Oxygen Isotope Profile and Age Determination of Venus Clam Mercenaria stimpsoni (Bivalvia: Veneridae) from the East Sea

Boo-Keun Khim, Jong-Geel Je', Sang-Joon Han', Kyung-Sik Woo''.

and Yong-Ahn Park'''

Research Institute of Oceanography, Seoul National University, Seoul 151-742, Korea "Korea Ocean Research and Development Institute, Ansan 425-600, Korea "Department of Geology, Kangwon National University, Chuncheon 200 701, Korea "Department of Oceanography, Seoul National University, Seoul 151-742, Korea

= 국문요약 =

동해산 뷔나스백합(Mercenaria stimpsoni)의 산소동위원소상과 연령추정

김부근·제종길··한상준·우경식··박용안··

서울대학교 자연과학대학부속 해양연구소, '한국해양연구소, "강원대학교 지질학과, ""서울대학교 해양학과

동해 연안에서 채취된 뷔나스백합(Mercenaria stimpsoni)의 연령과 성장률을 이매패의 표면에서 확인된 연륜과 이매패 각질에서 분석된 산소동위원소비의 성장에 따른 변화를 이용하여 비교하였다. 뷔나스백합의 산소동위원소상은 일련의 주기적인 변화를 뚜렷하게 보여주며 이러한 변화진폭은 이매패가 성장한 해수의 온도변화에 일차적으로 제어된다. 산소동위원소상의 주기와 연륜의 관계로부터 뷔나스백합의 연륜이 해마다 여름철에 형성됨을 보여준다. 해수 온도의 계절적 변화와 산소동위원소비에서 얻어진 예측 온도와의 비교로부터, 뷔나스백합은 겨울철에 성장이 멈추는 것으로 사료된다. 또한 산소동위원소비는 뷔나스백합의 성장에 따른 전형적인 노화현상을 보여준다. 따라서 이매패가 성장하는 해수의 물리화학적 조건에 의해 제어되는 산소동위원소비는 뷔나스백합의 경우 연령과 성장률을 측정하는 독립적인 시간 척도가 될 수 있다.

Key words: Oxygen Isotope, Age, Growth Rate, Mercenaria stimpsoni, East Sea

INTRODUCTION

Considerable economic importance and heavy fishing of shellfish stocks emphasize the reliable determination for correct age and growth rate of organisms. Age determination of population is also of essentially significance for the application of resource yield models used in shellfish fisheries

management (e.g., Ricker, 1975). A variety of techniques presently employed for age determination of the bivalve shells depend on the identification of growth checks visibly on the exterior of the shell (Stevenson and Dickie, 1954; Merrill *et al.*, 1965; Kennish and Olsson, 1975; Kennish and Loveland, 1980; Clark and Lutz, 1982; Tanabe, 1988; Jones *et al.*, 1989, 1990; Sephton and Bryan, 1990).

Development of cyclic growth increment ranging

in scale from day to year is the unique feature of the bivalve shells (Lutz and Rhoads, 1980). banding patterns have proven to be the most consistent and readily interpretable to receive wide attention in marine ecological views, particularly in determining age and growth rates. However, the identification of external checks as representing duration of growth for an individual bivalve is often complicated by disturbance or shock rings (Fritz An entire spectrum of growth and Lutz, 1986). disturbances, either periodic (e.g., annual spawning) stochastic (e.g., storms). is potentially interpretable from the bivalve shells (Kennish and Olsson, 1975). Thus, Jones et al. (1978) argued that the counting of growth checks seemed to be misleading because the age of young clams was overestimated due presumably to the presence of disturbance rings, and that of older ones was underestimated because largely of the erosion of early rings on the umbo and crowding of later rings at the ventral margin.

Distinguishment between annual growth and external disturbance lines is frequently very difficult macroscopically and often very subjective (Lutz and Rhoads, 1980). Other shell characteristics, such as seasonal variation in shell color, convexity of the shell profile, and activity of boring organisms, may provide additional information for the interpretation of external lines (e.g., Merrill et al., 1965). However, these criteria are still very subjective and not conclusive. With respect uncertainties involved in the accurate interpretation of growth checks, additional and potential method of establishing the periodicity of these characteristics was pursued in the mollusk species. Principal among these efforts is the utility of stable isotope chemistry across shell increments (Epstein and Lowenstam, 1953; Killingley and Berger, 1979; Wefer and Killingley, 1980; Arthur et al., 1983; Jones et al., 1983; Krantz et al., 1987; Weidman et al., 1994; Khim, 1997).

Present-day age estimate techniques for the venus

clam, *Mercenaria stimpsoni* rely on the subjective interpretation of growth lines on the shell exterior as representing periods of annual growth. The purpose of this study is to verify the seasonal cyclicity of the annual growth increments through the stable oxygen isotope method and to determine the age of venus clam, *Mercenaria stimpsoni* collected from the eastern coast of Korea.

MATERIALS AND METHODS

One valve of dead specimen HP-1 (Veneridae: *Mercenaria stimpsoni*) was collected from the dumped sediments that were dredged from the inner harbor of Hupo, east coast of Korea (Fig. 1). *Mercenaria stimpsoni* is a cold-water bivalve species distributed in the eastern coast of Korea whereby the fine sandy substratum are dominant with 10 to 20 m in water depth (Fig. 2a; Je, 1993; Jo *et al.*, 1995).

Specimen HP-1 was prepared for stable isotope analysis by first lightly grinding the exterior of the shell to eliminate any attached debris. Discrete sampling of carbonate powder were then made by drilling from the outer shell layer using a 0.5-mm dental drill bit. The calcium carbonate powders were collected in a series of grooves parallel to shell growth from 47 mm to 77 mm of shell height (Fig. 2b). Samples were taken only from the outer prismatic shell layer which is deposited sequentially along the shell margin during the growth.

Stable isotope measurements were done using a FINNIGAN MAT 252 gas isotope mass spectrometer with an automatic microprocessor—controlled carbonate preparation device (Kiel CARBO II) at GEOMAR, Germany. Each individual sample was treated with purified phosphoric acid at 70° C to produce CO_2 from which $^{18}O/^{16}O$ abundance was measured. Analytical precision is $\pm 0.03\%$ based on replicate standards. The values are reported relative to the Peedee belemnite (PDB) standard, and calibration to PDB have been done with NBS-19

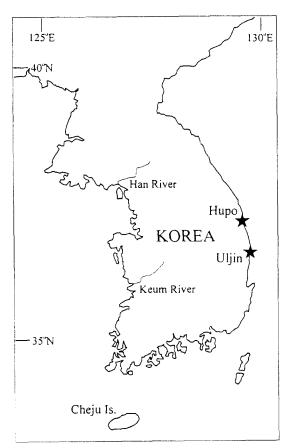


Fig. 1. Collection site of mollusk specimen HP-1 (Veneridae; Mercenaria stimpsoni). One valve was collected from the dumped sediments that were dredged from the inner harbor of Hupo.

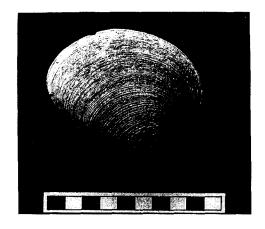
Mercenaria stimpsoni is a cold-water bivalve species distributed in the eastern coast of Korea whereby the fine sandy substratum are dominant with 10 to 20 m in water depth

(Craig, 1957).

RESULTS

Isotopic determinations were made on 35 discrete carbonate powders from the shell of specimen HP-1 with a shell height of about 100 mm. The oxygen isotope data are plotted in Figure 4 with the $\delta^{18}O$

(a)



(b)



Fig. 2. (a) Photograph of Mercenaria stimpsoni. The individual arrows marks the dark growth increments. (b) Sampling scheme of sectioned shell specimen HP-1. The growth marks are clearly visible on the surface. The each sampling groove is a drilled site for the collection of carbonate powder.

scale reversed; the lower $\delta^{18}O$ values, representing "warm" isotopic temperatures, are at the top of the vertical scale. The oxygen isotope profile of specimen HP-1 exhibits almost five complete cycles with approximately 2.58 ‰ variation between minimum and maximum $\delta^{18}O$ values (Fig. 3). The heaviest (most positive) $\delta^{18}O$ value in the record is 1.34 ‰ and the lightest (most negative) is -1.24 ‰. In each cycle, the variation from the $\delta^{18}O$ minimum value to the maximum is abrupt whereas the change from maximum to minimum looks fairly gradual. An another interesting feature is the gradual attenuation of amplitude in each cycle as

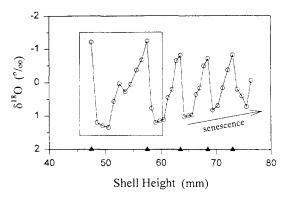


Fig. 3. The oxygen isotope profile of shell specimen HP-1 (Mercenaria stimpsoni). The δ^{18} O scale is reversed so that the lower (more negative) δ^{18} O values representing "warm" isotopic temperatures are at the top of the vertical scale. The solid triangles along the horizontal axis stand for the dark growth increments that are visible on the shell exterior. The inset box is shown in Fig. 5 as converting the estimated temperature of shell carbonate deposition.

each cycle becomes correspondingly lighter. The $\delta^{18}O$ curve is roughly sinusoidal although occasional deviations of the a few tenths of a permil are observed from the trend.

Specimen HP-1 was estimated to have completed 16 years of growth and finished shell deposition in the margin at the death of time. The determination was primarily based on an interpretation of the identifiable external growth lines represented diagrammatically in Figure 2b. The millimeter scale on the horizontal axis related the position of these external lines to shell height (as measured from the umbo to the margin) and the position of each carbonate powder sample drilled from the shell. Over the sampled intervals of oxygen isotope, the individual growth checks as representing dark growth lines match the each oxygen isotope cycle (Fig. 3). The dark growth lines are formed at the time just following the minimum δ¹⁸O value in each year.

DISCUSSION

growing. In addition, the maximum δ^{18} O value in

One of the characteristic features in the mollusk

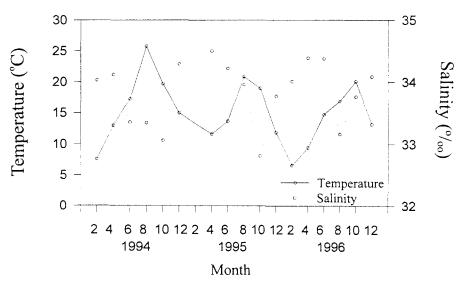


Fig. 4. Three-year (1994, 1995 and 1996) temperature and salinity variation observed off Uljin in water depth of 10 m (NFRDA, 1995, 1996, 1997).

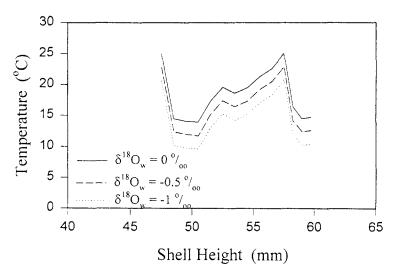


Fig. 5. Estimated temperature variation from the oxygen isotope data measured from shell carbonate using the paleotemperature equation of Grossman and Ku (1986). The seawater δ¹⁸O values are assumed as 0, -0.5, and -1.0% (SMOW), respectively.

shell is an accretionary growth presenting repeated and periodic shell increments (Lutz and Recent studies on the timing of Rhoads, 1980). growth increment formation reported that the geographic differences in annual shell growth patterns reflected seasonal fluctuations of ambient water temperature (Clark and Lutz, 1982; Peterson et al., 1983). In addition, Grizzle and Lutz (1988) recognized the wide latitudinal variations in the growth increment formation and underscored the requirements for the documentation of such patterns. In our coastal area in Korea, Kim et al. (1977) reported that Meretrix meretrix lusoria formed the annual increments during cold season between November and April. The growth pattern of Spisula sachalinensis showed the formation of annual banding in late summer from August to September (Kato and Hamai, 1975; Kang and Kim, Based on the oxygen isotope, Khim (1997) suggested that the annual increments of Cyclina sinensis were formed in winter, similar to those of Phacosoma japonicum (Tanabe, 1988).

This study also employs the isotope ratio between ¹⁸O and ¹⁶O in shell carbonate to interpret the growth pattern of Mercenaria stimpsoni. Based on the thermodynamic behaviors of the oxygen isotopes in chemical reactions, the δ^{18} O values of the product depend on the 818O values of the reactants and the temperature at which the reaction occurs (Urey, 1947; Epstein et al., 1953; Rye and Sommer, 1980). During the growth of a mollusk, the isotopic fractionation of shell carbonate is a function of the ¹⁸O/¹⁶O ratio of the ambient water in which the organism lives and the ambient temperature during In assumed case of constant shell precipitation. δ¹⁸O value for ambient water, relatively fewer ¹⁸O atoms are incorporated into shell carbonate during the warmer summer months ("lighter" isotopic ¹⁸O atoms are values) and proportionately more during the cooler winter assimilated ("heavier" isotopic values).

At a first approximation, the variations in the oxygen isotope profiles of specimen HP-1 can be interpreted as being controlled primarily by seasonal

changes of seawater temperature (Fig. 3). A series of periodic cycle in the oxygen isotope profile reflect the annual fluctuation of seawater temperature. In addition, the correspondence of each growth mark to the δ^{18} O cycle at least confirms that the formation of growth bands over the sampled intervals can be regarded as annual. The position of annual growth marks lies just over the δ^{18} O minimum value in the cycle. It means that the growth marks were formed just after the warmest season of late summer. Thus, the oxygen isotope profile confirms the visual identification of growth bands, exhibiting an apparent annual cycles. The gradual attenuation of amplitude and decrease of the maximum δ¹⁸O value in each cycle show the typical pattern of senescence in growth. Similar interpretations have been proposed for the attenuation of cycles in the isotopic record for conchs (Epstein and Lowenstam, 1953; Wefer and Killingley, 1980) and surf clams (Jones et al., 1983; Krantz et al., 1987; Weidman et al., 1994).

The controlling factors of temperature and δ¹⁸O value of water can be quantified in relation to oxygen isotopic composition of shell carbonate in terms of the aragonite paleotemperature equation (Grossman and Ku, 1986). The principal application of this equation is to calculate temperature of precipitation from a known carbonate isotopic value when water isotopic composition is known or can be reasonably estimated. Epstein et al. (1953) emphasized that seasonal temperature cycles produce significant variations in isotopic composition within Through a series of sampling from a mollusk shell at close intervals, it is possible to examine seasonal changes of the 18O/16O ratio and to compare these variations with the shell growth record (Wefer and Killingley, 1980; Arthur et al., 1983; Jones et al., 1983; Krantz et al., 1987; Weidman et al., 1994; Khim, 1997).

Temperature and salinity data between 1994 and 1996 obtained from 10 m water depth off Uljin south of the study area were displayed in Figure 4

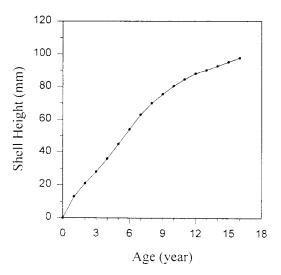


Fig. 6. Growth rate of *Mercenaria stimpsoni* determined from the external line technique that was confirmed by oxygen isotope profile.

(NSFDA, 1995, 1996, 1997). The study area seems to be essentially full marine with mean salinity of 33.8 \(\text{\(and an annual salinity range is about 1.2 \(\text{\(b\)} \). A certain degree of seasonality is associated with salinity in that the highest salinity values occur in the late spring and early summer, while the lowest salinity values are observed during late summer (Fig. 4). Monthly temperature for the same area range from approximately 7.6°C to a maximum of 25.6°C. approximately but generally Throughout most of the winter and early spring, water temperatures remain below 12°C. Beginning in late spring and continuing through the fall, water temperature steadily increase to an annual maximum at the time of August. An interannual variation of temperature was also figured out.

As previously mentioned, ambient temperatures during shell carbonate precipitation can be estimated from the aragonite paleotemperature equation (Grossman and Ku, 1986).

$$T(^{o}C) = 20.6 - 4.34 \times (\delta^{18}O_{c} - \delta^{18}O_{w})$$

using the $\delta^{18}O_c$ values of the individual carbonate samples and the $\delta^{18}O_w$ values of the ambient waters.

As a first approximation, if one makes the simplified assumption that changes in seawater δ^{18} O values at the collection site are negligible, an average seawater δ¹⁸O value can then be used to estimate temperature during shell deposition. In this study, considering the variation of salinity, the corresponding seawater δ¹⁸O value changes little significantly, but unfortunately the δ^{18} O values of seawater are not available. Thus, the seawater δ¹⁸O values are assumed as 0, -0.5 and -1.0 %, respectively. In this manner, the shell carbonate δ¹⁸O values can be converted to temperature maxima and minima (Fig. 5). Using this approximation, the minimum isotopic temperature recorded in the shell of HP-1 is about 10°C at the -1.0 % of seawater δ^{18} O value and the maximum is about 25°C at the 0 ‰ of seawater δ¹⁸O value. In this case, the calculated temperature range is smaller than the real fluctuation of temperature in Uliin (Fig. 4). The main reason is the minimum temperature that was recorded in the shell isotope data. In extreme case of Fig. 4, the estimated minimum temperature of 10°C reflects that either the shell mollusk did not grow below that temperature or the very slow growth rate under such temperature could not retrieve by the presently utilized analytical method. Similar feature of cessation of shell deposition related to cold threshold temperature has been already reported from other shell mollusks (Krantz et al., 1987; Weidman et al., 1994).

Because the oxygen isotopic composition of *Mercenaria stimpsoni* is controlled by seasonal hydrographic factors, the isotopic record from this venus clam should provide a functional time scale for determining the growth rate. The number of months from the beginning of shell deposition may be estimated for obvious seasonal peaks such as summer δ^{18} O minima and winter δ^{18} O maxima in the oxygen isotope profile. This time scale then be related directly to the positions on the shell of the respective samples. Constructed in this manner, a

standard graph of shell height to years of growth (Fig. 6) illustrates that specimen HP-1 (*Mercenaria stimpsoni*) shows an average rate of growth of approximately 6.1 mm per year (as interpreted from the isotopic record). This supports the growth rate interpretation by suggesting a similar trend in ontogenetic development.

CONCLUSIONS

Venus clam, Mercenaria stimpsoni, was collected from the Hupo Harbor, east coast of Korea. External growth lines visibly identified on the shell surface represent periods of apparently annual growth and provide the utility of present-day age determination technique. Such subjective estimate of Mercenaria stimpsoni was verified by the stable isotope profile across the shell surface. The present stable oxygen isotope study proves the shell age and growth estimates from the external growth lines. The oxygen isotope profile of venus clam, Mercenaria stimpsoni shows cyclic and annual pattern which is largely controlled by seawater temperature variation. On the basis of the match between the individual dark growth mark and the annual oxygen isotope cycle, the formation of growth marks looks apparently annual, although we cannot rule out the possible disturbance and shock marks. Because the oxygen isotopic composition of shell carbonate are controlled by the physicochemical condition of ambient seawater hydrographic factors, the oxygen isotope profiles of Mercenaria stimpsoni provide an independent time scale for age and growth rate determination.

ACKNOWLEDGMENTS

This research was partly supported by MECBES (PE9765) from Ministry of Marine and Fishery Affairs granted to KORDI through Dr. Sang-Joon Han and by the academic research fund from Ministry of Education to Dr. Kyung-Sik Woo. We

appreciate the two anonymous reviewers for their painstaking reading.

REFERENCES

- Arthur, M.A., Williams, D.F. and D.S. Jones (1983)
 Seasonal temperature-salinity changes and thermocline development in the mid-Atlantic Bight as recorded by the isotopic composition of bivalves.

 Geology, 11: 655-659.
- Clark, G.C. and Lutz, R.A. (1982) Seasonal patterns in shell microstructure of Mercenaria mercenaria along the U.S. Atlantic coast. Abstract and Program of Geological Society of America, 14: 464.
- Craig, H. (1957) Isotopic standards for carbon and oxygen and correction factors for mass spectrometric analysis of CO₂. *Geochimica et Cosmochimica Acta*, 12: 133–149.
- Epstein, S. and Lowenstam, H (1953) Temperature-shell growth relations of recent and interglacial Pleistocene shoal-water biota from Bermuda. *Journal of Geology*, **61**: 424-438.
- Epstein, S., Buchsbaum, R. Lowenstam, H. and Urey, H.C. (1953) Revised carbonate-water isotopic temperature scale. *Geological Society of America Bulletin*, 64: 1315-1326.
- Fritz, L.W. and Lutz, R.A. (1986) Environmental perturbations reflected in internal shell growth patterns of *Corbicula flucminea* (Mollusca: Bivalvia). *Veliger*, **28**: 401-417.
- Grizzle, R.E. and Lutz, R.A. (1988) Descriptions of macroscopic banding patterns in sectioned polished shells of *Mercenaria mercenaria* from southern New Jersey. *Journal of Shellfish Research*, 7: 363–370.
- Grossman, E.L. and Ku, T.L. (1986) Oxygen and carbon isotope fractionation in biogenic aragonite: temperature effects. *Chemical Geology*, **59**: 59-74.
- Je, J.G. (1993) Distribution of Molluscs in Soft Bottom of Korean Seas. 296 pp. Ph.D. Thesis, Seoul National University.
- Jo, M.K., Byun, K.S., Lim, K.B., Son, S.J. Lee, S.J., Baik, C.L., Park, Y.J., Choi, S.H., Hong, J.P., Kim, G.Y., Sung, K.T., Lee, S.C. and Kwun, K.S. (1995) Distribution and ecology of major shellfishes in the

- coastal areas of Kyongsangbuk-do. Bulletin of National Fisheries Research and Development Agency, 51: 23-66.
- Jones, D.S., Williams, D.F. and Arthur, M.A. (1983) Growth history and ecology of the Atlantic surf clam, Spisula solidissima (Dillwyn), as revealed by stable isotopes and annual shell increments. Journal of Experimental and Marine Biology and Ecology, 73: 225-242.
- Jones, D.S., Quitmyer, I.R., Arnold, W.S. and Marelli, D.C. (1990) Annual shell banding, age, and growth rate of hard clams (*Mercernaria* spp.) from Florida. *Journal of Shellfish Research*, 9: 215–225.
- Jones, D.S., Thompson, I. and Ambrose, W.G. (1978)
 Age and growth rate determinations for the
 Atlantic surf clam *Spisula solidissima*, based on
 internal growth lines in shell cross-sections. *Marine Biology*, 47: 63-70.
- Jones, D.S., Arthur, M.A. and Allard, D.J. (1989) Sclerochronological records of temperature and growth from shells of *Mercenaria mercenaria*, Narragansett Bay, Rhode Island. *Marine Biology*, 102: 225-234.
- Kang, Y.J. and Kim, C.K. (1983) Studies on the structure and production processes of biotic communities in the coastal shallow waters of Korea 3. Age and growth of Spisula sachalinensis from the eastern waters of Korea. Bulletin of Korean Fishery Society, 16: 82-87.
- Kato, Y. and Hamai, I. (1975) Growth and shell formation of the surf clam, Spisula sachalinensis (Schrenck). Bulletin of Faculty in Fishery Hokkaido University, 25: 291-303.
- Kenrish, M.J. and Loveland, R.E. (1980) Growth models of the northern quahog *Mercenaria mercenaria* (Linne). *Proceedings of National Shellfish Association* **70**: 230–239.
- Kennish, M.J. and Olsson, R.K. (1975) Effect of thermal discharges on the microstructural growth of Mercenaria mercenaria. Environmental Geology, 1: 41-64.
- Khim, B.K. (1997) Stable oxygen and carbon isotope profiles of the bivalve shells collected from coastal regions of Korea: comparison of the coastal water properties. *Journal of Korean Society of*

- Oceanography, 32: 28-37.
- Killingley, J.S. and Berger, W.H. (1979) Stable isotopes in a mollusk shell: detection of upwelling events. *Science*, **205**: 166–188.
- Kim, B.A., Kim, B.K. and Kim, S.U. (1977) Studies on the growth of hard clam, Meretrix meretrix lusoria (Roding). Bulletin of Fisheries Research and Development Agency, 17: 77-85.
- Krantz, D.E., Williams, W.F. and Jones, D.S. (1987) Ecological and paleoenvironmental information using stable isotope profiles from living and fossil molluscs. *Palaeogeography Palaeoclimatology Palaeoecology*, 58: 249–266.
- Lutz, R.A. and Rhoads, D.C. (1980) Growth patterns within the molluscan shell: an overview. *In:* Skeletal Growth of Aquatic Organisms: Biological Records of Environmental Change. (ed. by Rhoads, D.C. and Lutz, R.D.). pp. 203-254. Plenum Press. New York.
- Merrill, A.S., Posgay, J.A. and Nichy, F.E. (1965) Annual marks on the shell and ligament of the sea scallop (*Placopecten magellanicus*). Fishery Bulletin, 65: 299-311.
- NFRDA (National Fisheries Research and Development Agency) (1995) Annual Report of Oceanographic Observations for 1994. Vol. 43, 510 pp.
- NSFDA (National Fisheries Research and Development Agency) (1996) Annual Report of Oceanographic Observations for 1994. Vol. 44, 519 pp.
- NSFDA (National Fisheries Research and Development Agency) (1997) Annual Report of Oceanographic Observations for 1994. Vol. 45, 527 pp.
- Peterson, C.H., Duncan, P.B., Summerson, H.C. and Safrit, G.W. (1983) A mark-recapture test of annual periodicity of internal growth band deposition in shells of hard clams, *Mercenaria mercenaria*, from a population along the southeastern United States. *Fishery Bulletin*, 81: 765-779.
- Ricker, W.E. (1975) Computation and interpretation of biological statistics of fish population. *Bulletin of Fishery Research and Board Canada*, 191: 1-382.

- Rye, D.M. and Sommer, M.A. (1980) Reconstructing paleotemperature and paleosalinity regimes with oxygen isotopes. *In*: Skeletal Growth of Aquatic Organisms: Biological Records of Environmental Change. (ed. by Rhoads, D.C. and Lutz, R.D.). pp. 169–202. Plenum Press. New York.
- Sephton, T.W. and Bryan, C.F. (1990) Age and growth rate determinations for the Atlantic surf clam, Spisula solidissima (Dillwyn, 1817), in Prince Edward Island, Canada. Journal of Shellfish Research, 9: 177-185.
- Stevenson, J.A. and Dickie, L.M. (1954) Annual growth rings and rate of growth of the giant scallop, *Placopecten magellanicus* (Gmelin) in the Digby Area of the Bay of Fundy. *Bulletin of Fishery Research and Board Canada*, 11: 660-671.
- Tanabe, K. (1988) Age and growth rate determinations of an intertidal bivalve, *Phacosoma japonicum*, using internal shell increments. *Lethaia*, 21: 231-241.
- Urey, H.C. (1947) The thermodynamic properties of isotopic substances. *Journal of Chemical Society*, 1947; 562–581.
- Wefer, G. and Killingley, J.S. (1980) Growth histories of strombid snails from Bermuda recorded in their O-18 and C-13 profiles. *Marine Biology*, 60: 129-135.
- Weidman, C.R., Jones, G.A. and Lohmann, K.C. (1994)
 The long-lived mollusc *Arctica islandica*: a new paleoceanographic tool for the reconstruction of bottom temperatures for the continental shelves of the northern North Atlantic Ocean. *Journal of Geophysical Research*, **99**: 18,305–18,314

Received February 26, 1998 Accepted April 11, 1998