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Source: Journal of Shellfish Research, 30(1) : 35-38

Published By: National Shellfisheries Association

URL: https://doi.org/10.2983/035.030.0106

Journal of Shellfish Research, Vol. 30, No. 1, 35–38, 2011.

NEW SPECIES LONGEVITY RECORD FOR THE NORTHERN QUAHOG (=HARD CLAM), *MERCENARIA MERCENARIA*

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ABSTRACT Twenty-two large shells (>90 mm shell height) from a sample of live collected hard shell clams, *Mercenaria mercenaria*, from Buzzards Bay, Woods Hole, Cape Cod, MA, were subjected to sclerochronological analysis. Annually resolved growth lines in the hinge region and margin of the shell were identified and counted; the age of the oldest clam shell was determined to be at least 106 y. This age represents a considerable increase in the known maximum life span for *M. mercenaria*, more than doubling the maximum recorded life span of the species (46 y). More than 85% of the clam shells aged had more than 46 annual increments, the previous known maximum life span for the species. In this article we present growth rate and growth performance indicators (the overall growth performance and phi prime) for this record-breaking population of *M. mercenaria*. Recently discovered models of aging require accurate age records and growth parameters for bivalve populations if they are to be utilized to their full potential.

KEY WORDS: longevity record, *Mercenaria mercenaria*, maximum life span

INTRODUCTION

Bivalves are increasingly being used as new model organisms for the investigation of aging (Strahl et al. 2007, Abele et al. 2008, Abele et al. 2009, Philipp & Abele 2010, Ridgway & Richardson 2010, Ridgway et al. 2010). To fully utilize bivalves in the investigation of aging and to be able to select suitable species for comparative investigations, it is necessary to obtain accurate information on the maximum life span of a species and their population growth parameters. In this article we report a new longevity record for the northern quahog (=hard clam), *Mercenaria mercenaria*. This finding represents a more than doubling of the known maximum life span for the species. The oldest *M. mercenaria* previously reported was 46 y old (Peterson & Fegley 1986) ($n = 67$). However, Beukema (1988) cautioned that estimates of maximum longevity for bivalve populations are often underestimates unless a sufficient number of shells from a population are analyzed. So although many estimates of maximum life span for bivalve species are published, these should perhaps be considered highly provisional estimates until a large number of populations from a wide range of geographical locations have been studied.

M. mercenaria is of economic importance and is exploited as a food source along the Atlantic coast of the United States. To date, most of our knowledge of this species has focused on younger animals—their age of maturity and growth rate—and there has been relatively little attention on the larger and therefore older animals. Because of its application in aquaculture, interest has inevitably fallen on the faster growing and therefore shorter lived populations. As in other animal groups, life span and growth rate are inversely correlated in bivalves (Ridgway et al. 2010). The age of the bivalves investigated in the current study was determined through sclerochronological analysis of the shell. The annual periodicity of increment formation in the shell of *M. mercenaria* has been demonstrated by mark-and-recapture experiments (Peterson et al. 1983) stable isotope profiles (Jones et al. 1990, Jones & Quitmyer 1996, Surge et al. 2008), and sequential sampling (Clark 1979, Peterson et al. 1985, Jones et al. 1990, Arnold et al. 1991, Arnold et al. 1998). In this article, we report the new maximum age observed for this species as well as growth parameters of a population of *M. mercenaria* containing the longest lived members of the species.

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DOI: 10.2983/035.030.0106

METHODS

M. mercenaria were hand collected by scuba divers at a water depth of 15 m July 2010 from Buzzards Bay, Woods Hole, Cape Cod, MA (41.520° N, 70.728° W). After field collection, 50 the clams were transported to the Marine Aquatic Resources Center of the Marine Biological Laboratory (Woods Hole, MA), where the clams were shucked, their tissues removed, and shells scrubbed, cleaned, and couriered to the School of Ocean Sciences for age determination using sclerochronological techniques.

The shells of 22 of the largest clams were selected for age and growth-rate analysis. Individuals were not chosen randomly, but were selected to represent a range of the larger (and presumably older) size classes. The age and growth rate of 22 *M. mercenaria* were determined from acetate peels of the sectioned shells (Richardson 2001). Clean, dry shells were embedded in resin (Met-Prep; Kleer Set type FF, Coventry, UK) and sectioned along the major growth axis using a diamond saw (Isomet 2000, Buehler). The cut surface was ground on increasingly finer grades of wet and dry paper, polished, and then etched for 5 min in 0.1 M hydrochloric acid. Acetate peel replicas were prepared using the methodology described by Richardson (1989) and Wanamaker et al. (2008), and were viewed in a transmitted light microscope. The age of the 20 *M. mercenaria* were estimated by counting the number of clear annual growth lines present in the hinge and margin regions of acetate peels of the shell sections. Images of the acetate peel replicas of shell sections were captured by camera and analyzed using Omninet image analysis software (Buehler). Growth curves were constructed from age and height (umbo–rim axis) data obtained from the shells, and average curves constructed by calculating the mean shell height at age (i.e., size at age 1, size at age 2, and so on) for 3 clams from the sample. Growth of the clams was modeled by fitting a von Bertalanffy growth function (VBGF) to the age–size (shell height) data.

The VBGF ($L_t = L_\infty\ (1 - e^{-K(t\ -\ t0)})$) was fitted to the shell length-at-age data, and the growth constant (K) and asymptotic maximum shell length (L_∞) determined using the fisheries program Fishparm. The growth parameters estimated in this study were compared with data available from the literature for other *M. mercenaria* populations.

Because of the nonlinearity of the growth process, the comparison of growth among different organisms is often complex (Moura et al. 2009). To meliorate this difficulty, several growth performance indexes were used—namely, the overall growth performance (P) ($P = \log(K \times {L_\infty}^3)$ and the growth performance index phi prime (ϕ') ($\phi' = \log K + 2 \times \log L_\infty$) (Pauly 1979, Munro & Pauly 1983). The growth parameters were similarly compared with published growth data.

RESULTS

Counting the number of internal narrow, dark growth lines and wider translucent growth increments evident in acetate peel replicas in the hinge region of the shell (Fig. 1) provided age estimates ranging from 36–106 y in the 22 shells. The annual increments were more defined and clear in the hinge section compared with the lines in the shell margin. Of the shells sectioned, 85% were older than the previous longevity record for the species (Fig. 2).

The population VBGF growth equation fitted using data from the annual internal growth increments provided an estimated asymptotic size (L_∞) of 99.45 mm (±1.285 SE), a growth constant (K) of 0.06/y (±0.0031) and $t_0 = -2.184$ (±0.446; Fig. 3). The growth curve depicts a period of rapid growth up until ~5–10 y, after which the growth rate continues to decline until ~40 y of age. From then on, the species displays a low rate of indeterminate growth.

DISCUSSION

The previous oldest documented age of *M. mercenaria* is 46 y old, and our findings more than double the known maximum life span for the species. The clams in the current study were obtained from a deeper water population of *M. mercenaria*. Age and growth studies of populations at a depth of 15 m have not been undertaken. Their shallow-water conspecifics are more commonly investigated, because they are exploited for fisheries and aquaculture purposes.

Because the annual periodicity of growth increment formation in *M. mercenaria* has been established throughout its geographical range, and the growth increments are clear and distinct, we have great confidence that the ages we determined are reliable. In some shells, especially those from more disturbed areas (e.g., in areas heavily affected by fishing gears or those affected by storms), the lines can be less defined and may be confused with disturbance rings, making accurate age determination problematic. Only in the early part of the life of *M. mercenaria* were faint disturbance rings evident in the growth

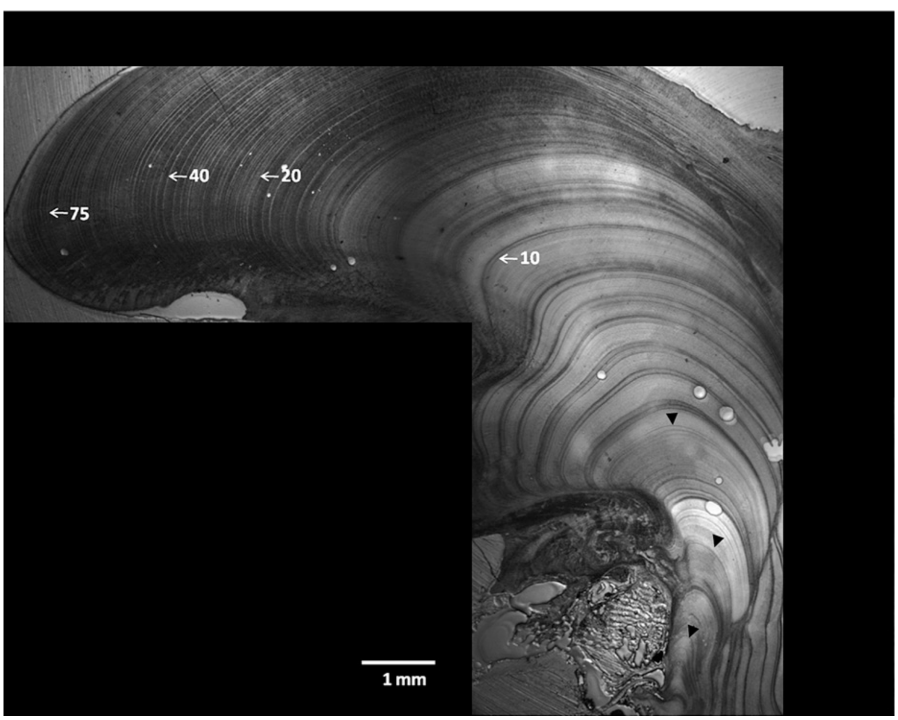

Figure 1. Micrograph of the annual growth increments in an acetate peel replica of the shell of the oldest *Mercenaria mercenaria* obtained from Buzzards Bay. The positions of the annually resolved growth increments (10, 20, 40, and 75) are indicated. Disturbance lines deposited during the early phase of growth are marked by black arrows. Scale bar = 1 mm.

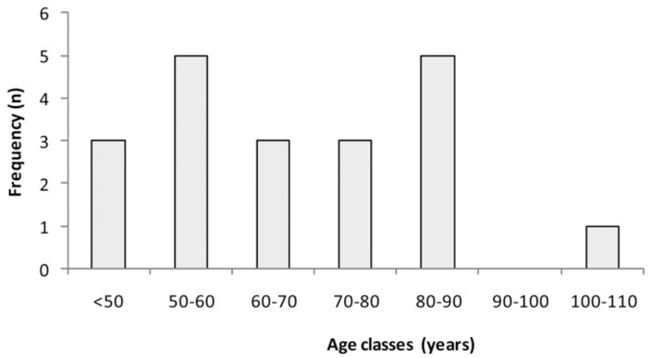

Figure 2. Age frequency distribution for the *Mercenaria mercenaria* population at Buzzards Bay, Cape Cod, MA. The figure is based on the 20 clams with age that was determined using sclerochronological techniques.

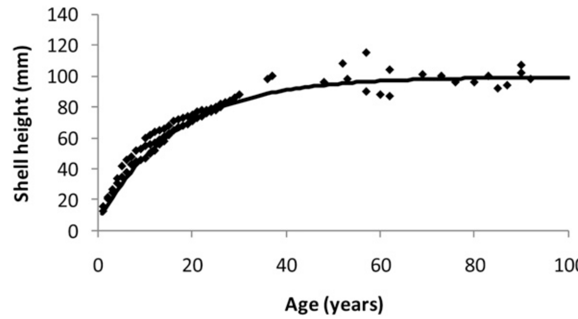

Figure 3. Variation in maximum shell height with age in the population of *Mercenaria mercenaria* from Buzzards Bay, Cape Cod, MA. The growth curve was fitted using the Von Bertalanffy growth equation ($L_t = 99.45$ mm $(1 - e^{-0.06(t - 2.184)})$). The population data points of age estimates and shell height have been pooled with the age-at-shell height estimates for 3 shells.

increments, but these were easily distinguishable from the more distinct annual increments.

Beukema (1988) discussed the importance of sampling effort in accurately determining the MLSP for bivalve populations. Here we have doubled the known MLSP for *M. mercenaria* while determining the ages from only a small sample containing a few large individuals. Our work here highlights the need to have accurate demographic information on bivalve populations under study. As bivalves become increasingly utilized as models for aging research (Abele et al. 2009, Philipp & Abele 2010, Ridgway & Richardson 2010, Ridgway et al. 2010) and biomonitoring (Byrne & O'Halloran 2001), it is essential to have an accurate grasp on what "old" is. The age structure at the sample site should be an important component in that process. Large intraspecific variations in MLSP occur across a species latitudinal and habitat range (Bauer 1992, Ziuganov et al. 2000, Sukhotin et al. 2007).

We recently documented maximum life span and growth rate correlates across bivalve species (Ridgway et al. 2010). In *M. mercenaria*, we document a similar observation here. This extremely longevous Buzzards Bay *M. mercenaria* population has the lowest VBGF growth constant (K = 0.06) reported for the species (Table 1). Similarly, the growth performance indices (P and ϕ') are also lower than other populations, and fall into the range of populations of the long-lived bivalve *Arctica islandica* (Begum et al. 2010). For *M. mercenaria* populations on the Atlantic coast, estimates of the VBGF growth constant K normally range between 0.20/y and 0.35/y (Jones et al. 1989, Harding 2007). In cooler areas—for example, Southampton water in the United Kingdom and in Snug Harbour, Cape Cod, MA—low growth constants been reported (0.149 (Brown et al. 2010) and 0.117 (Surge et al. 2008)), and these were in relatively shallow water.

CONCLUSIONS

Here we have documented that 85% of *M. mercenaria* collected live from Buzzards Bay, Cape Cod, MA, had an age in excess of the previous known MLSP for the species, which we have now doubled. This work highlights the importance of having accurate knowledge of the MLSP for each population of a species being investigated for aging research, especially in species that have received little historical attention, such as those in deeper waters, because even in one of the most comprehensively well-studied species like *M. mercenaria*, we have documented a substantial increase in its known MLSP.

ACKNOWLEDGMENTS

This work was supported by grants from the American Diabetes Association (to Z. U.), American Federation for Aging Research (to A. C.), the University of Oklahoma College of Medicine Alumni Association (to A. C.), the BBSRC (to C. A. R.),the National Institutes of Health (AT006526 and HL077256 to Z. U.; AG022873 and AG025063 to S. N. A.), and the DFG Cluster of Excellence "Future Ocean" (to E. P.). The analysis took place during the 2010 Biology of Aging Course at the Marine Biological Laboratory (Woods Hole, MA) organized by S. N. Austad and G. Ruvkun, for which we thank The Ellison Medical Foundation.

TABLE 1.

Von Bertalanffy growth parameters and other parameters by area for clams *Mercenaria mercenaria* from this study and published literature.

Population	L_∞	K	ϕ'	P	Lat °N	T_{max}	Reference
Southampton	80.13	0.149	2.981	4.885	50.51	30	Brown et al. (2010)
Narragansett Bay, RI	76.25	0.22	3.107	4.989	41	31	Jones et al. (1989)
Virginia	67.54	0.3257	3.172	5.002	37	n/a	Harding (2007)
Buzzard Bay, MA	99.45	0.06	2.773	4.771	41.50	90	Current study

Asymptotic shell length (L_∞ mm), von Bertalanffy growth constant (K/y^1), ϕ', overall growth performance (P), latitude (Lat °N), estimate of population longevity (T_{max}), and reference source.

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