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Smaller size-at-age menhaden with coastal warming and fishing intensity

R Eugene Turner

The size-at-age of one million *Brevoortia tyrannus and B. patronus,* harvested from Maine to Texas over 65 years, were analysed to determine if there was evidence of changes consistent with the well documented temperature size rules. The average *annual* weight and length for age 3-, 4- and 5-year-old fish declined on both the Atlantic and Gulf of Mexico (GOM) coasts. For example, the average size of a 4-year-old fish captured in 2010 from the Atlantic and GOM, relative to an average 4-year-old fish captured in 1987, is 15 per cent and 11 per cent lighter, respectively. Small changes in the year-to-year size of same-aged fish were closely related to variations in the annual air temperature (used as a proxy for water temperature) for fish on both coasts. The size-at-age of GOM fish are also smaller during overfished periods compared with underfished periods by 10–24 per cent, and decrease by about the same proportion as indicated by temperature changes. The most plausible explanation for these size changes is that they are a consequence of recent coastal and oceanic warming. These reductions in size-at-age by temperature and fishing pressure affect egg production, oil yield and prey community for one-half of the US Atlantic and GOM fish harvest. The future of menhaden fish size-at-age will be, it seems, smaller as oceanic temperatures rise.

Key words menhaden; size; *Brevoortia*; climate change; fisheries; Gulf of Mexico and Atlantic

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Introduction

The average body size of individual ecotherms in the ocean is declining for bacteria, benthic invertebrates, and fish as climate change warms the planet (Daufresne *et al.* 2009; Hiddink *et al.* 2015). The empirical basis for this changing body size is supported by Bergmann's Rule, James' Rule, and the Temperature Size Rule (TSR) [see reviews by Angilletta and Dunham (2003), Angilletta *et al.* (2004) Daufresne *et al.* (2009) and Millien *et al*. (2006)]. Briefly, Bergmann's Rule holds that the sizes of *species* in warmer environments will be smaller than species found in cold environments. Similarly, James' Rule suggests that the *mean body size of an individual species* for a unique population will be inversely related to average environmental temperature. Finally, the TSR applies to the inverse relationship between temperature and size for *individuals* of the same species and age. Two factors contributing to the decline in size-at-age are: (1) the respiratory demand of individual fish is more easily satisfied by the greater surface area-to-volume ratio of smaller organisms; and (2) the higher oxygen concentration at colder temperatures which increases the available oxygen for cross-cellular transport. Smaller-sized fish also have smaller cell sizes, with the cell size scaling directly with fundamental properties such as genome size, growth rate, protein synthesis rates and metabolic activity (Arendt 2007; Hessen *et al.* 2013). Daufresne *et al.* (2009), for example, described a temperature-dependent shift in the size-at-age for Herring and Sprat populations in the Baltic Sea, and in adult females of *Pseudocalanus* species grown in temperature-controlled mesocosms. Organism size, therefore, is affected by temperature in various ways, and the consequences extend to throughout the food web (Daufresne *et al.* 2009; Ohlberger 2013).

The increase in global air temperatures and sea surface temperature (SST) in the last century warmed at about equal rates (0.74°C and 0.67°C, respectively; Trenberth *et al.* 2007), and the SST from 1982 to 2006 on the Atlantic coast increased between 0.16–0.23°C

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and 0.31°C in the Gulf of Mexico (GOM) (Belkin 2009). The rise in temperature was 0.8°C over the coral reefs in the Florida Keys in the last century (Kuffner *et al.* 2015) and more than 3°C from 1979 to 2006 in GOM seagrasses (Fodrie *et al.* 2010). The temperature changes on the continental shelf are tracked by fish stocks (Nye *et al.* 2009; Pinsky *et al.* 2015). Some models of the effects of the anticipated *future* global changes in ocean temperature strongly suggest that the body size of the harvested oceanic organisms will be reduced, perhaps by 14–24 per cent from 2000 to 2050 (Cheung *et al. 20*13). Lefevre *et al*. (2017) conclude that some of the coefficients in Cheung *et al*.'s (2013) model include erroneous assumptions about gill size, body mass and respiratory demand, but that warming may 'lead to reductions in the average body size and size-at-age of fishes'. Also, Cheung *et al*.'s (2013) model results are the simulated landings of open ocean species, and are not about the coastal species with a different reproductive cycle involving estuarine waters. Documenting the changes in size-at-age would be useful to confirm the scale of changes and to improve the modelling coefficients for coastal fish. Information on the average size-at-age of individuals over many years would be informative, in this regards, and a compelling aspect for investigation as we evaluate the effects of future climate changes on fish stocks. Monitoring data from commercial fishing harvest are a principal source of such data.

Data from fishing, however, can complicate a time-series analysis of fish size when the size-at-age is unknown (Baudron *et al.* 2014). Fishing disproportionately removes the largest and oldest fish, for example, and the selectivity-at-size of the fishery may change temporally, so that different sizes of individual fish are targeted over time. Fishing may also reduce the size of the harvested similarly aged fish because of their capture at the beginning of a year, rather than later. Further, the age at maturation may change with fishing pressure as intraspecific competition is reduced. The average size of individual organisms over time may be the best data available, and fish size-at-age information is often restricted to less than two decades of data and without consideration of a changing genetics (Kuparinen and Merilä 2007). The results may be that the average size of the *harvested* fish may decrease, but we do not know if the size of the same-aged fish declines from changes in temperature, fishing effort, net selectivity, or another factor. Quantifying changes on the aged individuals that are due only to temperature may be, therefore, somewhat problematic.

The extensive fishery-dependent data on the United States (US) menhaden fisheries can be used to examine how regional temperature affects the size of the fish. The commercial purse seine landings of the two species of menhaden caught (*Brevoortia patronus* and *B. tyrannus*) were valued as US$129 million (dockside) and weighed 667 million mt in 2013 (NMFS 2014). The total weight was 53 per cent of the total Atlantic and GOM fisheries landings, but only 5 per cent of the value. The harvest record of both species since 1940 is shown in Figure 1.

The life history of both menhaden species is to spawn offshore, move to suitable estuaries where juveniles grow to 1- and 2-year-old fish, and then to return offshore where they are harvested with purse seines (VanderKooy and Smith 2015). The *B. tyrannus* occur on the Atlantic coast from Maine to northern Florida, and are now mostly caught around Virginia (Smith 1991; Reintjes 1969; SEDAR 2015; VanderKooy and Smith 2015). The results from genetic and tagging studies suggest that the Atlantic stock is a single population unit with extensive migratory range (SEDAR 2015). The *B. patronus*, also a single population unit, are landed principally (94% in 1996) in the central northern GOM (Nicholson 1978; SEDAR 2013). Almost all purse seine sets occur within 35 km of the shore, or in coastal bays in the Atlantic (SEDAR 2015) and almost entirely within 32 km from shore on the continental shelf in the GOM (Nicholson 1978). The growing season in the Atlantic appears to be defined by temperatures above 15°C, and the larger fish of a given age are captured further north than the same aged smaller fish (SEDAR 2015). Sexual maturity and fecundity are considered to be directly dependent on length and biomass (condition) rather than age *per se*. One-year-old fish can be sexually mature, but it is the 2- and 3-year-old fish that produce most of the total eggs in most years. The smaller biomass of 4-year-old fish contributed significantly in recent years because of increasing fecundity with age (SEDAR 2013 2015).

The size and age of more than one million coastal clupeids have been determined for the last six decades

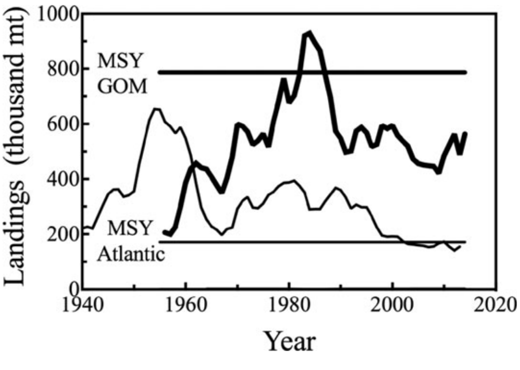

Figure 1 The landings (thousand mt) of the Atlantic and GOM menhaden fishing fleet from 1940 to present. The maximum sustainable yield (MSY) was estimated from the Beaufort Assessment Model Correction made on 11 September 2018 after first publication: The unit of measurement for landings is corrected.

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in a consistent manner. These size-at-age data were used to investigate temporal changes in the size-at-age of the menhaden, and to test the hypothesis that variations in temperature and fishing pressure affect the size-at-age of individual fish.

Materials and methods

Regional temperature

Water temperatures on both coasts are increasing with air temperature, especially in estuaries where there is an efficient exchange of heat between air and water (Smith and Kierspe 1981). The winter estuarine water and air temperatures track each other on the Atlantic coast with an effect on fish and shrimp abundances (Hettler and Chester 1982; Hare and Able 2007). The annual cycle of monthly temperatures and changes in the summer temperature on the Louisiana continental shelf are closely related (Turner *et al*. 2017). The period of record for water temperatures, however, is not as prolonged as for air temperature measurements, and the rate increases (°C year^{-1}) may not be equivalent for both because of various physical reasons, including differences, for example, in reflectance, reservoir size, reservoir turnover, and specific heat content. There is no systematic collection of water temperature for the Atlantic and GOM coastal waters for all months of all years of the menhaden data collection. The regional annual air temperature from each coast was used as a surrogate of water temperature changes, therefore, to explore how the annual variations in size-at-age are related to annual variations in water temperature. These temperature data are the monthly averages of the daily air temperature at weather stations that are available at the NOAA National Centers for Environmental Information (www.ncdc.noaa.gov/cdo-web/). The annual average monthly temperature for the Southeast Region of Maryland, located in the middle of the fishing zone, was used for the Atlantic menhaden data (US Department of Commerce 2016). The monthly data were summed for an average annual mean of each year. Station GHCND:USW00012916 is for the New Orleans International Airport, which is in the middle of the fished zone for the remaining four contemporaneous GOM processing plants located between Moss Pt, MS and Cameron, LA (Smith and Vaughan 2011).

Fish size and age data collection

The weight, length and age of menhaden have been determined through sampling of 495,000 *B. tyrannus* collected between 1955 and 2008 (Atlantic States Marine Fisheries Commission 2010, 30) and 510,000 *B. patronus* between 1964 and 2010 (Vaughan *et al.* 2010, 5), respectively. Port agents measured the fish's fork length (mm) and weight (g), and removed a scale patch (*c*. 10–25 scales) from the mid-portion of the flank below the dorsal fin for age determination. The analysis of the age data began in 1955 and has been under the continuous supervision of Ethel A. Hall at the National Marine Fisheries Service (NMFS) Beaufort Laboratory, Beaufort, NC since 1969. At least six scales per fish are read for counts of growth intervals. The independent scale reader data have been replicated with independent observers, and verified with otolith age determinations (SEDAR 2015, 24). NMFS personnel demonstrated that only one ring forms annually by measuring on menhaden impounded for up to 14 months (SEDAR 2015, 23). Menhaden are assigned ages based on a 1 March 'birthdate', based on the peak period of annulus formation (SEDAR 2015, 23).

Fish size-at-age

The sources of the average fish size-at-age data for the GOM are from Vaughan *et al*. (2010), and from Atlantic States Marine Fisheries Commission (2010) for the western Atlantic (US) seaboard. These reports include the average measured fork length, and the total number and weight of the aged harvested menhaden from 1955 to 2012 for each year. The mean size-at-age in each year from 1955 to 2012 was calculated separately for each species using the number of fish and the total weight for each age class. The standard error term of the weight is not reported in these NOAA reports. The average number of fish aged each year was 10,922 from 1964 to 2010 for the GOM, and 9267 from 1955 to 2008 for the Atlantic. A simple linear regression of the weight or length (Y) versus year (X) was made for each age class using:

$$\mathrm{Y} = \mathrm{aX} + \mathrm{b} \tag{1}$$

where a is in °C year^{-1}.

Various transformations of the independent data did not yield stronger alternative descriptions of variable variance as a function of year. The weight and fork length of individual age classes were compared for both coasts.

Under- and overfishing intervals

A period of over- or under-harvest is based on the results from the NMFS Beaufort Assessment Model (BAM) (SEDAR 2013 2015; Vaughan *et al. 2*010). The BAM was developed as a benchmark to estimate the maximum sustainable yield (MSY) for both stocks (Williams and Shertzer 2015) and includes a spawner–recruit curve and values for growth, natural mortality, maturity, and selectivity to estimate the MSY as the maximum equilibrium landing. The estimate of total allowable catch (TAC) by the Atlantic menhaden fisheries was 170.8 million mt in 2013 after a coefficient for age at maturity ('ogive') was adjusted (SEDAR 2015, 27). The current TAC has not been exceeded by

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the reduction fisheries since 2003. There are no harvest limits for the GOM menhaden harvest (SEDAR 2013, 203), but the mean estimate of the MSY for the GOM menhaden is 787 million mt (CI = 772–831 million mt; SEDAR 2015, 205). The current GOM harvest in 2012 is not considered to be 'overfished' in terms of the BAM modelled MSY. A rough estimate, therefore, is that the Atlantic harvest was 3.8 times the modelled MSY at a peak in 1954, and 2.0 times the MSY in 1972. Menhaden landings were 1.2 times the GOM MSY after 1982, but less than 1 after 1988. The interval of over-harvest was estimated to be for between 1983 and 1987 for the GOM fisheries. A two-year separation between over-harvest and underfished time period was used to account for the carryover effect of the density of menhaden (over- or underfished) population age on fecundity, which increases with age (SEDAR 2013). The temporal relationship between the harvest and MSY for each coast is given in Figure 1.

Multiple regression models

The size-at-age and temperature data described above were entered into a multiple regression model to predict the variations in the dependent variable average weight (g) or length (cm). The data were divided into three datasets: the GOM, Atlantic, and combined GOM and Atlantic. A p value was calculated for each model equation, and the p value for the type III sum of squares calculated to test if the individual contribution to the total model was significant. A further division of the GOM data was made for the weight at age in years that were above or lower than the BAM estimates of MSY, as described above. A test was made to detect if the slope and intercept of a simple regression of weight (Y) and temperature (X) were different for when the harvest was above or below the BAM estimate of the MSY. The p value (two tailed) was used to test the null hypothesis that the slopes were identical (parallel lines). If the slopes were identical, then a second p value was calculated to test the null hypothesis that the lines had identical zero intercepts. If this second p value was high, then there was no compelling evidence to conclude that the lines are different. The same analysis was done to test if the air temperature in New Orleans and Southeastern Maryland changed at the same rate. The best two-variable model was selected using the type III sum of squares results from a multiple regression model to choose between age, year and temperature categories as independent values.

Results

Air temperature

The air temperature increased at a nearly identical rate of 0.0163 and 0.01768°C year^{-1} since 1940, at New Orleans, LA and at Southeastern Maryland, respectively ($p < 0.0001$) (Figure 2). There was no difference in the regression line slopes. The temperature variations from one year to the next were as large as the average change over a decade or more.

Fish weight and length variations each year

The size of the Atlantic menhaden is about 50–60 per cent larger than GOM menhaden in the first two years of growth, but then becomes twice as large by year 5. The separation among groups, between being statistically significant at over 95 per cent or not ($p < 0.05$), occurs between years 2 and 3 (Figure S1). In general, the average annual weight- and length-at-age of fish captured decreased from 1955 to 2008 for the Atlantic menhaden, and from 1964 to 2010 for the GOM menhaden (Figure 3). The results for the individual linear regression equations for the weight and fork length of each fish are given in Table I. The coefficient of loss per year for fish *weight* or *length* at 0–1 year old in the GOM was not significant, but was significant for 2-, 3- and 4-year-old fish. The annual decline in the weight and length of Atlantic menhaden was significant for the 0- 4- and 5-year-old fish. The size change is such that the weight of a 4-year-old fish in 2015 is 15 per cent smaller than the same aged fish in 1980 (–0.43% year^{-1}). The annual Atlantic and GOM menhaden size (weight or length) declines at the same rate per year (Figure S2).

Variations in size with temperature and fishing pressure

The best two-variable model included the 'age' and 'temperature' variable to predict size, but not the 'year' variable. The results from the multiple regression analysis indicate that the variability in average size-at-age (weight and length) of GOM fish is negatively related to the variability in the annual temperature for

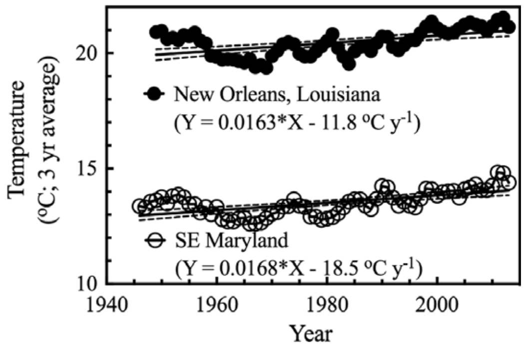

Figure 2 The average annual air temperature at New Orleans, LA (top) and southeast Maryland (bottom) from 1946 to 2014. A linear fit of the data is shown together with the 95 per cent confidence interval ($p < 0.001$)

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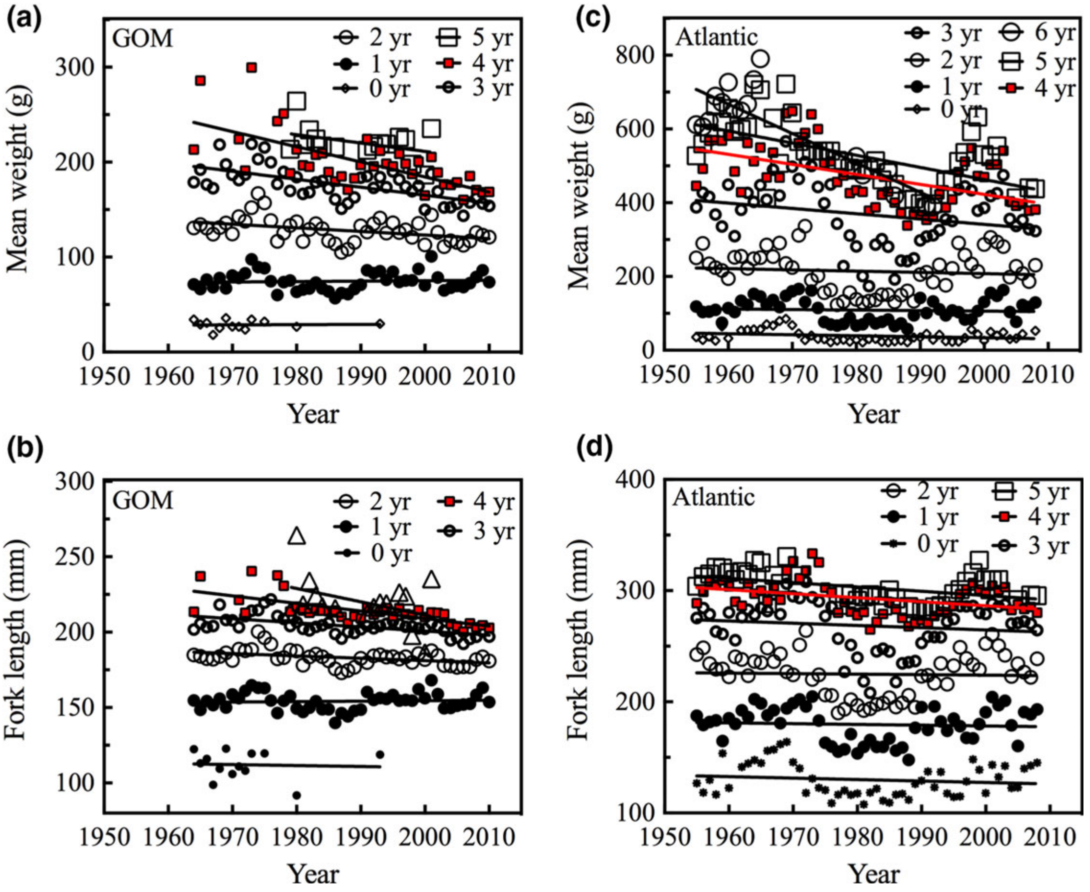

Figure 3 The weight (g) and length (mm) of aged fish for the GOM (a, b) and Atlantic (c, d) menhaden from 1955 to 2012. The equations of each linear regression line is in Table I. The statistical significance, if any, for the simple linear regression line for each age group is shown to the right (*p* values)

that year (Table II; $R^2 > 0.87$; $p < 0.01$). Temperature was not a significant factor describing variations in length for the Atlantic dataset, but was for the variations in weight (Table II; $R^2 = 0.88$; $p < 0.01$). The variations in temperature were a significant factor describing the variations in length and weight for the combined dataset (Table II; $R^2 > 0.86$; $p < 0.01$).

The size-at-age of fish in the GOM is lower at the same temperature during periods when the total harvest is greater than the MSY, compared with when it is less than the MSY (Figure 4). There was no difference in the slopes of the regression analysis, indicating that the statistical relationship between temperature and declining size was the same, but the intercept was lower for fish caught during periods when fishing was greater than the MSY ($p < 0.01$; Table III). The average size for 1- to 4-year-old GOM fish taken at 20°C, for example, is 10–23 per cent smaller than for fish harvested during underfished years. The slope (g °C) declined faster with increasing size. A 200 g 3-year-old fish in water that warmed 2°C would become 33.6 g (17%) smaller. There was no statistically significant effect of fishing pressure on the size of fish from the Atlantic fisheries revealed in this analysis when the Atlantic dataset was analysed by itself, but there was a highly significant effect on both weight and length when the GOM and Atlantic datasets were analysed together within one dataset (Table II). The statistical significance in the combined datasets may be driven solely by the temperature effects in the GOM dataset.

Discussion

The menhaden length- and weight-at-age for both species demonstrate a convincing decline in most size classes for the same aged fish on both coasts. The annual changes in the weight and fork length of both Atlantic and GOM menhaden decreased from 1955 to 2012 for the older fish, but not the younger ones, whereas there was a difference for 1-, 2-, 3- and 4-year-old GOM fish. The size decline in the same aged fish

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Table I Summary statistics for the data in Figure 3 showing the average weight and fork length for different aged fish in the Gulf of Mexico (GOM) and Atlantic fisheries. The *p* values in bold are significant at the <0.05 confidence interval

	N	*Y (g or mm)*	*=a* (year) + b*	p
A. GOM: weight (g) at age				
0 year	13	Y	=0.02147*X – 13.63	0.91
1 year	47	Y	=0.04370*X – 12.25	0.67
2 years	47	Y	=–0.3805*X + 884.2	**0.0038**
3 years	47	Y	=–0.8398*X + 1845	**0.0001**
4 years	39	Y	=–1.595*X + 3375	**0.0001**
5 years	16	Y	=–0.8813*X + 1974	0.13
B. GOM: fork length (mm) at age				
0 year	13	Y	=–0.06288*X + 236.1	0.87
1 year	47	Y	=0.02863*X + 97.27	0.65
2 years	47	Y	=–0.1561*X + 493.3	**0.0039**
3 years	47	Y	=–0.2729*X + 746.6	**0.0001**
4 years	39	Y	=–0.5017*X + 1212	**0.0001**
5 years	16	Y	=–0.8813*X + 1974	0.126
C. Atlantic: weight at age				
0 year	52	Y	=–0.2733*X + 580.4	**0.06**
1 year	54	Y	=–0.1422*X + 390.5	0.59
2 years	54	Y	=–0.3390*X + 885.7	0.49
3 years	54	Y	=–1.441*X + 3224	0.59
4 years	50	Y	=–2.714*X + 5850	**0.0001**
5 years	50	Y	=–3.293*X + 7049	**0.0001**
6 years	17	Y	=–7.968*X + 16284	**0.0001**
D. Atlantic: fork length (mm) at age				
0 year	53	Y	=–0.1317*X + 390.7	0.32
1 year	54	Y	=–0.06920*X + 316.7	0.62
2 years	54	Y	=–0.04585*X + 315.7	0.79
3 years	54	Y	=0.2022*X + 669.1	0.31
4 years	54	Y	=–0.3609*X + 1008	**0.007**
5 years	44	Y	=–0.3878*X + 1071	**0.0023**

transcends the variability from year to year for the multi-decadal record and the variable fishing effort. What are the explanations for this overall decline?

Possible explanations for size-at-age variations

The size differences between the two species at the same age cannot be explicitly described as supporting Bergmann's Rule. The temperature on each coast is different, but the size differences between species may be because the two species occupy different tidal regimes and life-history trajectories found on each coast. *B. tyrannus* travel broadly over 15° latitude (Maine to northern Florida) with an estuarine tidal range of up to 5 m (ME), whereas *B. patronus* is captured within 4° latitude for a region with a tidal range of 0.5 m, and in warmer temperatures. But the size changes with temperature in both Atlantic and GOM coasts for the individual species suggests that a global causative agent supersedes the influence of local causal agents (e.g. tides, continental shelf hypoxia or wetland loss).

Fishing pressure Fishing pressure may influence the observed average size-at-age of the fish at capture because of targeting or gear selectivity. The total yield (mt) per set for the GOM fisheries, however, has remained fairly stable in the last few decades (Figure S3), whereas the size-at-age of individual fish kept declining in proportion to temperature. Yet the fish size-at-age decreases (not increases) almost continually from before, during and after fluctuations in harvest. Fishing has an effect in addition to the overall decline in size-at-age with small variations in temperature (Figure 3). Fish-at-age are smaller if the total fish harvest is defined as 'overfished' using the BAM model. The apparent response to temperature in size-at-age, and then reversal over a few years for Atlantic menhaden under varying fishing pressure, seems quite fast for evolutionary pressures to express themselves, although it cannot be absolutely ruled out. The parallel regression lines of fish size-at-age versus temperature for the same-aged GOM fish that are overfished or not suggests that fishing *per se* is not the principal agent of the size decline, but a secondary factor. The strong relationship between small changes in temperature and size over a few years for the GOM fish implies that phenotypic plasticity occurs there.

Co-linearity between time and temperature The size-at-age of menhaden harvested on two coasts, therefore, declined as both fishing pressure and temperature increased. The average annual temperature and year are co-related (Figure 2; $R^2 = 0.69$; $p = 0.0001$), and so there may be another factor involved that is co-related with time that is misunderstood to be that from a rising temperature. But the selection of the variable 'temperature' over 'year' in the multiple regression equation suggests that the primary factor is not 'year'. A temperature effect, however, is supported by other analyses that Sheridan and Bickford (2011) summarise for plants, fish, birds, mammals and other species. One of the key elements is that metabolism may increase with rising temperatures, but that the availability of oxygen solubility and physiological access declines, and with a consequential reduction in net production as adults. Further, a 1°C increase has been shown to result in a 6–22 per cent reduction in fish size (Sahin 2001; Desai and Singh 2009), which bounds the observed size decline measured for menhaden. The conclusion that climate change is driving these changes, therefore, although not experimentally tested with menhaden, is based on the commonality of the changes on two coasts, the steady and declining size, the direction of change, physiological expectation and observations, experiments with a wide range of other species, and modelling results.

Evaluating the changing average size of the same-aged Atlantic fish with temperature, however, has some complications that the GOM fisheries does not: (1) the number of years included for the fish harvested during underfished season equals only four; (2) the fisheries

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Table II Results of a multiple regression analysis of the relationship between temperature (°C) and age (years) on menhaden weight (g) and length (cm) for the Gulf of Mexico (GOM), Atlantic, and combined datasets

	Model variance					*Type III sum of squares*		
Region	n	R^2	*Adj.* R^2	F	p	*Parameter*	F	p
A. GOM								
Weight	209	0.89	0.84	796.0	<0.0001	temperature	9.4	0.002
						age	1584.0	<0.0001
Length	209	0.87	0.87	693.9	<0.0001	temperature	18.8	<0.0001
						age	1369.0	<0.0001
B. Atlantic								
Weight	354	0.88	0.88	1291.0	<0.0001	temperature	6.3	0.012
						age	2535.0	<0.0001
C. Combined GOM and Atlantic								
Weight	563	0.86	0.86	1705.0	<0.0001	temperature	519.7	<0.0001
						age	2577.2	<0.0001
Length	558	0.87	0.86	1776.4	<0.0001	temperature	461.6	<0.0001
						age	2811.8	<0.0001

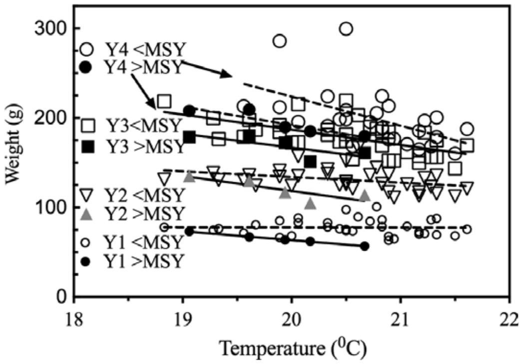

Figure 4 The average menhaden weight for the 1, 2, 3 and 4-year-old aged fish in the GOM fisheries (g) versus regional temperature. The dataset for each year class is divided into years when the total harvest was < or > than the modelled maximum sustainable yield (MSY). The slopes were not significant among year classes, whereas the intercept was different

Table III Results of tests for whether or not the slopes and intercepts of a linear regression of weight (g) versus temperature (°C) are different in years whose harvests are above and below the MSY. Four age classes of Gulf of Mexico menhaden landings were tested

	Slope			*Pooled slope*	*Elevation*		
Year	F	p	*Are slopes different?*	*(coef. X, °C)*	F	p	*Are intercepts different?*
1	1.7	0.200	no	–0.9	9.3	0.004	yes
2	1.1	0.310	no	–7.2	6.7	0.014	yes
3	0.0	0.900	no	–16.8	7.1	0.011	yes
4	0.2	0.625	no	–30.4	4.4	0.044	yes

have been confined to a smaller geographical area in the last 20 years (although it remains large compared with the GOM); and (3) the catch-per-set is increasing in the Atlantic (Figure S3). The catch-per-set is a measure of effort for the boat for that part of the day; it is not the same as the number of days fished. It indicates potential changes in gear (Smith 1991; SEDAR 2015), skill, fish schooling or combinations thereof. Furthermore, fish movements extend north and south along the coast to cover a wide range of temperature conditions that one station record at the centre of the fish's offshore range is not likely to capture. The annual variations in temperature at one weather station are clearly not representative of the regional complexities except for year 1 fish caught in the Atlantic, whose habitat temperature is in estuaries influenced by air temperature, whereas the oceanic temperatures of the older fish are more weakly related to regional coastal air temperatures. The temperature of one year carries forward into the temperature of the next year, and so forth; the upward rise in temperature is predicated on the warming from the previous years, and so the effects cannot be easily separated with significant step functions.

It would be interesting to incorporate a changing temperature coefficient into the various modelling indices of fecundity, growth and mortality. The models could be probed to see how well the observed sizes are simulated. Then future temperature projections can be evaluated to see what effects may appear on the size of individual fish, and the MSY on both coasts.

Ecological implications

There are consequences of these size changes for the menhaden population, and for the community of its predators, regardless of how well we understand and model them. The fishing of menhaden, for example,

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has consequences for nekton food webs in the estuaries and offshore (Hartman and Brandt 1995; Pruell *et al*. 2003; Uphoff 2003; Vaughan *et al*. 2007; Walter *et al.* 2003). Smaller sized fish of the same age will appear as fishing pressure increases, and fish maturation may accelerate (Kuparinen and Merilä̊ 2007). There is more egg production as fish age (Nelson *et al*. 1977). The 5+-year-old fish, for example, produce two to three times more eggs than females aged 3 years old (SEDAR 2015). The percentage of body oil increases with age and size for clupeids (Bruce 1924), which affects the caloric yield and quality for predators. Further, the gape size and swimming speed of prey and predator change with size. The sum effect of these subtleties, as modelled by Audzijonyte *et al.* (2013), is that there may be significant consequences from a 0.4 or 0.8 per cent year^{-1} body length reduction, which is a rate similar to what has already occurred for a 4-year-old or older menhaden caught on both coasts. The effect of the fishing, if present, can be reversed, whereas the consequences of temperature changes are permanent for now, and anticipated to increase. The effects of temperature changes on these fish for the last six decades are documented and will expand as the warming of the Earth's atmosphere and oceans accelerates, as anticipated (Strauss 2013). The future of menhaden, it seems, will be even smaller.

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References

Angilletta Jr M J and Dunham A E 2003 The temperature-size rule in ectotherms: simple evolutionary explanations may not be general *American Naturalist* 162 332–42

Angilletta Jr M J, Steury T D and Sears M W 2004 Temperature, growth rate and body size in ectotherms: fitting pieces of a life-history puzzle *Integrated Comparative Biology* 44 498–509

Arendt J 2007 Ecological correlates of body size in relation to cell size and cell number: patterns in flies, fish, fruits and foliage *Biological Review* 82 241–56

Atlantic States Marine Fisheries Commission 2010 *Stock assessment report No 10-02 of the Atlantic Menhaden Stock Assessment and Review Panel Reports* Atlantic States Marine Fisheries Commission

Audzijonyte A, Kuparinen A, Gorton R and Fulton E A 2013 Ecological consequences of body size decline in harvested fish species: positive feedback loops in trophic interactions amplify human impact *Biology Letters* 9 20121103

Baudron A R, Needle C L, Rijnsdorp A D and Marshall C T 2014 Warming temperatures and smaller body sizes: synchronous changes in growth of North Sea fishes *Fisheries Bulletin* 20 1023–31

Belkin I M 2009 Rapid warming of large marine ecosystems *Progress Oceanography* 81 207–13

Bruce J R 1924 Changes in the chemical composition of the tissues of the herring in relation to age and maturity *Fisheries Bulletin* 18 469–85

Cheung W W L, Sarmiento J L, Dunne J, Frölicher T L, Lam V W Y, Palomares M L D, Watson R and Pauly D 2013 Shrinking of fishes exacerbates impacts of global ocean changes on marine ecosystems *Nature Climate Change* 3 254–58

Daufresne M, Lengfellenr K and Sommer U 2009 Global warming benefits the small in aquatic ecosystems Proceedings National Academy of Sciences of the United States of America 106 12788–93

Desai A S and Singh R K 2009 The effects of water temperature and ration size on growth and body composition of fry of common carp, *Cyprinus carpio Journal of Thermal Biology* 34 276–80

Fodrie F J, HeckJr K L, Powers S P, Graham W M and Robinson K L 2010 Climate-related, decadal-scale assemblage changes of seagrass-associated fishes in the northern Gulf of Mexico *Global Change Biology* 16 48–59

Hare J A and Able K W 2007 Mechanistic links between climate and fisheries along the east coast of the United States: explaining population outbursts of Atlantic croaker *(Micropogonias undulatus) Fisheries Oceanography* 16 31–45

Hartman K J and Brandt S B 1995 Trophic resource partitioning, diets, and growth of sympatric estuarine predators *Transactions of the American Fisheries Society* 124 520–37

Hessen D O, Daufresne M and Leinaas H P 2013 Temperature-size relations from the cellular-genomic perspective *Biological Review* 88 476–89

Hettler F and Chester A J 1982 The relationship of winter temperature and spring landings of pink shrimp, *Penaeus duorarum*, in North Carolina *Fisheries Bulletin US* 80 761–8

Hiddink J G, Burrows M T and Molinos J G 2015 Temperature tracking by North Sea benthic invertebrates in response to climate change *Global Change Biology* 21 117–29

Kuffner I B, Lidz B H, Hudson J H and Anderson J S 2015 A century of ocean warming on Florida Keys coral reefs: historic in situ observations *Estuaries Coasts* 38 1085–96

Kuparinen A and Merilä J 2007 Detecting and managing fisheries-induced evolution *Trends Ecology and Evolution* 22 652–9

Lefevre A, McKenzie D J and Nilsson G E 2017 Models projecting the fate of fish populations under climate change need to be based on valid physiological mechanisms *Global Change Biology* 23 3449–59

ISSN 2054-4049 doi: 10.1002/geo2.44

Millien V, Lyons S K, Olson L, Smith F A, Wilson A B and Yom-Tov Y 2006 Ecotypic variation in the context of global climate change: revisiting the rules *Ecology Letters* 9 853–69

National Marine Fisheries Service (NMFS) 2014 *Fisheries of the United States (2013)* Current Fishery Statistics No 2013. National Marine Fisheries Service, Washington DC

Nelson W R, Ingham M C and Schaaf W E 1977 Larval transport and year-class strength of Atlantic menhaden, *Brevoortia tyrannus Fisheries Bulletin* 75 23–41

Nicholson W R 1978 Gulf menhaden, *Brevoortia patronus*, purse seine fishery: catch, fishing activity, and age and size composition, 1964–73 NOAA Tech Report NMFS SSRF-722, Washington DC

Nye J A, Link J S, Hare J A and Overholtz W J 2009 Changing spatial distribution of fish stocks in relation to climate and population size on the northeast United States continental shelf *Marine Ecology Progress Series* 393 111–29

Ohlberger J 2013 Climate warming and ectotherm body size – from individual physiology to community ecology *Functional Biology* 27 991–1001

Pinsky M, Worm B, Fogarty M J, Sarmiento J L and Levin S A 2015 Marine taxa track local climate velocities *Science* 341 1239–42

Pruell R J, Taplin B K and Cicchelli K 2003 Stable isotope ratios in archived striped bass scales suggest changes in trophic structure *Fisheries Management and Ecology* 10 329–36

Reintjes J W 1969 *Synopsis of biological data on the Atlantic menhaden Brevoortia tyrannus* FAO Fisheries Synopsis 42 and US Wildlife Service Circular 320

Reish R L, Deriso R B, Ruppert D and Carroll R J 1985 An investigation of the population dynamics of Atlantic menhaden *(Brevoortia tyrannus) Canadian Journal of Fisheries and Aquatic Sciences* 42(Suppl 1) s147–57

Sahin T 2001 Effect of water temperature on growth of hatchery reared Black Sea Turbot, *Scophthalmus maximus (Linnaeus, 1758)Turkish Journal of Zoology* 25 183–6

SEDAR 2013 *SEDAR 32A – Gulf of Mexico menhaden stock assessment report* SEDAR, North Charleston, SC (http://sedarweb.org/sedar-32a) Accessed 24 December 2012

SEDAR 2015 *SEDAR 40 – Atlantic Menhaden stock assessment report* SEDAR, North Charleston, SC (http://sedarweb.org/sedar-40) Accessed 14 July 2015

Sheridan J A and Bickford D 2011 Shrinking body size as an ecological response to climate change *Nature Climate Change* 1 401–6

Smith J W 1991 The Atlantic and Gulf menhaden purse seine fisheries: origins, harvesting technologies, biostatistical monitoring, recent trends in fisheries statistics, and forecasting *Marine Fisheries Review* 53 28–41

Smith J W and Vaughan D S 2011 *Harvest, effort, and catch-at-age for Gulf Menhaden* SEDAR Southeast Data, Assessment, and Review, SEDAR 27-DW05, South Atlantic Fisheries Management Council, North Charleston, SC (http://sedarweb.org/s27dw05-harvest-effort-and-catch-age-gulf-menhaden) Accessed 24 December 2012

Smith N P and Kierspe G H 1981 Local energy exchanges in a shallow, coastal lagoon: winter conditions *Estuarine Coastal Shelf Science* 13 159–67

Strauss B H 2013 Rapid accumulation of committed sea-level rise from global warming *Proceedings National Academy of Sciences of the United States of America* 110 13699–700

Trenberth K E, Jones P D, Ambenje P, Bojariu R, Easterling D, Tank A K, Parker D, Rahimzadeh F, Renwick J A, Rusticucci M, Soden B and Zhai P 2007 Observations: surface and atmospheric climate change in **Solomon S, Qin D, Manning M, Chen Z, Marquis M, Averyt K B, Tignor M and Miller H L** eds *Climate change 2007: the physical science basis contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change* Cambridge University Press, Cambridge, UK and New York, USA

Turner R E, Rabalais N N and Justić D 2017 Trends in summer bottom-water temperatures on the Northern Gulf of Mexico continental shelf from 1985 to 2015 *Plos ONE* 12 e0184350

US Department of Commerce 2016 National Climatic Data Center, Washington, DC (www7.ncdc.noaa.gov/CDO/CDODivisionalSelect.jsp#) Accessed 10 September 2017

Uphoff Jr J H 2003 Predator-prey analysis of striped bass and Atlantic menhaden in upper Chesapeake Bay *Fisheries Management and Ecology* 10 313–22

VanderKooy S J and Smith J W eds 2015 *The menhaden fishery of the Gulf of Mexico, United States: a regional management plan* Gulf States Marine Fisheries Commission, Ocean Springs, MS

Vaughan D S, Shertzer K W and Smith J W 2007 Gulf menhaden (*Brevoortia patronus*) in the U S Gulf of Mexico: fishery characteristics and biological reference points for management *Fisheries Research* 83 263–75

Vaughan D S, Smith J W and Schueller A M 2010 SEDAR 27-DW02 Age, growth and reproduction of Gulf menhaden NOAA Fisheries Beaufort, NC (http://sedarweb.org/s27dw02-age-growth-and-reproduction-gulf-menhaden) Accessed 10 September 2017

Walter J F III, Overton A S, Ferry K H and Mather M E 2003 Atlantic coast feeding habits of striped bass: a synthesis supporting a coast-wide understanding of trophic biology *Fisheries Management and Ecology* 10 349–60

Williams E H and Shertzer K W 2015 *Technical documentation of the Beaufort Assessment Model (BAM)* US Department of Commerce, NOAA Technical Memorandum NMFS–SEFSC–671

ISSN 2054-4049 doi: 10.1002/geo2.44