

# Latitudinal variation in shell growth patterns of *Phacosoma japonicum* (Bivalvia: Veneridae) from the Japanese coast

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**ABSTRACT:** Shell growth patterns of *Phacosoma japonicum* (Reeve) were examined from 5 locations around the Japanese coast, using annual increments within the internal shell sequence. Recognition of annual increments is based on the presence of growth cessation marks or biochecks (= slow growth bands), both of which were formed by winter of each year. Northern individuals generally possess a smaller growth parameter in von Bertalanffy equations and a longer life span than southern ones. Toward the south, the number of microincrements within each annual increment tends to increase, whereas the mean microincrement width gradually decreases. Winter growth cessation marks are especially conspicuous in individuals from Seto Inland Sea and northward. The range of temperatures calculated from <sup>18</sup>O/<sup>16</sup>O ratios of 2 selected specimens correlates well with the season of phytoplankton abundance in the habitats. These lines of evidence strongly suggest that the north-south cline detected results mainly from the difference in the length of the growing season among local populations, depending on both temperature and trophic resource seasonality.

## INTRODUCTION

Periodic structures of different magnitudes are commonly observed within the marginally growing skeletons of invertebrates. Of these, annual increments may be most important for life history analysis of living organisms. Annual layering is actually present in the majority of Recent bivalves studied in detail (Lutz & Rhoads 1980), and has been utilized in age and growth rate determinations of local populations (Mason 1957, Hallam 1967, Jones et al. 1978, Seed & Brown 1978, Bachelet 1980, Jones 1980, Tanabe 1988) and in documenting conspecific variation of shell growth patterns (Hall et al. 1974, Beukema & Meehan 1985, Harrington 1987).

The venerid *Phacosoma japonicum* (Reeve) treated in this paper also preserves large-scale repeating structures in the outer aragonite layer of the shells. This species is common in the sandy-to-muddy sediments of intertidal to lower subtidal environments, distributed on the coasts of Japan, Korea and China (Habe 1977). Recent sclerochronological analysis of marked and recovered individuals from the coast of the Seto Inland Sea demonstrated that the large-scale repeating layers

in this species can be used as annual increments for age and growth rate determinations (Tanabe 1988). Using this approach, this paper considers the latitudinal variation of shell growth patterns in this species over a wide geographic range around the Japanese Islands, and discusses its ecological implications.

## MATERIAL AND METHODS

Samples of *Phacosoma japonicum* were collected from 5 locations along the Japanese coast: (1) subtidal sand flat of Wakkanai Port, northern Hokkaido, (2) subtidal sand flat of the Kamiiso Coast, Hakodate Bay, southern Hokkaido, (3) intertidal sand flat of the Kaneda Coast, Kisarazu, Tokyo Bay, central Honshu, (4) intertidal sandy mud flat of the Kawarazu Shore, Toyo, Seto Inland Sea, Shikoku, and (5) intertidal sandy mud flat of the Arao Coast, Ariake Bay, Kyushu (Fig. 1). The Wakkanai coast is presumed to be at the northern limit of the zoogeographic range of this species. Sea-surface temperature tends to decrease with increasing latitude (Fig. 2). The range of annual temperature variation in the northern locations is much

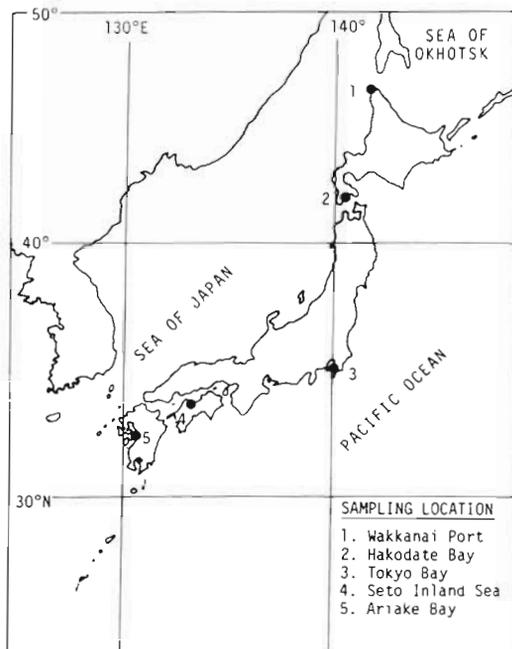


Fig. 1. Sampling locations of *Phacosoma japonicum*

larger than that in the southern locations. This is largely a reflection of the flow patterns of the warm Kuroshio current from the south and the cold Oyashio

current from the north. Very low winter temperatures in the Wakkanai water result from influx of floating ice from the Sea of Okhotsk.

After having removed soft tissues from the shells, a single valve for each specimen was sectioned from umbo to ventral margin along the maximum shell growth axis with the aid of an Isomet low speed saw (Buehler Co.). Following the methods described in Tanabe (1988), the sectioned surface was polished, etched, and then acetate peels were prepared for every specimen. The etched surface of several specimens was coated with platinum, and the microtexture was observed under the SEM (Hitachi S-430). Measurements of the internal increment sequence were made on the peeled specimens using a profile projector (Nikon Co., model V-16), attached to a digital micrometer (accuracy  $\pm 1 \mu\text{m}$ ) (magnifications  $\times 200$ ). Recognition of annual increments in the shell cross-sections is based on the criteria described in Tanabe (1988). The annual increments are distinguishable by gradual narrowing of microincrements in their marginal portion and the presence of a clear growth cessation mark at the boundary of 2 annual increments (Fig. 3). In the population on the Kawarazu Shore, the growth cessation mark is formed annually during winter (November–February), and is expressed by discontinuity (break) in microincrement growth (Tanabe 1988). Winter formation of growth cessation

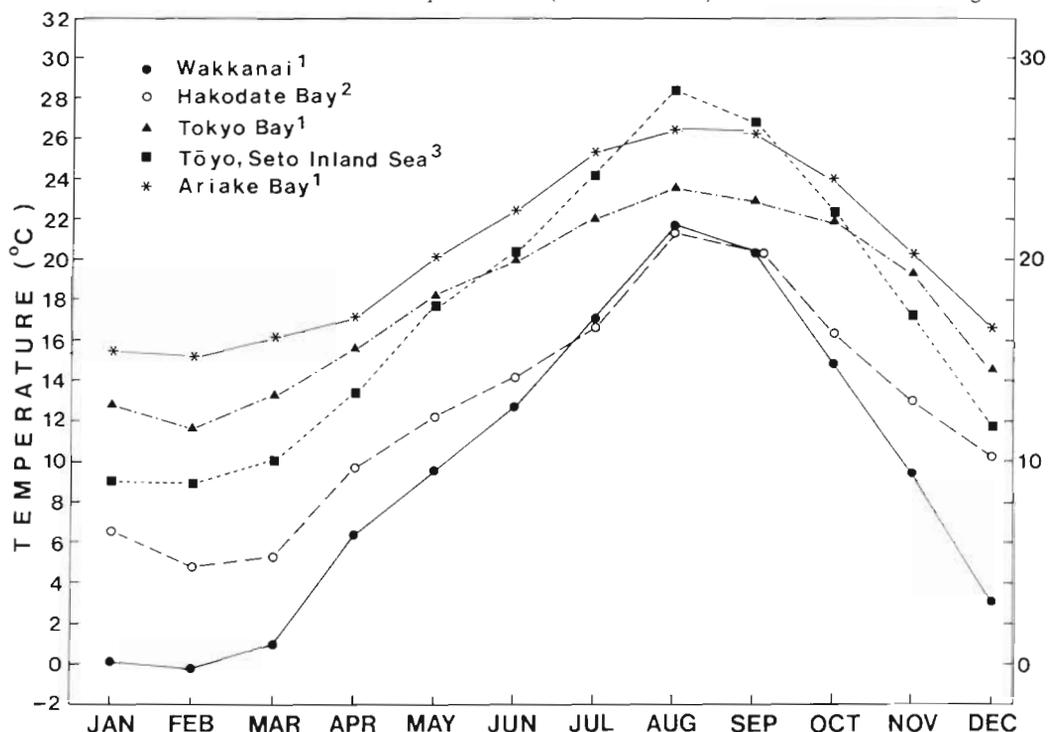


Fig. 2. Monthly mean water temperatures near the sampling locations. Data sources: (1) Oceanographic observations by the Japan Meteorological Agency in 1985 (Japan Meteorological Agency 1986), (2) unpubl. data of the marine biological station of the Hokkaido University of Education during 1979–1980; (3) unpubl. data of the Ehime Prefectural fisheries experiment station in 1985

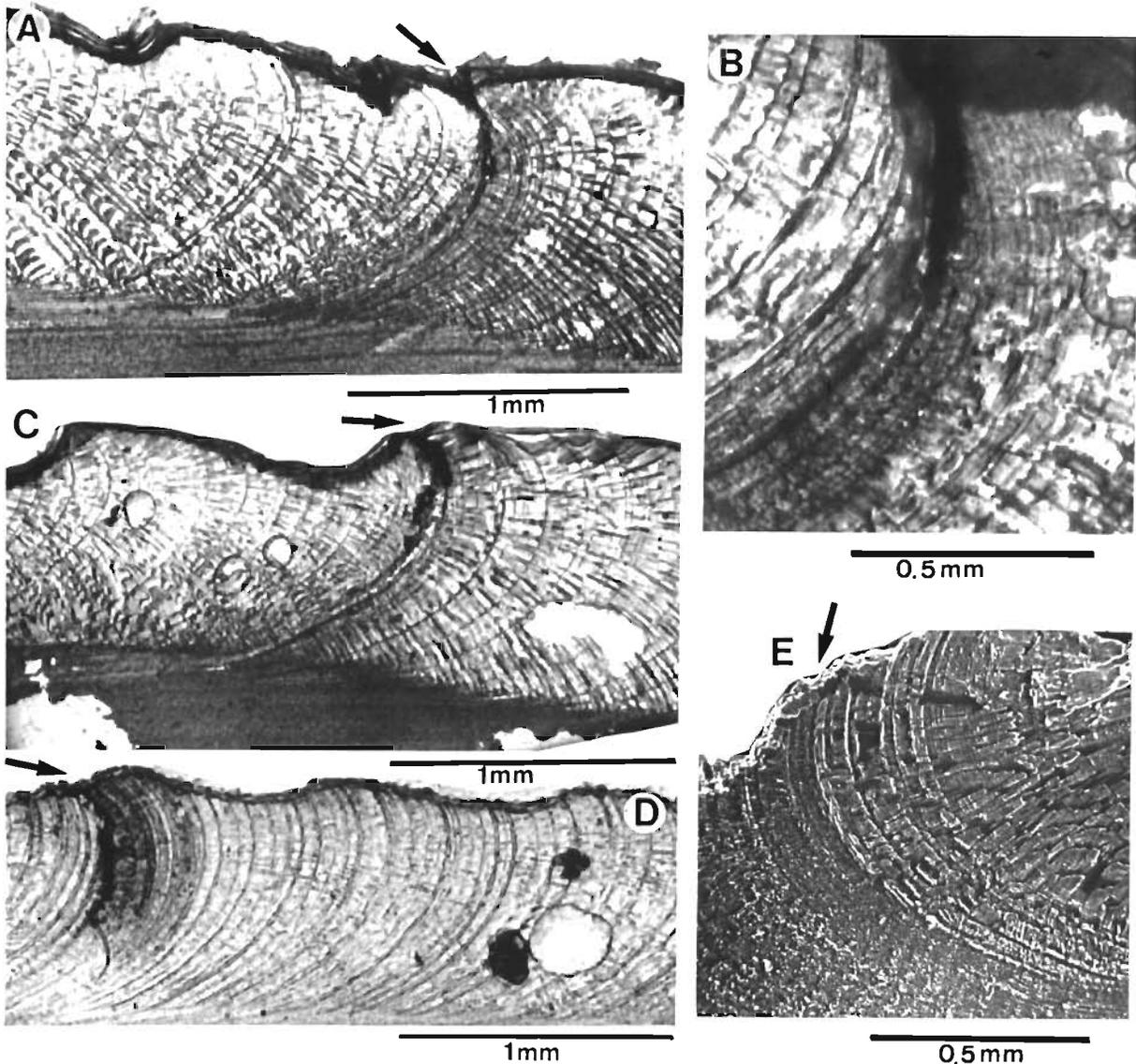


Fig. 3. *Phacosoma japonicum*. Boundary (arrows) between 2 annual increments for specimens from different locations. (A & B) Growth cessation mark between 4th and 5th annual increments in a specimen from Wakkani Port. (C) Growth cessation mark between 3rd and 4th annual increments in a specimen from Kamiiso Coast, Hakodate Bay. (D) Growth cessation mark between 3rd and 4th annual increments in a specimen from Kaneda Coast, Tokyo Bay. (E) Biocheck between 5th and 6th annual increments in a specimen from Arao Coast, Ariake Bay

marks is strongly suggested for specimens from other localities by the microincrement sequence near the ventral shell margin and its comparison with sampling date.

Shell height from umbo to the ventral margin of each annual increment was first measured in each specimen of *Phacosoma japonicum*. Average shell heights for each annual increment were used to describe shell growth patterns at the 5 sample sites examined. Shell growth of each population was modeled by fitting the von Bertalanffy equation (von Bertalanffy 1938) to the age/mean shell height data:

$$H_t = H_\infty (1 - e^{-K(t-t_0)}) \quad (1)$$

where  $H_t$  = shell height of an animal at time  $t$ ;  $H_\infty$  = maximum asymptotic shell height;  $K$  = a growth constant; and  $t_0$  = theoretical time when  $H_t = 0$ . We also computed Gallucci & Quinn's (1979) growth parameter  $\omega$  ( $\omega = K \cdot H_\infty$ ) for each sample.

Shells of 2 specimens (nos. K72 and W29 from Toyo and Wakkanai areas) were used in stable isotopic analysis. In this analysis, small amounts of powdered calcium carbonate sample (ca 0.1 mg each) were collected in a series by drilling the outer prismatic layer

parallel to the shell increments from umbo to ventral margin. Each sample was reacted in 100% phosphorous acid at 60°C, and the oxygen and carbon isotopic compositions of the evolved carbon dioxide gas were determined on a Finnigan MAT 251 mass spectrometer. Isotopic values are expressed relative to the carbon dioxide gas derived from the Pee Dee Belemnite (PDB) standard carbonate powder (Epstein et al. 1953) in conventional delta notation. Analytical precision was less than 0.03%.

## RESULTS

### Growth parameters

A plot of mean shell height data versus annual increments for each site provides a generalized growth curve (Fig. 4). In every sample the growth curve predicts a decrease of the specific growth rate as the shell height approaches the upper limit. Maximum attainable shell size and specific growth rate both seem to be markedly different among the 5 sites. The shell growth curves for the 5 sites, based on annual increments, are nicely fit by the von Bertalanffy equation, although the actual growth patterns of living individuals cannot be approximated by a simple curve owing to the annual fluctuation in growth rates (Tanabe 1988). Both the growth constant  $K$  and the  $\omega$  parameter of Gallucci & Quinn (1979) systematically decrease to the north, although no latitudinal trend was detected for the maximum asymptotic shell height ( $H_\infty$ ) (Table 1). The Arao population shows the largest variation in shell height at a given age.

### Microincrement growth

Ontogenetic changes of the microincrement growth patterns in the present species can be expressed by plotting their number and mean width in relation to annual increments (Figs. 5 and 6). In every sample,

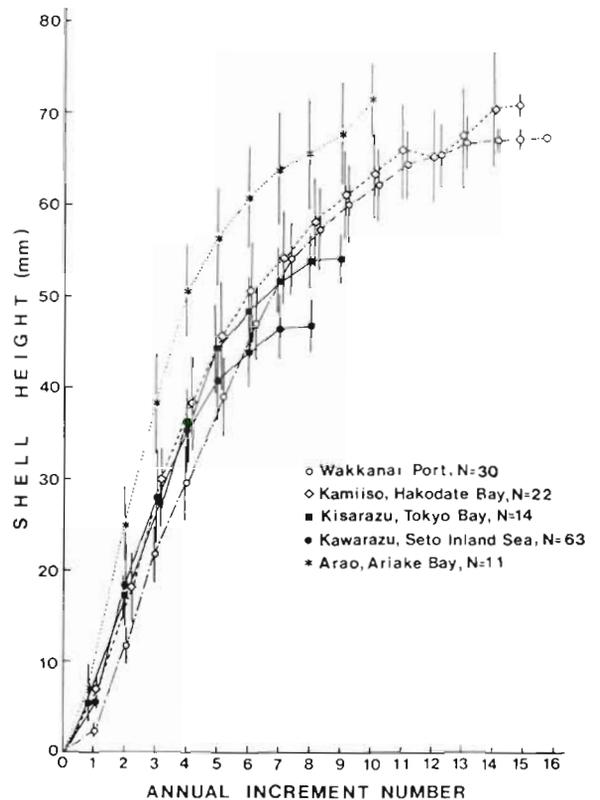


Fig. 4. *Phacosoma japonicum*. Generalized growth curves for samples from different locations. Sample mean and range of standard deviation are indicated for each sample

both number and mean width of yearly formed microincrements tend to decrease with age. At the same age, the number of annually formed microincrements in the southern individuals is much larger than that in the northern individuals. In contrast, the mean growth rate at a given age tends to increase towards the north.

### Oxygen isotope ratios

$\delta^{18}\text{O}$  profiles in the 2 specimens from the Wakkanai and Kwarazuru areas are shown in Fig. 7. A clear annual

Table 1. *Phacosoma japonicum*. Growth parameters of von Bertalanffy equations for samples from Japanese coast. Age/mean shell height data shown in Fig. 4 are used in this calculation.  $H_\infty$ : maximum asymptotic shell height,  $K$ : growth constant,  $\omega$ : growth parameter,  $t_0$ : theoretical time when shell height ( $H_t$ ) is zero

| Locality        | Mean annual temp. (°C) | $H_\infty$ (mm) | $K$   | $\omega$ | $t_0$ (yr) |
|-----------------|------------------------|-----------------|-------|----------|------------|
| Wakkanai Port   | 9.7                    | 78.95           | 0.159 | 12.58    | -0.205     |
| Hakodate Bay    | 12.3                   | 74.46           | 0.203 | 15.11    | -0.471     |
| Tokyo Bay       | 18.0                   | 61.06           | 0.262 | 16.00    | -0.379     |
| Seto Inland Sea | 17.5                   | 55.46           | 0.295 | 16.35    | -0.383     |
| Ariake Bay      | 20.5                   | 76.44           | 0.403 | 23.10    | -0.335     |

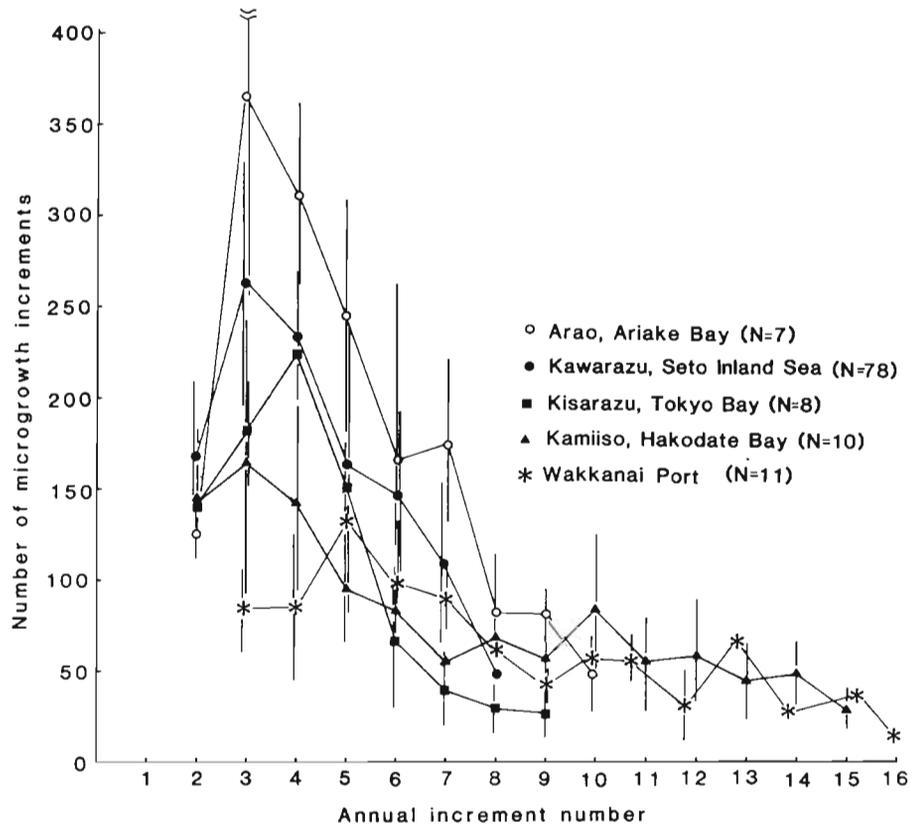


Fig. 5. *Phacosoma japonicum*. Plot of the number of microincrements within an annual increment versus annual increment number for samples examined. Sample mean and range of standard deviation indicated for each sample

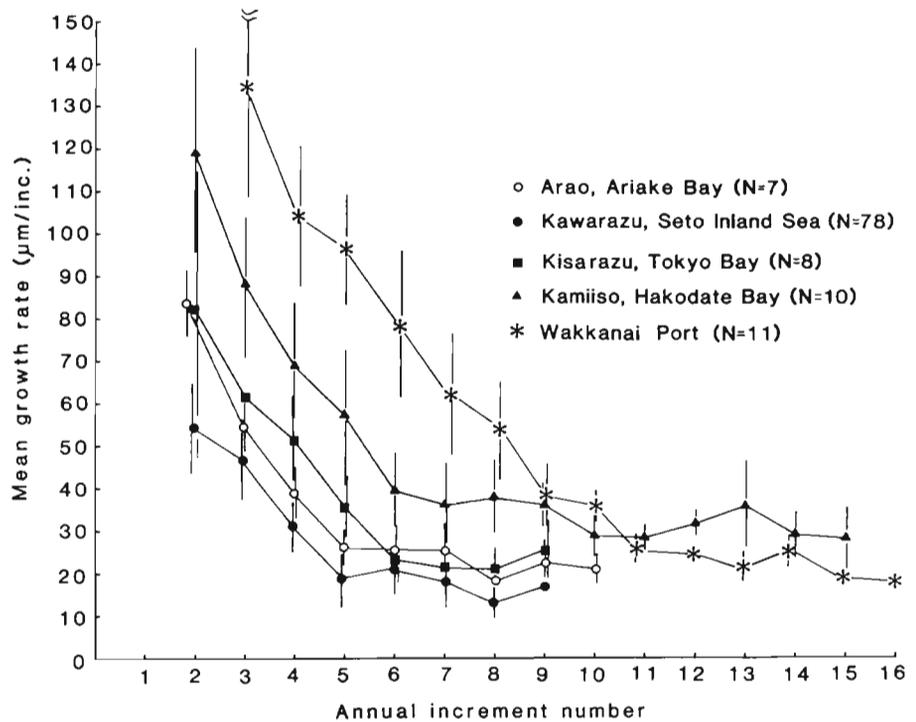


Fig. 6. *Phacosoma japonicum*. Plot of the mean microincrement width within an annual increment versus annual increment number for samples examined. Sample mean and the range of standard deviation indicated for each sample

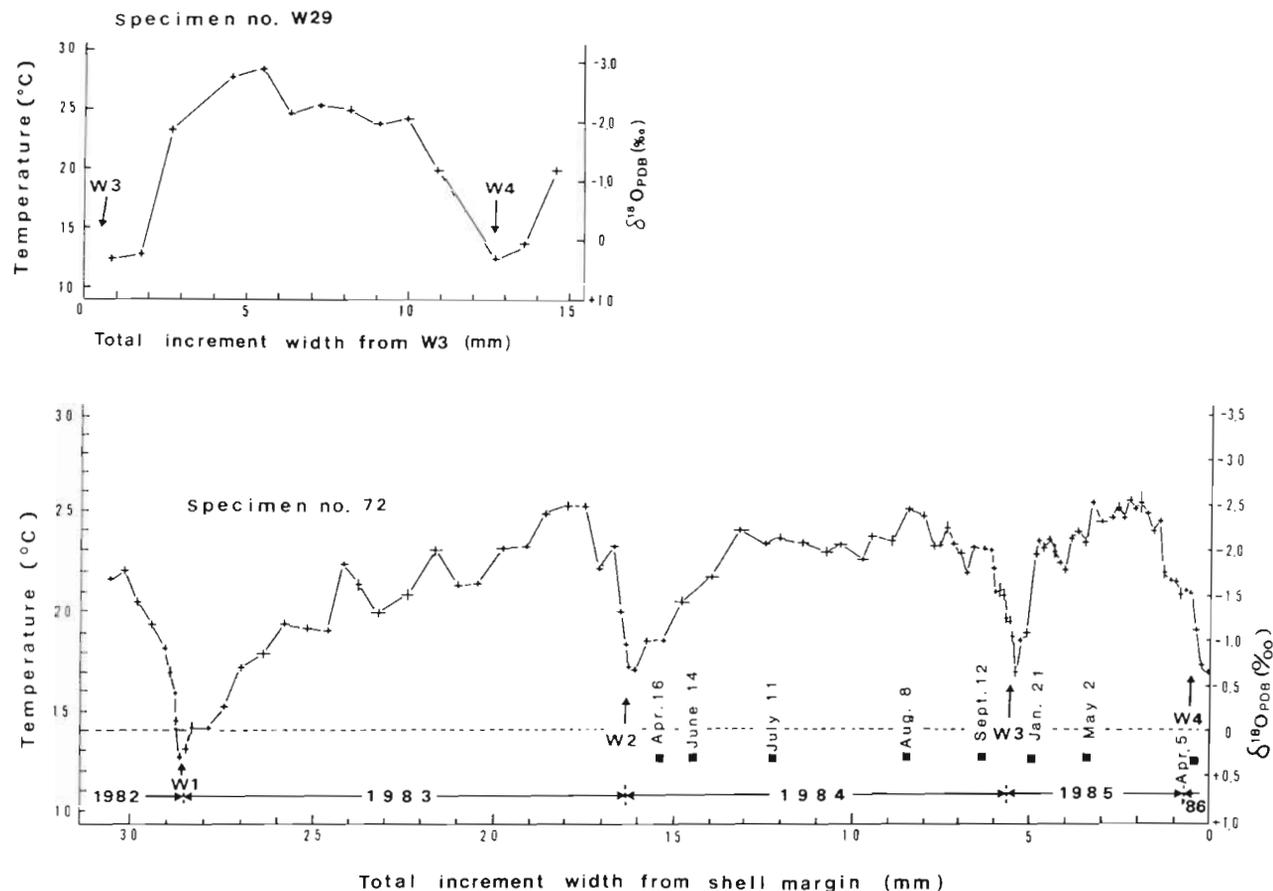


Fig. 7. *Phacosoma japonicum*. Oxygen isotopic profiles and corresponding temperatures in 2 specimens from Wakkanai Port and Kawarazu Shore (Seto Inland Sea). Sclerochronological data are added for the Kawarazu specimen.  $W_i$  (=  $W_1 - W_4$ ) means  $i$ -th winter growth cessation mark

$\delta^{18}\text{O}$  cycle is discernible in the 2 profiles, and the portions with highest  $\delta^{18}\text{O}$  value are located near the winter growth cessation mark. It is well known that  $^{18}\text{O}/^{16}\text{O}$  ratios of the calcified tissue in an aquatic animal are changeable with water temperature and salinity of the habitat (Dodd & Stanton 1981). Annual fluctuation of salinity is minimal at least for the sampling station of the Kawarazu Shore (31 to 33‰), and this suggests the cyclic patterns in the  $\delta^{18}\text{O}$  profiles mostly reflect the annual fluctuation of water temperature.

Growth history of the Kawarazu specimen was traced for more than 2 yr by the mark-and-recovery method, together with the record of temperature and salinity at the planting site (Tanabe 1988). The plot of  $\delta^{18}\text{O}$  ratios at the 4 portions of the specimen formed during the season of rapid shell growth versus water temperatures of corresponding dates provides a linear relationship between the isotopic ratio and the water temperature (Fig. 8). The temperature scale shown in  $\delta^{18}\text{O}$  profiles of the Kawarazu and Wakkanai specimens (Fig. 7) was estimated from the linear relationship. In both specimens, temperatures calculated from  $\delta^{18}\text{O}$  ratios in the

central portion of annual increments correlate well with the water temperatures of the summer season. The lowest temperatures detected near the winter growth cessation marks of the 2 specimens (ca 12°C) are, by contrast, higher by 5 to 10°C than the winter water temperatures of the sampling locations.

## DISCUSSION

*Phacosoma japonicum* from the Japanese coast shows latitudinal trends in the growth parameters of von Bertalanffy equations and accretionary patterns of microincrements. Especially, high negative correlation between rate of growth deceleration and mean annual temperatures (Table 1) suggests a dependence of growth on temperature. Based on the samples examined, northern individuals generally possess more numerous annual increments than the southern ones, suggesting a longer life span in the former (Fig. 4). However, exact longevity cannot be determined from annual increment counting, because large animals

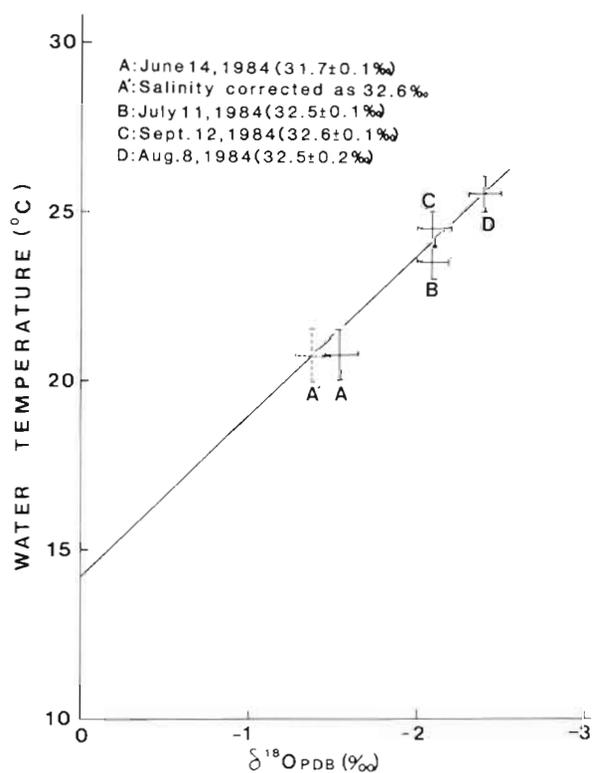


Fig. 8. *Phacosoma japonicum*. Linear relationship between  $\delta^{18}\text{O}$  ratios at the 4 portions of the Kawarazu specimen and water temperatures of corresponding dates. Vertical and horizontal bars indicate ranges of errors in measurements. Regression line by the least squares fit

inhabiting the Kawarazu Shore can survive for more than several years after completion of shell growth (Tanabe 1988). Therefore, the above hypothesis must be tested by other methods such as long-term growth analysis of marked individuals.

Reductions of growth rate in the colder areas of distribution (higher latitudes) have been observed in many marine bivalves hitherto investigated. Furthermore, longer life span and shorter growing seasons in northern individuals than southern ones has been suggested in *Siliqua patula* (Weymouth & McMillin 1931), *Macoma balthica* (Gilbert 1973, Bachelet 1980) and *Protothaca staminea* (Harrington 1987). Most previous authors also regarded temperature as a dominant factor affecting the difference in growth patterns of marine bivalves over a wide geographic range (e.g. Appeldoorn 1983, Beukema & Meehan 1985).

It has been generally accepted that accretionary patterns of microincrements reflect the seasonal variation in shell growth rate (Rhoads & Pannella 1970, Lutz & Rhoads 1980, Jones 1985). Annual cycles in oxygen isotope ratios and corresponding temperatures were detected in the shells of many bivalve species (e.g.

*Spisula solidissima*, Jones et al. 1983; *Placopecten magellanicus*, Krantz et al. 1984), but little was investigated about the exact relationship between the length of growing seasons and temperature from the sclero-chronological point of view.

The present study on *Phacosoma japonicum* strongly suggests slow and continuous winter growth for the southernmost individuals from Ariake Bay, judging from the narrow and crowded microincrements near the end of an annual increment without a growth cessation mark (Fig. 3E). In contrast, the presence of a clear growth cessation mark at the boundary between 2 adjoining annual increments in specimens from other locations (Figs. 3A to D) indicates a partial dissolution of microincrements at the ventral shell margin during winter. The degree of disagreement between temperatures estimated from  $\delta^{18}\text{O}$  ratios near the winter growth cessation marks and the sea-surface temperatures of habitat for the Wakkanai specimen is more conspicuous than that for the Kawarazu specimen (Fig. 7). Furthermore, the number of annually formed microincrements at a given age tends to decrease with increasing latitude (Fig. 5). These lines of evidence strongly suggest a latitudinal decrease in the length of growing seasons in this species. A similar idea was suggested by Harrington (1987) for the eastern Pacific *Protothaca staminea*, based on the latitudinal decrease

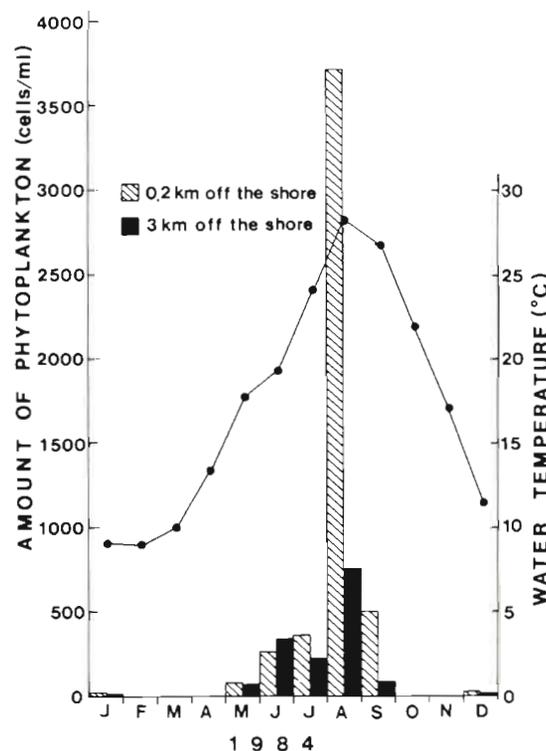


Fig. 9. Seasonal variation in phytoplankton abundance in the water of the Kawarazu Shore, Seto Inland Sea

in the number of microincrements within the first annual increment. Harrington (1987) used external growth bands for age determination, but did not show sufficient documentation for their annual origin.

In the population of the Seto Inland Sea, remarkable shell growth occurs in a limited interval between April and September (Tanabe 1988). Furthermore, sclero-chronology of a single shell (no. 72, same specimen used in this study) revealed especially high rates of microincrement growth (1.2 to 1.7 increments  $d^{-1}$ ) during June to September (Tanabe 1988). The above seasonal pattern of microincrement growth correlates well with that of phytoplankton abundance in the Kawarazu Shore (Fig. 9). The range of temperatures obtained from oxygen isotope ratios in the second annual increment (= 2 yr-old stage) of the Kawarazu specimen (13 to 25°C) (Fig. 7) is compared with that of sea-water temperatures during March to November. Meanwhile, the oxygen isotopic temperatures in the fourth annual increment of the Wakkanai specimen (13 to 28°C) show a close correspondence to the water temperatures between June and October at the sampling station.

In conclusion, latitudinal variation of growth patterns observed in *Phacosoma japonicum* from the Japanese coast results mainly from the difference in the length of the growing season among local populations, depending on both temperature and trophic resource seasonality.

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