Validated age, growth, and mortality estimates of the ocean quahog (*Arctica islandica*) in the western Atlantic

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The age structure of offshore (Sable Bank) and inshore (St Mary's Bay) populations of eastern Canadian ocean quahogs (*Arctica islandica*), and of a northwestern Iceland population, is investigated. Age estimates for eastern Canadian ocean quahogs were validated through analysis of bomb-produced ¹⁴C in quahog shell growth increments deposited before, during, and after the atmospheric atomic bomb testing periods of the 1950s and 1960s. Delta ¹⁴C from shells with presumed birthdates between the late 1950s and 1970s clearly reflects the sharp increase in oceanic radiocarbon attributable to nuclear testing. The results validate our age interpretations of Sable Bank quahogs to an age of 45 y, and support longevity estimates of more than 200 y for the same population. Longevity calculations for the other populations exceeded 60 y. Von Bertalanffy growth parameters were estimated for the three populations; the growth rate of all three was relatively rapid for the first 20–30 y of life, but thereafter was very slow. The instantaneous rate of natural mortality (*M*), calculated using the age–frequency distribution of the unexploited populations, was estimated to be 0.03 and 0.10 for the Sable Bank and St Mary's Bay populations, respectively.

Keywords: age determination, Arctica islandica, bomb radiocarbon, ocean quahog validation.

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Introduction

The ocean quahog (*Arctica islandica*) is widely distributed in the North Atlantic, ranging from the Bay of Cadiz in Spain, north to Iceland in the northeast Atlantic, and from Cape Hatteras in North Carolina, USA, to the Canadian Arctic in the northwest Atlantic (Nicol, 1951; Merril and Ropes, 1969; Abbott, 1974; Brey *et al.*, 1990; Witbaard *et al.*, 1999). The depths at which they are found usually ranges from 10 to 280 m, with northern populations found shallower than southern populations (Thompson *et al.*, 1980a, 1980b).

The species has been a target for a major offshore clam fishery in the USA since the mid-1970s, especially in the Mid-Atlantic Bight and along the east coast of Maine (Beal and Kraus, 1989), and more recently in Iceland (Thorarinsdottir, 1997). As a result, research on the population characteristics of A. islandica has become increasingly important in the past two decades. For example, the age of this species was investigated for the Mid-Atlantic Bight population (Thompson et al., 1980a, 1980b; Kennish et al. 1994), near New York (Ropes et al., 1984a, 1984b), and in Iceland (Steingrimsson and Thorarinsdottir, 1995; Thorarinsdottir and Steingrimsson, 2000). The population structure and seasonal reproductive cycle were described for the southern New England shelf (Mann, 1982), New Jersey (Fritz, 1991; Kennish and Lutz, 1995), Iceland (Thorarinsdottir and Johan-nesson, 1996; Thorarinsdottir and Einarsson, 1996; Thorarinsdottir 2000), the Baltic Sea (Zettler et al., 2001), and Georges Bank (Lewis et al., 2001). However, little is known about the species in Canadian waters.

With the growth in the development and utilization of quahog products in the USA, considerable interest has been aroused as to the possibility of developing an expanded Canadian fishery. The species is abundant in offshore Canadian waters on Sable Bank as well as inshore off southwestern Nova Scotia (Rowell and Chaisson, 1983; Rowell *et al.*, 1990). These areas may support a fishery, but information on age composition, mortality, and growth rate is required to estimate levels of sustainable harvest. Rowell *et al.* (1990) provide estimates of the minimum age of sexual maturity in St Mary's Bay using a sample of small quahogs, but they did not collect larger animals. The age composition covering most of the size range of the ocean quahog population on the Scotian Shelf has never been determined, nor has the accuracy of the quahog ageing method been validated. Nevertheless, age validation is critical to fisheries management of quahogs on Sable Bank, where large numbers of presumably old quahogs may be collected.

The bomb radiocarbon (¹⁴C) spike from atmospheric testing of atomic bombs in the late 1950s and early 1960s provides one of the best age-validation approaches available for long-lived marine organisms such as corals, bivalves, and fish (Kalish, 1993, 1995a, 1995b; Campana, 1997, 1999; Kalish *et al.*, 1997; Campana *et al.*, 2002). The technique has been used successfully as a dated marker to confirm the age interpretations of various marine organisms (Weidman and Jones, 1993; Campana and Jones, 1998; Campana, 2001; Dwyer *et al.*, 2003).

Here we describe the age structure, growth, and longevity of populations of ocean quahog in Canada and compare it with those of Iceland. In Canadian waters, the inshore (St Mary's Bay) and offshore (Sable Bank) quahog populations with potential commercial importance were examined intensively for the first time. To confirm the accuracy of shell-section rings as indicators

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of absolute age in the species, we compare the known pre- and post-bomb ¹⁴C chronology of Scotian Shelf waters with radiocarbon assays of growth increments whose date of formation was inferred from reading shell sections. The focus of the radiocarbon age validation was the Sable Bank population, presumably the longest lived of the three populations studied. On the basis of the validated age readings, the age composition and the rate of instantaneous natural mortality (*M*) were estimated for the two Canadian locations. The intention of this study is to provide the basis for stock assessments of ocean quahogs in unexploited populations, especially in Canada.

Material and methods

The sampling areas in Canada were chosen according to their potential commercial importance. On the Scotian Shelf, the area with the greatest biomass of the ocean quahog is Sable Bank ($61^{\circ}00'W 44^{\circ}00'N$) (Rowell *et al.*, 1990), where fishing activities will soon begin. An inshore population in St Mary's Bay at the mouth of the Bay of Fundy ($66^{\circ}15'W 44^{\circ}15'N$) is also currently unexploited. The Canadian results were contrasted with those for Iceland ($18^{\circ}15'W 65^{\circ}50'N$), where quahog fisheries were started recently and few estimates of the age composition of the population are available.

Hydraulic dredges were used to collect samples of ocean quahog from St Mary's Bay (n = 183) from depths of 27–60 m, and on Sable Bank (n = 336) from depths of 11–104 m, during stock assessment surveys in October 2002 and September 2003, respectively. The sample from Iceland (n = 55) was collected by divers in February 2004 from depths of 11–47 m.

For St Mary's Bay, the samples from the survey did not include animals <48.5 mm, so could not provide a complete size range of the population for growth modelling. In order to provide a wider

size range, the age data reported by Rowell *et al.* (1990) for small ocean quahogs from the same location in St Mary's Bay (n = 104) were pooled with the age results from the current study. Both data sets showed similar growth patterns for the sizes that overlapped, indicating that pooling of the age data was justified.

The age of quahogs was estimated by the acetate peel technique (Thompson et al., 1980a, 1980b; Ropes et al., 1984a, 1984b), in which the left valve is sectioned using a low-speed diamond saw, embedded in epoxy resin. The sections were then ground with silica carbide grinding powder of successively finer grit (240, 400, and 600), then polished with a commercial polishing compound used to polish gemstones and etched with 1% hydrochloric acid for 1 min. Acetate peels were made by applying an acetate sheet (0.013 mm thick) over the etched surface after flooding it with acetone. After a 1 h drying period, the acetate was peeled off and sandwiched between glass slides for examination under a compound microscope. The internal growth bands were counted both in the hinge tooth and along the entire section (Figure 1). Although the number of bands was consistent in both section margin and hinge area, the former was usually used because the growth bands were wider and therefore provided greater resolution. The von Bertalanffy growth curves for all age-length data were fitted by non-linear regression using the statistical package SYSTAT (1997):

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

where L_t is the length at age *t*, *k* a growth coefficient, L_{∞} the asymptotic length, and t_0 the theoretical age at zero length. Likelihood ratio test (Kimura, 1980) was used to compare the growth curves between areas.



Figure 1. Acetate peel of polished cross-section through a 61-y-old ocean quahog (Sample 11) from umbo to ventral margin. The upper photographic inset indicates the clear growth bands at the ventral margin, and the black circles indicate growth bands presumed to be deposited annually between 2002 and 1990. The lower photographic inset indicates the growth bands (black circles) presumed to be formed annually between 1990 and 1980. A series of false growth bands (some of them shown by arrows) could be counted in the same region, which would lead to the conclusion that the bands were formed between 1973 and 1990.

Validation of the periodicity of shell deposition using the bomb radiocarbon method requires a sample of shells which are believed (based on growth band counts) to span the period of atomic bomb testing in the 1950s and 1960s. Six quahogs meeting this requirement were selected from the aged sample from Sable Bank. Sections (1.0-1.5 mm thick) of each shell were prepared in the same way used in age estimation. Digital images of each section were taken and enhanced using Adobe Photoshop. The growth bands in the acetate sheet, where the age readings were recorded, were clear and prominent, whereas in the shell section, greater magnification and digital enhancements were needed to resolve bands on the shell-section surface after taking the acetate sheet as reference. Growth bands for assay were selected based on the age and year of formation inferred from increment counts. Shell material for bomb radiocarbon assay was extracted from the outer prismatic layer (banded aragonite), with a Merchantek computer-controlled micromilling machine using steel cutting bits and burrs. Three samples were extracted from each individual from bands presumed to be deposited before, during, and after the atomic bomb testing periods between the 1950s and the early 1960s. As sample weights from individual growth bands were insufficient for assay (3 mg is required), pooled cores from adjacent bands (three to four bands) were extracted so as to bring the total sample weight to at least 3 mg. To minimize the possibility of surface contamination, all samples were sonified in Super Q water after extraction. After drying, the sample was weighed to the nearest 0.1 mg, in preparation for assay with accelerator mass spectrometry. All samples were also assayed for δ^{13} C, which was used to correct for isotopic fractionation effects. Radiocarbon values were subsequently reported as Δ^{14} C, which is the ‰ deviation of the sample from the radiocarbon standard (19th century wood), corrected for sample decay prior to 1950 according to the methods outlined by Stuiver and Polach (1977).

The onset of nuclear testing in the late 1950s resulted in a marked and widespread increase in Δ^{14} C in marine dissolved inorganic carbon, which is easily detected in all marine carbonates growing in surface waters during the 1960s (Druffel, 1989; Campana and Jones, 1998). To assign dates of formation to an unknown sample, it is essential that the Δ^{14} C of the sample be compared with a Δ^{14} C chronology for the area based on known-age material (a reference chronology). The reference Δ^{14} C carbonate chronology for the northwest Atlantic was derived from assays of known-age fish otoliths formed between 1949 and 2000. The collection and radiocarbon assay of 56 age 1-3 haddock (Melanogrammus aeglefinus) and redfish (Sebastes spp.) otoliths have been described elsewhere (Campana, 1997; Campana et al., 2002); the chronology was supplemented by 17 age 1-2 haddock and yellowtail flounder (Limanda ferruginea) otoliths collected between 1980 and 2000 and prepared in a similar manner. There was no detectable difference between the haddock, redfish, and yellowtail chronologies, so they were pooled and used as the reference carbonate chronology. The Δ^{14} C chronology of aragonitic fish otoliths in the NW Atlantic parallels that of North Atlantic corals and bivalves (Campana, 1997), and is therefore a good proxy for the Δ^{14} C history of quahogs growing in the upper 200 m of the water column on the Scotian Shelf.

Instantaneous natural mortality rate (M) was estimated on the basis of age-frequency distributions (Ricker, 1975) on Sable Bank and in St Mary's Bay. These locations have little or no commercial fishing history, so it was assumed that total mortality (Z) was equivalent to natural mortality. Z was estimated by calculating the slope of the regression between the natural log of the frequency at age and age. Only quahogs >24 y old were included so as to restrict the analysis to mature quahogs that were fully vulnerable to the sampling gear and therefore on the descending right limb of the age-frequency curve.

Samples used in the catch curve to estimate *M* should be representative of the population. This was not the case during the age estimation of St Mary's Bay and Sable Bank samples, which were collected by length-stratified sampling. To meet the random sampling requirement, the lengths of aged animals (n = 183 and 336 for St Mary's Bay and Sable Bank, respectively) were assembled in age–length keys, then converted to overall age-frequency distributions to represent the two populations. This was done using the total length frequency recorded during the two surveys (n = 93 219 and 310 252 for St Mary's Bay and Sable Bank, respectively). The keys were then used to convert the length frequency to age frequency.

Results

Age validation

The quahog δ^{13} C data were relatively constant, averaging 2.33‰ (s.e. = 0.54), although there was a suggestion of more depleted values in growth increments formed later in life (Table 1). In contrast, the Δ^{14} C of quahog samples showed a strong trend of presumed date of deposition, in which the values increased sharply from around -70 in the pre-bomb period to >90 in 1968, followed by a decline to around 75 after 1975 (Table 1; Figure 2). These assay results paralleled those evident in the reference chronology based on fish otoliths: low and constant prior to the late 1950s, increasing sharply to a peak in the mid-1960s with the flux of bomb radiocarbon from the atmosphere to the ocean (Figure 2). The maximum rate of increase was between 1958 and 1964 and was easily differentiated from the adjacent time periods; thereafter, Δ^{14} C values continued to decline.

The Δ^{14} C chronology of the Sable Bank quahogs showed a strong phase similarity with other North Atlantic histories derived from otoliths in the NW Atlantic and ocean quahogs from Georges Bank (Figure 3). In particular, the period of initial increase is similar in all chronologies.

Age and growth

Growth band counts were consistent and reproducible between independent age readers and methods, generating confidence that we were not inadvertently missing a portion of the shell growth history. An exception was noticed in one animal (Sample 11) in which the growth bands were not as clear and were over-counted by both readers, as indicated by the out-of-phase 1957 radiocarbon assay. This may have been due to over-counting of crowded growth increments in the region of sample extraction (Figure 1). After it was identified as one that had too high an age, results compatible with the $\Delta^{14}C$ were easily obtained. Nevertheless, to avoid bias, it was decided to use the original counts, which had little effect on the overall results.

A broad range of sizes and ages were seen in quahogs from all three areas. Quahogs from Sable Bank ranged between 2 and 210 y for animal lengths of 8–118 mm. For St Mary's Bay the age range was 3–72 y for quahogs with lengths of 22–90 mm. The sample from NW Iceland had an age range of 11–105 y for shells between 32 and 86 mm. In all three populations, growth rate was most rapid (about 2 mm y⁻¹) in animals <20 y old, declining to very

Table 1. Summary of δ^{13} C and Δ^{14} C assay results for samples from growth increments of ocean quahog (*Arctica islandica*) shells collected from Sable Bank in September 2003.

Sample ID	Length (mm)	Water depth (m)	Age (y)	Assumed period of deposition	δ ¹³ C	$\Delta^{14}C$
22 A	69.9	70	44	1963	2.27	44.6
22 B	69.9	70	44	1971	1.93	58.2
17 A	88.2	33	46	1960.5	3.12	- 9.3
17 B	88.2	33	46	1964.5	3.13	77.5
17 C	88.2	33	46	1976	1.72	66.3
19 A	94.0	33	46	1960.5	2.75	- 27.9
19 B	94.0	33	46	1963.5	3.00	12.7
19 C	94.0	33	46	1975	2.15	79.0
21 A	94.5	33	55	1959.5	2.78	- 38.7
21 B	94.5	33	55	1964	2.38	52.5
21 C	94.5	33	55	1976.5	1.42	76.2
11 A	90.1	37	61	1957	2.38	27.7
11 B	90.1	37	61	1968	2.19	90.7
11 C	90.1	37	61	1981	1.72	70.9
15 A	90.5	37	74	1956	2.85	- 69.3
15 B	90.5	37	74	1969.5	2.15	66.4
15 C	90.5	37	74	1978.5	1.69	78.4

low growth rates $({\leq}0.5 \text{ mm y}^{-1})$ after an age of about 50 y (Figure 4).

Calculations of growth rate suggest that maximum sizes (L_{∞}) were similar in all populations and that L_{∞} underestimated maximum observed size by a large margin in the Sable Bank population (Table 2). The growth parameter k for the Iceland population was the lowest of those examined, whereas that for St Mary's Bay was the highest, almost equivalent to that reported for Georges Bank. Despite containing both the largest and the oldest of the quahogs examined (Figure 4), the growth of the unexploited Sable Bank population was estimated to be intermediate between those of the other populations. Although there was no significant difference in the growth curves between Sable Bank and St Mary's samples (Likelihood ratio test, $X^2 = 7.104$,



Figure 2. Δ^{14} C in growth increments of ocean quahog shells in relation to the year of formation estimated from counts of presumed annular bands. Lines connect the Δ^{14} C assay results from the same individual, whereas open circles show the Δ^{14} C of the reference chronology (fitted with a LOWESS curve). The arrow points to an individual (Sample 11) in which the presumed 1957 year of formation was shifted towards an earlier year through overcounting in a crowded area in the shell section (see text and Figure 1).

P = 0.069), there was a significant difference between Sable's Bank and Iceland samples (Likelihood ratio test, $X^2 = 11.704$, P = 0.0008).

Mortality

The age composition in the samples of Sable Bank and St Mary's Bay was dominated by quahogs between 25 and 35 y of age, although substantial numbers of animals up to 100 y old were found in the Sable Bank sample (Figure 5).

The estimates of *M* were significantly different from each other (ANCOVA, p < 0.05; Figure 5). The estimate for St Mary's Bay (0.10) was higher than that for Sable Bank (0.03). As might be expected, the populations with the lowest rate of natural mortality contained the oldest quahogs.



Figure 3. Δ^{14} C in individual growth bands of ocean quahog shells plotted against year of formation estimated from counts of presumed annular bands (closed circles). The Δ^{14} C chronology of ocean quahogs from Georges Bank (dashed line) (Weidman and Jones, 1993) is similar to that of the reference chronology based on fish otoliths (solid line). All chronologies are fitted with LOWESS curves.



Figure 4. Growth curves of ocean quahogs in (a) St Mary's Bay (crosses, age data from Rowell *et al.*, 1990; open circles, age data from the present study), (b) Sable Bank, and (c) northwest Iceland fitted with a von Bertalanffy growth curve (the parameters are listed in Table 2).

Discussion

The interpretation of Δ^{14} C chronology in the quahog shells is straightforward; the Δ^{14} C chronology of the shell should match the reference chronology from the same region as long as the



Figure 5. Age – frequency of ocean quahogs at different locations. The fitted regression line was used for the mortality estimate. Only the solid symbols were included in the descending arms of the catch curves for estimating M (values in parenthesis are the upper and lower 95% confidence intervals of M).

growth band counts are correct. Any under-ageing would phaseshift the shell ¹⁴C chronology towards more recent years, whereas over-ageing would phase-shift it towards earlier years. The Δ^{14} C in ocean quahog samples increased sharply between 1958 and 1964, with a timing and magnitude that was similar to that of the reference chronology. The correspondence between the two ¹⁴C chronologies indicates that the growth bands in the ocean quahogs from Sable Bank were deposited annually and that the number of bands read corresponds to absolute age. Therefore, these results validate our age interpretations of Sable Bank quahogs to an age of at least 45 y and strongly suggest that the older ages are also accurate. It is reasonable to assume that Sable Bank quahogs are broadly representative of quahogs elsewhere in the western Atlantic, indicating that the age-estimation method applied in this study should yield accurate ages in other quahog populations too.

Table 2. Von Bertalanffy growth parameters by area for ocean quahogs from this study and published reports (values in parenthesis are the upper and lower 95% confidence intervals of the estimated parameter).

Parameter	L_{∞} (mm)	k	t ₀ (y)	Maximum observed size (mm)	Maximum observed age (y)
Baltic Sea (Zettler <i>et al.,</i> 2001)	Not available			52.0	40
Georges Bank (Lewis et al., 2001)	97.6 m	0.06	-8.47	97.3	90
Mid-Atlantic Bight (NEFSC, 1995)	97.3	0.03	14.967	93.1	90
Iceland (Thorarinsdottir and Jacobson, 2005)	99.9	0.02	- 22.5	99.0	202
Iceland (present study), $n = 45$, $r^2 = 0.62$	92.5 (89.71–99.0)	0.03 (0.01-0.05)	-7.24 (-10.5 to -4.2)	88.8	100
St Mary's Bay (present study), $n = 287$, $r^2 = 0.84$	87.6 (82.9–92.16)	0.05 (0.04 - 0.06)	-4.02 (-5.49 to -2.55)	90.7	72
Sable Bank (present study), $n = 335$, $r^2 = 0.79$	90.48 (88.10-92.86	5) 0.05 (0.041–0.05)	-1.44 (-2.90 to 0.02)	118.1	210



Figure 6. Comparison of age – length relationships of ocean quahogs from different locations.

The longevity and growth of ocean quahogs differed among areas, although all populations appeared to reach a similar maximum size. In each population, growth rate was relatively rapid for the first 20-30 y of life, slowing substantially thereafter. The minimum marketable size (62 mm) (Duggan, 1998) would be reached in 22 and 20 y in the Sable Bank and St Mary's Bay populations, respectively. All three populations in this study were characterized by impressive longevities: >60 y in all populations and >100 y in two populations. For the Sable Bank sample, the oldest observed quahog was 210 y, which compares well with the maximum longevity estimate of 221 y recorded by Ropes (1985).

The longevity observed in this study differed from those reported for other locations such as the Mid-Atlantic Bight and George's Bank (Table 2), presumably because of the limited size ranges examined in other studies. For example, Murawski *et al.* (1982) studied the age and growth of the ocean quahog in the Mid-Atlantic Bight on the basis of a sample with maximum lengths of <60 mm. Kraus *et al.* (1992) used a sample with a maximum length of 65.5 mm to estimate the growth curve of the juveniles of this species in eastern Maine, USA. In Europe, Zettler *et al.* (2001) investigated the distribution and abundance of the species in the Baltic Sea, where the quahog samples had a maximum shell length of 55 mm. Given that the maximum shell lengths in our study sometimes exceeded 100 mm, it is not surprising that the longevities we observed substantially exceeded values reported in those studies.

Despite the greater longevities in Canadian and Icelandic waters, the overall growth pattern observed in this study was broadly similar to that reported in the Mid-Atlantic Bight (Murawski et al., 1982). In contrast, the Baltic Sea study reported a substantially slower growth rate (Zettler et al., 2001), whereas that for Georges Bank reported a much faster growth rate (Lewis et al., 2001; Figure 6). Lewis et al. (2001) estimated the growth curve functions of A. islandica on Georges Bank using 144 animals and reported that L_{∞} , k, and t_0 were 97.6 mm, 0.06, and -8.5 y, respectively. There are two possible explanations for this difference. The use of thin shell sections by Lewis et al. (2001) rather than acetate peels may have provided less accurate ages. In our study, we could not use the section surface of some animals older than 50 y to determine the clam's age, because the bands were not as clear as on the acetate peel. Alternatively, the growth rate on Georges Bank may be intrinsically faster than that in other regions, either because of genetic characteristics or because of physico-chemical features. Dahlgren et al. (2000) determined the

sequence of the mitochondrial cytochrome b gene of *A. islandica* and found little genetic differentiation between quahogs from Nova Scotia, Canada, Georges Bank, and Virginia, USA. Therefore, there is no evidence at present for a genetic basis for the growth rate differences among areas. However, the productivity and mean annual water temperature on Georges Bank are higher than those in other areas (Backus and Bourne, 1987; O'Reilly *et al.*, 1987), implying that food availability and the conditions for growth may be better on Georges Bank than elsewhere. This explanation is supported by the results of Kraus *et al.* (1992), who recorded faster growth in the laboratory than in the field owing to food availability in surface waters.

In Canada, the growth curves of ocean quahog populations on Sable Bank and in St Mary's Bay are similar (Figure 6). Therefore, the difference in maximum observed sizes (118 and 91 mm for Sable Bank and St Mary's Bay, respectively) may be largely attributable to the difference in the instantaneous rate of natural mortality: 0.03 and 0.10 on Sable Bank and in St Mary's Bay, respectively. The source of the natural mortality includes invertebrate predators such as brachyuran crabs (Cancer irroratus) (Stehlik, 1993), sea stars (Kennish et al., 1994), other crustaceans (Kraus et al., 1992), and teleost predators such as longhorn sculpin (Myoxocephaus octodecempinosus) (Langton and Bowman, 1980). Medcof and Caddy (1971) noted that predators such as cod, winter flounder, sculpin, skates, moon snails, and hermit crabs fed on quahogs damaged by dredging. Most of these same predators were observed on Sable Bank and in St Mary's Bay (pers. obs.), although their relative abundance is unknown.

The value of M = 0.02 assumed for use in US quahog stock assessments (NEFSC, 1995) is close to that calculated here for the Sable Bank population (0.03). As the Sable Bank population appears to grow more slowly than do quahogs in the US, and in light of the observed positive relationship between M and growth rate, it is possible that a slightly higher value of M might be more suited to the faster-growing US quahog populations.

In conclusion, the present study documents the population age structure, growth rate, longevity, and natural mortality of ocean quahogs in eastern Canada. Management of the resource in a sustainable manner will clearly need to take into account the great longevity of the species, as well as the limited growth of animals older than 30 y. More investigations are required to determine the environmental factors influencing the distribution and abundance of the species.

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