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Journal

Earth and Planetary Science Letters, 89(1)

ISSN

0012-821X

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Publication Date

1988-06-01

DOI

10.1016/0012-821x(88)90030-1

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Bomb-produced radiocarbon in the shell of the chambered nautilus: rate of growth and age at maturity

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Received October 20, 1987; revised version received March 21, 1988

The temporal pattern of bomb-produced radiocarbon in the oceans provides a chronometer to estimate the rate of growth of marine organisms. Radiocarbon measurements by tandem accelerator mass spectrometry of samples from the septa and shell wall of a mature specimen of *Nautilus macromphalus* reveal progressively increasing values in more recently formed shell material. This pattern is similar to that recorded in a banded coral from surface waters of the Great Barrier Reef, Australia. However, the pre-bomb values of $\Delta^{14}\text{C}$ are lower in the nautilus than in the coral. This offset is probably due to the difference in the respective habitat depths of the two animals. Taking this difference into account, we have used the temporal pattern of $\Delta^{14}\text{C}$ in the coral as a point of reference to help interpret the pattern of $\Delta^{14}\text{C}$ in the nautilus. According to our calculations, the age of the specimen of *N. macromphalus* is 10–12 years and the timing of septal formation ranges from ≥ 80 to 240 days/septum.

1. Introduction

The chambered nautilus is the only surviving member of a large group of extinct shelled cephalopods, and therefore, information about its life history is particularly important. Yet its rate of growth and age at maturity are poorly known. Previous estimates of these parameters have been based on mark-recapture studies [1,2] and observations of *Nautilus* in aquaria [3–5]. An alternative approach involves the use of chronometers incorporated into the shell during growth. Naturally occurring radionuclides of the uranium and thorium decay series have been used to determine the growth rates of a variety of marine organisms [6–16]. In particular, the radionuclides ^{228}Ra (half-life = 5.75 y) and ^{210}Pb (half-life = 22 y) present in sea water are incorporated into the shells of marine organisms where they undergo radioactive decay to ^{228}Th (half-life = 1.9 y) and ^{210}Po (half-life = 138 days), respectively. These daughter radionuclides are not directly incorporated into the shells from sea water, but only appear as a result of radioactive decay. Therefore,

the change in the daughter/parent activity ratio with time serves as a chronometer for growth. In *Nautilus*, ^{210}Po is excluded from the aragonitic shell during its formation, and the $^{210}\text{Po}/^{210}\text{Pb}$ activity ratio increases from 0 to an equilibrium value (1.0) in approximately five half-lives of ^{210}Po . The $^{210}\text{Po}/^{210}\text{Pb}$ activity ratio thus can be used as a chronometer to measure the rate of growth over the two most recent years of growth [15,16]. In a mature specimen, however, the relatively short half-life of ^{210}Po prevents this method from providing information on the age of the animal or its rate of growth early in its ontogeny.

The atmospheric testing of thermonuclear weapons during the 1950's and early 1960's introduced fallout radionuclides into the oceans, and the temporal pattern of these tracers also may be used as a chronometer to measure the rate of growth of marine organisms. Bomb-produced radiocarbon increased the $\Delta^{14}\text{C}$ (per mil deviation with respect to the activity in 19th century wood) of the atmosphere to nearly 1000‰ by 1964. In the surface ocean, the record of $\Delta^{14}\text{C}$ is well documented in hermatypic corals [17–21] and ex-

hibits an increase above the pre-bomb level starting in the late 1950's and continuing into the mid-1970's. This pattern of ^{14}C variation with time has been used as a chronometer to determine the growth rate of the marine bivalve, *Arctica islandica*. Turekian et al. [14] used the record of $\Delta^{14}\text{C}$ observed in the growth increments of this bivalve to evaluate the hypothesis that these increments form annually. In this paper, we use the record of $\Delta^{14}\text{C}$ in the septa and shell wall of a mature specimen of *Nautilus macromphalus* to infer its age and rate of growth.

2. Experimental methods and results

The specimen of *Nautilus macromphalus* was collected in July, 1969 by Dr. J. Redmond (Iowa State University) near Noumea, New Caledonia ($22^{\circ}18'S$, $166^{\circ}48'E$). It was caught in traps set between 50 and 80 m depth, although, in fact, this species may live as deep as 600 m [22]. The specimen is 16.5 cm in diameter with 31 septa. The most recent septum is approximated (closely spaced) and thicker than the preceding septum. The angular length of the body chamber, measured from the last septum to the apertural edge, equals 120° . The approximated last septum and large body chamber angle suggest that this animal is nearly to fully mature [1,23,24].

Six samples of the septa and shell wall were collected for radiocarbon analysis (Fig. 1). Five of the samples are septa ranging from the most recently formed septum (#31) to septa 8 and 9, which were combined to form a single sample. Stable isotopic and morphologic data on other specimens of *Nautilus* have indicated that septa 8 and 9 are the initial postembryonic septa [15,25]. The sixth sample was obtained by breaking off 3–5 mm of shell from the apertural edge. All samples were rinsed in distilled water to remove any surface material. Sample masses (see Table 1)

DIAMETER = 16.5 cm
NUMBER OF SEPTA = 31
BODY CHAMBER ANGLE = 120°

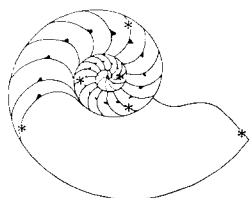


Fig. 1. Schematic drawing of a median section of the specimen of *N. macromphalus*. Asterisks indicate locations of samples.

TABLE 1

Radiocarbon analyses of samples from the specimen of *Nautilus macromphalus*

Sample	Mass (g)	$\Delta^{14}\text{C}$ (‰)
Septum 8, 9 ^a	0.06	-60 ± 12
15	0.17	-71 ± 12
20	0.22	-48 ± 8
25	0.88	-21 ± 8
31	4.06	$+20 \pm 10$
Aperture	1.41	$+68 \pm 6$

^a Septa are numbered from the first formed (#1) to the most recently formed (#31).

ranged from less than 0.1 g (septa 8/9) to several grams (septum 31). Due to the small masses, particularly for the early septa, ^{14}C was determined by tandem accelerator mass spectrometry (TAMS) at the NSF-Arizona Accelerator Facility for Radioisotope Analysis [26]. Samples were converted to graphite for TAMS and the analytical procedures are detailed elsewhere [27].

To provide a comparison with the $\Delta^{14}\text{C}$ record in the nautilus, we present the $\Delta^{14}\text{C}$ record in a hermatypic coral from the Great Barrier Reef, Australia. Cores of *Porites australiensis* were collected from 10 m depth on the outer reef area of Heron Island in November 1983. The coral was sectioned into annual bands and the post-1950 portion measured for radiocarbon according to methods reported by Griffin and Druffel [28]. The radiocarbon measurements for both the nautilus and the coral are reported as $\Delta^{14}\text{C}$ according to the definition of Stuiver and Polach [29]. In the nautilus, the $\Delta^{14}\text{C}$ values were calculated using $\delta^{13}\text{C}$ values of the graphite prepared from the carbonate samples.

The results of the ^{14}C measurements of the nautilus samples are listed in Table 1 and the coral data are plotted in Fig. 2. The coral data vary over time from an average of -46‰ prior to 1958 to a maximum of 150‰ in 1976. In comparison, the nautilus values range from -60 to -71‰ in early septa (8/9 and 15) to $+68\text{‰}$ in the apertural sample.

3. Discussion

In constructing a chronology from the nautilus data, we begin by a consideration of the temporal variation in $\Delta^{14}\text{C}$ in the surface ocean. Previous

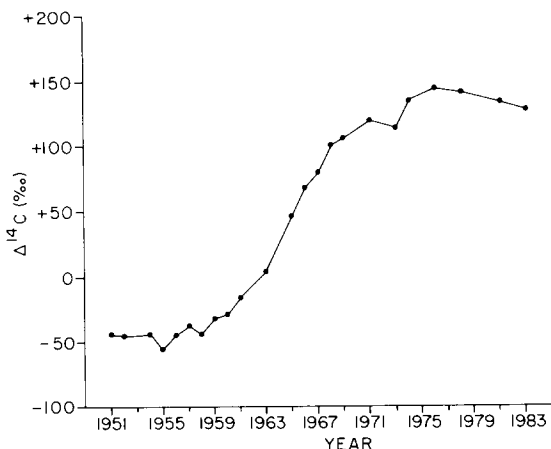


Fig. 2. $\Delta^{14}\text{C}$ in the annual growth bands of a coral (*Porites australiensis*) from the Great Barrier Reef, Australia plotted as a function of the year which the growth band formed.

work has demonstrated that such variation is recorded in the radiocarbon content of the annual growth bands of corals. Data are available from corals collected in many locations including Bermuda [17], Florida and Belize [18], the Galapagos Islands [20], Tahiti [21], the Fiji Islands [30] and Australia (Fig. 2). The patterns from all these locations are similar in showing an increase in $\Delta^{14}\text{C}$ in surface water starting in the late 1950's and continuing until the 1970's, when the pattern levels off and begins to decrease in temperate regions and continues to increase in tropical regions.

Several features of the coral data are relevant to any interpretation of the ^{14}C record in the nautilus. First, the earliest evidence of bomb-produced radiocarbon observed in the surface ocean occurs in 1957-58. Second, corals from different locations exhibit slightly different pre-bomb values of $\Delta^{14}\text{C}$ as well as slightly different temporal patterns. These discrepancies are caused chiefly by upwelling which brings deeper water with a lower $\Delta^{14}\text{C}$ signature to the surface [17,31]. Corals growing in areas where upwelling occurs on a more or less continuous basis, such as those from the Galapagos Islands, display pre-bomb values of $\Delta^{14}\text{C}$ approximately 20‰ lower than those in corals from other areas [20]. In areas in which upwelling occurs sporadically, for example, Bermuda, the values of $\Delta^{14}\text{C}$ recorded in corals are depressed for the period of time over which the upwelling occurs

[17]. The record of $\Delta^{14}\text{C}$ in the Australian coral illustrated in Fig. 2 is similar to those from Belize and Florida [18], where upwelling is uncommon. The data from the Australian coral represent a typical temperate ocean trend and we will use this pattern to interpret the pattern in the nautilus.

The pattern of $\Delta^{14}\text{C}$ in the nautilus is similar to that in the Australian coral. In the nautilus the values of $\Delta^{14}\text{C}$ in septa 8/9 and 15 are low and approximately the same within the reported one sigma error ($-60 \pm 12\text{‰}$ and $-71 \pm 12\text{‰}$). The rest of the samples exhibit a monotonic increase to positive values of $\Delta^{14}\text{C}$ reaching a maximum of $+68 \pm 6\text{‰}$ in the apertural sample. Based on comparison with the coral record, we interpret septa 8/9 and 15 as having formed prior to the first appearance of bomb radiocarbon in the water in which the nautilus grew its shell. In the coral, the pre-bomb values of $\Delta^{14}\text{C}$ average -46‰ . In the nautilus the average pre-bomb values are lower than those in the coral, $\sim -66\text{‰}$. This difference may be due to upwelling as described above, but it is more likely due to the fact that *N. macromphalus* is a mobile animal and, in New Caledonia, commonly lives at depths between 300 and 500 m [22]. Thus, on the average, the nautilus is living in deeper water than the coral and this difference in depth is reflected in its record of $\Delta^{14}\text{C}$.

Broecker and Peng [31], using water column data collected in the 1950's, reconstructed the pre-bomb depth profile of $\Delta^{14}\text{C}$ in the South Pacific. Values range from approximately -50‰ in the surface ocean (comparable to that recorded in the Australian coral prior to 1959) to $\sim -100\text{‰}$ at a depth of 800 m. A pre-bomb $\Delta^{14}\text{C}$ value of -66‰ occurs at depths of about 250-350 m, well within the range of *Nautilus*. It thus appears that the nautilus is recording the radiocarbon content at depth in the water column, and therefore, its record of $\Delta^{14}\text{C}$ will probably be offset from that of the Australian coral much like the radiocarbon record of the Galapagos coral is offset from those of other temperate corals.

In order to assign a chronology to the record of $\Delta^{14}\text{C}$ in the nautilus, we assume that the regular increase in $\Delta^{14}\text{C}$ from the oldest to most recently formed shell material results from shell secretion at a consistent depth or range of depths. We also assume that: (1) septa 8/9 and 15 were formed prior to the first appearance of bomb radiocarbon

in the water in which the nautilus grew and the average value of $\Delta^{14}\text{C}$ in these samples represents the baseline, pre-bomb level, (2) septa 20, 25, and 31 were formed after 1958 (the last year before the appearance of bomb radiocarbon in the Australian coral) but before 1969, the date of collection of the nautilus specimen, and (3) the apertural sample was formed in 1969. Our task is then to reconstruct the temporal change in $\Delta^{14}\text{C}$ in the water in which the nautilus grew and compare this change with that recorded in the nautilus shell.

We have information on the depth profiles of $\Delta^{14}\text{C}$ at two times in the South Pacific: pre-bomb, as mentioned above (1955–1957, [31]), and 1974 (GEOSECS, [32]). By 1974, bomb radiocarbon had been mixed to about 800 m at GEOSECS station 269 [32], and decreased linearly with depth. The pre-bomb and 1974 $\Delta^{14}\text{C}$ profiles are plotted in Fig. 3a. The coral data indicate that bomb ^{14}C first appears in the surface water after 1958, and assuming a rapidly mixed layer of 100 m, the average rate of penetration of bomb ^{14}C must have been 44 m/y from 1958 to 1974 for the signal to reach a depth of 800 m by the end of this time period. Using this rate of penetration of the bomb ^{14}C signal, we have calculated $\Delta^{14}\text{C}$ vs. depth profiles for 1959–1974 by fixing the $\Delta^{14}\text{C}$ values of the mixed layer on the basis of the coral data and drawing simple linear profiles connecting the mixer layer value and the pre-bomb value for any given depth of penetration. The profiles that result are illustrated in Fig. 3a. On the basis of these profiles, we calculate a single depth, 200 m, and a range of depths, 0–360 m, for which the values of $\Delta^{14}\text{C}$ most closely match the range of

values expressed in the nautilus data. At 200 m, the values of $\Delta^{14}\text{C}$ range from -57‰ (pre-bomb) to $+68\text{‰}$ at 1969 and are plotted in Fig. 3b. Between 0 and 360 m, the depth-weighted average values of $\Delta^{14}\text{C}$ span about the same range, -57‰ to $+69\text{‰}$, and are plotted in Fig. 3c. In terms of the habitat of the nautilus, Fig. 3b represents the temporal pattern of $\Delta^{14}\text{C}$ observed by the animal

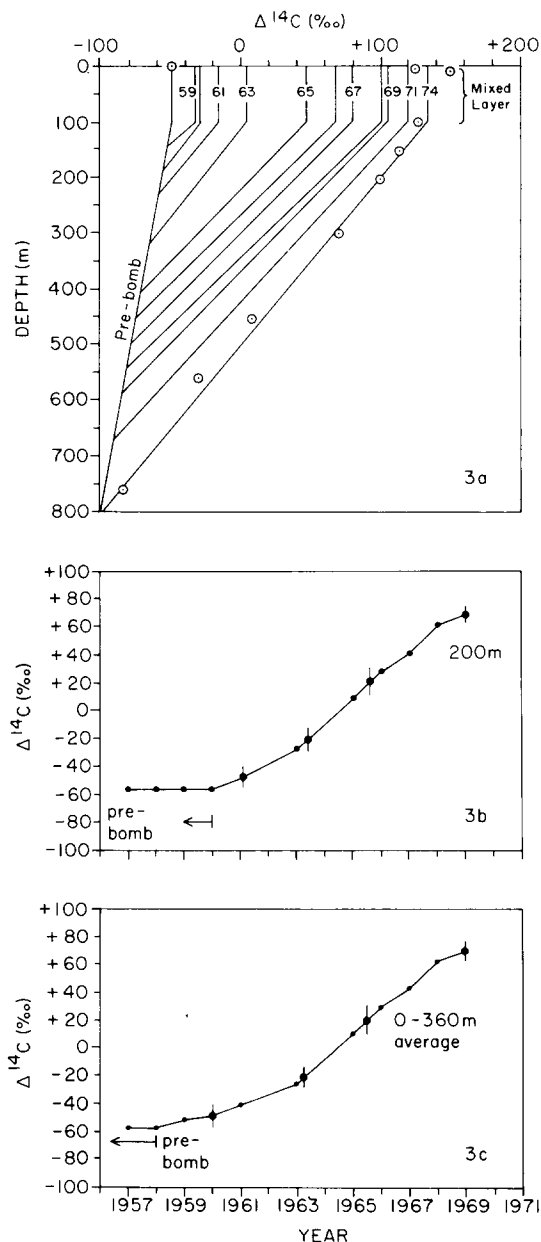


Fig. 3. Reconstruction of the $\Delta^{14}\text{C}$ variation in the water in which the specimen of *N. macromphalus* grew. (a) $\Delta^{14}\text{C}$ vs. depth in the South Pacific water column. The pre-bomb and 1974 profiles are based on data (open circles) from water samples analyzed for ^{14}C [31,32]. Simple linear profiles are drawn. Intermediate profiles are constructed assuming a mixed layer depth of 100 m and a rate of penetration of the bomb ^{14}C signal of 44 m/y. The Australian coral data (Fig. 2) are used to define the temporal variation of $\Delta^{14}\text{C}$ in the mixed layer and the profiles are labelled according to the year they represent. (b) $\Delta^{14}\text{C}$ vs. time at a depth of 200 m, based on the depth profiles of Fig. 3a. The large filled circles represent the nautilus $\Delta^{14}\text{C}$ data. (c) $\Delta^{14}\text{C}$ vs. time based on a depth-weighted average of values from 0 to 360 m (Fig. 3a). The large filled circles represent the nautilus $\Delta^{14}\text{C}$ data.

if it lived solely at 200 m and Fig. 3c represents the pattern observed by the animal if it lived in the upper 360 m and incorporated an average value of $\Delta^{14}\text{C}$ in its shell.

We have assigned dates to the values of $\Delta^{14}\text{C}$ in the nautilus samples on the basis of Fig. 3b and 3c and the results are listed in Table 2. Although the two methods yield similar results as the bomb radiocarbon signal penetrates deeper into the water column over time, the results differ for the early record. The method of averaging from 0 to 360 m implies that the bomb radiocarbon signal is incorporated into the shell shortly after its first appearance in the surface water (1958), whereas the 200 m method delays the first appearance of bomb radiocarbon in the shell until this signal has penetrated to a depth of 200 m (~ 1960 -61). In both approaches the age of the aperture is approximately 3 years older than the most recent septum (#31), suggesting that the animal continued growing at the aperture after secreting the last septum. This result is supported by the large angular length of the body chamber, which is characteristic of mature specimens [1,23,24].

Using the $\Delta^{14}\text{C}$ chronologies, we calculated the time intervals required for septal formation. The values range from 130 to 240 days/septum for septa 20 to 31. Within the uncertainties of the measurements listed in Table 2, these values compare well with previous estimates of 50–100 days/septum in *N. macromphalus* maintained in aquaria [5] and up to 300 days/septum in *N. belauensis* in nature [1,16].

The methods we have used to assign ages to the nautilus samples do not allow us to calculate the dates at which septa 8/9 and 15 formed because these septa predated the first appearance of the bomb ^{14}C signal. However, we can set lower limits on the ages of these samples. The bomb ^{14}C signal was first recorded in the nautilus shell between septa 15 and 20. If we assign the last year before the bomb ^{14}C signal first appeared in the water in which the nautilus grew as the date of formation of septum 15 (Fig. 3b or 3c), we produce a lower limit for the time elapsed between septa 15 and 20 (and a lower limit for the timing of septal formation in this interval). The assigned dates depend on the method used to construct the $\Delta^{14}\text{C}$ vs. time

TABLE 2
Chronology and rates of growth of *Nautilus macromphalus*

Sample	Measured $\Delta^{14}\text{C}$ (‰)	Method I (200 m) ^a				Method II (0–360 m average) ^a			
		year of formation	time after first appearance of bomb ^{14}C in shell (y)	time between successive samples (y)	time of septal formation (days/septum) ^c	year of formation	time after first appearance of bomb ^{14}C in shell (y)	time between successive samples (y)	time of septal formation (days/septum) ^c
Septum 8/9	–60	–	–	–	–	–	–	–	–
15	–71	1960	0 ^b	1.1	≥ 80 ^b	1958	0 ^b	2.0	≥ 150 ^b
20	–48	1961.1	1.1	2.3	170^{+70}_{-90}	1960	2.0	3.3	240^{+180}_{-120}
25	–21	1963.4	3.4	2.2	130^{+80}_{-60}	1963.3	5.3	2.2	130^{+70}_{-50}
31	+20	1965.6	5.6	3.5	–	1965.5	7.5	3.5	–
Aperture	+68	1969 ^d	9.0	–	–	1969 ^d	11	–	–

^a Both methods are based on reconstruction of $\Delta^{14}\text{C}$ depth profiles over time (Fig. 3). Method I uses the temporal variation in $\Delta^{14}\text{C}$ values at a depth of 200 m whereas method II uses a weighted average of $\Delta^{14}\text{C}$ values in the upper 360 m of the water column. In both approaches the $\Delta^{14}\text{C}$ values range from -57‰ to $+68$ – 69‰ , comparable to those observed in the specimen of *N. macromphalus*.

^b Assumes that septum 15 was the last septum formed before the first appearance of bomb radiocarbon.

^c Uncertainties are estimated by using the 1σ errors on the $\Delta^{14}\text{C}$ values of the samples to calculate upper and lower limits on the time interval between successive samples and hence on the time of septal formation.

^d Assumes that the apertural sample was formed in 1969, the date of collection of the specimen.

curve and are 1958 for the 0–360 m method and 1960 for the 200 m method (Table 2). The corresponding times of septal formation are ≥ 150 days/septum or ≥ 80 days/septum respectively (Table 2). Although these values are lower limits, they are comparable to the estimates cited earlier based on other studies.

Finally, we would like to use the ^{14}C chronology to calculate the age of the specimen and hence its age at maturity. Our samples bracket the entire postembryonic development of the animal because septa 8/9 are the first septa formed after the animal hatched from its egg capsule [15,25,33]. In addition to our previous calculations, we must calculate the time elapsed between septa 8/9 and 15 in order to calculate this age. We adopt a conservative approach and use the shortest time of septal formation reported for *N. macromphalus*, ~ 50 days/septum. This value, based on aquarium studies [5], yields an elapsed time of approximately one year between septa 8/9 and 15. The age at maturity of this specimen of *N. macromphalus* is, therefore, at least 10–12 years, depending on the method used to construct the ^{14}C chronology (Table 2). This estimate exceeds values of 2.5 to 6 years for this species based on aquarium studies [4] but is comparable to values of 10–15 years for *N. belauensis* in nature based on mark-recapture and radiometric studies [1,16]. These results emphasize the striking difference between the life history of *Nautilus* and that of most other modern cephalopods, which rapidly reach maturity in 1–3 years [34].

Acknowledgements

We thank Dr. Jim Redmond for supplying the specimen of *N. macromphalus*. We gratefully acknowledge National Science Foundation support to E.R.M.D. (grant OCE83-15260) to J.K.C. (grant OCE86-13844) and to D.J.D. and A.J.T.J. (grant EAR85-12761). This is Contribution No. 580 from the Marine Sciences Research Center, SUNY at Stony Brook, and Contribution No. 6507 from the Woods Hole Oceanographic Institution.

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