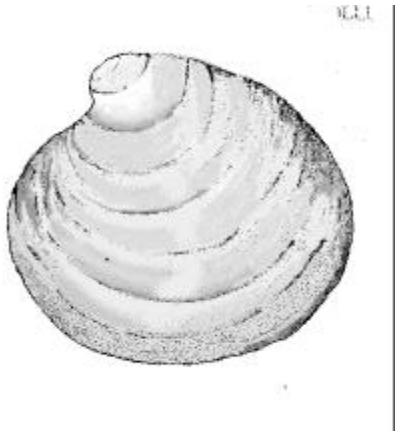
Tree of the sea

Witbaard, Rob

The growth rate decreases drastically .
At this age the shell height is approximately 6 cm. The periostracum starts to change in colour. New growth increments deposited along the shell margin become so crowded that it is hardly possible to separate them externally from each other. The periostracum starts to turn black by the deposition of iron and manganese complexes.

CHAPTER 3

Verification of annual growth increments in *Arctica islandica* L. from the North Sea by means of oxygen and carbon isotopes



CHAPTER 3

Verification of annual growth increments in *Arctica islandica* L. from the North Sea by means of oxygen and carbon isotopes

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ABSTRACT

^{14}C analysis of material from the shells of *Arctica islandica* supports the hypothesis that the clear and definite banding of these shells are of annual origin. The pulse of ^{14}C around 1960, resulting from atmospheric nuclear bomb testing was recorded in the shells at a location in concurrence with that expected from band counting. The observed cyclic variation in stable isotopes of oxygen and carbon coincides with growth bands. This variation, at least for ^{18}O, agrees with annual temperature variations. This suggests that growth bands are a reflection of seasonally determined differential growth rates. The longevity of this species, coupled with variations in increment width, may provide important information regarding growth and productivity, as well as a record of past environmental conditions.

INTRODUCTION

The ocean quahog, *Arctica islandica* L. has a maximum shell length which can be as high as 10 cm and it is speculated that its longevity may be as long as 225 years (Ropes, 1985). *Arctica* is widely, but patchy, distributed in coastal waters of the North Atlantic. It is a sublittoral species, generally inhabiting sandy-mud to mud bottoms at depths as shallow as 4 m (Rowell *et al.*, 1990) to as deep as 482 m (Nicol, 1951). The

species tolerates temperatures from 0° to 19°C (Nicol, 1951). Because of its inability to tolerate temperatures less than 0°C, *Arctica* is considered a boreal, but not an arctic genus (Nicol, 1951). The distribution of *Arctica* in the North Sea was first documented by Nicol (1951). A more detailed picture of this distribution resulted from the 1986 Synoptic Benthic Survey of the North Sea (Duineveld *et al*., 1990, Duineveld *et al*., 1991) (Figure 3.1). Since most of the individuals in this collection were juveniles, this distribution pattern may not accurately reflect the distribution of adults.

Figure 3.1

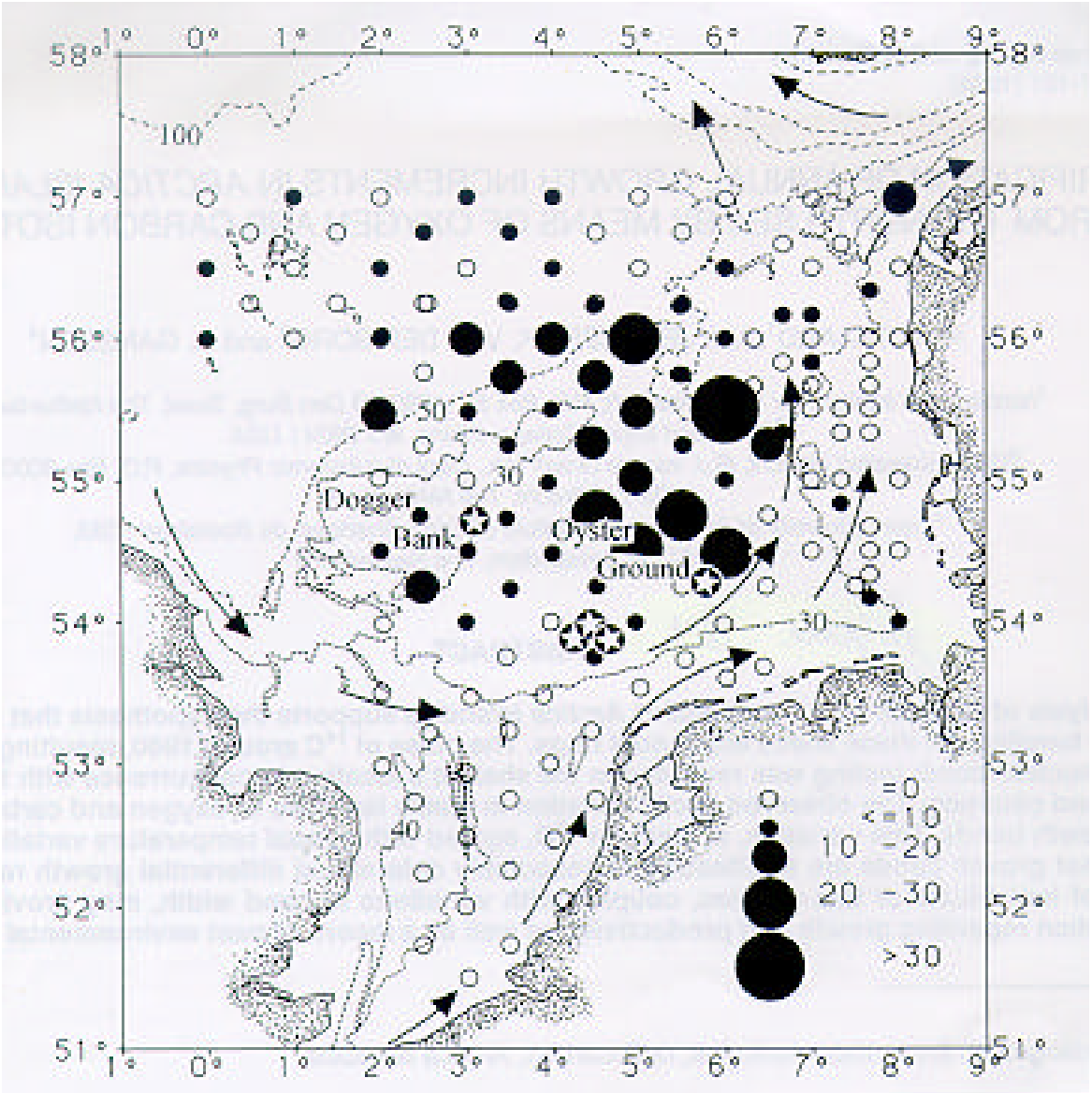

Figure 3.1. Map of central and southern North Sea showing distribution of *Arctica islandica*. Size of black circles reflects density in numbers/m² (After Duineveld *et al*., 1991). Arrows indicate residual currents. Position from where the shells used in this study have been collected is indicated by ✪.

For a number of reasons, there is increased interest regarding growth and productivity measurements of *Arctica* (Brey *et al*., 1990). In American coastal regions, the ocean quahog has become commercially important for human consumption as a replacement for dwindling stocks of the surf clam (*Spisula solidissima*) (Thompson *et al*., 1980a). While *Arctica* is rarely fished commercially in Europe, it has been shown by Arntz (1974) that *Arctica* is an important food source for codfish in the Baltic Sea. Finally, because of its supposed longevity and the continuous record of its growth in variable width of growth bands, *Arctica* is now being seen as a potentially valuable tool for evaluating present environmental changes in terms of past events (Thompson & Jones, 1977; Jones, 1980; Witbaard & Duineveld, 1990).

Growth and productivity measurements depend on the reliability of the observed growth bands as accurate indicators of age. The earliest attempts to measure growth rates relied on external growth checks found on the shells of relatively small (<60 mm shell length) specimens of *Arctica* (Lovén, 1929). Larger specimens (>60 mm shell length) or those with more than 10 checks were difficult to evaluate because the rings near the margin of the valves were too tightly crowded or were partially obscured by the thick black periostracum or because of erosion of the earliest formed checks.

Recent investigations have relied on microscopic examination of internal banding patterns of *Arctica* shells. Because the bands in *Arctica* are narrow with little color contrast, they are not easily discerned. However, by cutting, polishing, and making acetate peels of the cross-section of *Arctica* shells, Thompson *et al*. (1980a; b), Jones (1980), and Ropes *et al*. (1988) were able to discern unambiguous growth bands, even in the most ancient individuals.

Evidence supporting the hypothesis that these are in fact annual bands, is given by Thompson *et al*. (1980a). This evidence includes: finding similar bands in surf clams (*S. solidissima*) which were proven to be annual; finding a low number of bands formed during the onset of sexual maturity that were not explained by less than an annual frequency; finding an expected number of bands formed sequentially in samples taken frequently during a 2-year period that reflected only an annual periodicity; finding a line deposited during the fall-winter, a period coinciding with spawning; and finding a consistent number of bands in a settlement and recovery experiment with young shells.

The results of a mark-release and recovery study (Murawski *et al*., 1982; Ropes *et al*., 1984a) provided more support of the hypothesis of annual band formation. Of 41816 specimens whose valve margins had been indelibly scored, 267 were re-covered and examined one and two years after release. In all cases, acetate peels made of the valves

of the recaptured quahogs revealed the expected number of bands formed beyond the score-marks.

The age of deposited shell material can also be estimated using time-dependent signals from naturally occurring (Smith *et al*., 1991) or anthropogenically produced radionuclides taken up by organisms from the surrounding water. Radionuclide measurements on *Arctica* growth rates have been reported by Turekian *et al*. (1982). Using both naturally occurring ^{228}Ra and ^{228}Th as well as bomb-produced ^{14}C, they concluded that the radiometrically determined growth rates for *Arctica*, at least for deep-water specimens, are compatible with those estimated from band counting.

While their ^{228}Ra and ^{228}Th studies returned expected results, the results from the ^{14}C studies were less definitive; *i.e.* they found a better fit of the data if a semi-annual banding was assumed, particularly for shallow living specimens. These results may be partly due to the method (Beta decay) used which required several shells representing different time windows to produce a composite ^{14}C chronology. This lack of confidence in shell deposition periodicity for shallow water specimens, coupled with the potential for differences due to geographical location were primary considerations for undertaking the present study. The relatively recent improve-ments in radionuclide measurement techniques were also a major factor.

To this end, sequential growth bands were examined by two independent procedures: 1) ^{14}C analysis and 2) analysis of stable oxygen and carbon isotopes.

Nydal & Lövseth (1983) and Nydal *et al*. (1984) reported that tropospheric radioactive carbon reached a peak in 1963. The Levels were twice their natural production rate (Berger, 1979). This increase was a direct result of atmospheric testing of nuclear weapons in the late 1950s and early 1960s. After 1963, input of ^{14}C from this source came to a virtual halt as a result of a partial test-ban treaty. Since that time, atmospheric levels of radioactive carbon have shown a continuous decline. A similar, but somewhat dampened pulse has also been reported for oceanic waters (Nydal *et al*., 1979; Nydal *et al*., 1984). The existence of this radioactive pulse provides an unequivocal chronological marker.

The stable oxygen isotope ratio (δ^{18}O) in carbonate shells has been shown (Krantz *et al*., 1984; Wefer, 1985; Wefer & Berger, 1991; Kalish, 1991; Epstein *et al*., 1953) to be a function of temperature and the δ^{18}O of the water. This latter is influenced by evaporation as well as the admixture of other water masses having different temperature and salinity characteristics. Since δ^{18}O values are inversely related to temperature, higher water temperatures correspond to lower δ^{18}O values of the carbonate deposited under such conditions.

Thus *Arctica* found in waters having an uniform salinity but a definite annual periodicity in bottom water temperature would be expected to show an annual periodicity in the $\delta^{18}O$ composition of its shell. Examples of this approach illustrating the periodicity of band deposition are given by Krantz *et al*. (1984) and Tan *et al*. (1988).

Because the stable carbon isotope ratios ($\delta^{13}C$) in carbonate shell materials are influenced by metabolic factors as well as by thermodynamic conditions (Fry & Sherr, 1988; Wefer, 1985; Kalish, 1991) the effect of temperature on $\delta^{13}C$ is less clear than for $\delta^{18}O$. Although Grossman & Ku (1986) found a small negative relationship between temperature and $\delta^{13}C$ for aragonitic mollusks, Romanek *et al*. (1992) did not find a temperature effect for abiogenic carbonates.

The role of metabolism is regarded as much more important (Wefer, 1985; Wefer & Berger, 1991; Kalish, 1991). Since metabolism is directly related to temperature and food supply, both of which vary in an annual cycle in the area under study, an annual periodicity for this isotope is to be expected.

Figure 3.2

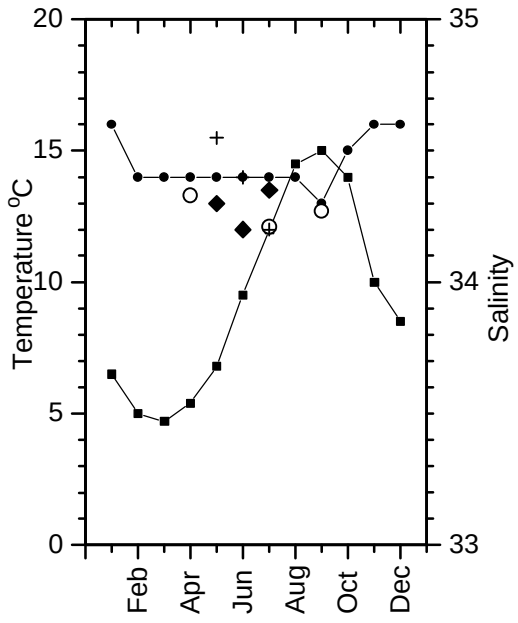

Figure 3.2. Long-term average seasonal variation in bottom water salinity (●) (Goedecke *et al*., 1976) and temperature (■) (Tomczack & Goedecke, 1964) for the southern Oyster Ground together with recent observations of salinities of Central North Sea bottom water (◆) and bottom frontal water (+) in 1986 (Li *et al*., 1989) and of Central North Sea bottom water in 1981 (❍) (Tijssen & Wetsteyn, 1983).

METHODS

Sample area and environmental setting

The animals used in this study were collected from the Oyster Ground, a 30-50 meter deep basin south-east of the Doggerbank. The area is covered with fine sandy sediments mixed with 10-20% clay (Creutzberg, 1984) and has an estimated annual primary production of 250 gC/m² (Gieskes & Kraay, 1984). The average bottom water temperature overlying the area varies between 5 and 15°C (figure 3.2) (Tomczack & Goedecke, 1964). Bottom water salinity variations are small, with the long-term average varying between 34.4 and 34.8 ‰ (Goedecke *et al*., 1967). In 1981, Tijssen & Wetsteyn (1983) found a bottom water salinity of 34.16 in July and 34.44 in May. More recently Li *et al*. (1989) found a similar range, *i.e.* 34.2 in June 1986 and 34.35 in July 1986 (figure 3.2).

At the southern border of the Oyster Ground, a hydrographic tidal front is present which separates the well mixed waters in the south from the summer stratified waters in the north. The position of this front roughly follows the 30 meter depth contour. Associated with this front, a chlorophyll maximum is found (Creutzberg, 1985) together with a rich benthic fauna (Creutzberg, 1984).

Three of the shells used for ^{14}C analysis came from this frontal area. A fourth shell used for ^{14}C was collected from the northwestern part of the Oyster Ground just south of the Doggerbank. The shell which was used for stable isotope analyses was collected north-east of the frontal area.

Analysis of ^{14}C

Sample Preparation

For the ^{14}C analyses 31 samples were taken from four shells which were collected from the southern North Sea. Sampling details are given in table 3.1.

Table 3.1

Shell nr.	Height (cm)	Latitude	Longitude	Date dd/mm/yr	Number of bands	Number of samples
RWL7	8.2	53°41' N	04°25' E	14/03/88	66	12
140	7.2	54°06' N	04°45' E	06/09/88	47	13
RW4C	6.9	53°41' N	04°19' E	14/03/88	27	5
BH40C	9.4	54°45' N	02°59' E	06/05/80	155	1

Table 3.1. Sampling details for the shells used in ^{14}C analyses.

The internal growth bands were made visible by making acetate peels (Ropes, 1985) of epoxy embedded cross-sections. Based on these peels sampling location from the shell cross-section was determined and $CaCO_3$ cores were extracted by using a diamond tipped hollow coring bit (Ø 3x1.8 mm). Thus the samples were taken parallel to the shell surface thereby minimizing contamination with carbonate from the inner nacrous layer. Every sample was assigned to a band count, starting with band 1 at the distal shell margin, *i.e.* the most recently deposited increment. When possible individual bands were sampled but most samples taken refer to a group of bands. This because it was not possible to sample bands from the later growth phases separately due to their narrow width.

From shell RWL7 each of the opposing cross-sections was sampled. The first series consisted of four samples (UtC 1013-1016) representing growth band 1 to 10, band 33 to 38, band 50 to 55 and band 60 to 63. The second batch was taken from the other half of the cross-sectioned shell and consisted of 8 samples of 5 band width intervals (UtC 1070-1077) covering the 40 most recently deposited increments.

Shell 140 contained 47 growth bands of which 13 samples were taken covering the 37 most recently deposited increments.

Five cores were taken from shell RW4C representing 5 * 5 band intervals for the 25 most recently formed growth bands.

From the very large specimen BH40C a single core was taken from 5 bands which represented juvenile growth which was located 150 to 155 bands from the distal shell margin.

Measurement

The samples of 10 to 30 mg carbonate were dissolved in 4 % HCl. The emerging CO_2 was trapped and converted into graphite targets by reduction in an excess of hydrogen with iron powder as a catalyst (Vogel *et al.*, 1984). The graphite targets containing 0.5 to 3 mg carbon were used for analysis with the Utrecht tandem accelerator (Borg *et al.*, 1987). The $\Delta^{14}C$ values were calculated from the ^{14}C-activity (A_{sn}) normalized to $\delta^{13}C$ =-25 per mil with $\Delta^{14}C = (A_{sn}/A_{abs\ -\ 1}) * 1000$ per mil, where A_{abs} is the absolute activity of the international standard (Stuiver & Polach, 1977).

Analysis of ^{18}O and ^{13}C

Sample preparation

Shell material from a relatively small specimen of *Arctica* (shell no. 195; shell height = 2.6 cm) was used for the analysis of oxygen and carbon isotopes. This specimen was collected on March 6th 1991, at 54°22'N, 05°40'E. An acetate peel of the cross-section

of the left-hand valve was prepared as described by Ropes *et al*. (1984a; 1984b). From this peel both internal growth bands and external growth checks were easily discerned. This information was used to determine where to take samples from the right hand valve. To do this, the concave side of the right-hand valve was first filled with epoxy to reinforce it. Then, using a scalpel and dental drills, the periostracum and irregularities in the shell material were removed from the convex surface.

Table 3.2

Shell nr.	growth band (1)	Estimated year (2)	UtC nr (3)	$\delta^{13}C$ (4)	$\Delta^{14}C$ (5)	error (6)
RWL7	1-5	1984-1988	1070	1.5	147	± 8
RWL7	1-10	1979-1988	1013	1.46	157	± 7
RWL7	10-15	1974-1979	1071	1.5	136	± 10
RWL7	15-20	1969-1974	1072	1.07	168	± 14
RWL7	20-25	1964-1969	1073	1.67	180	± 13
RWL7	25-30	1959-1964	1074	1.85	-16	± 7
RWL7	30-35	1954-1959	1075	1.8	-45	± 8
RWL7	33-38	1951-1956	1014	1.29	-25	± 8
RWL7	35-40	1949-1954	1076	1.3	-64	± 8
RWL7	40-45	1944-1949	1077	1.77	-58	± 7
RWL7	50-55	1939-1934	1015	2.55	-15	± 9
RWL7	60-63	1926-1929	1016	2.03	-39	± 6
140	1-6	1983-1988	2712	2	129	± 7
140	7-13	1976-1982	2711	2	105	± 10
140	14-17	1972-1975	2710	2	203	± 7
140	18-24	1965-1971	2709	2	201	± 7
140	25-26	1963-1964	2708	2	213	± 7
140	26-27	1962-1963	2707	2	138	± 9
140	27	1962	2706	2	171	± 12
140	28-30	1959-1961	2705	2	40	± 10
140	31-32	1957-1958	2704	2	-44	± 14
140	33-34	1955-1956	2703	2	-45	± 8
140	35	1954	2702	2	-44	± 7
140	36	1953	2701	2	-64	± 12
140	37	1952	2700	2	-51	± 15
RW4C	1-5	1984-1988	1078	.18	114	± 22
RW4C	5-10	1979-1984	1079	1.5	142	± 13
RW4C	10-15	1974-1979	1080	1.5	166	± 17
RW4C	15-20	1969-1974	1081	2.81	139	± 20
RW4C	20-25	1964-1969	1082	1.83	206	± 6
BH40C	150-155	1826-1831	1017	2.93	-33	± 6

Table 3.2. Results of the ^{14}C analyses from sequential cores from four shells from the North Sea. (1), reference to growth bands sampled, counting backwards from most recent deposited. (2), Estimated absolute time scale. (3), Laboratory number UtC. (4), $\delta^{13}C$ with respect to PDB measured at Utrecht geology department, the "2" values are estimates. (5), $\Delta^{14}C$ with respect to 100 % modern (after normalization to delta 13=-25 per mil; age corrected). (6), Standard error of $\Delta^{14}C$.

In total, six growth increments were sampled. Within each individual growth increment, shell material was sampled by cutting concentric grooves on the convex surface parallel to the growth checks and the outer shell margin. In this way, 2 to 14 sample points were collected from each growth increment, which allowed chronological growth sequence to be established. From the most recently deposited increment VI, only one sample could be taken. Collected material was stored in small glass jars until analysed for stable-isotope composition. After collection of the samples a cross-section of the right hand valve was made to check the depth of sampling (figure 3.4).

Measurement

Samples were dissolved for approximately 10 minutes at 50°C with 100% phosphoric acid (H_3PO_4 in vacuum) by adding droplets of the acid to the samples. The evolved CO_2 gas was frozen at -180°C in glass bottles after being purified from water at -80°C. The isotope composition of the gas was analyzed with a Finnigan MAT 251 mass-spectrometer. The results are expressed as deviations in per mil from the PDB standard, where:

$$\delta^{18}O = \frac{(46/44_{sample} - 46/44_{standard})}{(46/44_{standard})} \times 1000$$

and

$$\delta^{13}C = \frac{(45/44_{sample} - 45/44_{standard})}{(45/44_{standard})} \times 1000$$

Analytical precision from a working standard was 0.04 ‰ for $\delta^{13}C$ and 0.08 ‰ for $\delta^{18}O$ during the period of measurement.

RESULTS

^{14}C

Table 3.2 lists the results of the ^{14}C analysis on the sequential cores taken from various shells. The ^{14}C values of the growth bands from all shells are also illustrated in figure 3.3. The time intervals indicated on the horizontal axis of this plot represent the periodic growth increments revealed in the cross sections made of the shells.

$\Delta^{14}C$ levels from the oldest bands vary from -64 per mil to -15 per mil for shell RWL7. An abrupt increase in $\Delta^{14}C$ to about +180 per mil occurs at the 25th growth band prior to the most recently deposited. Thereafter, a gradual reduction in $\Delta^{14}C$ values occurs, reaching a level of about 148 per mil in the youngest growth bands. Shell 140 showed essentially the same pattern. Maximum $\Delta^{14}C$ was 213 per mil for the sample taken from band 25-26 prior to most recently deposited.

Figure 3.3

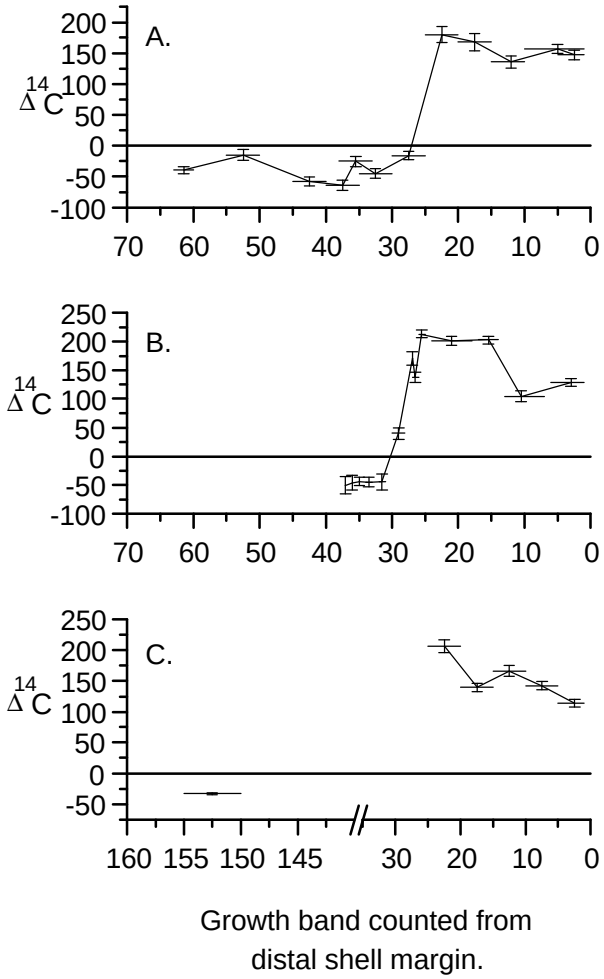

Figure 3.3. Graph of $\Delta^{14}C$ values (per mil) found in sequential cores of four shells of *Arctica islandica*. Horizontal axis represents number of increments with most recently formed (1988) on right. Abrupt increase in $\Delta^{14}C$ occurs about 25 increments before time of collection. (a), Shell RWL7. (b), Shell 140. (c), Shells RW4C and BH40C.

The cores taken from shell RW4C included the 25 growth increments deposited prior to 1988. Only high $\Delta^{14}C$ values were observed from this shell, similar to those found in the 25 most recently deposited growth increments of the other shells, with an equal decrease over time. The single measurement from growth bands 150-155 in shell BH40C gave a ^{14}C value of -33 per mil. This is somewhat more enriched than the values found in the older (prebomb) growth increments of shells RWL7 and 140.

^{18}O and ^{13}C

Both $\delta^{18}O$ and $\delta^{13}C$ values show cyclic variations (figure 3.4). And for both isotopes, a break in the pattern occurs between increments III and IV. The $\delta^{18}O$ values found over all sampled increments varied from a minimum of 1.15 to a maximum of 3.99 per mil. Intra-incremental $\delta^{18}O$ ranges varied from 0.67 to 1.5 per mil. The pattern within all individual increments is essentially the same: a sharp increase between the termination of one band and the beginning of the next followed by a gradual decrease through the major portion of the band. The higher values are thus found in the earliest deposited portion of a given increment while the lowest values are found in those parts deposited just before the observed growth stops. Further, an overall trend of decreasing values with time, superimposed on the cyclic variations, can be observed. For $\delta^{13}C$, a gradual increase in values with time was found with values ranging from 0.58 per mil for the oldest increment formed to 2.39 for increment V. Within individual increments differences ranged from 0.56 to 1.06 per mil. Minimal values are for all increments found in the first deposited parts.

DISCUSSION

^{14}C

The abrupt increase in ^{14}C values observed in figure 3.3 almost certainly resulted of the bomb-produced pulse which peaked in the troposphere in 1963. The time difference between this peak and the collection date of the shells (1988) was 25 years which coincided closely with the number of growth increments represented between the peak signal in the shells and the collection date. The difference in both the exact position of the peak and the absolute values for shell RWL7 and shell 140 is probably due to the precision of sampling. The growth increments are so narrowly spaced in the later growth phase that it was not possible to extract samples from all individual years. Thus most of the ^{14}C values represent an average for a number of years.

However, these data are direct evidence that the growth bands in the shell represent an annual event. Results similar to those described above have been reported by Weidman & Jones (1993a) using a specimen from Georges Bank. Their record of ^{14}C for a North Sea specimen (Weidman & Jones, 1993b) was incomplete but shows a trend very similar to that presented here.

The close coincidence between the number of growth bands counted backwards and the occurrence of the rapid increase in $\Delta^{14}C$ was not necessarily expected; it would not have been unreasonable to expect a time-lag between finding this peak in the atmosphere and its appearance in the North Sea.

Figure 3.4

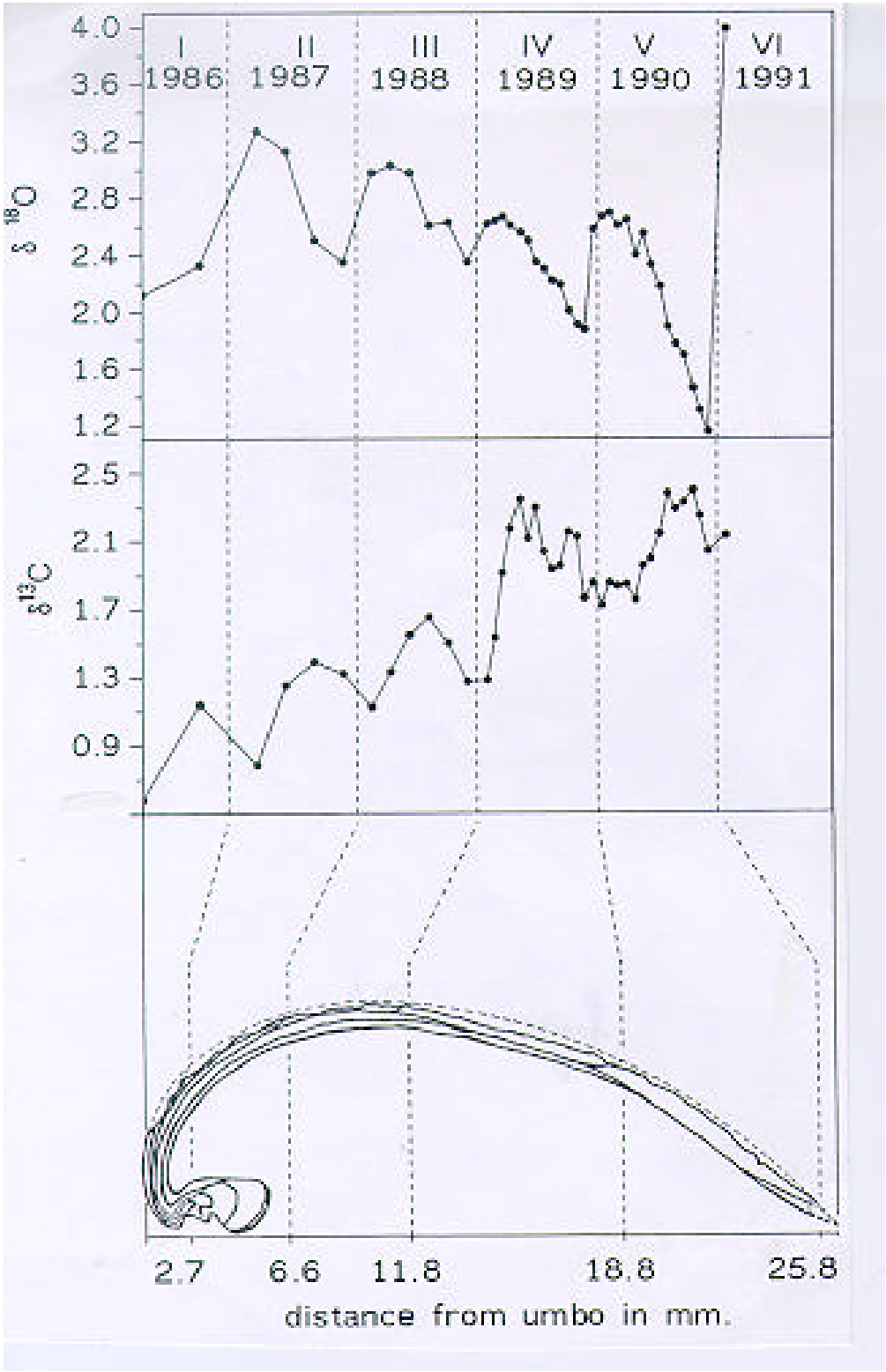

Figure 3.4. Cross-section of shell no. 195 after being sampled. Dotted vertical lines indicate increment boundaries, curved dotted line approximates the presampled outer shell surface. Obtained $\delta^{18}O$ ‰ (PDB) and $\delta^{13}C$ ‰ (PDB) results of sequential samples are given for corresponding shell segments. Six increments were sampled with most recent increment shown on right. Increment number (I,II,III,IV,V,VI) together with the represented year is given in the upper part of the figure.

Model estimations of Broecker *et al*. (1985) for instance, demonstrated that peak height, and the date and time interval in which the maximum $\Delta^{14}C$ is reached differs among oceans and with latitude within an ocean basin. They noted that the rise towards maximum values in the northern temperate Atlantic Ocean surface waters is far steeper than for other latitudinal zones. Unfortunately the measure-ments for the northern North Atlantic (45°N-75°N) are only available from 1965 until 1967 (Nydal *et al*., 1984). Consequently, the effect of the nuclear bomb testing on the northern North Atlantic Ocean surface has to be assessed from data collected from more southern areas, *i.e.* from a latitude between 25° and 39°N.

It seems likely from these data that for the northern North Atlantic Ocean surface waters the ^{14}C pulse mainly peaked in the period 1967-1969 (Nydal *et al.*, 1979), some four years after the occurrence of the peak in the troposhere. Since that time, ^{14}C levels in the ocean surface waters have declined gradually (Nydal & Löveseth, 1983).

Because the southern North Sea is so shallow and well mixed, it might be expected that interchange with the atmosphere would be more rapid here, with the maximum ^{14}C values occurring somewhat earlier than in the surface waters of the large ocean basins. This may especially be true for the region from where the shells for this study were collected. It is a region where a tidal front generates vertical water transport which is accompanied by an increased primary production. Hence, the $\Delta^{14}C$ signal might be expected to be more rapidly transferred to the benthic fauna when compared to deeper sites where such vertical transport with increased production is lacking.

In this regard, it is interesting to note that the results of the Georges Bank specimen from Weidman & Jones (1993a) shows maximum peak in $\Delta^{14}C$ somewhat later compared to both their own North Sea specimen and the results presented here. Hence they have suggested that *Arctica* could well be used as an indicator to measure the arrival time of the ^{14}C pulse to the different regions of their extensive range and to use it in studies on watermass transport.

The pre-bomb values for the period 1944 -1952 are on average -53 per mil, a value comparable to those given by Tanaka *et al*. (1990) and Weidman & Jones, (1993a; 1993b). The pre-bomb value obtained from shell BH40C is, however, less depleted (-33 ± 6 per mil). This difference can be explained by the effect of the combustion of fossil fuels (Suess, 1958). The sample represents the pre-industrial time period of the early 19th century (1826-1831). Since the later part of the 19th century the industrial revolution caused a massive release of CO_2 (^{14}C free) leading to a depletion of the atmospheric $\Delta^{14}C$. This effect was overshadowed since the onset of nuclear bomb testing in the late 1950s.

Stable isotopes

The cyclic periodicity shown by both the $\delta^{18}O$ and $\delta^{13}C$ data closely follows the increment band patterns (figure 3.4), providing further evidence that these bands are annual in nature.

The geographical region from which shell 195 was collected is characterized by a distinct annual temperature cycle as well as an annual cycle of phytoplankton abundance. Variation in salinity within any given year are minimal, usually not exceeding 0.4 ‰. The expected variation in $\delta^{18}O$ values due to these small variations in salinity would be around 0.2 per mil as calculated using the empirical relationship developed for North Atlantic waters (Ganssen, unpublished):

$$\delta^{18}O = -14.555 + 0.417 * \text{salinity}$$

The long-term average bottom water temperature for this area fluctuates annually between 4 and 15°C (figure 3.2). The expected maximum annual variation in $\delta^{18}O$ due to these temperature differences would be 2.5 per mil. The observed differences within any given increment of shell deposition, however, did not exceed 1.65 per mil (figure 3.4).

The most rapid observed changes are almost invariably found at the inter-incremental boundaries with the largest occurring between increments V & VI. The magnitude of this change (2.84 per mil.) closely resembles the expected value of 2.5 based on an annual temperature variation of 11°C. These observations suggest that carbonate is deposited during only a fraction of the annual temperature cycle, with the initiation and termination of growth occurring at different bottom water temperatures.

To explain these observations, we propose a mechanism in which the steep inter-incremental changes reflect a "winter stop" in which growth stops at the end of summer and does not resume again until the following spring. Thompson *et al*. (1982b) have suggested that the formation of the growth line for *Arctica* found in North American waters takes place in fall or at the end of summer in close coincidence with reproduction, and that most growth takes place during the spring and early summer. *Arctica* seems to have a similar reproductive cycle in European waters (Oertzen, 1972), which would imply that growth line formation in this region also occurs at a time with maximum bottom water temperatures, resulting in minimum $\delta^{18}O$ values just prior to increment termination. This, together with the expectation that significant shell growth is probably not resumed before the following spring, is illustrated by the narrow band width of the sixth increment in the specimen we studied. This narrow increment must have been deposited between the autumn prior to the

sampling date and the time of sampling, *viz.* March. During this period, bottom water temperatures are low and would have yielded maximum $\delta^{18}O$ values in juxtaposition to the depleted $\delta^{18}O$ carbonate deposited during the end of the previous growing season. This would result in a rapid change in carbonate composition at the increment boundary as observed. A complete winter stop in growth is proposed because the main food supply (the spring phytoplankton bloom) is not present before the month of March (Creutzberg, 1985; Reid *et al*., 1990).

During the development of the spring bloom, the bottom water temperature increases slowly, a pattern which seems to be mirrored in the slowly decreasing $\delta^{18}O$ values for the earliest deposited materials within each band. This is especially noticeable in increments III, IV and V.

Thus, the mean seasonal temperature cycle can explain most of the observed variation in $\delta^{18}O$ levels. The gradual decrease within each increment reflects the gradual warming of the bottom water between spring and autumn. The rapid $\delta^{18}O$ increases at the increment boundaries mark a winter stop in growth beginning at the end of summer (high temperatures) and ending the following spring (low temperatures). The slowly decreasing $\delta^{18}O$ values for the earliest parts of each increment thereby reflects the period during spring in which the phytoplankton bloom develops but increases in temperature are still small.

The difference in magnitude between inter- and intra-annual $\delta^{18}O$ variations might also be an effect of the sampling technique. Because growth increments tend to be overlapping, sampling too deeply near the outer incremental boundary would result in contamination of the sample with shell material from the deeper internal nacrous layer, material which had been deposited more recently. Analysis of such contaminated material would result in less depleted $\delta^{18}O$ values than would be expected for so late in the growing season. Since the most recently deposited increment would have no deposits underlying it, it would be minimally contaminated and thus would more accurately reflect the complete seasonal temperature change. From the cross-section made (figure 3.4) it can be seen that this might indeed have influenced the stable isotope values for the first three increments sampled.

Another explanation for the differences observed in intra- and inter-incremental variation as proposed by Weidman *et al*. (1994) might be due to a shutdown temperature below which growth stops. This mechanism also implies a growth season shorter than an entire year. Weidman *et al*. (1994) concluded from their results that this temperature was approximately 8°C, at least for the specimen they studied.

Absolute temperatures cannot be derived from our data as we did not measure the $\delta^{18}O$ values of the bottom water. However, if one assumes a maximum bottom water

temperature of 15°C coinciding with band termination, growth must have started at a temperature of approximately 4°C (March, see figure 3.2) based on the $\delta^{18}O$ difference between increment V and VI. This indicates that growth can take place at a much lower temperature than proposed by Weidman *et al*. (1994). This is corroborated by experiments where an average shell growth of 1.3 mm/3 months for ~15 mm high shells was achieved at a temperature of 3°C (chapter 4).

We therefore suggest that the onset of growth is mainly determined by food availability which in turn is closely regulated by the seasonal cycle. The start of growth is thereby triggered by the development of the spring bloom (Graf *et al*., 1984; Davies & Payne, 1984; Smetacek, 1984) which will begin each year at approximately the same time and temperature. This might suggest a "shutdown" temperature, but more likely reflect the temperature at which the food supply to the benthos starts. If so, different populations of *Arctica* from different environmental settings could appear to have different "shutdown" temperatures.

The interpretation of $\delta^{13}C$ is much more difficult than for $\delta^{18}O$. First of all there is no agreement on the effect of temperature on $\delta^{13}C$ values of aragonitic carbonate. Based on literature Kalish (1991) concluded that the temperature effect would be small and may even be uncertain. Latter supposition has been confirmed by the observations of Romanek *et al*. (1992) who did not find an effect of temperature on $\delta^{13}C$ values for abiogenic carbonates.

Metabolism is generally regarded as much more important (Wefer, 1985; Wefer & Berger, 1991) in determining variation in $\delta^{13}C$ values, but because metabolism is directly controlled by both temperature and food supply a cyclic variation in the ^{13}C composition of the increments could be expected. However, Erlenkeuser (1976) found that the shell carbonate was deposited in isotopic equilibrium with the bicarbonate of the surrounding bottom water which thus suggests that a vital effect is likely to be absent.

Local watermass variations may also influence $\delta^{13}C$ ratios and there might also be a seasonality in the local DIC (Dissolved Inorganic Carbon) composition of the bottom water. A phytoplankton bloom may result in a relative enrichment of the water. And if *Arctica* indeed deposits its carbonate shell in equilibrium with surrounding DIC a gradual enrichment in the carbonate during the phytoplankton bloom may be seen. After the bloom collapse local DIC values come back to normal values resulting in a gradual decrease before band termination. Again a cyclic pattern will be the result.

Between increment III and IV there is a sharp transition in both $\delta^{13}C$ and $\delta^{18}O$ which might be related to the effects of ontogenetic development. Because such effects involve major metabolic changes, e.g. changes in weight specific metabolism, the onset

of reproduction and changes in age specific growth, it is likely that they may well effect $\delta^{13}C$ ratios. These effects may, however, be spread over several growing seasons and thus would tend to change gradually rather than enhance cyclic patterns.

An environmental change to explain the observed transition can however not be excluded. Indications for such an environmental change was first given by Lindley *et al*. (1990) who observed a massive occurrence of Doliolids in the German Bight. This planktonic organism is regarded as an indicator of oceanic waters. They also noted that the sea surface temperature (SST) in June was 2 to 3°C higher than normal. Later Becker & Wegner (1993) reported that the mean annual SST for 1990 was 0.7 °C higher than the decadal mean. In 1992 Becker *et al*. also reported an anomalous high salinity in the southern North Sea and the Channel. There are thus indications of abnormal hydrographic conditions in the early 1990s so it is reasonable to suppose that these abnormal hydrographic conditions also affected the bottom water and consequently its isotopic compositon. The observed transition might also have been an indirect effect in terms of a prolonged food supply, which caused growth under warmer conditions, hence more depleted $\delta^{18}O$ values.

Despite the uncertainties in the interpretation of the stable isotope data, we conlude on the basis of the $\Delta^{14}C$ results together with the repeating cyclic variation in stable isotopes, which are in close coincidence with the growth bands, that these bands, are indeed annual.

Additional evidence for an annual deposition pattern for North Sea specimens comes from our observations of a population found at 140 m in the northern North Sea (59°20'N 0°30'E) (see chapter 7). This population was sampled twice; first in 1983 and again in 1991. The earlier sample consisted of 6 young shells and the later sample of 18 shells. From acetate peels (Ropes, 1985) prepared of the hinge part of these shells, measurements of the internal growth increments were made. Because the date of sampling was known for each group, a known year could be assigned to each of the growth increments. For those shells from which the period of overlap was long enough, the % similarity of growth variations or "Gleichläufigkeit" (Schweingruber, 1989) was calculated. The average value found for all possible pairs was 73%, indicating that both groups of shells showed similar growth variations for the pre-1983 period. This implies an annual deposition periodicity because the number of deposited increments in the 1991 sample was equal to the number of years since 1983.

While we recognize that this study is based on only a limited number of shells, it is deemed significant that the complementary results of the different methods employed all support the conclusion that the observed growth rings are annual.

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