


REGULAR PAPER

Temporal variability in size and growth of Atlantic herring in the Gulf of Maine

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Abstract

Variability in life history traits and structural diversity of commercially exploited fishes in response to stress can impact their population dynamics and sustainability. Using data from a fishery dependent sampling program from 1978 to 2011, we evaluated temporal variability of size and growth of adult Atlantic herring (*Clupea harengus*) in the Gulf of Maine. We then developed and tested the hypotheses on the links of such temporal changes to population density and environmental factors and found decreases in size and growth potential. Generalized additive models found that density dependence was the main driver of such changes over sea surface temperature and salinity. Our results highlight the importance of density dependent processes in regulating growth and population size structure for Atlantic herring in the Gulf of Maine.

1 | INTRODUCTION

The structural diversity of life history traits (e.g., size and age) within and among fish populations is an important consideration that may impact the population dynamics and productivity of managed fish stocks (Hilborn & Walters, 1992; Ricker, 1975). Large variations in size and age diversity have been demonstrated among populations, as well as within populations among years, and can be related to various biotic and abiotic factors (e.g., population density, prey availability, temperature and salinity) (Blaxter, 1992; Chen & Mello, 1999; Hare *et al.*, 2016; Yan *et al.*, 2012). Additionally, truncated size and age distributions can indicate a stressed stock due to overfishing (Brunel & Piet, 2012). As such, an understanding of the complex relationship between fish populations and their environment is

important for investigating the potential impact of environmental changes on fish population dynamics (Fischer *et al.*, 2013).

An inverse relationship between spawning stock biomass (SSB) and growth, as well as a decline in asymptotic length per unit biomass density, has been described (Lorenzen & Enberg, 2002; Walters & Post, 1993). The parameters of the Von Bertalanffy growth function (VBGF) maximum attainable length (L_{∞}), maximum attainable weight (W_{∞}) and the Brody growth rate (K) are influenced by density-dependent growth. This is often dictated by competition for food (Beverton & Holt, 1957; Lorenzen & Enberg, 2002). For example, an increase in biomass and subsequent decrease in food supply can lead to lower growth manifested as decreases in L_{∞} and W_{∞} (Froese *et al.*, 2008; Lorenzen & Enberg, 2002).

Temperature, both directly and indirectly, influences biological operations of all organisms. At a molecular level, it controls the activities of intracellular operations, and at an ocean-basin scale it influences decadal scale productivity of entire ecosystems (Blaxter, 1992). Metabolic processes, physiology, early-life growth and behaviour are linked to

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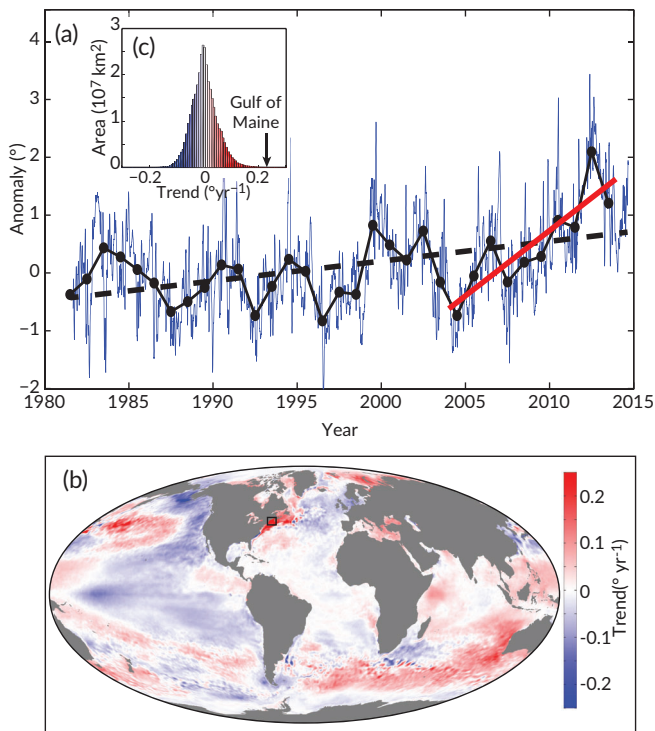


FIGURE 1 Gulf of Maine sea surface temperature deviation from the mean for the years 1980–2013, highlighting the extreme increase from 2005–2013. (Reproduced with permission from Pershing *et al.*, 2015.) (—) 15d smoothed; (●) yearly mean; (---) overall trend; (—) trend since 2004

temperature. Growth especially is strongly responsive to temperature (Blaxter, 1992). Meta-analysis across taxa has indicated predictable correlations between temperature and growth, ontogenic duration and mortality rates among fishes (Houde, 1989; Pepin, 1991). Link and Sherwood (2019) found positive correlations between growth (K) and temperature, and an inverse relationship between L_{∞} and temperature.

The Gulf of Maine (GoM) sea surface temperature (SST) has increased at a rate of about 0.01°C since the 1890s (Figure 1) and has recently accelerated (Pershing *et al.*, 2015; Shearman & Lentz, 2011). Moreover, the GoM is warming faster than many other areas of the world's oceans (Pershing *et al.*, 2015). The GoM SST increased at about 0.03°C per year from 1982 to 2004, about three times the planet's average rate. There is high uncertainty associated with long-term forecasts of ocean temperature, but it is hypothesized that population fluctuations and community reconfiguring will be species-specific depending on life history traits (Hare *et al.*, 2016).

Salinity influences the survival of all fishes (Bishai, 1961). Survival depends on an organism's ability to acclimate to unstable salinity (Taugbol *et al.*, 2014; West-Eberhard, 2005; Yan *et al.*, 2012). Variable salinity is linked to elevated metabolic activity among teleosts, necessary for osmoregulation in extreme saline environments. If substantial energy is diverted toward osmoregulation, less is available for growth of somatic tissue (Barton, 1987).

Ocean freshening can influence the winter–spring phytoplankton communities in the GoM (Ji *et al.*, 2008). Negative impacts on primary

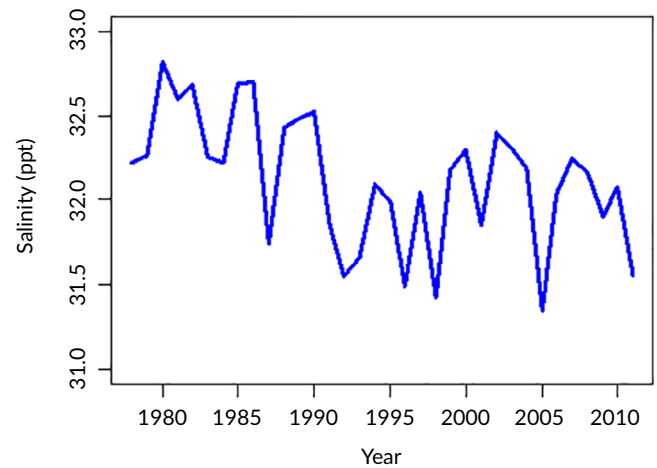


FIGURE 2 Gulf of Maine mean annual salinity (NOAA, 2016)

productivity can negatively influence secondary productivity, like the abundance of the zooplankton *Calanus finmarchicus*, which comprises up to 76% of the diet of herring during the summer (Runge *et al.*, 2015). Salinity recorded in the Atlantic demonstrated a freshening trend north of 40°N and south of 25°S (Curry *et al.*, 2003). Furthermore, salinity in the GoM has been on a decreasing trend since 1978 (Figure 2).

Generalized additive models (GAMs) have been considered to deal with the nonlinear relationships between environmental data and fish community metrics (Murase *et al.*, 2009; Zhao *et al.*, 2014;). A GAM is a nonparametric regression technique not limited by linear relationships and is flexible to the statistical distribution of data (Swartzman *et al.*, 1995). As such, it can be more suitable for investigating the relationships between fish community metrics and their surrounding environment.

The purpose of this study is to apply GAMs to examine changes in life history traits of commercially caught adult (≥ 3 years) Atlantic herring (hereinafter “herring”) from 1978 to 2011 within the GoM and to investigate a relationship with population density and abiotic environmental factors.

2 | MATERIALS AND METHODS

1. Were fishes collected as part of faunal surveys?
No
2. Were fishes killed during or at the end of your experiment (e.g., for tissue sampling)? No
3. Were surgical procedures performed?
No
4. Did the experimental conditions severely distress any fishes involved in your experiments?
No
5. Did any procedures (e.g., predation studies, toxicity testing) cause lasting harm to sentient fishes?
No

FIGURE 3 Four management areas for the US Atlantic herring fishery: (—) US *Clupea harengus* management areas; (—) area A1; (—) *Clupea harengus* sample sites

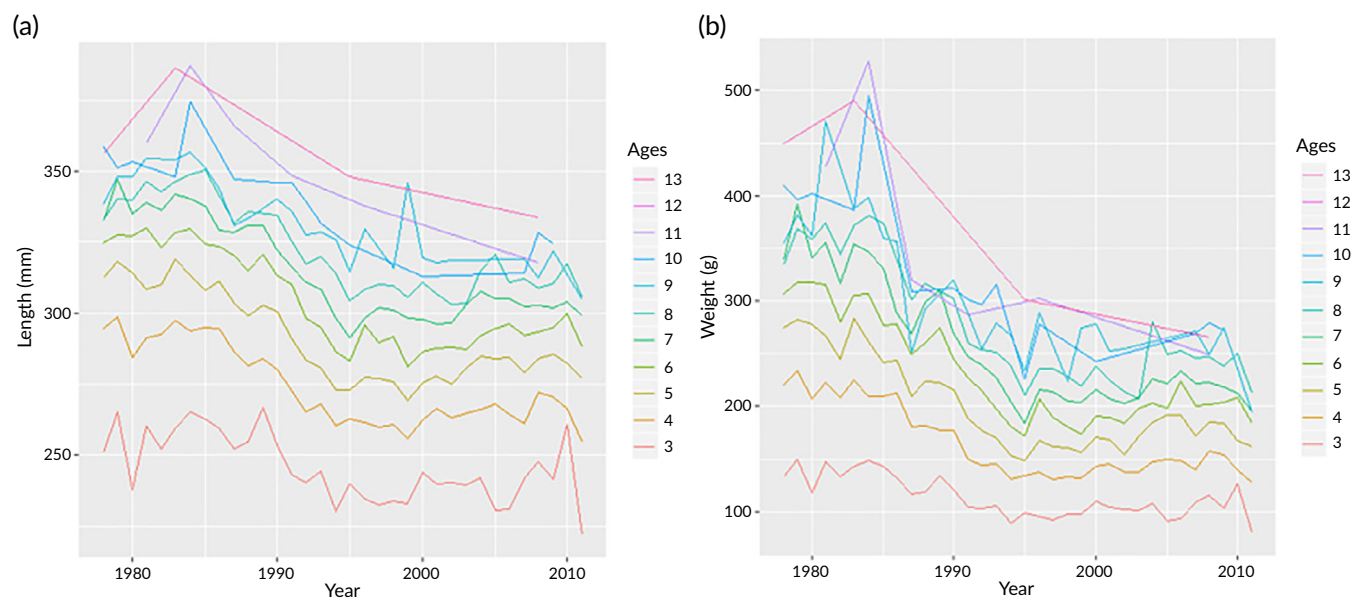
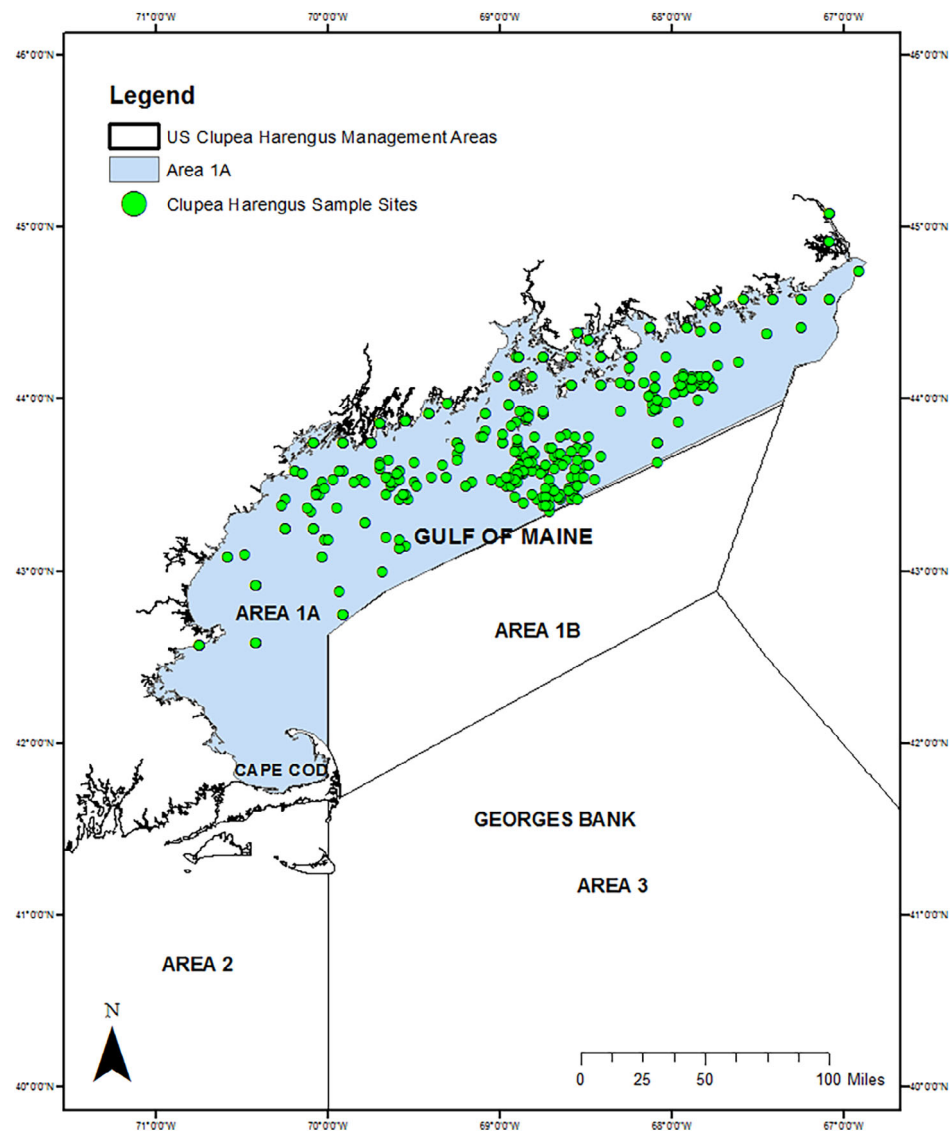


FIGURE 4 Variations in adult mean length-at-age (a), and mean adult weight-at-age (b) of *Clupea harengus*

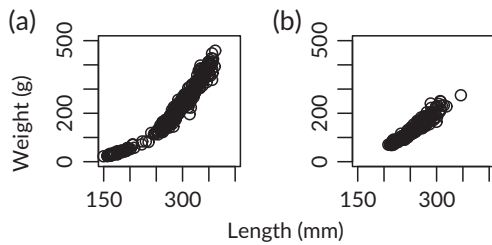


FIGURE 5 WLR for 1979 (a) and 1999 (b) of *Clupea harengus*

6. Did any procedure involve sentient, unanaesthetized animals that were subjected chemical agents that induce neuromuscular blockade, such as muscle relaxants?

No

To examine these changes, 824 commercially caught samples containing a total of 15,589 herring landed from 1978 to 2011 were processed and analysed. Biological samples have been collected annually throughout the entire range of the US herring fishery since 1960 as part of a Maine Department of Marine Resources (DMR) dockside monitoring program to assess the stock status. To maintain an uninterrupted consistent time series and data set, and to rule out size influences and bias from different gear types and inter-annual growth of gonads during the autumn spawning processes, a subset of samples from the purse seine fleet fishing in Area 1A (Figure 3) during the months of June and July were used for this study.

2.1 | Sea surface temperature and salinity

SST and salinity data were analysed and used from the Northeast Fishery Science Center (NEFSC) bottom trawl surveys for the years 1978–2011 and were collected from within the GoM (NEFSC, 2014) (Figure 3).

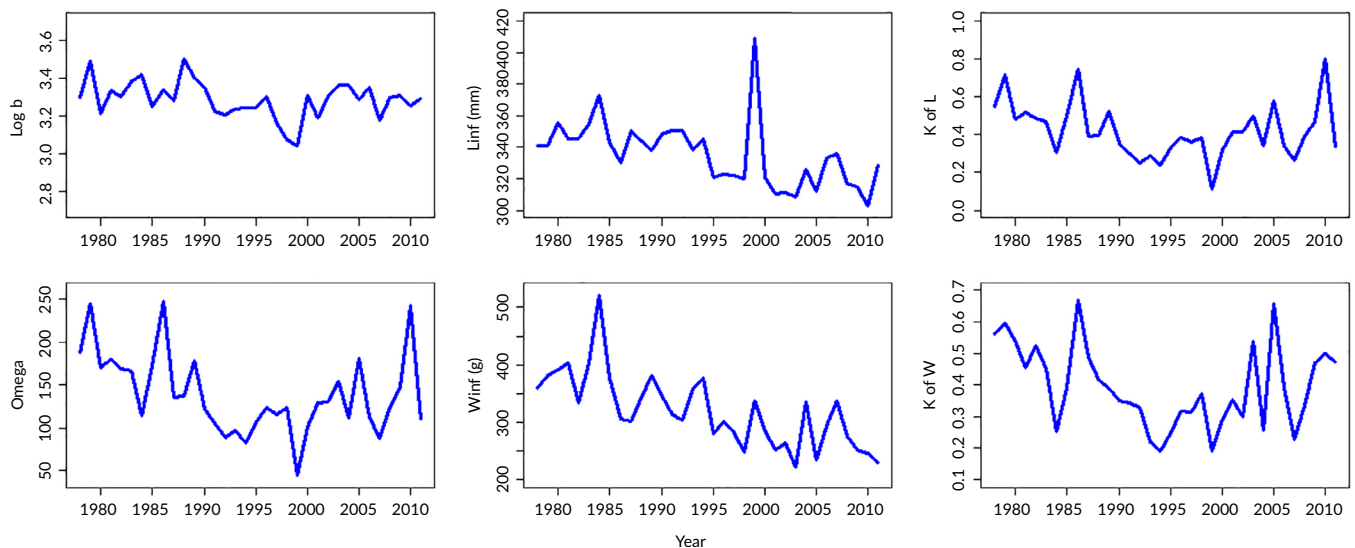


FIGURE 6 Variations in the log transformed allometric factor (a), maximum attainable length (b), Brody growth of maximum attainable length (c), omega (d) maximum attainable weight (e) and Brody growth of maximum attainable weight (f) of *Clupea harengus*

2.2 | Spawning stock biomass

Values for female spawning stock biomass (SSB) were derived using a statistical catch-at-age approach as described in the Atlantic herring assessment report (NEFSC, 2018). Data were made available by National Marine Fisheries Service (NMFS) staff directly from the output of the base model run (NEFSC, 2018; their table B4-2) and have not been adjusted for retrospective bias (Figure 9). In short, female SSB is calculated by multiplying numbers-at-age by the maturity schedule, multiplying by weight-at-age during the spawning season, and then dividing by two.

2.3 | Analysis of the weight–length relationship and size-at-age data

The weight–length relationship (WLR) can be described as:

$$W = aL^b e^{\epsilon} \epsilon \in N(0, \sigma^2)$$

where W is the weight (g), L is the length (mm), the parameter a is a scaling coefficient for the weight at length of the fish, the parameter b is a shape parameter called the allometric factor, and ϵ is a multiplicative error term (Brodziak, 2012; Ricker, 1975).

The WLR was log transformed into a linear model to stabilize the variance and to make the error additive:

$$\log W = \log a + b \log L + \epsilon$$

A least squares (LS) method was used to estimate parameters a and b for each year. The functional regression and specific standard value $b = 3$ describe isometric growth, which would characterize a fish of unchanging body form and specific gravity, with increasing length (Safran, 1992).

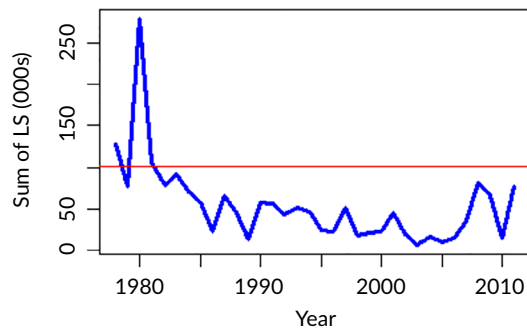


FIGURE 7 The sum of LS by year for length within the VBGF of *Clupea harengus* including the 95% confidence intervals. (—) LS; (■) 95% CI

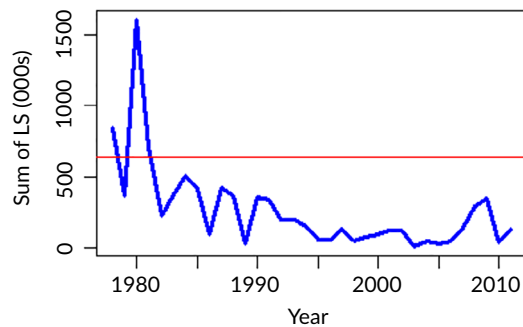


FIGURE 8 The sum of LS by year for weight within the VBGF of *Clupea harengus* including the 95% confidence intervals. (—) LS; (■) 95% CI

Size-at-age data for length and weight were described by the commonly used VBGF, expressed as:

$$L_t = L_{\infty} \left(1 - e^{-k(t-t_0)} \right)$$

in length and:

$$W_t = W_{\infty} \left(1 - e^{-k(t-t_0)} \right)^3$$

in weight, where L_t is the whole fish length (mm) and W_t is the whole-body weight (g) at age t (years), L_{∞} is the maximum attainable length, W_{∞} is the maximum attainable weight, K is the Brody growth parameter and t_0 is the hypothetical age at which the length or weight is zero (Ricker, 1975). The above parameters were estimated by the method of LS. For a well-defined VBGF, t_0 usually has a negative value or a value close to 0 (as fish have nonzero length and weight at age 0). For length, omega (ω) was used as the growth parameter proposed by Gallucci and Quinn (1979) and was estimated as:

$$\omega = KL_{\infty}$$

for each year; ω is useful for describing the overall growth potential of fish at young ages (Chen & Harvey, 1994).

2.4 | Analysis of factors influencing life history

To investigate potential significant drivers of declines and temporal variability in size and growth, two types of GAMs were constructed. The first had zero lag in time between the environmental data and the response data, and the second had a 1-year lag to account for and better fit the delayed response of life history traits to changes in environmental variables (Gasparrini *et al.*, 2010). The following life history traits were individually used in both types of GAMs: $\log b$, L_{∞} , w , W_{∞} and K of W_{∞} , making a total of 10 models. Deviance, adjusted R^2 , GCV, AIC, and P value scores were calculated to best describe the goodness-of-fit and main drivers for each model. The “mgcv” package (version 1.8–27) of the R program was used to conduct all GAMs.

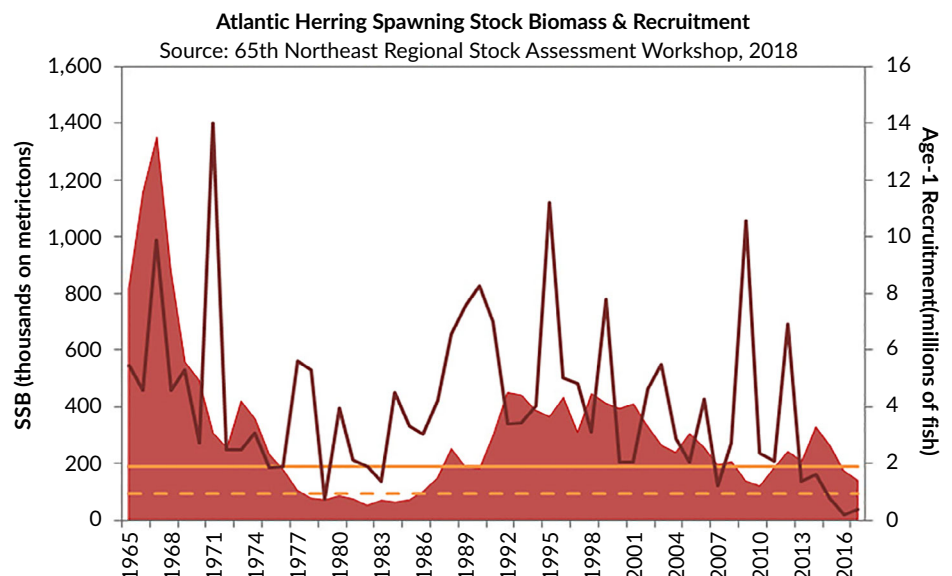


FIGURE 9 SSB for US *Clupea harengus* for the years 1965–2017 (plot by ASMFC, 2018). (—) SSB

GAMs with a gamma distribution and a log-link function were used to accommodate the continuous nature of the response variables written in R code as.

$\text{gam}(\text{logb} \sim s(\text{SSB_2018}) + s(\text{GOM_SST}) + s(\text{GOM_SSS}), \text{family} = \text{Gamma}(\text{link} = \text{log}))$

for the allometric factor b ,

$\text{gam}(\text{Linfs}(\text{SSB_2018}) + s(\text{GOM_SST}) + s(\text{GOM_SSS}), \text{family} = \text{Gamma}(\text{link} = \text{log}))$

for L_{∞} ,

$\text{gam}(\text{OmegaS}(\text{SSB_2018}) + s(\text{GOM_SST}) + s(\text{GOM_SSS}), \text{family} = \text{Gamma}(\text{link} = \text{log}))$

for ω ,

$\text{gam}(\text{Winfs}(\text{SSB_2018}) + s(\text{GOM_SST}) + s(\text{GOM_SSS}), \text{family} = \text{Gamma}(\text{link} = \text{log}))$

for W_{∞} ,

$\text{gam}(K_Winfs(\text{SSB_2018}) + s(\text{GOM_SST}) + s(\text{GOM_SSS}), \text{family} = \text{Gamma}(\text{link} = \text{log}))$

and for K of W_{∞} , where s is a spline smoother, SSB_2018 is the SSB from the 2018 herring stock assessment (NEFSC, 2018), GOM_SST is SST and GOM_SSS is salinity for the GoM from the NEFSC bottom trawl survey (NEFSC, 2014).

All analyses were conducted using R statistical software (R Core Team, 2019).

3 | RESULTS

3.1 | Temporal variability in size and growth

Mean size-at-age for both length and weight of herring exhibited a decrease. The largest decrease occurred between 1978 and the mid-1990s (Figure 4a,b). Herring older than 9 years displayed a fragmented absence for many of the years, but the overall declining trend remained.

Scatterplots of the WLR showed a decline and truncation in size ranges, exposing the absence of small and large fish, and a narrowing range over time. More profound was the increase in the absence of larger herring when comparing 1979 to 1999 (Figure 5a,b). For instance, 1979 showed a broader range in weight and length, and the second highest value of logb , while in 1999 the range and logb were the lowest (Figures 5 and 6a). The parameter logb displayed a variable decline (Table 1), reaching its lowest value in 1999 of 3.04, increasing afterwards through 2011 (Figure 6a).

Maximum attainable size decreased for both length and weight from 1978 through 2011 (Table 2 and 3). L_{∞} decreased from 373.14 mm in

TABLE 1 Summary of the parameter estimation in fitting the log transformed Weight Length Model for *Clupea harengus*

Year	a	logb
1978	-13.33	3.30
1979	-14.46	3.49
1980	-12.82	3.21
1981	-13.52	3.33
1982	-13.45	3.30
1983	-13.84	3.38
1984	-14.09	3.42
1985	-13.15	3.25
1986	-13.68	3.34
1987	-13.38	3.28
1988	-14.58	3.50
1989	-14.01	3.40
1990	-13.77	3.35
1991	-13.07	3.22
1992	-12.92	3.20
1993	-13.11	3.23
1994	-13.15	3.24
1995	-13.19	3.24
1996	-13.46	3.30
1997	-12.70	3.16
1998	-12.23	3.07
1999	-11.99	3.04
2000	-13.48	3.31
2001	-12.80	3.18
2002	-13.49	3.30
2003	-13.82	3.36
2004	-13.80	3.36
2005	-13.37	3.28
2006	-13.69	3.35
2007	-12.73	3.17
2008	-13.43	3.30
2009	-13.49	3.31
2010	-13.23	3.25
2011	-13.41	3.29

1984, spiked in 1999 to 409.18 mm, then dropped to a low of 302.78 mm in 2011 (Figure 6b). when ω displayed an overall decrease (Figure 6c). Initially, ω increased, reaching its highest value in 1986 of 247.09, then dropped to its lowest in 1999 of 45.85. From 1999 through 2011, ω increased variably, and ended in 2011 at 109.67. W_{∞} declined, with a high of 520.86 g in 1984 to a low in 2003 of 221.71 g (Figure 6d). Lastly, K of W_{∞} displayed a precipitous decline into the mid-1990s, with a high of 0.68 in 1986, then declined through 2007 to a low of 0.23, and ended in 2011 slightly lower than in 1978, at 0.47 (Figure 6e). The sum of LS for both VBGF models breached the 95% confidence interval for 3 years, 1978, 1980, and 1981 (Figures 7 and 8).

TABLE 2 Summary of the parameter estimation in fitting the von Bertalanffy growth function to the length-at-age data for *Clupea harengus*

Year	L_{∞} (mm)	K	t_0	Sum of LS
1978	341.19	0.55	0.53	127,741
1979	340.97	0.72	0.97	77,451
1980	355.52	0.48	0.66	279,069
1981	345.63	0.52	0.49	106,489
1982	345.40	0.49	0.31	78,372
1983	354.82	0.47	0.17	90,524
1984	373.13	0.31	-1.05	70,889
1985	343.25	0.50	0.12	57,930
1986	329.90	0.75	0.95	22,612
1987	350.18	0.39	-0.35	65,546
1988	343.94	0.40	-0.28	45,099
1989	337.76	0.53	0.43	13,372
1990	348.49	0.35	-0.66	56,800
1991	350.09	0.30	-0.97	55,345
1992	350.52	0.25	-1.57	43,036
1993	338.33	0.29	-1.35	51,728
1994	345.70	0.24	-1.62	45,751
1995	320.41	0.33	-1.00	24,059
1996	322.97	0.38	-0.32	22,985
1997	321.95	0.36	-0.56	51,362
1998	319.75	0.39	-0.36	17,014
1999	409.17	0.11	-4.56	20,205
2000	321.05	0.32	-1.33	21,959
2001	310.65	0.41	-0.58	44,001
2002	311.40	0.42	-0.46	18,723
2003	308.26	0.50	0.02	6524
2004	325.99	0.34	-0.95	15,574
2005	312.27	0.58	0.68	9584
2006	332.95	0.34	-0.56	14,891
2007	335.82	0.26	-1.82	34,311
2008	317.37	0.39	-0.86	81,490
2009	314.72	0.47	-0.14	66,163
2010	302.78	0.80	0.94	14,686
2011	328.48	0.33	-0.40	77,503

TABLE 3 Summary of the parameter estimation in fitting the von Bertalanffy growth function to weight-at-age data for *Clupea harengus*

Year	W_{∞} (g)	K	t_0	Sum of LS
1978	360.08	0.56	0.70	846,695
1979	381.76	0.59	0.84	370,509
1980	391.84	0.54	0.93	1,601,255
1981	402.81	0.45	0.33	718,313
1982	332.67	0.52	0.48	227,308
1983	402.52	0.45	0.24	375,998
1984	520.86	0.25	-1.25	512,905
1985	378.05	0.39	-0.32	411,504
1986	305.59	0.67	0.91	101,397
1987	301.71	0.49	0.26	422,394
1988	343.95	0.41	0.08	370,801
1989	381.45	0.39	0.22	30,380
1990	344.99	0.35	-0.49	360,013
1991	314.32	0.34	-0.42	339,727
1992	303.14	0.33	-0.63	198,717
1993	357.28	0.22	-2.00	200,257
1994	376.74	0.19	-2.09	149,524
1995	279.52	0.25	-1.72	58,142
1996	301.44	0.32	-0.53	64,088
1997	281.58	0.31	-0.72	133,324
1998	247.34	0.37	-0.46	48,501
1999	337.90	0.19	-2.74	76,971
2000	285.64	0.29	-1.43	100,492
2001	252.64	0.35	-0.86	129,762
2002	264.41	0.30	-1.32	121,992
2003	221.71	0.54	0.29	15,566
2004	335.18	0.25	-1.54	52,276
2005	233.13	0.66	1.01	29,369
2006	293.48	0.39	0.01	46,510
2007	337.73	0.23	-2.05	144,549
2008	276.23	0.33	-1.13	294,508
2009	251.10	0.47	0.02	348,470
2010	246.34	0.50	0.43	44,086
2011	229.05	0.47	0.40	137,769

3.2 | Factors influencing life history

In relation to the time frame of this research (1978–2011) and concurrent with the variability of these life history traits are fluctuations in the SSB of herring. Starting with the lowest value in 1982 of 53,084 t, the population began an increase in the mid-1980s into the early 1990s, with the highest value of 452,094 t in 1992 (Figure 9). Through the 1990s, SSB remained in a relatively high phase, then declined through 2010, with a spike in 2011 to 185,013 t.

3.2.1 | Zero lag GAM

The performance of each zero lag GAM model varied with each response variable (Table 4). Deviance explained ranged from 56.9% for K of W_{∞} , to 19.2% for L_{∞} , with a mean of 44.9%. The mean adjusted R^2 value was 0.35 and spanned from 0.49 for K of W_{∞} to 0.08 for L_{∞} . SSB had the lowest P values over SST and salinity on three of the five response variables. Logb, ω and K of W_{∞} were significant, while L_{∞} and W_{∞} were not, with $P = 0.436$ and 0.071 , respectively. The mean P value for SSB was 0.085. Salinity was only

TABLE 4 Results for GAM models of life history parameters of *Clupea harengus* in response to environmental variables

Parameter	Response variables						Mean
	logb	L_{∞}	K of L_{∞}	ω	W_{∞}	K of W_{∞}	
Adjusted R^2	0.38	0.08	0.31	0.42	0.40	0.49	0.35
Deviance explained (%)	49.1	19.2	41.2	52.0	50.2	56.9	44.77
Generalized Cross-Validation	0.000	0.004	0.099	0.073	0.027	0.068	0.045
Akaike Information Criterion	-68.06	305.03	-43.74	340.84	365.66	-61.00	139.79
P values							
Smoothed covariates							
SSB	0.005	0.436	0.000	0.000	0.071	0.000	0.085
SST	0.938	0.293	0.406	0.468	0.105	0.254	0.411
Salinity	0.144	0.412	0.346	0.243	0.136	0.014	0.216

Note: AIC, xxx; GCV, xxx; SSB, spawning stock biomass; SST, sea surface temperature.

TABLE 5 Results for GAM models of 1-year lagged life history parameters of *Clupea harengus* in response to environmental variables

Parameter	Lagged response variables						Mean
	logb	L_{∞}	K of L_{∞}	w	W_{∞}	K of W_{∞}	
Adjusted R^2	0.30	0.49	0.34	0.42	0.42	0.27	0.37
Deviance explained (%)	40.2	66.4	40.4	49.5	49.2	34.8	46.75
Generalized Cross-Validation	0.001	0.003	0.097	0.075	0.028	0.095	0.050
Akaike Information Criterion	-62.43	282.44	-42.445	332.43	356.05	-47.64	136.40
P values							
Smoothed covariates							
SSB	0.009	0.035	0.000	0.000	0.112	0.001	0.026
SST	0.929	0.076	0.798	0.868	0.787	0.797	0.709
Salinity	0.528	0.025	0.140	0.273	0.154	0.371	0.248

Note: AIC, akaike information criterion; GCV, generalized cross-validation; SSB, spawning stock biomass; SST, sea surface temperature.

significant for K of W_{∞} , $P = 0.014$. None of the dependent variables responded significantly to SST.

3.2.2 | Lagged GAM

Once the response variables were offset with a 1-year lag, the overall performance of each model and significance to SSB strengthened (Table 5). The mean deviance explained increased to 46.75%, ranging from 66.4% for L_{∞} to 34.8% for K of W_{∞} . Adjusted R^2 values increased to a mean of 0.37 and spanned from 0.49 for L_{∞} to 0.27 for K of W_{∞} . The mean P value of SSB decreased below the set alpha of 0.05 to 0.03. logb, L_{∞} , K of L_{∞} , ω and K of W_{∞} responded significantly to SSB, while W_{∞} did not, $P = 0.112$. L_{∞} was the only variable to respond significantly to salinity, $P = 0.25$.

4 | DISCUSSION

Analysis of fishery-dependent data suggests that herring from commercial catches within the GoM demonstrated temporal variability

and a decline in various size and age metrics from 1978 to 2011 and that density dependence was the most important factor when compared to temperature and salinity.

Size and age diversity are important considerations for determining resilience and productivity in fish stocks (LeBris *et al.*, 2015). This study demonstrated decreases in the length and weight range, the mean adult size-at-age, the maximum attainable size and the growth potential of Atlantic herring between the years 1978 and 2011. This may have implications for the stock since larger and older fish are pivotal for a population as they are more fecund (Bobko & Berkeley, 2004) even at sustainable exploitation rates, therefore sustained fishery yield can be reduced by size and age truncation of the resource (Berkeley *et al.*, 2004).

The morphology of herring varied profoundly throughout the time frame of this research. The allometric factor logb decreased from 1978 to 1999 and increased from the late 1990s to 2011. Moreover, a decrease in both W_{∞} and the adult mean weight-at-age were apparent. Combined, these decreases support the change in condition and shift towards a more truncated size structure. This change in morphology is aligned with density dependence, with an increase in SSB and a potential decrease in food supply through the 1990s. Indeed, the

preferred prey of herring, *Calanus finmarchicus*, were depressed through the 1990s and into the early 2000s (Pershing *et al.*, 2005; EcoMon Gulf of Maine Copepod Time Series (n.d.)), perhaps as a result of high grazing pressure by herring, but also potentially related to freshening impacts on zooplankton community structure as inferred by Pershing *et al.* (2005). L_{∞} , K of L_{∞} and ω decreased, supporting a decline in growth potential. These decreases indicate that herring were not growing as large as they once did in the 1970s.

Beverton and Holt (1957) indicated that density-dependent growth in relation to the physiological concepts of the VBGF influence the asymptotic size of fishes. As such, L_{∞} , K of L_{∞} , W_{∞} , K of W_{∞} , ω and $\log b$ all displayed significant inverse relationships to SSB. This relationship supports life history theory: with an increasing SSB of herring comes an increase in competition for food and a decrease in food availability, *i.e.*, zooplankton (Lorenzen & Enberg, 2002; Walters & Post, 1993). A negative impact on herring diet could hamper growth potential, like the effects of low food availability on any organism. Coincidentally, the highest SSB for this time frame was during the 1990s, when $\log b$, K of L_{∞} , ω and K of W_{∞} were at their lowest. Furthermore, the highest values of these parameters occurred during the lowest values of SSB, from the late 1970s into the mid-1980s, suggesting that the opportunity for larger growth potential occurred during a period of low herring biomass. Moreover, the length and weight size range were the largest in 1979, when SSB was at its lowest, and were at their narrowest in 1999, when SSB was at its highest.

For the VBGF models, the LS only exceeded the 95% CI for 3 years, 1978, 1980 and 1981. This time frame occurs during the collapse of this fishery, where landings and therefore sampling were significantly low. During the late 1970s and throughout the 1980s, the SSB was at its lowest population and in what is now referred to as a collapse and rebuilding phase (Overholtz, 2002).

SSB was identified as the most significant variable for both types of GAMs, except for L_{∞} and W_{∞} , with zero lag, and W_{∞} , with a 1-year lag. With the 1-year lag of the response variables, an overall better fit and tightening of the models and reduction of P values was apparent, supporting the sometimes delayed response that occurs within organisms between their life history traits and changes in their surrounding environment. For example, a substantial decrease in food supply would not instantly impact the condition of a fish population, it would take some time for noticeable changes to be detected.

Although these GAMs suggested SSB was the main driver, it should not be overlooked that significant relationships with SST were observed *via post hoc* individual regression and correlation, and salinity was found to be significant within both types of GAMs.

For over 100 years, SST in the GoM has been on a variable increase, with a substantial increase since 2003 (Pershing *et al.*, 2015; NEFSC, 2016). Temperature influences entire ecosystems, from life history and metabolic activities to spatial arrangements of marine organisms (Dell *et al.*, 2011; Houde, 1989; O'Connor *et al.*, 2007).

Since the late 1970s, salinity in the GoM and the continental north-west Atlantic has been decreasing, with a striking decrease in the 1990s (Ji *et al.*, 2008). Increased freshwater on the Labrador Shelf during the

1990s played a key role in this salinity anomaly (Häkkinen, 2002). Again, even though the GAMs suggested the overall driver was SSB, salinity was significant, with K of W_{∞} in the zero lag GAM and L_{∞} in the lagged GAM. This freshening event may have influenced certain life history traits of herring, as well as the plankton communities (Pershing *et al.*, 2005). In addition, GoM salinity was at a low in 1998, aligning around the time of the high SSB and low *C. finmarchicus* biomass, $\log b$, K of L_{∞} , ω and K of W_{∞} , and inversely was at its highest in the late 1970s, aligning with a high $\log b$, L_{∞} and W_{∞} , and low SSB.

These noticeable changes in SST and salinity can alter primary and secondary productivity of entire ecosystems. As such, plankton and therefore food sources for higher trophic species can be shifted in both distribution and abundance.

C. finmarchicus plays a pivotal role in the GoM ecosystem (Bigelow, 1924; Johnson *et al.*, 2011). The later lipid-rich stages (CV–VI) are the primary food for herring (Runge, 2007). Significant abundance declines in *C. finmarchicus* could lead to negative impacts on the local metazoan energy budget and affect the biomass and distribution of planktivores and their predators (Johnson *et al.*, 2011). Studies identified significant declines of *C. finmarchicus* within the GoM from the late 1990s into the 2000s: “*C. finmarchicus* experienced a dramatic decline in 1998 to levels not seen since the 1960s” (MERCINA, 2001; Greene *et al.*, 2003). The deep basins of the GoM, where *C. finmarchicus* over-winter, have also seen significantly low population abundances around 1998 (Greene *et al.*, 2003; Runge *et al.*, 2015). Greene *et al.* (2003) linked these declines in abundance to climate variability associated with the North Atlantic Oscillation. This timing aligns around the high herring SSB found throughout the 1990s and early 2000s, and low values of life history traits during the 1990s. Moreover, SSB was at its highest value on record in the late 1960s (Figure 9), around the time of the earlier low biomass of *C. finmarchicus*.

Perhaps a top-down effect during the high SSB of herring created a density-dependent competition for *C. finmarchicus*. During the high SSB in the 1990s, it could be argued that the herring population forced significant predator/prey pressure on this vital zooplankton, in the process depleting its abundance and grazing down its own food supply (Brooks & Dodson, 1965). This scenario supports the decrease in the values of the life history traits, the presence of population stressors in the mid-to-late 1990s and life history dynamics in general (Lorenzen & Enberg, 2002; Walters & Post, 1993).

Long-term sustainability among a fish population is strengthened by structural diversity (Wheeler *et al.*, 2009). However, these results suggest that significant variability and decreases among important life history traits occurred within this population because of changing population size. These results may further enhance our understanding and knowledge of this and other fisheries, and in particular better inform both management and population models during stock-wide transitions in life history traits.

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