Journal of Shellfish Research, Vol. 26, No. 2, 443–450, 2007.

AGE DETERMINATION, VALIDATION, GROWTH AND MINIMUM SIZE OF SEXUAL MATURITY OF THE GREENLAND SMOOTHCOCKLE (*SERRIPES GROENLANDICUS*, BRUGUIERE, 1789) IN EASTERN CANADA

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ABSTRACT The Greenland smoothcockle (*Serripes groenlandicus*) has a circumpolar distribution in the northern hemisphere. Despite such a wide range and potential commercial importance, little is known about most aspects of the biology of this species. As part of studying the growth rate of this cockle species, we compared 3 methods that could be used to estimate the age of *S. groenlandicus*: (1) reading the external rings on the shell, (2) counting the growth rings on thin sections of the chondrophore, and (3) counting growth rings of whole shell sections. The chondrophore proved to be the best region to count the growth bands compared with the other regions in the cockle shell. Age bias plots and the coefficient of variation indicated that our ageing method represents a nonbiased and precise approach. This age method was validated by using Marginal increments Ratio method (MIR) to confirm that the growth bands are deposited annually. Marginal increments were significantly different between months (Kruskal-Wallis $P < 0.001$); a distinct trend of increasing monthly increment growth began in August. We estimated age in 425 cockles, which were collected from the Banquereau Bank ($n = 240$) and Grand Bank ($n = 185$). This data was used to determine the von Bertalanffy growth parameters for the 2 populations: $L_\infty = 95.64$ mm and 96.29 mm (Length), $k = 0.21$ and 0.17 and $t_o = 0.97$ and 0.33 for the Banquereau Bank and Grand Bank, respectively. There was a significant difference in growth curves between the 2 populations (Likelihood ratio test: $X^2 = 33.40$, $P < 0.05$). Minimum size and age at sexual maturity were 27.92 mm and 2.83 y for male tissues and 37.22 mm and 3.69 y for female tissues, respectively. This is the first time that age determination, growth, and minimum size of sexual maturity of the Greenland smoothcockle has been investigated.

KEY WORDS: age determination, validation, sexual maturity, marginal increment ratio, Greenland smoothcockle, smoothcockle, *Serripes groenlandicus*

INTRODUCTION

The Greenland smoothcockle (*Serripes groenlandicus*, Bruguiere 1789) belongs to the family Cardiidae and is an infaunal suspension feeder. It is cosmopolitan in the Arctic and boreal regions, from the subtidal zone to about 100-m deep (Khim 2001). Its distribution extends in the North Atlantic from Greenland south to New England and in the Pacific from Puget Sound, WA, to the Bering Sea, Aleutian Islands and south to Japan. (Kafanov 1980, Coan et al. 2000). The Greenland smoothcockle was found to comprise a main constituent in the diet of the Atlantic walrus (*Odobenus rosmarus rosmarus*) in the Northwest Territories in Canada and of the Pacific Walrus (*Callorhinus ursinus*) in Bering Sea (Miles & Hills 1994; Fisher & Stewart 1997). In the last five years, *S. groenlandicus* has become a valuable by-catch in the Arctic surfclam (*Mactromeris polynyma*) fishery in eastern Canada.

There is lack of information about the general biology, in particular the growth rate and size and age at sexual maturity for the Greenland smoothcockle. Few studies have been done on the species, but it has been used in a number of studies examining growth rate differences in relation to environmental variables. Andrews (1972) studied the growth rates of some recent and fossil bivalves including *S. groenlandicus*. He used the growth lines on the external shell surface to compare the growth rates recent and fossil cockles from the Arctic and Subarctic to draw inferences on the Late-Quaternary marine environment. To conduct the study he examined the growth rate of recent cockles, from the Arctic and Subarctic, along with a sample from the Gulf of St. Lawrence. Khim (2001) analyzed the stable oxygen and carbon isotopic composition in shells of the Greenland smoothcockle to trace the variation in hydrographic conditions of the ambient sea water in the Canadian Arctic. Ambrose et al. (2006) examined cockle growth rate variations in relation to physical variables and climatic forcing.

Validated growth rate and age structure are essential for fisheries models to assess the health of a fishery resource or to correctly interpret the dynamics of a fish population. Typically in marine animals, it is assumed that growth increments are laid down annually on hard parts, such as scales, otoliths, or shells. However, without age validation studies, some aging methods may not provide the true age of the fish, or certainty that an "annulus" is formed each year (Campana 2001). Therefore age validation should be a priority in the ageing of commercial species (Beamish & MacFarlane 1983, Campana 2001). Panfili et al. (2002) go so far as to state that theoretically, a validation should be made of every population of any given species, because there may be important differences between them. There are published studies relating the position of the external shell bands to annual cycles in stable isotope ratios (Ambrose et al. 2006, Strontium-Calcium ratios; Khim 2001, Khim 2002, Khim 2003; $\delta^{18}O$ and $\delta^{13}C$), which show that the bands are annual, and thus validate the use of external growth bands for aging Greenland smoothcockles. For our study we show that there is a correspondence between the external and internal growth bands, and use the marginal increment ratio method to validate our aging for the populations studied.

In this study, we compared three methods that could be used to estimate the age of *S. groenlandicus*. These methods were: (1) reading the external rings on the shell; (2) counting the growth

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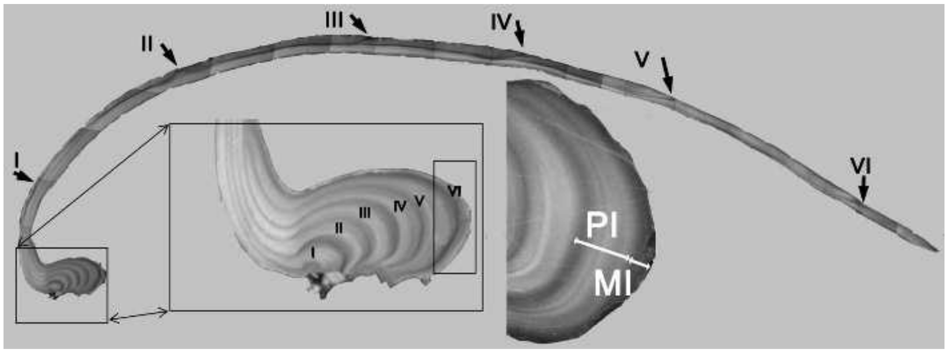

Figure 1. Transverse section of chondrophore thin-section from a shell of the Greenland smoothcockle viewed under reflected light. Growth bands are indicated by roman numerals on the chondrophore showing 6 growth rings and the end of the corresponding bands are indicated on the whole thin section (roman numerals and arrows). The enlarged edge of the chondrophore indicates the appearance of the marginal increment (MI) and previous increment (PI), measurements used for marginal increment ratio (MIR).

rings on thin sections of the hinge plate (chondrophore); and (3) counting growth rings of whole shell thin sections. The age and size at sexual maturity of the Greenland smoothcockle on the Scotian Shelf were also determined. The intent of this study is to provide information critical for stock assessments of *S. groenlandicus* in Eastern Canada.

Besides age structure, minimum size and age at sexual maturity are vital for fisheries management to ensure that the target species has a chance to reproduce before it is harvested. We examined 86 small cockles collected during a clam survey of Banquereau Bank to provide estimates of size and age at maturity for this species.

MATERIAL AND METHODS

Age Determination: Comparison of Methods

The specimens used in this part of the study were 84 individuals collected during an offshore clam survey of Banquereau in July to August 2004 for the sexual maturity investigation.

The length of each animal was measured to the nearest 0.1 mm and the shell was separated from the flesh and air dried. For consistency, the right valve was chosen for ageing if intact, otherwise, the left shell was used in the study. The shells were first aged by counting the external growth rings. Each shell was then sectioned by cutting the shell from the ventral margin through the umbo with a low-speed saw mounted with two diamond blades, 2 mm apart. The cut surface was hand ground using 2 successively fine grits (240 grit or 53.5 μm, and 400 grit or 23.6 μm) to remove any saw marks. The section was bonded to a microscope slide with epoxy and ground down to 0.20–0.35-mm thickness with a Buehler PETRO-THIN thin sectioning system. The section surface was hand ground using the same grits as used before, rinsed with tap water and left to dry. Shell sections were examined using a Nikon microscope under transmitted light at ×40 magnification. The number of translucent annuli was counted in the whole shell section and the chondrophore.

The three methods for age determination were compared: counting external rings on the shell; internal rings in whole shell thin sections; and internal rings in thin sections of the chondrophore.

Once a method had been selected from the previously mentioned analysis, ageing accuracy and precision was examined using 425 individuals, which were collected as following. A sample of 156 cockles was collected as bycatch of the commercial

TABLE 1.

Statistics comparing bias between methods for Greenland smoothcockles Serripes groenlandicus. Bias is between method bias, nominal age is mean, averages are weighted by number of cockles.

	Age (y)	Count	Agreement %	CV %	Bias (y)	Bias %
Chondrophore thin sections *versus* external shell bands						
	1	1	100.0	0.0	0.00	0.0
	2	10	100.0	0.0	0.00	0.0
	3	5	80.0	4.0	0.20	1.9
	4	17	88.2	1.8	0.00	0.0
	5	8	75.0	3.2	0.00	0.0
	6	13	100.0	0.0	0.00	0.0
	7	3	100.0	0.0	0.00	0.0
	8	1	100.0	0.0	0.00	0.0
	9	1	100.0	0.0	0.00	0.0
Average			91.53	1.31		
Chondrophore thin sections *versus* whole shell thin sections						
	1	1	0.0	47.1	1.00	66.7
	2	12	83.3	4.7	0.17	3.3
	3	5	60.0	21.5	0.20	1.3
	4	19	73.7	9.1	0.42	2.6
	5	4	100.0	0.0	0.00	0.0
	6	9	77.8	2.4	0.00	0.0
	7	3	100.0	0.0	0.00	0.0
Average			77.36	7.66		
External shell bands *versus* whole shell thin sections						
	1	1	0.0	47.1	1.00	66.7
	2	9	88.9	3.1	0.11	2.2
	3	5	60.0	18.9	0.00	0.0
	4	12	75.0	11.8	0.67	4.2
	5	5	60.0	5.1	0.00	0.0
	6	7	85.7	1.6	0.14	0.4
	7	2	100.0	0.0	0.00	0.0
Average			75.61	8.48		

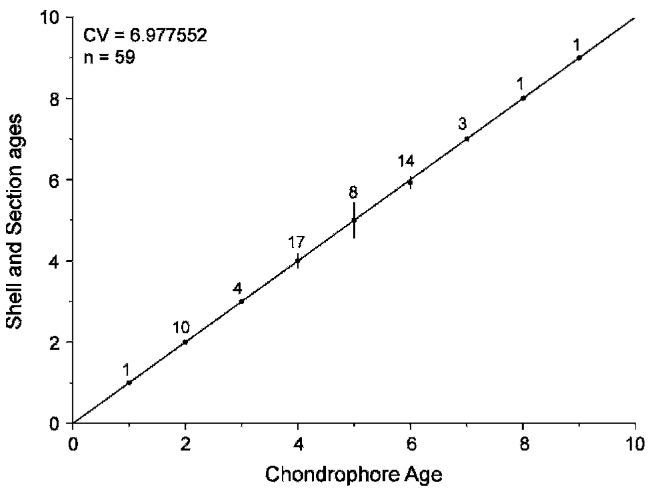

Figure 2. Age bias plot for ageing using external shell bands and whole shell thin sections *versus* thin sections of the chondrophore. Each error bar represents the 95% confidence interval about the mean age assigned by using whole shell or shell sections to all cockles assigned a given age by reading the chondrophore thin section. The values indicate the number of cockles aged at each age group. The solid line represents one-to-one equivalence.

Arctic surfclam (*Mactromeris polynyma*) fishery on Banquereau (44°30′N, 58°W) from 1998 to 2005. This was combined with 84 individuals (used in the sexual maturity investigation) collected during an offshore clam survey of the same bank in July to August 2004. Finally, 185 animals were taken from samples collected by commercial clam vessels on Grand Bank (44°30′N, 50°W) between 2001 and 2005. All individuals were sectioned and aged in 2006.

To examine precision, band counts on the chondrophore thin sections were made independently by two readers for each specimen without prior knowledge of the cockle's length or of previous counts. Age determination bias between readers ($n = 318$) was assessed through the use of an age-bias plot. This type of graph displays band counts of one reader against a second reader in reference to an equivalence line where reader 1 has the same results as reader 2. Specifically, for all animals assigned a given age by reader 1, the mean age and 95% confidence intervals of the ages assigned by reader 2 are plotted against the reader 1 age (Campana et al. 1995, Campana 2001). A linear regression of Reader 1 *versus* Reader 2 ages was used as a statistical test of between reader bias. A slope significantly different from 1 would indicate a between reader bias in counting rings, and an intercept different from 0 would indicate a between reader offset, caused by a difference in such decisions as determining what is counted as the first ring. Precision estimates were calculated by using the coefficient of variation

TABLE 2.

Coefficients and their approximate 95% Confidence Intervals for a generalized linear regression of the ages assigned by reader 2 versus those assigned by reader 1.

	Lower	Estimate	Upper
Intercept	–0.143	0.102	0.347
Slope	0.974	0.991	1.007

TABLE 3.

Statistics comparing reader bias for Greenland smoothcockles Serripes groenlandicus. Bias is between reader bias, nominal age is mean, averages are weighted by number of cockles.

Age (y)	Count	Agreement %	CV %	Bias (y)	Bias %
1	1	0.0	47.1	–1.00	–66.7
2	15	53.3	13.2	0.20	4.0
3	8	50.0	10.1	0.25	2.4
4	28	39.3	9.5	–0.11	–0.6
5	9	77.8	4.6	–0.11	–0.5
6	19	68.4	3.4	–0.21	–0.5
7	20	55.0	4.2	–0.05	–0.1
8	18	94.4	0.5	–0.06	–0.1
9	5	60.0	4.6	0.20	0.3
10	10	20.0	5.4	0.40	0.4
11	14	50.0	4.0	0.50	0.4
12	28	64.3	2.0	0.14	0.1
13	23	56.5	3.7	–0.17	–0.1
14	16	50.0	4.7	–0.31	–0.2
15	18	50.0	3.6	0.33	0.1
16	8	25.0	4.9	0.13	0.0
17	10	80.0	1.2	0.10	0.0
18	17	41.2	2.5	–0.18	–0.1
19	8	62.5	3.7	0.00	0.0
20	2	100.0	0.0	0.00	0.0
22	1	0.0	6.4	2.00	0.4
23	1	0.0	3.0	–1.00	–0.2
24	2	50.0	1.4	–0.50	–0.1
25	7	14.3	4.4	–0.71	–0.1
26	3	0.0	4.4	1.67	0.2
27	4	0.0	5.2	0.50	0.1
28	4	25.0	5.0	0.00	–0.0
29	6	16.7	3.6	0.50	0.1
30	4	25.0	2.9	–0.75	–0.1
31	3	33.3	2.3	0.33	0.0
32	1	0.0	6.5	3.00	0.3
33	4	50.0	3.7	–1.75	–0.2
39	1	100.0	0.0	0.00	0.0
	Average	51.57	4.68		

(CV) as described by Chang (1982) and Morales-Nin and Panfili (2002):

$$CV_j = 100*\frac{\sqrt{\sum_{i=1}^{R}\frac{(X_{ij}-\overline{X_j})^2}{R-1}}}{\overline{X_j}}$$

where X_{ij} is the ith age estimate of the jth clam, $\bar{X}$ is the mean age of the jth clam, and R is the number of times each clam is aged. CV is then averaged across clams to produce a mean. CV is more flexible and statistically more robust than other measures of precision, such as percent agreement or average percent error (Kimura & Lyons 1991).

Age Validation: Marginal Increment Ratio (MIR)

Marginal increment ratio or relative marginal distance has been used to validate the annual periodicity of growth ring deposition in different fish species (see Campana 2001, and Panfili & Morales-Nin 2002 for reviews) including winter skate;

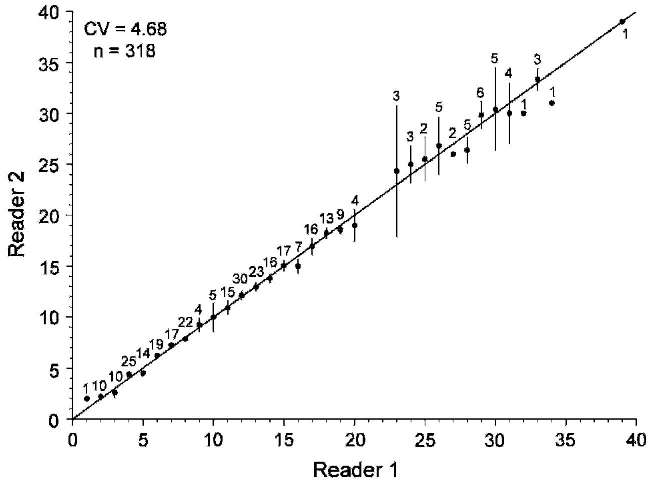

Figure 3. Age bias graph for Age Reader 1 and 2 ageing the Greenland smoothcockle by counting the growth rings on the chondrophore. Each error bar represents the 95% confidence interval about the mean age assigned by Ager 2 to all cockles assigned a given age by Ager 1. The values indicate the number of cockles aged at each age group. The solid line represents one-to-one equivalence.

Leucoraja ocellata (Sulikowski et al. 2002), and yellowtail flounder *Limanda ferruginea* (Dwyer et al. 2003). The marginal increment (MI) and penultimate increment (PI) were measured for each shell section. The MI is defined here as the distance between the chondrophore margin and the distal edge of the last-completed opaque increment, and the PI is the distance between the distal edges of the outermost two opaque increments (Fig. 1). An Optimus 6.2 image analysis system was used to record the two measurements at ×40 magnification. The MIR was calculated as:

$$MIR = \frac{MI}{PI} * 100$$

Growth

The relationship between the number of growth rings, "age," and clam length was modeled with a von Bertalanffy Growth Function (VBGF), which takes the form:

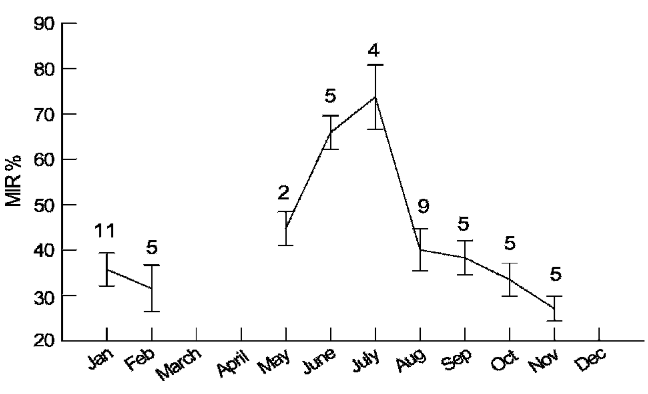

Figure 4. Mean monthly marginal increments of opaque bands for the Greenland smoothcockles. The values indicate the number of aged cockles at each month. Error bars represent ±1 SE.

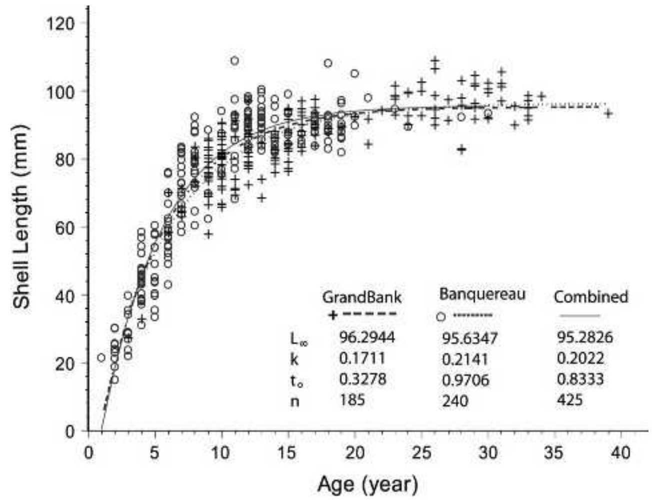

Figure 5. Growth curves of Greenland smoothcockles for Banquereau Bank, Grand Bank and combined samples.

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

where L_t is the cockle's length-at-age t; L_∞ is the asymptotic maximum length; t_0 is the hypothetical age at zero length and k is a growth rate parameter. The parameters L_∞, k and t_0 were estimated by using nonlinear least squares (SYSTAT 2001). The VBGF was calculated separately for samples collected from Banquereau ($n = 240$) and from the Grand Bank ($n = 185$). A likelihood ratio test (Kimura 1980) was used to compare the growth curves between the 2 areas.

Comparisons to published growth curves were made by scanning the figures from Andrews, 1972 (see Fig. 3 later) and Khim, 2001 (see Fig. 3 later) and overlaying a grid to extract the size at age data from the figures.

Minimum Size and Age at Sexual Maturity

To estimate the minimum size and age at sexual maturity, a sample of 86 cockles ranging in size between 14.9 mm and 75.9 mm was used. Each animal was measured to the nearest 0.1 mm and fixed in 10% formalin in sea water. The preserved samples were transported to the laboratory where the foot portion, which contains the gonad material, was separated for histological processing to define the gonad maturity stages in different months. Histological processing and classification was done at the Aquatic Diagnostic Services, Atlantic Veterinary College, Charlottetown, Prince Edward Island, Canada. Gonad sections were examined under a microscope and visually classified into six maturity stages (Ropes 1968, Rowell et al. 1990, Thorarinsdottir, 2000). Because Greenland smoothcockles are hermaphroditic, the minimum size and age of sexual maturity were estimated for male and female sections of the gonads. The proportion of mature individuals was plotted against size aggregated into 5-mm intervals. A logistic curve was fit to the data by maximum likelihood using the S-PLUS statistical package (Insightful Corp. 2003). The logistic curve is:

$$P = e^{(a+bL)}/(1 + e^{(a+bL)})$$

where P is the proportion of mature individuals in the sample, L is the shell length (mm), a and b are the model parameters. The

TABLE 4.

Calculated von Bertalanffy equation for the Greenland smooth cockles collected from the Banquereau Bank, the Grand Bank and combined samples. Values between parentheses are the lower and upper 95% confidence limits for the parameter.

Location	L_∞ (mm)	k	t_o (y)	*n*	r^2
Banquereau Bank	95.635	0.214	0.971	240	0.883
	(93.001–98.270)	(0.189–0.240)	(0.682–1.259)		
Grand Bank	96.294	0.171	0.328	185	0.712
	(94.256–98.334)	(0.142–0.200)	(–0.852–1.507)		
Combined	95.283	0.202	0.833	425	0.863
	(93.001–98.270)	(0.189–0.240)	(0.682–1.259)		

cockle length corresponding to 50% mature individuals was calculated as: $L_{50} = -a/b$. The shells were retained and aged with chondrophore thin sections as described earlier. A logistic curve was fit to the age at maturity data using maximum likelihood method as earlier.

RESULTS

Age Determination: Comparison of Methods

Of the 86 cockles in our sample, 2 had shells, which were too damaged to age with any of the methods, leaving 84 cockles for comparison of methods.

Age determinations of Greenland smoothcockles available in the literature were based on counting the external growth rings on the shell (Andrews 1972, Khim 2001, Ambrose et al. 2006). In this study, we found that the bands on the shell external surface were only clear in younger cockles, older growth rings being closely spaced and difficult to distinguish. Even on our sample of young cockles, we were only able to age 70 of the 84 cockles using this method. Although this method would be the fastest, requiring only the cleaning of the shell surface before reading, it is not suitable for all shells, and there would be few older shells where it could be used with confidence.

The whole shell thin sections were difficult and time consuming to prepare, as the sections broke easily, and 53 of the 84 cockles were aged using this method.

TABLE 5.

Mean length and age of cockle shells used in the minimum sexual maturity estimation. Greenland smoothcockles are hermaphroditic, so maturity of both male and female gonads were observed for each specimen.

	Male	Immature	Mature	Immature	Mature
	Female	Immature	Immature	Mature	Mature
Shell Length (mm)	Mean	27.76	38.82	49.45	50.60
	Std. Err.	2.92	2.30	4.45	1.46
	Minimum	14.9	26.9	45.0	21.2
	Maximum	65.0	56.5	53.9	75.9
	n	16	14	2	54
	Male	Immature	Mature	Immature	Mature
	Female	Immature	Immature	Mature	Mature
Age	Mean	2.87	3.86	5.00	5.02
	Std. Err.	0.38	0.29	0.00	0.19
	Minimum	1.0	2.0	5.0	2.0
	Maximum	7.0	6.0	5.0	9.0
	n	15	14	2	53

Rings were readily distinguishable on thin sections of the chondrophore of all 84 of the cockles in our sample, and the method was also successful with older cockles.

Table 1 shows the comparisons of the three methods used with different statistics that have been used for comparison. The agreement between external shell bands and chondrophore thin sections is excellent (Cv = 1.3%), whereas the agreement between those methods and the whole shell sections are not (7.7 and 8.5%). Figure 2 shows an age-bias plot comparing the chondrophore ages to the other two methods combined. There is no bias evident in the age determination between the methods.

For the rest of the analysis the chondrophore thin section method was chosen as the aging method for the Greenland smoothcockles.

In examining between reader bias using the chondrophore thin sections, an examination of a Q-Q (Quantile-Quantile) plot of the residuals from a regression of the ages assigned by reader 2 against those assigned by reader 1 showed that they were not normally distributed. A generalized least squares model was fit by REsidual Maximum Liklihood (REML) and the approximate 95% confidence intervals for the intercept and slope are shown in Tables 2 and 3. The slope is not significantly different from 1 and the intercept is not significantly different from 0, indicating that there is no significant difference in the age results obtained by the two readers by counting the growth bands on the chondrophore. The Bias plot comparing the results of the two readers also indicated no appreciable bias in the ageing process (Fig. 3) and the mean coefficient of variation was 4.68%. There is no absolute rule for an acceptable CV for ageing studies,

TABLE 6.

Minimum size and age (–a/b) of sexual maturity estimated from the logistic equations $P = e^{(a + bL)}/(1 + e^{(a + bL)})$ for males and females of Greenland smoothcockles in the Banquereau Bank (Plots are shown in Figure 6–7). (P: proportion mature, L: shell length or age, *a* and *b* are the equation constants).

	Size		Age	
Parameter	Male	Female	Male	Female
a	–7.4405	–4.97796	–3.324	–3.830
b	0.26651	0.133748	1.1730	1.039
–a/b	27.92	37.22	2.83	3.69
R	0.59	0.89	0.79	0.89
n	86	86	84	84
(84 aged of 86 cockles processed for maturity)				

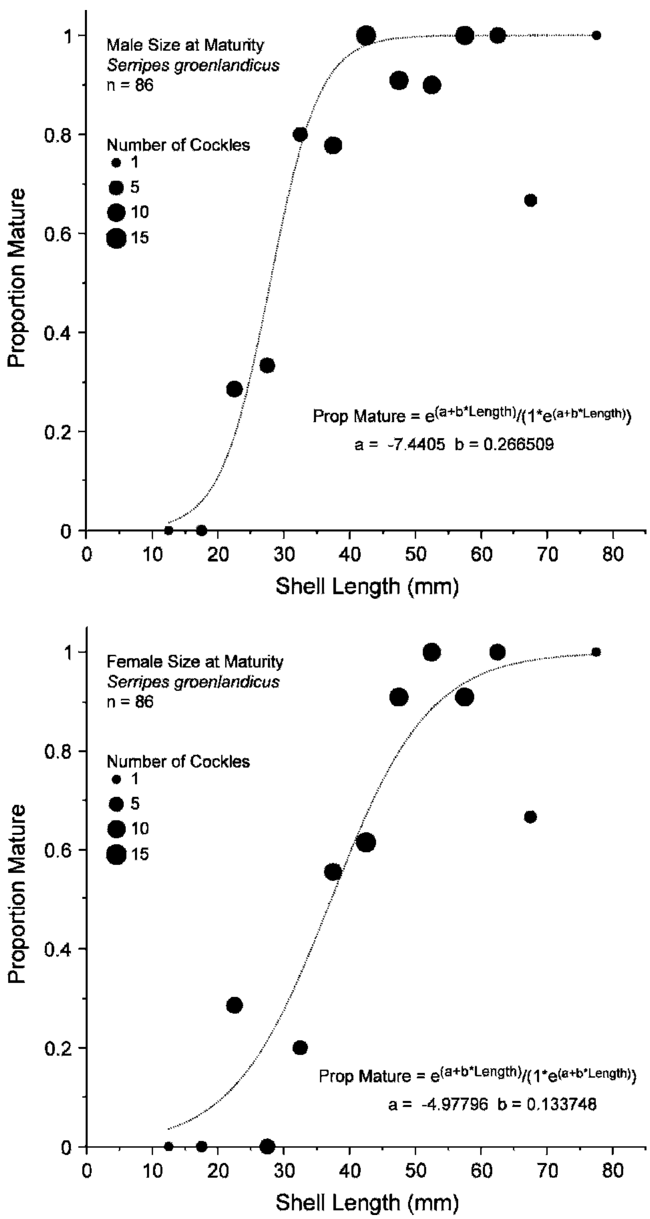

Figure 6. Minimum size of sexual maturity of Greenland smoothcockles on Banquereau Bank. (see Table 6 for equation)

because the precision is affected by longevity, the structure used for aging and the difficulty in reading annuli. Laine et al. (1991) suggested a CV of 5% as the limit of precision for acceptable age readings for short lived species (<10 age classes). Campana (2001) states that 5% serves as a reference point for many fishes of moderate longevity and reading complexity, but shows in a review of 117 published precision values that CV's exceeding this are common. Our results were thus considered precise and unbiased, and therefore the counts generated by one reader for the entire set of shells were used for the analyses.

Age Validation: Marginal Increment Ratio (MIR)

To avoid the effects of proportionally large measurement errors in closely spaced growth bands, the marginal increment analysis included only individuals less than 12 y in age. The mean monthly MIR was calculated from clams ranging in number between 2 and 11 specimens for each month (total of 51 cockles) from August 2001 to January 2005, with the exception of March, April, and December when specimens were not available. The MIR was significantly different between months (Kruskal-Wallis $P = 0.0013$). There was a distinct trend of increasing monthly increment growth that peaked in July, followed by a large decline by August (Fig. 4). Based on this information, the increment analyses show that a single opaque band is formed annually in the cockle shell starting in August or September for the Banquereau Bank area.

Growth

After confirming that the growth rings counted on the chondrophore were deposited annually, the maximum observed age in all samples was 39, which was found in a 93.3 mm cockle. Von Bertalanffy growth curves (Fig. 5) were fit to samples collected from both Banquereau and Grand Bank, and the growth curves for the 2 samples were significantly different (Likelihood ratio test: $X^2 = 33.40$, $P < 0.05$, Table 4).

Minimum Size and Age of Sexual Maturity

Greenland smoothcockles are hermaphrodite and the gonad tissues of each sex can be at different maturity stages within the same individual. Of the 86 cockles processed for maturity, 68 and 56 had mature male and female gonad tissue respectively and 18 and 30 had immature male and female respectively (Table 5). The parameters for the fit of a logistic curve to the proportion mature by size and sex are given in Table 6, and shown in Figure 6 and Figure 7 by size and age respectively. The male tissues were found to reach maturity earlier than the female tissues. The 50% sexual maturity level was reached at 27.92 mm and 2.83 y for males and 37.22 mm and 3.69 y for females.

DISCUSSION

We found that in our samples, the method of counting the external rings on the shell for aging was not possible for older cockles with very crowded growth rings. Two of the published age estimates based on external rings are based on cockles younger than 10 y of age (Andrews 1972, Khim 2001), whereas Ambrose et al. (2006) was able to age a 20-y-old cockle from a high Arctic fjord using external rings. Whereas this method could be used for young and/or fast growing cockles, it is believed that in most situations a single method that could be applied to all cockles in a sample would be preferred. Using external rings does have an advantage over the other methods in that it does not require any processing of the shells and thus is faster than the other methods.

The method of using whole shell thin sections was time consuming and difficult. In our study it produced age estimates that had a lower agreement than the other two methods, but it was felt that this could be improved with modifying the protocol to reduce breakage and further processing to improve the readability of the rings. This however would involve more processing time simply to make it consistent with the chondrophore thin section method.

The annuli in the chondrophore thin sections were readily distinguishable in older animals, and the age estimates using this method were highly reproducible.

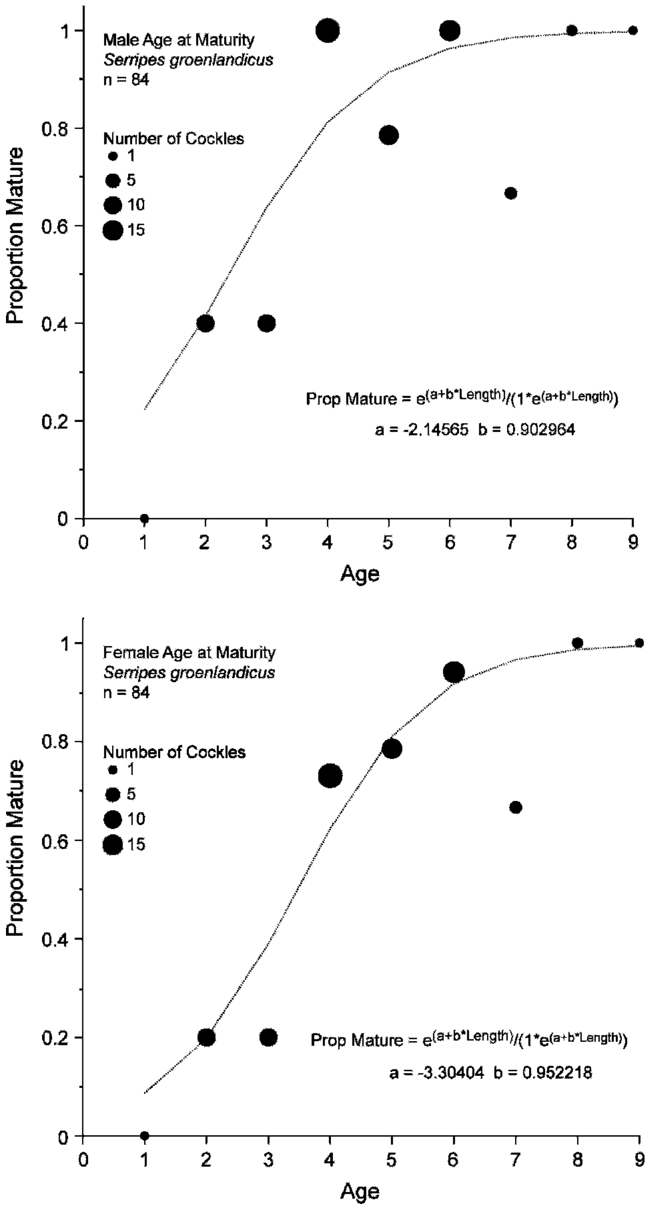

Figure 7. Minimum age of sexual maturity of Greenland smoothcockles on Banquereau Bank. (see Table 6 for equation)

Our results indicate that, of the 3 methods examined, the chondrophore thin section provides an accurate estimate of age, could be used to age the older cockles in our samples, and required less preparation than whole shell thin sections, making it the best choice of the methods examined.

Thin sections have been used to age many bivalve species (Penttila & Dery 1988). To confirm that the growth rings are deposited annually, the method should be validated and thus a number of different validation methods have been used. These include mark and recapture (Ropes et al. 1984), chemical marking using tetracycline (Pirker & Schiel 1993), or by marking the shells with Strontium chloride (Fujikura et al. 2003). In ocean quahogs, *Arctica islandica*, thin sectioning of the shell has been validated by using assays of bomb radiocarbon content (Kilada et al. 2007). For Greenland smoothcockles, there have been a number of papers relating stable isotope profiles recorded in the shells to ambient hydrographic conditions during the period of growth (Ambrose et al. 2006, Strontium-Calcium ratios; Khim 2001, Khim 2002, Khim et al. 2003, $\delta^{18}O$ and $\delta^{13}C$). Whereas these studies were not designed to validate the ageing performed, they do validate that the external growth rings are deposited annually for the areas they studied. We have shown that the external lines are reflected in the shell structure, and that the corresponding internal bands provide a precise estimate of age.

We applied the Marginal increment method to validate the chondrophore rings for our samples. The sharp drop in the width of the marginal increment in July to August (Fig. 4) supports the hypothesis of annual band formation of this species. This pattern was similar to that observed for thorny skates in the Western Gulf of Maine (Sulikowski et al. 2003), in which the opaque bands were proven to be deposited in August and September. To avoid the effects of proportionally large measurement errors in closely spaced growth bands, the marginal increment analysis included only individuals less than 12 y in age. Nevertheless, we assume that the annual nature of band deposition continues throughout the cockles life.

The growth rate of *S. groenlandicus* is rapid during the first 9 y, until the cockle reaches about 80–90 mm in size and slows down thereafter. Our growth rates for Banquereau and Grand Bank are higher than that in the Gulf of St. Lawrence (Andrews 1972) but similar to those in the Bearing Sea (Khim 2001) for the first 5–10 y. Those two authors relied on the external rings on shells to estimate age (Fig. 8). The difference in growth rates are probably caused by differences in environmental factors between sampling locations.

There is no published literature on the reproduction biology of the Greenland smoothcockle. Our study shows that *S. groenlandicus* is hermaphroditic, like some other members of the family Cardiidae such as *Clinocardium nuttallii* (Gallucci & Gallucci 1982). The female tissues in *S. groenlandicus* reach sexual maturity after the male tissues. The 50% maturity level was reached in the male and female tissues at 27.92 and 37.22

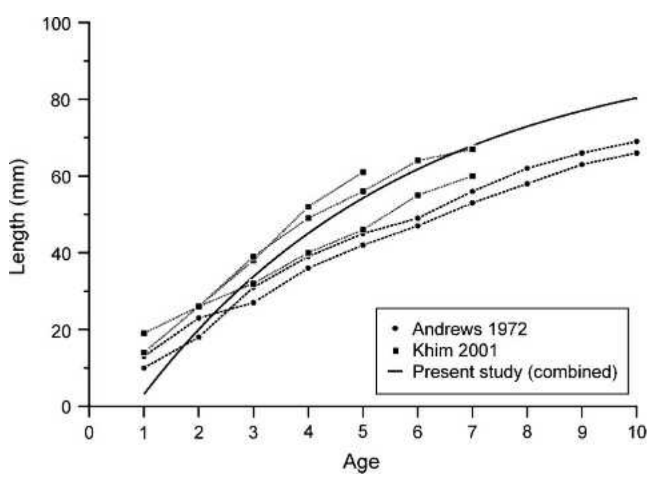

Figure 8. Age at length of Greenland smoothcockles for the first 10 y on Banquereau Bank and other locations, estimated from chondrophore thin sections (present study) and from external growth rings (Andrews 1972, Khim 2001).

mm after 2.83 and 3.69 y, respectively. Therefore, any management plan for this species should ensure that the mean size at capture is above 35 mm. Our study provides growth rate, age, and size at sexual maturity as a first step to understanding the biology of the Greenland smooth cockles and its growth performance in various areas.

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