

Coherent long-term body-size responses across all Northwest Atlantic herring populations to warming and environmental change despite contrasting harvest and ecological factors

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Abstract

Body size is a key component of individual fitness and an important factor in the structure and functioning of populations and ecosystems. Disentangling the effects of environmental change, harvest and intra- and inter-specific trophic effects on body size remains challenging for populations in the wild. Herring in the Northwest Atlantic provide a strong basis for evaluating hypotheses related to these drivers given that they have experienced significant warming and harvest over the past century, while also having been exposed to a wide range of other selective constraints across their range. Using data on mean length-at-age 4 for the sixteen principal populations over a period of 53 cohorts (1962–2014), we fitted a series of empirical models for temporal and between-population variation in the response to changes in sea surface temperature. We find evidence for a unified cross-population response in the form of a parabolic function according to which populations in naturally warmer environments have responded more negatively to increasing temperature compared with those in colder locations. Temporal variation in residuals from this function was highly coherent among populations, further suggesting a common response to a large-scale environmental driver. The synchrony observed in this study system, despite strong differences in harvest and ecological histories among populations and over time, clearly indicates a dominant role of environmental change on size-at-age in wild populations, in contrast to commonly reported effects of fishing. This finding has important implications for the management of fisheries as it indicates that a key trait associated with population productivity may be under considerably less short-term management control than currently assumed. Our study, overall, illustrates the need for a comparative approach within species for inferences concerning the many possible effects on body size of natural and anthropogenic drivers in the wild.

KEY WORDS

bottom-up effects, comparative approach, density-dependence, life history theory, size-at-age, size-selective mortality, synchrony, thermal optimum

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1 | INTRODUCTION

Body size is a major organismal trait given its expected role in physiology (e.g. metabolism; Brown et al., 2004), productivity (e.g. via fecundity; Barneche et al., 2018) and ecological interactions (e.g. predation; DeLong et al., 2015). Many of the world's marine fish have sustained rapid decreases in body size over the past century, a trend which has been widely associated with climate warming (Gardner et al., 2011) and the industrialization of fishing (Barnett et al., 2017; Trippel, 1995). Although both temperature and mortality are expected to affect mean body size in fish (Crozier & Hutchings, 2014; Marshall & McAdam, 2007; Swain et al., 2007), their importance relative to each other and to other known drivers of change such as resource availability generally remains uncertain. Given the potentially large implications of changing body size for the fisheries and ecosystems these populations support (Hočvar & Kuparinen, 2021; Laugen et al., 2014), partitioning the effects of each driver and evaluating their potential interactions is both a timely and necessary objective for conservation.

Global warming is expected to elicit both plastic and genetic responses in body size, implying that consequences to populations may not be uniform across contexts. In most experimental settings, growth rate increases slowly with temperature up to a certain optimum, then declines rapidly to a critical temperature maximum (Brett et al., 1969; see also Neuheimer et al., 2011, for a study in the wild). The direction of response to warming, therefore, will depend mainly on the average temperature experienced relative to the optimum (Ohlberger, 2013). Notably, the parameters of this phenotypic response will also be subject to local adaptation (Tüzün & Stoks, 2018). This further implies the potential for differences in response among populations driven by temperature (Angilletta et al., 2003), in combination with specific trade-offs among traits (e.g. age at maturity; Berrigan & Charnov, 1994) and ecological factors such as the availability of resources (Brett et al., 1969; Carozza et al., 2019) and predation risk (Lankford et al., 2001). Although laboratory experiments predict greater impediments to growth rate for ectotherms in warmer environments (e.g. Deutsch et al., 2008), it is important to acknowledge that a thermal optimum may not (fully) materialize for that process in nature; some relationships may appear monotonic due to sampling only at temperatures that characterize either the ascending or descending limb of an otherwise parabolic function, or there may be concurrent shifts of the optimum toward lower temperature values (see Childress & Letcher, 2017; van Denderen et al., 2020). Moreover, the capacity of responses to evolve and interact with other processes relevant to body size implies that relationships observed in the laboratory may not directly apply to wild populations.

Size at a given age—an imperfect, but widely monitored proxy of individual fitness—does not only integrate the effects of temperature on growth (e.g. Huss et al., 2019; Lindmark et al., 2022) but possibly also the (context-specific) responses in reproduction and survival (e.g. Carozza et al., 2019; Kuparinen et al., 2011; see also Gislason et al., 2010). More generally, it is expected to reflect any driver of

change likely to affect size from the year of birth, which includes—for harvested fish populations—the key role of harvest (Kuparinen & Festa-Bianchet, 2017). The effect of this added source of mortality on size-at-age is almost always negative, though the overall response reflects the magnitude of fishing mortality and the type and degree of selection (Millar & Fryer, 1999). By reducing population abundance, exploitation may also elicit compensatory increases in juvenile growth, presumably at the expense of size at subsequent ages (Croll et al., 2023; Rose et al., 2001). Theory further indicates that sufficient mortality, selective or not, can generate selection favoring decreased age and length at maturity (Handford et al., 1977; Heino et al., 2002), which in turn is associated with a decrease in prospects for adult growth (Enberg et al., 2012; Stearns & Koella, 1986). Finally, in addition to the effects on size-at-age, the mortality imposed by fishing generally leads to truncation of population age and therefore also size distribution (Barnett et al., 2017; see also the key contribution by Lee, 1912, for effects on apparent growth). Overall, therefore, warming and fishing are both largely capable of reducing size-at-age, with several studies on marine fish having argued for the combined importance of the two drivers (e.g. Marty et al., 2014; Neuheimer & Grønkjær, 2012; Sinclair et al., 2002).

Although most of the literature on size-at-age published so far has focused on climate warming and harvest, there are many other selective pressures which can affect the mean values of this trait in the wild. Like fishing, predation tends to be highly selective with respect to body size (Andersen et al., 2009; Law et al., 2009), with potentially strong implications for the life-history traits of the targeted populations (e.g. maturation schedules; Swain, 2011) and associated feedbacks at the community level (DeLong et al., 2015; Shackell et al., 2010). Moreover, in most observation-based studies, responses to temperature need to be disentangled from other effects on somatic growth, reproduction and survival, including those resulting from variations in the availability of (Holsman et al., 2019; Korman et al., 2021) and competition for resources (Lorenzen & Enberg, 2002; Oke et al., 2020), and independent shifts in demography (e.g. carry-over effects across the age structure; Ciannelli et al., 2020; Whitten et al., 2013). These various effects, along with the many possible differences in the strength and selectivity of harvest across locations (e.g. Schindler et al., 2010), have the potential to generate widely diverging patterns of size-at-age over time and across space (e.g. Lorenzen, 2016). In turn, such variations may lead to large but differing outcomes for ecosystems and fisheries (e.g. Audzijonyte et al., 2020; Lorenzen, 2016; Schindler et al., 2010), emphasizing the importance of examining any and all relevant hypotheses on variations in that trait in the wild.

Comparative analyses can help disentangle the variations in body size associated with temperature from those caused by other key drivers by exploiting available contrasts in selection over time and among populations. The present study aims to resolve, for the 16 principal populations of Atlantic herring (*Clupea harengus*) in the Northwest Atlantic (NWA), the potentially complex interplay among factors known or expected to affect mean length-at-age for individual cohorts. Specifically, we quantified the magnitude and extent of

age-specific size declines in herring over the past five decades, a period over which these ecosystems have undergone significant warming of the sea surface layer (Cyr et al., 2022; Galbraith et al., 2022; Hebert et al., 2023). In light of these thermal responses, we examined how local differences in other selective pressures, especially harvest (e.g. Trochta et al., 2020) but also density-dependence (e.g. Brunel & Dickey-Collas, 2010), shifting ecological structure (e.g. Bundy et al., 2009) and environmental factors (e.g. Nye et al., 2014), might have affected the coherence of variations in size-at-age across the NWA. Considering temperature and fishing related effects is particularly relevant as our study covers the period of industrialization of fishing in these ecosystems, both directed at herring (e.g. Day, 1970) and at other species, notably the groundfish predators of herring (Fogarty & Murawski, 1998; see also Swain & Benoît, 2015). This industrialization has led to large changes in population abundance and the structure of the fish communities and therefore plays a key part in the expectation of variability in size-at-age over time and among populations.

Our comparisons focus on the mean length-at-age 4, which is early in adult life, and is the youngest point in ontogeny where size was representatively sampled in herring surveys and, therefore, suitable for testing most relevant hypotheses on size-at-age. We employed a series of empirical models intended to represent (shared) thermal response curves involving an optimum and to evaluate different hypotheses for locally adapted variations in the parameters of that response. The optimum in this framework was not intended for direct inference of plasticity in growth but, rather, to acknowledge that effects of temperature on body size may be positive, negative or optimal, depending on key trade-offs and the selective context. Then, retaining the most probable model variants, we analyzed the residuals of the thermal response, using the shared and unshared variations among populations as a basis for disentangling effects by each factor. Given herring populations in the NWA have experienced a wide range of harvest and ecological pressures historically, each associated with different hypothesized effects on size-at-age, our expectation was for a low degree of coherence in the model residuals among populations.

2 | METHODS

2.1 | Study background

Our dataset included herring born from 1962 to 2014 in populations with centers distributed from the historically warm Gulf of Maine, United States, to the colder White Bay in Newfoundland, Canada (Figure 1). The naming system for the sixteen populations reflects the known geographic locations of spawning, many of which have been established by tagging experiments (e.g. Wheeler & Winters, 1984) and structural analyses of the otoliths (e.g. Messieh, 1972). For populations in the Gulf of St Lawrence (GSL) and off coastal Newfoundland, the populations names also specify the season of spawning—either spring or fall—given that these

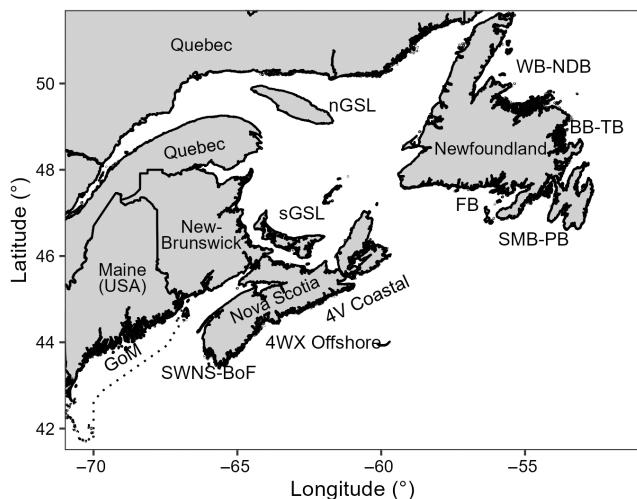


FIGURE 1 Locations for the sixteen Atlantic herring populations examined in the present study, with the full names corresponding to each abbreviation given in Figure 2. The dashed line refers specifically to the USA Herring Fishery Management Area for the Gulf of Maine (GoM) population.

populations are distinct and are assessed and managed separately (Melvin et al., 2009); all other populations are known to spawn exclusively in the fall.

The populations considered for analysis have experienced key differences in their harvest histories (Figure 2), while also exhibiting a high degree of ecological (e.g. Melvin et al., 2009) and genetic discreteness (e.g. Lamichhaney et al., 2017). Differences in harvest history were quantified by population, decade or, when relevant and possible, half-decade (i.e. 5 years; represented as two adjacent dots in Figure 2), using harvest intensity as the main basis for classification. The assessments for these populations differed in their sophistication, with some providing detailed estimates of annual fishing mortality derived from age-structured analytical assessment models (e.g. McDermid et al., 2018; McQuinn et al., 1999), and others providing qualitative assessments only based on indicators (e.g. Bourne et al., 2023). Consequently, we developed a three-level scheme to classify harvest intensity wherein 'elevated' referred to any harvest pressure likely to have caused population decline or collapse, 'intermediate' referred to harvest with possible to unlikely adverse effect on the population, and 'low' for harvest unlikely to represent a significant source of mortality. Moreover, for each time period and population, we distinguished the classifications informed by fully analytical assessment models, considered here to be more accurate, from those based on indicators and fishery removals (see references in Figure 2 for details on inputs and assumptions).

Briefly, exploitation levels in the Gulf of Maine (GoM; NEFSC, 2018), Southwest Nova Scotia / Bay of Fundy (SWNS-BoF; Singh et al., 2016), southern GSL (sGSL; Cleary, 1981), Saint Mary's Bay / Placentia Bay (SMB-PB) and Fortune Bay (FB; Winters & Moores, 1980) were most elevated prior to 1980, following which they either decreased significantly (e.g. FB, SMB-PB; Bourne et al., 2023) or continued to fluctuate between high and low (e.g.

Population	1960s	1970s	1980s	1990s	2000s	2010s	References / Remarks
Gulf of Maine (GoM)	●	●	●	●	●	●	See Figure B1 (bottom panel) in NEFSC (2018)
Southwest Nova Scotia / Bay of Fundy (SWNS-BoF)	○	●	●	●	●	●	Based on landings and relative exploitation rates in Singh et al. (2016)
Scotian Shelf Offshore Banks (4WX Offshore)	○	○	○	○ ○	○	○	Exploited by foreign vessels in 1963–1973 and by a directed fishery since 1996 (Singh et al. 2016)
Coastal Nova Scotia (4V Coastal)	○	○	○	○	○	○	Negligible landings (<0.1 t) for most of the time series (Singh et al. 2016)
Southern Gulf of St. Lawrence Fall Spawners (sGSL Fall)	○	●	●	● ●	● ●	●	Fishing mortalities available from peer-reviewed assessment models (Cleary 1981; McDermaid et al. 2018)
Southern Gulf of St. Lawrence Spring Spawners (sGSL Spring)	○	●	● ●	●	● ●	●	Fishing mortalities available from peer-reviewed assessment models (Cleary 1981; McDermaid et al. 2018)
Northern Gulf of St. Lawrence Fall Spawners (nGSL Fall)	○	●	● ●	●	○	○	Based on population model from 1973 to 1997 (McQuinn et al. 1999); not overfished since 2000 (Chamberland et al. 2022)
Northern Gulf of St. Lawrence Spring Spawners (nGSL Spring)	○ ●	● ●	● ●	●	○	○	Based on population model from 1965 to 1998 (McQuinn et al. 1999); low exploitation since 2000 (Chamberland et al. 2022)
Fortune Bay Fall & Spring Spawners (FB Fall, FB Spring)	●	● ●	○	○	○	○	Fishing known as the main cause of collapse in the mid-1970s (Winters and Moores, 1980); harvest rates believed to be low since the early 1980s (Bourne et al. 2023)
Saint-Mary's Bay / Placentia Bay Fall & Spring Spawners (SMB-PB Fall, SMB-PB Spring)	○	○	○	○	○	○	Exploitation likely similar to FB Fall and FB Spring; harvest rates believed to be low since the early 1980s (Bourne et al. 2023)
Bonavista Bay / Trinity Bay Fall & Spring Spawners (BB-TB Fall, BB-TB Spring)	○	○	○	○	○	○	Known to have been exploited in a very small fishery since the early 1960s (Bourne et al. 2023)
White Bay / Notre Dame Bay Fall & Spring Spawners (WB-NDB Fall, WB-NDB Spring)	○	○	○	○	○	○	Known to have been exploited in a very small fishery since the early 1960s (Bourne et al. 2023)



FIGURE 2 Contrasts over time and among populations in the known or perceived harvest pressures since 1960 (elevated=likely to have caused population decline or collapse, i.e., unsustainable harvest; intermediate=possible to unlikely adverse effect on the population, yet still a non-negligible source of mortality; low=unlikely to be a significant source of mortality). Note that variations in the overall fishing intensity occurring within the same decade are represented by two separate dots, one for each 5-year period.

sGSL; McDermaid et al., 2018). Fishing for the Offshore Scotian Shelf (4WX Offshore; Singh et al., 2016) and northern GSL (nGSL; Chamberland et al., 2022) populations was largely perceived as having been weaker than in other regions, though the specific levels

likely varied extensively among years as well. Finally, the available landings records and knowledge on the Coastal Nova Scotia (4V Coastal; Singh et al., 2016), White Bay / Notre-Dame Bay (WB-NDB; Bourne et al., 2023) and Bonavista Bay / Trinity Bay (BB-TB; Bourne



et al., 2023) populations have suggested consistently low exploitation rates overall.

The effects of a thermal gradient across locations (5.5–13.1°C) and differences in harvest pressures summarized in Figure 2 have occurred within the context of major changes in ecosystem structure and functioning. In particular, the collapse of several groundfish populations in the late-1980s to early-1990s relaxed the predation on most forage fish (Bundy et al., 2009; Morissette et al., 2009; Savenkov et al., 2007), but to varying degrees among species and NWA ecosystems (e.g. lower for herring in the sGSL; Benoît & Rail, 2016). Herring populations also differed with respect to the timing and location of spawning—and fishing—within each location (Melvin et al., 2009; see also Figure 2 in Beaudry-Sylvestre et al., 2022), the environmental conditions that appear to affect recruitment (e.g. colder-water copepods for spring-spawners; Brosset et al., 2019) and degree of rebuilding following collapse (Trochta et al., 2020), thereby leading to even greater expected differences in size-at-age among populations.

2.2 | Trends in temperature and size

Water temperatures have generally increased over the past century in the NWA (Cyr et al., 2022; Galbraith et al., 2022; Hebert et al., 2023). Although the analysis on thermal responses used annual data from the past five decades, we compiled data for as far back in time as possible for a broader overview of the historical context for warming.

The thermal history for each cohort, that is fish of the same population born in the same year, was defined as an average sea surface temperature (SST) experienced from birth up to the year of capture at age 4 (hereafter, lifetime SST). The SST values employed for this average were extracted from the National Oceanic and Atmospheric Administration's (NOAA) monthly global 2°×2° Extended Reconstructed Sea Surface Temperature v5 model (years 1880–1981; Huang et al., 2017) and Fisheries and Oceans Canada's (DFO) Atlantic Zonal Monitoring Programme (years 1982–2018; strata delineated in Figure 1 of Galbraith & Larouche, 2013) over the May to November period each year. These estimates of lifetime SST were deemed physiologically relevant to herring given that they primarily spawn and feed in the surface layer (depth generally 0–75 m, depending on season and location). Lifetime SST estimates closely related to the mean SST recorded in the year of birth, suggesting that any lagged effect of temperature on length-at-age would not significantly affect our conclusions (Figure S1).

All herring populations had an associated time series of lifetime SST taken from the areas which best corresponded to their known locations of spawning and residence (see Figure 1; $N=9$). The SMB-PB and FB populations were attributed the same lifetime SST values given that neither of the two SST datasets generally distinguished between these two adjacent and geographically proximate areas.

Data on Canadian herring populations were obtained from surveys conducted by DFO over the cohorts born from 1962 to 2014 (see Methods in Benoît et al., 2018). Given our aim to disentangle the effects of various external drivers on size-at-age, only fish captured with the least size-selective gear were retained for analysis, principally purse seines and scientific multi-mesh gillnets (different from and excluding commercial gillnets; see frequency of each gear type in Table S1). Samples from these principal gear types produced comparable estimates of mean length-at-age 4 over time and among populations (Figure S2), suggesting minimal impact of gear-specific selectivity on perceptions of size variability among populations or over time. The influence on the analysis of potential within-sample correlation, wherein fish of the same or spatiotemporally adjacent samples might exhibit more similar lengths than fish in non-adjacent samples, was also deemed negligible given that most samples comprised few individuals, usually less than 10, relative to total number of fish and samples available for analysis for any given cohort (Tables S1 and S2).

Individually resolved length-at-age values were adjusted to a common date in the year of capture, September 30th, by applying a version of the growing degree-day method developed by Neuheimer et al. (2008) intended specifically for seasonal (within-year) variation in temperature within each cohort. The corrections applied were small and relatively consistent across cohorts of each population, with analyses based on adjusted and non-adjusted (original) values leading to very similar results overall (Table S3; Figures S3 and S4). We note that these corrections did not account for seasonal changes in survival associated with either the timing of fishing or predation. Variations in these factors could have affected the mean size-at-age in our dataset, but their influence does not appear to have been important given the results we report below.

The dataset for Canadian herring populations was complemented with published estimates of mean length-at-age 4 for herring from the Gulf of Maine obtained from Figure 4a of Becker et al. (2020). These data had originally been collected by purse seines in the months of June and July and subsequently adjusted to the same date of capture, and include herring aged 4 years in cohorts from 1974 to 2007. The full dataset for lifetime SST and mean length-at-age 4 comprised 722 cohort-specific sets of values across a total of sixteen populations.

The response variable in our first set of analyses was the mean length-at-age 4 of individual cohorts, a measure that integrates the contribution of numerous age or size-specific processes from birth, principally somatic growth, reproduction and survival. Four years is the youngest age at which herring in the NWA are fully recruited to spawning populations and, therefore, representatively sampled in scientific surveys and commercial fishery sampling. It is also an age at which the average length is well-correlated with length at maturity and maximum observed length, indicating that it represents age-related length values over a substantial portion of the herring lifespan, and suggesting a consistent link to individual fitness (Beaudry-Sylvestre et al., 2022).

Although studies of growth rate typically focus on juvenile fish, a life stage during which length is not also affected by reproductive investment (see Enberg et al., 2012), we still combined values across maturity stages to preserve variations in age at maturity associated with maturity-dependent mortality (Beaudry-Sylvestre et al., 2022). Moreover, despite immature fish not being representatively sampled across all locations, trends in their mean lengths-at-age 4 were overall very similar to those for mature herring at the same age, suggesting an overall weak impact of such investment on the results (Figure S5).

2.3 | Thermal response model

The response of fish and other ectotherms to warming has been described in the laboratory as generally involving a thermal optimum, with more negative effects expected near the warmer edge of species' geographic ranges (e.g. Brett et al., 1969; Deutsch et al., 2008). Although the general applicability of laboratory findings to natural contexts remains unclear, given the other abiotic and biotic factors that can influence temperature-performance relationships (Childress & Letcher, 2017; van Denderen et al., 2020), the potential for positive, negative, and optimal responses in body size at a given age to warming is clear (e.g. Huss et al., 2019). It is therefore important to consider this range of possibilities when evaluating responses in the wild over as long a period and across as many populations of the same species as we have. We specified the association between lifetime SST (T) and mean length-at-age 4 (I) with a three-parameter parabolic function that heuristically represents an optimum in the thermal response of body length. The model employed the general form:

$$I = I_{\max} + k (T - T_{\text{opt}})^2 + \varepsilon, \quad (1)$$

where I_{\max} is the intercept or elevation (cm), k is the thermal sensitivity or breadth ($\text{cm}^{-1}\text{°C}^{-2}$), T_{opt} is a thermal optimum ($^{\circ}\text{C}$), and ε is a vector of model residuals. This equation assumes symmetrical rates of change in I along the ascending ($T < T_{\text{opt}}$) and descending portions of the curve ($T > T_{\text{opt}}$), a necessary assumption given there were few values in the range of temperatures below the optimum in the data, precluding estimation of a more complex function.

TABLE 1 Empirical support for the four model variants describing the association between mean length-at-age 4 (I) and lifetime SST (T) over the cohorts from 1962 to 2014. Each variant has a shared parameter for curvature or breadth (k) whereas model variants 2, 3 and 4 also include interactions with a categorical population term (parameters which varied among populations are denoted as $[s]$) for thermal optima (T_{opt}) and/or vertical elevations (I_{\max}). Model variants are compared with respect to adjusted R^2 and the differences (Δ) in BIC and AICc relative to the model with the smallest value obtained.

Variant	Equation	Adjusted R^2	Δ BIC	Δ AICc
1	$I = I_{\max} + k \cdot (T - T_{\text{opt}})^2 + \varepsilon$	0.28	245.4	317.2
2	$I = I_{\max}[s] + k \cdot (T - T_{\text{opt}})^2 + \varepsilon$	0.55	0	3.98
3	$I = I_{\max} + k \cdot (T - T_{\text{opt}}[s])^2 + \varepsilon$	0.52	35.0	39.0
4	$I = I_{\max}[s] + k \cdot (T - T_{\text{opt}}[s])^2 + \varepsilon$	0.56	62.5	0

Organisms are expected to develop some degree of adaptation to the environmental conditions where they reside (Tüzün & Stoks, 2018). The response to warming is therefore expected to depend, at least in part, on the selective pressures experienced locally over several generations. To evaluate the possibility of locally adapted response, we specified model variants with (1) all three parameters represented by single values (common cross-population responses; as in Equation 1) or population-specific estimates for either (2) I_{\max} , (3) T_{opt} , or (4) both I_{\max} and T_{opt} (Table 1). These model variants provided a simplified representation of the following four processes, which are commonly observed in the laboratory but may also affect body size in the wild: (1) an absence of local adaptation across the study system (an implicit assumption when extrapolating population-level parameters to the species level; reviewed Sinclair et al., 2016); (2) countergradient variation in somatic growth and other processes contributing to I_{\max} (the pattern wherein plasticity and adaptation presumably act in opposition along a thermal gradient; Conover & Present, 1990); (3) local adaptation in T_{opt} in response to a change in the external selective constraints which determine the optimal point of the curve (Angilletta et al., 2003); and (4) combinations of patterns (2) and (3), depending on context (see examples in Villeneuve et al., 2021). Although local adaptation may also involve a change in thermal breadth, for example as part of thermal specialization (e.g. Angilletta et al., 2003), a common cross-population parameter k was maintained in all model variants for the same reasons we assumed a symmetrical response function.

The four model variants were compared, using the adjusted R^2 , Bayesian Information Criterion (BIC) and small-sample version of Akaike's Information Criterion (AICc) as relative measures of fit and parsimony (Table 1). Then, retaining the most probable model variant(s), we examined whether and how the properties of the thermal response might have varied along a spatial gradient of mean lifetime SST ranging in values from 5.5 to 13.1°C.

2.4 | Coherence and variation in model residuals

The variations in mean length-at-age not explained by temperature, that is the residuals of the thermal response, were expected to reflect responses to a variety of other length- or growth-selective



pressures over time and across populations. The common signals contained in these residuals were extracted via dynamic factor analysis (DFA), a state-space modelling framework which combines factor and time-series analysis (Zuur et al., 2003). By quantifying the extent of shared variability among time-series, the DFA can help to separate the effects of large-scale drivers acting on multiple populations from the more localized roles of demographic and ecological factors (e.g. Olmos et al., 2020). Thus, in our study system, a DFA analysis on the model residuals was expected to reveal a low degree of spatial coherence in the variations in size among the sixteen populations, resulting for instance from differences in fishing histories. The standardized residuals (zero mean, unit variance) of model variant 4 at time t , denoted y_t and calculated as $y_t = \frac{\epsilon - \bar{\epsilon}}{SD(\epsilon)}$, were modelled as:

$$y_t = Zx_t + v_t, \text{ where } v_t \sim \text{MVNormal}(0, R), \quad (2)$$

$$x_t = x_{t-1} + w_t, \text{ where } w_t \sim \text{MVNormal}(0, Q), \quad (3)$$

where Equations 2 and 3 model the observations and a random-walk process error, respectively. In these equations, Z is a matrix of factor loadings on a small finite number of hidden states x_t (here, restricted to either one or two), and v_t and w_t are multivariate normally distributed (MVNormal) observation and process errors with zero mean and variance-covariance matrices R (*diagonal and unequal*) and Q (*identity*), respectively. The residuals of model variant 4 were employed as the response variable for this analysis, though we note that they were strongly correlated with the residuals from the other variants; this suggested that the results of the DFA would be very similar regardless which set of residuals was employed (see Results). Model parameters were estimated with the R package developed for multivariate autoregressive state-space analysis (MARSS; Holmes et al., 2012) in R version 4.1.1 (R Core Team, 2021).

A more specific aim for the analysis of model residuals was to identify factors which could explain the dominant common trend(s) detected across populations. This could not be entirely achieved statistically, given a lack of covariate data at scales matching the observation dataset; however, for seven populations with sufficient assessment history, it was possible and relevant to test for a common manifestation of (within-population) density-dependence, the expected negative association between the natural log of population biomass and growth, and thus size at a given age (Croll et al., 2023; Rose et al., 2001). The strength of density-dependence is expected to be a function of the abundance of herring, as well as their weight given allometric weight-dependent consumption (Post et al., 1999). Consequently, we employed biomass as the readily available measure of population size (see sources and temporal trends in Table S4; Figure S6), noting that effects were likely strengthened by the reductions in length-at-age themselves (see Stawitz & Essington, 2019). As in the thermal response models, the values for population biomass employed for correlations with the common trend were averaged from birth up to the age of 4 years within each cohort.

We also considered a possible association between the common trend in model residuals and the North Atlantic Oscillation (NAO)

index, which affects climate variability in the North Atlantic. We do not report those results here in the main text given the weak association we estimate, and our view that an association would be difficult to interpret mechanistically in the context of this study (details provided in Supplementary Material S7).

3 | RESULTS

3.1 | Trends in temperature and size

The lifetime SST experienced by each cohort has been increasing since at least the early 1900s, with the increase for the cohorts from 1962 to 2014 averaging 1.4°C across the study area (Figure 3a). Slopes of the temperature trends differed between the nine locations considered (analysis of covariance over cohorts 1962–2014: cohort \times location: $F_{8,459} = 11.4$; $p < 0.0001$; see also Table S5), although most of the variation was explained by a common response (partial R^2 for a common effect of cohort: 0.98). The differences in slope among regions did not appear to vary in a systematic manner geographically (e.g., latitudinally). The ranking of locations from slowest to fastest rate of warming was 4V Coastal, 4WX Offshore, BB-TB, GoM, nGSL, sGSL, SMB-PB + FB, SWNS-BoF, and WB-NDB.

Trends in mean length-at-age 4 differed mainly between the warm GoM, Scotian Shelf and sGSL (range of mean lifetime SST: 10.6–13.1°C) and the colder nGSL and Newfoundland regions (range: 5.5–10.1°C) (Figure 3b,c). In the former group, lengths fluctuated without trend until about 1980, and have declined more or less continuously since, with reductions for each population ranging from 3.4 to 7.4 cm, or 11 to 22% over the study period. In contrast, estimates for the latter populations increased from the early 1960s until the mid-1970s, declined until the late-1980s, and then slowly increased from the mid-1990s onward, resulting in net declines averaging 1.4 cm, or <5% over the temporal extent of analysis.

3.2 | Thermal response model

Consistent with a thermal optimum framework applied to body size (Ohlberger, 2013), the effects of increasing lifetime SST on the mean length-at-age 4 were more steeply negative in warm than in cold locations (Figure 4). The most parsimonious fits for these responses were given by model variant 2 (based on BIC) or variant 4 (based on AICc), with these two models leading to very similar predictions of length as a function of lifetime SST (Table 1; see also the turquoise and yellow lines in Figure 4). The predictions by model variant 2 were associated with a relatively narrow k of -0.14 ± 0.02 (SE) $\text{cm}^{-1} \cdot \text{°C}^{-2}$, values of I_{\max} ranging from 29.8 to 38.3 cm across populations and a shared T_{opt} at 4.63 ± 0.81 °C. In contrast, the more complex model variant 4 was associated with an estimated k of -0.41 ± 0.17 $\text{cm}^{-1} \cdot \text{°C}^{-2}$, and across population variation in I_{\max} between 28.9 and 36.7 cm and T_{opt} between 4.9 and 10.9 °C.

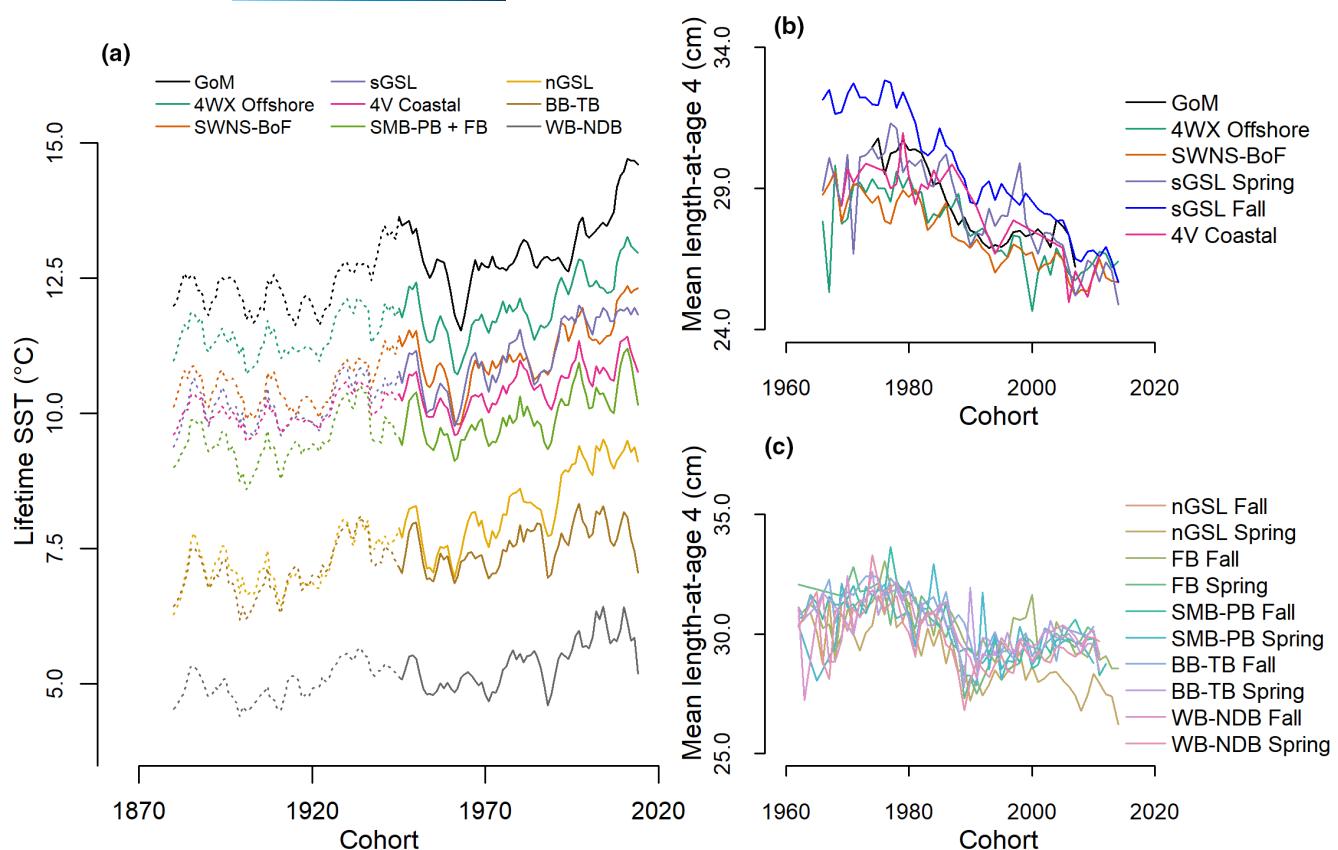


FIGURE 3 Trends across cohorts in (a) the mean lifetime SST experienced within nine specific locations over the cohorts from 1880 to 2014; (b) the (seasonally adjusted) mean length-at-age 4 over the cohorts from 1962 to 2014 for the six southern-most populations, which occur in the sGSL, Scotian Shelf and GoM; and (c) 10 northern-most populations, which occur in the nGSL and along the south and east coasts of Newfoundland. The dotted lines for lifetime SST values for cohorts born prior to 1945 intend to illustrate the greater uncertainty associated with these earlier data (Huang et al., 2017). The plus symbol in the 'SMB-PB+FB' label is for the shared attribution to the same time-series of lifetime SST values given the geographic proximity of the populations and the spatial resolution of the available temperature data.

In accordance with a framework involving local adaptation in the thermal response, estimates for population-specific parameters in the two selected variants varied in a somewhat continuous manner with respect to the historical mean temperature where each population resides (Figure 5). In variant 2, population-specific l_{\max} values increased nearly linearly from cold to warm locations. In variant 4, the population-specific l_{\max} estimates were flat with respect to mean temperature, whereas T_{opt} increased monotonically towards warmer locations.

3.3 | Coherence and variation in model residuals

The standardized (length-at-age) residuals of model variant 4 exhibited very little of the asynchrony that would have been expected given the substantial differences between populations in their fishing and ecological histories. Rather, trends in the residuals were highly coherent among the sixteen populations (Figure 6). This finding was robust to the choice of thermal response model, as evidenced by the strong correlations with residuals of model variant 2 (Pearson's

correlation $r = 0.98$) and for that matter with those of model variants 1 ($r = 0.77$) and 3 ($r = 0.95$). Irrespective of the model variant used, residuals displayed a general increasing trend up to the mid-1970s, a decline until the early-1990s, and a return to intermediate values for the remainder of the time period across all populations.

The coherence in model residuals among cohorts and populations was well accounted for by a DFA with a single temporal trend (Figure 6). Although the patterns for certain populations were more parsimoniously explained by a model with two common trends (see factor loadings for sGSL herring in Figures S8 and S9), both models yielded very similar predictions with respect to length (see orange and blue lines in Figure 6).

The common trend of the residuals (x_t of DFA model 1) displayed no consistent association with lifetime population biomass across populations (Figure 7). Furthermore, an expected negative association between residuals and biomass was only found in three of the seven populations examined (GoM, sGSL Fall, and FB Spring), suggesting that any such density-dependence might have at best been important for length-at-age within certain non-neighboring ecosystems.

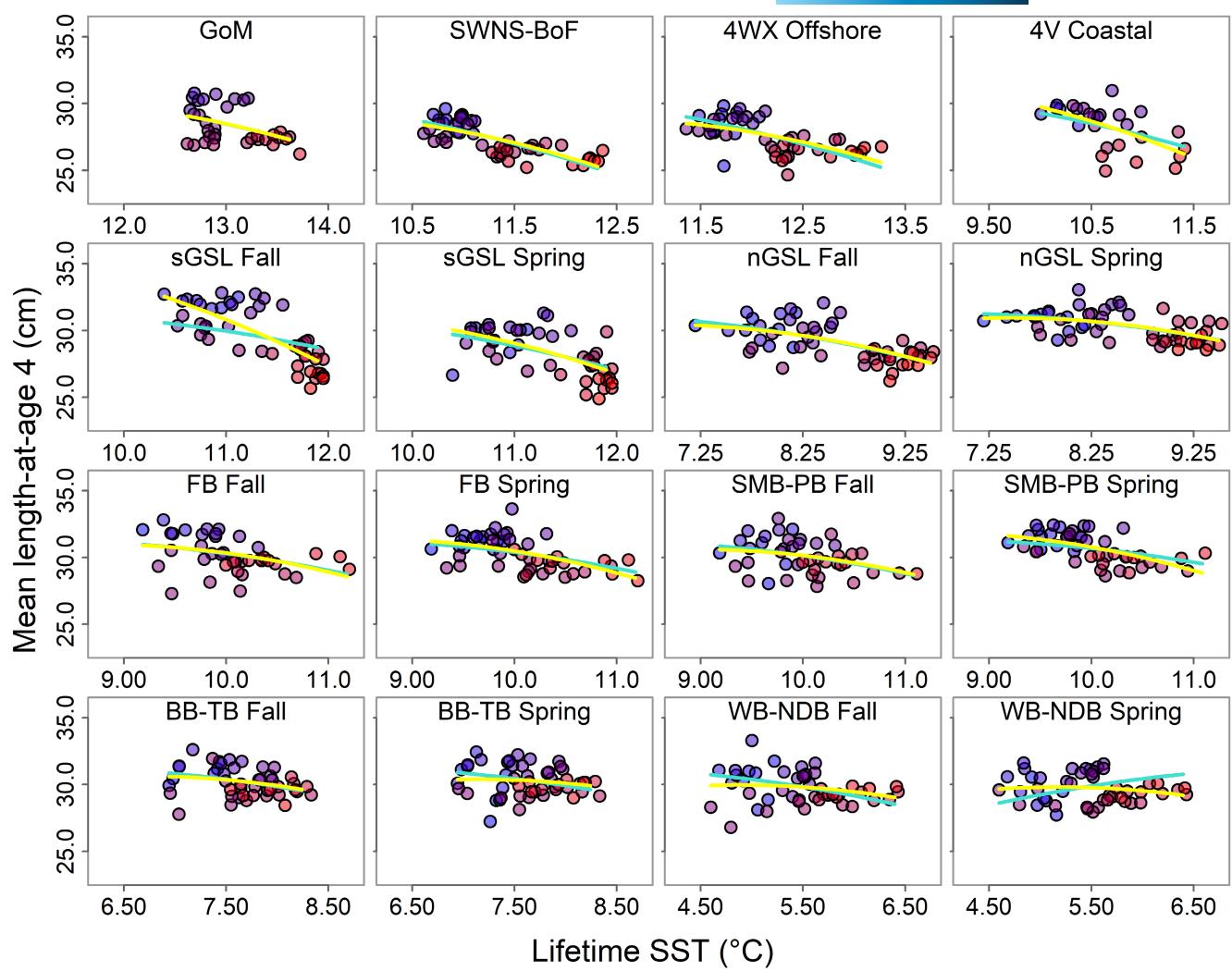


FIGURE 4 Estimates of mean length-at-age 4 as a function of lifetime SST across cohorts of the sixteen populations examined, with predictions of model variants 2 (population-specific I_{\max}) and 4 (population-specific I_{\max} and T_{opt}) illustrated as yellow and turquoise lines, respectively. The color gradient from blue to red illustrates the temporal progression of cohorts from 1962 to 2014. Note that the x-axis scales differ across panels.

4 | DISCUSSION

Declining body size has been observed for numerous fish populations worldwide, but the relative importance of warming and harvest in this trend, as well as the interplay with other key factors, generally remain uncertain (Gardner et al., 2011; Huss et al., 2019; Trippel, 1995). By analyzing an extensive dataset of length-at-age for a widely monitored, moderately long-lived pelagic fish in the NWA, we demonstrate that simple optimal responses to warming can account for most of the size variation experienced by populations over more than five decades. Contrary to prior expectations that length-at-age would differ among populations and over time due to numerous factors including harvest pressure, population density and ecological context, changes in mean length were well and parsimoniously explained by a shared response to temperature and, in appearance also, a common environmental driver. These findings provide a compelling example of body size appearing to be dominated by

climatic factors operating at the scale of an entire ocean basin rather than the many other pressures hypothesized to differ in their effects at a local scale. Moreover, by providing evidence against a dominant role of human exploitation on body size (Darinot et al., 2009), our study raises important questions concerning the short-term management control on this key aspect of productivity and ecological functioning in the wild.

Our analysis provides some of the strongest evidence to date for the differential effects of warming on body size across the full distributional and contemporary thermal range of a species in an ocean basin. The faster declines in length-at-age for herring populations in the southern end of their range agree with many experimental and field-based comparisons on ectotherm growth in relation to temperature (e.g. Deutsch et al., 2008; Neuheimer et al., 2011). Although our analysis does not permit isolating the contributions of growth and growth-selective mortality to length-at-age, coherent growth-related change among populations seems to us most

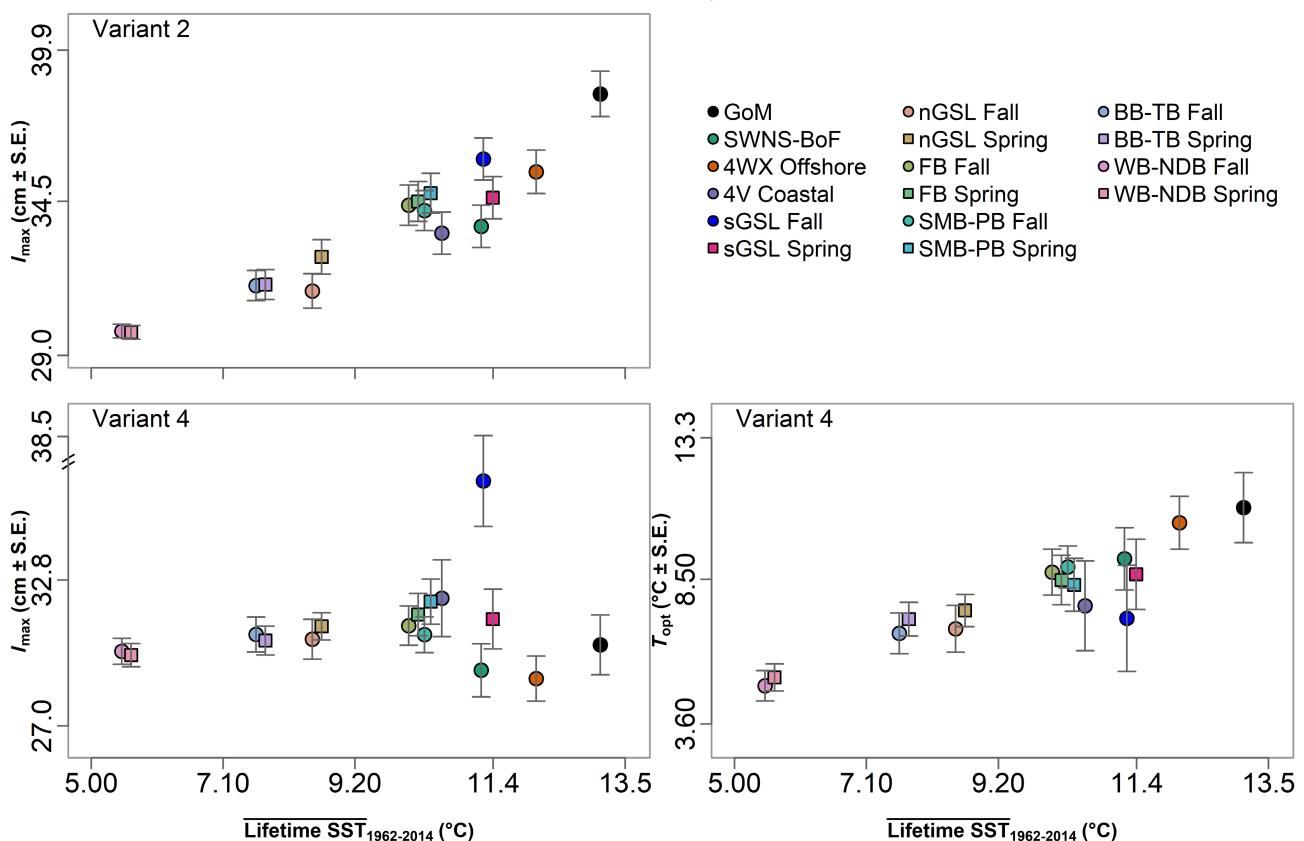


FIGURE 5 Comparisons of L_{\max} and T_{opt} for model variants 2 and 4 and their associated standard errors along a continuous gradient of mean thermal history from 5.5 to 13.1°C. For populations with the same or similar estimated thermal history, values were jittered with respect to the x-axis for ease of distinction between data points.

likely in light of the evidence available for key trade-offs and drivers. Notably, the strength, form and temporal variations of mortality are known to have differed amongst the populations, yet appear to have contributed very little to length variation (see Figure 2 and Study background in the Methods). For example, the mean values for populations in Fortune Bay, Newfoundland, increased during a period of strong harvest (~1960–70s) but then decreased during the near moratorium that followed (Winters & Moores, 1980). Also inconsistent with a dominant role of fishing is the rapid decline observed in 4V Coastal, a population which has experienced very low exploitation over the study period (Singh et al., 2016). The contrasts evident in mean length-at-age 4 were therefore indicative of more adverse impacts of increasing temperature in warm than cold locations, a finding with direct implications for individual fitness (Beaudry-Sylvestre et al., 2022) and more generally marine ecosystems (e.g. Hočevar & Kuparinen, 2021; Laugen et al., 2014).

We emphasize that the aim of the present study was to disentangle the effects of climate warming and other drivers of change in body size, not to infer plasticity in any particular process. Still, the use of a parabolic temperature response framework was deemed important given the link to somatic growth (e.g. Huss et al., 2019) and evidence for both positive (e.g. Audzijonyte et al., 2020; Ikpewe et al., 2021; Solokas et al., 2023) and negative (e.g. Baudron et al., 2014; van Rijn et al., 2017) associations in natural systems. The predominance of

negative responses in our study is perhaps unsurprising given that ocean warming in the NWA was initiated several decades prior to the beginning of our time-series. That other studies reported positive effects of temperature on body size, despite presumably also studying populations in waters that were already warming, could be explained by changes in available resources for growth or by the confounding actions of other traits relevant to size (e.g. age at maturity; Neuheimer & Grønkjær, 2012). The influence of such effects is expected to be minor for NWA herring given the strong coherence in length-at-age response observed among populations.

Given a premise of local adaptation, the parameters of the phenotypic response were expected to vary among populations, reflecting in part the interplay between historically relevant thermal and ecological conditions (Angilletta et al., 2003). The probable increases in L_{\max} toward warmer locations, as proposed by model variant 2, may reflect countergradient variation in relation to temperature, i.e. selection on L_{\max} compensating for the faster declines in length-at-age in these waters (see Figure 3). Such a process has been previously described for growth rate across latitudes (e.g. Conover & Present, 1990; Villeneuve et al., 2021), but effects on L_{\max} in our model likely involved other mechanisms (see below). The relative evidence for an increase in T_{opt} with temperature, as estimated by model variant 4, potentially indicates greater tolerance to warming in these waters, provided sufficient availability of resources (Brett et al., 1969; Holsman

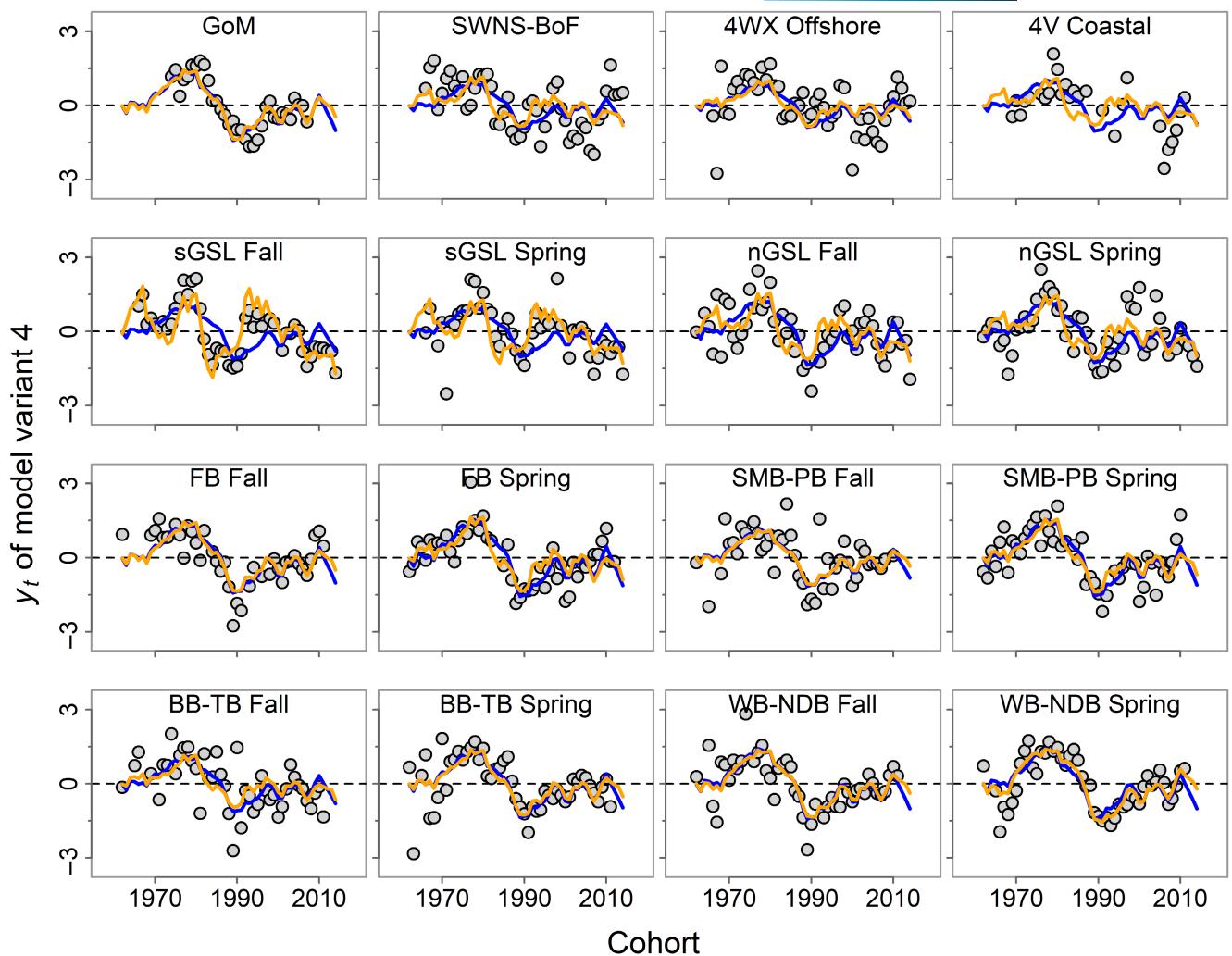


FIGURE 6 Standardized residuals from model variant 4 and estimated trends for the sixteen populations examined, with the predictions of DFA models with one and two common trends illustrated as blue and orange lines, respectively.

et al., 2019) and limited predation (Lankford et al., 2001). These hypotheses, albeit consistent with several other findings on ectotherms in the wild (e.g. Baumann & Conover, 2011; Villeneuve et al., 2021), must be interpreted in light of key assumptions. Notably, the breadth of response or parameter k was assumed as being symmetrical around the optimum and shared by all of the populations considered (Sinclair et al., 2016). Moreover, responses apply to cross-sectional data which reflect not only longitudinal growth patterns, as in back-calculated length increments for individual fish (see Swain et al., 2007, for a specific example), but also integrate the results of size-dependent changes in survival, although variation caused by that process was at best minor in our analyses. Whether they truly reflect adaptation can only be evaluated by a common garden experiment, and this constitutes a valuable research avenue.

We predicted the trends in length-at-age unrelated to warming, that is the thermal response residuals, to vary extensively over time and among populations, especially in response to human exploitation (Darinot et al., 2009). Yet, neither the magnitude nor the direction of trends in the model residuals differed between herring populations

having experienced elevated, intermediate and low harvest in our study system, nor was there a change in trend in populations for which the pattern of mortality varied over time (Figure 2). A consistent pattern of size selectivity also seemed implausible given the contrasts in the mode of exploitation summarized in a previous study on these populations (fisheries either targeting mature or both mature and immature herring; Beaudry-Sylvestre et al., 2022) and the known differences in predator fields over time and between ecosystems (e.g. in relation to the collapse of several groundfish predators in the late-1980s to early-1990s; Bundy et al., 2009; Morissette et al., 2009; Savenkovoff et al., 2007). These results suggest that, contrary to what had been proposed in other comparisons based on intensity of harvest (e.g. Devine et al., 2012; Sharpe & Hendry, 2009), fishing mortality was not a significant driver of size-at-age in our study system.

Another key hypothesis for the synchrony observed was that local density-dependence, the process wherein population biomass limits the prospects for somatic growth (Post et al., 1999; Whitten et al., 2013), might generate consistent outcomes on length-at-age across all the populations. However, the finding that only three of

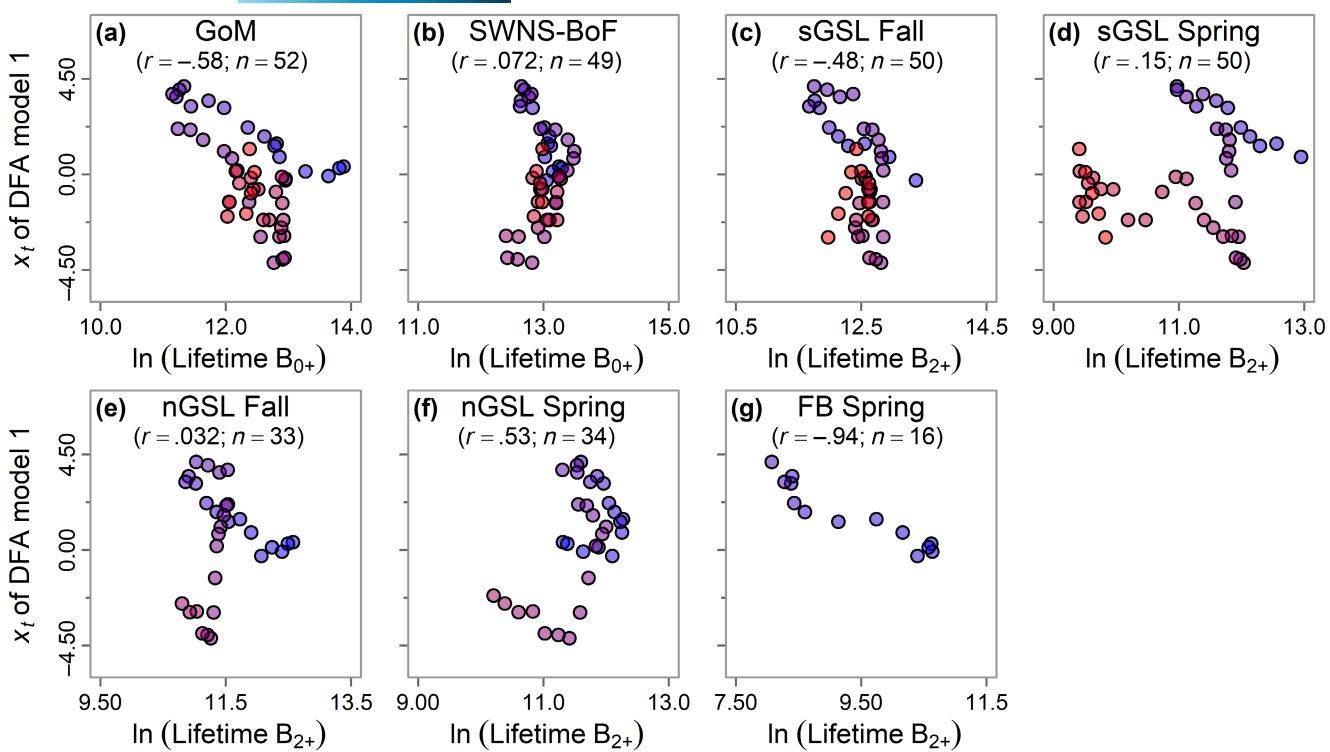


FIGURE 7 Correlations between the common trend in the (standardized) residuals of model variant 4 (x_t of a single-trend DFA) and the natural log of lifetime population biomass (denoted as B , where the subscript indicates the ages included in the biomass estimate). The color gradient from blue to red illustrates the temporal progression of data points for cohorts from 1962 to 2014. The values within each panel provide the strength of the correlation (r) and the number of points used in the correlation (n).

the seven time-series examined were negatively correlated with lifetime average biomass contradicts this expectation. The lack of consistency in density-dependence among populations, despite large changes in herring biomass in a number of locations, suggests that the importance of this process may well have been overestimated in previous analyses on some of these populations (Becker et al., 2020; Brunel & Dickey-Collas, 2010). It also implies that reductions in population density associated with overfishing and/or low recruitment are unlikely to have resulted in shared compensatory increases in juvenile growth rate across the NWA (Croll et al., 2023; Rose et al., 2001; Trochta et al., 2020). The discrepancy observed with previous work could reflect the longer time-series of data available in the present study, though the correlation strengths for specific population may also be affected by statistical methods and assumptions (e.g. nature of covariates; Lorenzen, 2016; Lorenzen & Enberg, 2002) and, more broadly, ecological context.

Synchrony over large geographic distances can be driven by animal movement and exchanges between populations (Liebhold et al., 2004; e.g. Luo et al., 2021). Herring have historically maintained a high degree of population integrity across their NWA range, a characteristic which implies low connectivity or exchange of individuals among populations (Stephenson et al., 2009). Such integrity has been realized, for example, by temporally stable patterns of natal homing and larval retention within the spawning ground (Wheeler & Winters, 1984) and, within several locations also, by differences between spring and fall spawners with respect to numerous trade-offs

(e.g. size and number of offspring; Bradford & Stephenson, 1992) and other aspects of productivity (e.g. resource availability in the larval stage; see Brosset et al., 2019). We also note that the main agents of mortality acting upon herring—fisheries and natural predators—have been largely constrained in space given fishery regulations that are established at the population level and some key bathymetric features of the environment (e.g. Laurentian Channel). The common trend in the model residuals we report cannot be explained by exchanges of fish for the foregoing reasons, but also because such exchanges would be expected to generate a common trend in length-at-age, which was not observed particularly when considering the trends for the warmer and colder water populations.

Finally, given the lack of empirical support for a shared influence of either mortality, competition for resources or animal movement on length-at-age, we considered in our last step a role of common environmental effects associated with climate. Environmental factors can synchronize somatic growth either directly via common effect on individuals (as inferred for individually resolved otolith chronologies; e.g. Campana et al., 2023; Morrongiello et al., 2021) or indirectly via a common indirect response of the main herring prey (Liebhold et al., 2004). In the NWA, for example, several zooplankton assemblages have experienced marked shifts in biomass and composition over past decades, with some of the trends also linked to key climatic factors (e.g. strength of dominant winds; Nye et al., 2014; Pershing et al., 2010). Comparisons for other study systems further indicate that synchrony in zooplankton availability can

occur at spatial scales equal or greater than those observed for the forage fish that feed upon them (Batchelder et al., 2012). Although most of the data needed to evaluate these hypotheses were lacking, we emphasize that bottom-up effects by lower trophic levels likely dominated the top-down control by fishing and natural predators. Based on this knowledge, and also given the extensive temporal and spatial coverage of the evidence, a common role of the environment on length-at-age may provide the most parsimonious explanation for the common trend.

A major strength of the present analysis has been the ability to evaluate patterns of size-at-age for many populations of the same species and over a period spanning several generations. Indeed, while differences in thermal response have also been explored in comparisons across species (e.g. Audzijonyte et al., 2020; Ikpewe et al., 2021; Solokas et al., 2023; van Rijn et al., 2017), our study is the first in our knowledge to report a unified pattern of response over such a broad range of selective contexts and for a single species in the wild. Using data on length at a specific age also excluded the confounding effects of truncation of age structure caused by poor survival to advanced ages (e.g. Barnett et al., 2017) and its replenishment via recruitment (e.g. Hansen & Nate, 2014). This again is in contrast with a large portion of the published literature on ectotherm responses to warming, which instead has focused on the mean body length irrespective of age (e.g. Oke et al., 2020) or the maximum or asymptotic body size (e.g. Baudron et al., 2014; Brunel & Dickey-Collas, 2010). Last, we emphasize the key importance of a comparative approach in achieving our study objectives. Taken singly, the populations analysed would likely not have revealed a reliably interpretable pattern in the residuals, opening the door for speculation and spurious correlation with regards to potential drivers. Viewed in a comparative framework, however, the data largely indicated a role of environmental factors operating across multiple ecosystems, thereby also implying a weak short-term impact of local management decisions on body size and associated metrics of productivity and persistence.

We conclude that a more comprehensive understanding of the factors which affect body size in fish and other ectotherms will require expanding the traditional focus on exploitation as the main or only valid alternative hypothesis to a role of warming. Clearly, harvest is capable of causing population-level characteristics to covary over scales comparable to those of climate; this is exemplified by the synchronous collapse in abundance of 22 North Atlantic cod populations in the late-1980s to early-1990s, a phenomenon ascribed to a common or repeated management scheme (Frank et al., 2016) rather than a common effect of the environment (see Rothschild, 2007). However, the lack of support for a dominant effect of fishing in our study system suggests that plasticity in the response to climate—both temperature and some other factor—may have played a more important role than has been acknowledged to date. In this regard, our findings echo recent calls in the literature on climate warming (Audzijonyte et al., 2019; Gardner et al., 2011) and exploitation (Hutchings & Kuparinen, 2021), and more generally on size-at-age (Lorenzen, 2016), for a more integrated view of the different factors

which may affect individual fitness within populations of the same species in the wild.

AUTHOR CONTRIBUTIONS

Manuelle Beaudry-Sylvestre: Conceptualization; formal analysis; writing – original draft; writing – review and editing. **Hugues P. Benoît:** Conceptualization; data curation; supervision; writing – original draft; writing – review and editing. **Jeffrey A. Hutchings:** Conceptualization; supervision; writing – review and editing.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are openly available in Dryad at <https://doi.org/10.5061/dryad.c866t1gdx>.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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