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Two-hundred year record of increasing growth rates for ocean quahogs (*Arctica islandica*) from the northwestern Atlantic Ocean

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ABSTRACT

Ocean quahogs [*Arctica islandica* (Linnaeus, 1769)] are the longest-lived, non-colonial animal known today, with a maximum life span exceeding 500 years. Ocean quahogs are a commercially important bivalve, inhabiting the continental shelf of the North Atlantic basin. We examined growth rates of ocean quahogs that were fully recruited to the commercial fishery (> 80-mm shell length) from four sites covering the range of the stock along the east coast of the U.S. through analysis of annual growth lines in the hinge plate. Both geographic and temporal differences (on a scale of decadal or longer) in growth rates exist throughout the range of the stock. The age at which animals reached 60, 80, and 90 mm decreased significantly, and average growth rates to 60, 80, and 90 mm increased significantly with birth year at a New Jersey and a Long Island site, both located in the southwestern portion of the stock, since the late 1700s/early 1800s, likely in response to increasing bottom water temperatures. That is, growth rates vary temporally with birth date at the southwestern sites, with younger animals growing at a much faster rate in recent decades than those born many decades previously, whereas at the northern sites off southern New England and on Georges Bank, changes in growth rates through time are limited to older adult animals or absent altogether. Thus, at the southern portion of the range, variation in growth rate over time exists in all phases of ocean quahog life, whereas on Georges Bank, little evidence exists for any differential in growth rate over the last ~200 years. The fact that ocean quahogs record the rise in ocean temperatures after the Little Ice Age in the Mid-Atlantic Bight southeast of southern New England, yet demonstrate little evidence of such a rise in the southern New England and Georges Bank region, would suggest a differential response of ocean circulation and its control of bottom water temperature between the northern and southern portions of the Mid-Atlantic Bight over the last 200+ years.

1. Introduction

The ocean quahog, *Arctica islandica*, is a widespread, biomass dominant on the continental shelf throughout the northwestern North Atlantic (Merrill and Ropes, 1969; Cargnelli et al., 1999; Dahlgren et al., 2000). These bivalve molluscs grow slowly to a shell length of about 130-mm, with a life span capable of exceeding 500 years (Butler et al., 2013). The long life span and the sensitivity of the species to interannual variations in the environment, particularly temperature, have supported the use of time series of growth as a temperature proxy to track long-term trends in climate (Schöne et al., 2003; Butler et al., 2010; Butler et al., 2013) and shorter term climate cycles (Schöne et al., 2005a; Butler et al., 2013; Lofmann and Schöne, 2013; Beierlein et al., 2015). In addition to the importance of this clam as a benthic biomass dominant and its value in elucidating long-term trends in climate, the ocean quahog also supports a commercial fishery that provides clam meat for most commercial chowders. Indeed, a commercially valuable fishery for this species has existed in the U.S. since the late 1960's (NEFSC, 2009, 2017a). An essential element in the sustainable management of this fishery is information on growth rate, which controls the age at which animals reach a size that can be selected by the commercial dredge.

The growth of ocean quahogs varies substantially throughout the lifetime of an individual, and proceeds through ontogeny and into old age in a manner that is unlike the growth process of most other bivalves. Juvenile ocean quahogs grow rapidly, displaying near exponential growth until the onset of maturity, whereupon growth rate slows, yet growth continues throughout the lifetime of the individual. Although numerous authors have applied a von-Bertalanffy growth model to this species (e.g., Brey et al., 1990; Lewis et al., 2001; Kilada et al., 2007), the continuation of growth into old age contradicts the basic assumption of asymptotic growth in this model. Pace et al.

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(2017a) showed that an alternative growth model specified by Tanaka (1982, 1988) provides a better description of this growth dynamic by combining both the near exponential growth of the juvenile phase with the continuous indeterminate growth of the adult into old age.

Geographic differences in growth rates of ocean quahogs are also well documented (Murawski et al., 1982; Brey et al., 1990; NEFSC, 1995; Lewis et al., 2001; Thórarinsdóttir and Jacobson, 2005; Kilada et al., 2007; Ridgway et al., 2012). Witbaard et al. (1999) suggest that the regional differences in growth rates are predominantly due to differences in primary production, but it is certain that a combination of several environmental factors contribute to the varying growth rates throughout the range of the stock and, indeed, Marali and Schöne (2015), Mette et al. (2016), Reynolds et al. (2017) and others have shown that variations in growth of individual animals over their life span can be explained in part by changes in sea surface, and by inference, bottom water temperatures. Additionally, sex-related differences in growth rate of ocean quahogs have been described (Ropes et al., 1984; Steingrímsson and Thórarinsdóttir, 1995). Regardless of the mechanism behind variable growth rates of this species, the result is an inability to create a single age-length key for the species. Varying growth rates, observed throughout the range of the ocean quahog stock, produce not only regional differences in growth rate, but also differential localized growth rates such that a wide range in age at length is found throughout most of the post-juvenile phase of life (Pace et al. 2017b). Thus, any age-at-length key that might be developed from a local population could result in inaccurate age estimates for more distant populations of ocean quahogs (Pace et al. 2017b).

Characteristics of age and growth of various ocean quahog populations from the U.S. mid-Atlantic continental shelf have been described (Murawski et al., 1982; NEFSC, 1995; Lewis et al., 2001; Pace et al. 2017b), but the number and geographic scope of these studies is limited. In addition, variations in growth as a function of environmental change remain undescribed for this species in the northwest Atlantic, though one anticipates that such variations should exist, as the species is found at latitudes farther south off the U.S. coastline than elsewhere in its boreal circumambience (Merrill and Ropes, 1969; Dahlgren et al., 2000; for further documentation of the North Atlantic range, see Brey et al., 1990; Rowell et al., 1990; Witbaard et al., 1999; Ragnarsson and Thórarinsdóttir, 2002; Butler et al., 2009). Thus, a need for understanding the age-at-length relationships throughout the range of the U.S. stock exists to inform fishery management, provide a basis for age-structured stock assessment models, and also to elucidate regional shifts in ocean climate over the last few centuries. The objective of this study was to investigate growth rates of selected individuals from four ocean quahog populations covering much of the mid-Atlantic range of the stock through the analysis of annual growth increments. To do this, growth increment time series for animals covering the age range observed in the four populations were used to determine the age at 60-, 80-, and 90-mm, and the average growth rates from birth to 60 mm, 60 to 80 mm, 80 to 90 mm, and post-90 mm. These data were evaluated as a function of birth year, within and between populations, to elucidate regional trends in growth and uncover time-dependent trends in growth, should they exist.

2. Material and methods

2.1. Sample collection and preparation

Ocean quahog samples were collected from New Jersey and Long Island from the *F/V Christie* in March 2015 and from Southern New England and Georges Bank from the *F/V Pursuit* in May 2015 using hydraulic dredges (Fig. 1). Initially, five clams were arbitrarily selected from each 5-mm size bin starting with 80 mm through the maximum shell length (anterior-posterior) collected at each site. For the New Jersey and Long Island sites, an additional five clams were selected from each 5-mm size bin to better define trends in growth rate with birth year. Clams were sectioned along the height axis (dorsal-ventral) using a modified commercial tile saw. Sectioned clams were ground and polished on a wet polishing wheel on 400-μm and 600-μm sandpaper grit, followed by 6-μm and 1-μm diamond suspensions on polishing pads. Additional details are provided by Pace et al. (2017a).

Images of the hinge region of all sectioned clams were captured using either a high definition Olympus DP73 digital microscope camera using the Olympus cellSens microscope imaging software or a high definition Olympus America microscope camera using Olympus MicroSuite software. Many photographs of the hinge region were required to produce a continuous image of the hinge at high magnification. Each individual image was automatically stitched together by the cellSens microscope imaging software. Hinge photographs taken using the Olympus MicroSuite software were stitched together using the open source software ImageJ (FIJI) to create a complete image of the hinge section. Through the use of the ObjectJ plugin in ImageJ, annual growth lines in the hinge region of each individual were annotated (see Fig. 2 in Pace et al. 2017b) and the growth increment widths (distance between consecutive annual growth lines) measured in units of pixels. The total shell length (mm) of an individual divided by the cumulative sum of all growth increment widths (pixels) provided a pixel-to-mm conversion.

2.2. Correlation analysis

Age estimates and measurements of growth increment widths were recorded for 205 individuals throughout the Mid-Atlantic [New Jersey (80), Long Island (65), Georges Bank (35), southern New England (25)]. Using this growth increment information, the age at which individuals reached 80 mm was compared to the year each individual was born. This shell length was initially selected because the capture efficiency of commercial dredges declines at clam lengths < 80 mm so that the abundance of smaller animals in the catch is not representative of their abundance in the population (NEFSC, 2017a); thus animals ≥ 80 mm are of a size of interest to the fishery and management of the species. To investigate whether any trends relating to birth year were specific to 80 mm, or if they held true throughout a larger size range, the ages at which animals reached 60- and 90-mm in shell length were also compared to the birth year of each individual. The 60-mm size was chosen because it approximates size a maturity (Rowell et al., 1990; Thórarinsdóttir and Jacobson, 2005; NEFSC, 2017a). The 90-mm size is a convenient size well within the adult length and age spans, but under the maximum size obtained at each of the four sites.

A Pearson's correlation test was used to test the strength of correlations between birth year and these variables at each site. Additional Pearson's correlation tests were used to test for correlations between birth year and shell length. Specifically, the variables examined were the average growth rate from birth to 60 mm, from 60 to 80 mm, from 80 to 90 mm, and the average growth rate from 90 mm to size at time of collection at each of the four sites. Hereafter, the former three average growth rates will be referenced by the upper size boundary, e.g., average growth rate from birth to 60 mm will be referred to as growth rate to 60 mm. The final growth increment from 90 mm to size at time of collection will be referred to as post-90 mm.

2.3. ANCOVA and regression analysis

Analyses of covariance and post-hoc least squares means tests were used to identify the relationship between the age at which animals reached each size (60, 80, 90 mm) and the intervening growth rates as a function of birth year and location. Each ANCOVA retained the interaction term if significant ($\alpha \leq 0.05$). We use ANCOVA because birth year is a discrete variable in this analysis rather than a main effect and thus serves as a covariate.

Multiple linear regression using the maximum R-square improvement method (Freund and Littell, 2000) was used to examine the ability