.	Mat.	Immat.	Mat.	Immat.	Mat.
1968	0	0	75	0	185	31
1969	21	0	74	0	64	1
1970	0	0	128	0	453	1195
1971	65	0	313	69	149	226
1972	132	0	792	31	737	510
1973	16	0	335	3	82	15
1974	3	0	141	0	15	8
1975	135	0	38	0	418	176
1976	1	0	443	5	420	133
1977	3	0	84	1	168	84
1978	10	0	382	18	392	228
1979	12	0	333	23	362	71
1980	1	0	226	1	101	39
1981	75	0	149	0	313	69
1982	2	0	173	0	245	109
1983	16	0	136	0	197	35
1984	31	0	180	1	84	3
1985	9	0	67	0	191	23
1986	26	0	376	1	190	23
1987	183	0	142	0	119	18
1988	49	0	81	1	53	61
1989	5	0	50	1	34	31
1990	1	0	111	4	56	34
1991	22	0	169	16	173	218
1992	24	0	142	12	54	77
1993	20	0	101	7	37	85
1994	6	0	3	1	22	3
1995	0	0	77	1	28	6
1996	13	0	20	0	29	40
1997	0	0	248	11	27	8
1998	0	0	3	0	0	0
1999	0	0	3	1	4	19
2000	0	0	28	5	0	0
2001	0	0	0	0	18	74
2002	0	0	18	2	24	39
2003	11	0	70	6	13	29
2004	13	0	45	2	95	43
2005	8	0	44	1	5	15
2006	21	0	8	4	18	40

Cohort	Age 2		Age 3		Age 4	
	Immat.	Mat.	Immat.	Mat.	Immat.	Mat.
2007	11	0	91	35	13	26
2008	17	0	29	7	29	70
2009	2	0	103	5	11	48
2010	17	0	34	9	18	13
2011	67	0	1142	12	1077	271
2012	2	0	0	0	0	1
2013	0	0	0	0	4	31
2014	67	0	33	2	0	0

Table B5 Number of immature and mature fish available for the estimation of PMRNs in the nGSL Fall stock.

Cohort	Age 2		Age 3		Age 4	
	Immat.	Mat.	Immat.	Mat.	Immat.	Mat.
1968	0	0	0	0	0	0
1969	0	0	0	0	0	0
1970	0	0	0	0	0	0
1971	0	0	0	0	0	0
1972	0	0	0	0	0	0
1973	0	0	0	0	0	0
1974	0	0	0	0	0	0
1975	0	0	0	0	0	0
1976	0	0	0	0	0	0
1977	0	0	0	0	0	0
1978	0	0	0	0	0	0
1979	0	0	0	0	0	0
1980	1	0	0	2	3	38
1981	0	0	12	0	0	21
1982	19	0	0	0	2	10
1983	0	0	4	1	5	11
1984	0	0	10	0	1	16
1985	10	0	21	2	5	12
1986	2	0	7	2	10	63
1987	18	0	14	5	71	62
1988	49	0	38	9	11	40
1989	51	0	36	2	16	32
1990	3	0	1	0	21	154
1991	0	0	22	20	3	27
1992	40	0	35	9	33	71
1993	55	2	42	5	10	63
1994	4	0	7	1	112	238
1995	0	0	102	14	31	49
1996	13	0	7	2	3	16
1997	18	0	52	1	33	158
1998	4	0	27	2	26	27
1999	4	0	5	0	40	17
2000	0	0	22	0	20	20
2001	0	0	23	3	186	53
2002	2	0	16	0	24	8
2003	27	0	19	0	72	24
2004	0	0	129	1	32	46
2005	0	0	2	1	50	48
2006	0	0	27	1	9	7

Cohort	Age 2		Age 3		Age 4	
	Immat.	Mat.	Immat.	Mat.	Immat.	Mat.
2007	14	0	28	0	46	39
2008	4	0	48	0	25	19
2009	1	0	3	0	32	29
2010	1	0	2	0	27	27
2011	0	0	0	0	0	0
2012	16	0	114	9	44	181
2013	1	0	15	0	9	6
2014	3	0	14	1	15	62