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Environmental controls on daily shell growth of *Phacosoma japonicum* (Bivalvia: Veneridae) from Japan

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ABSTRACT: This study examined the environmental factors controlling the daily shell deposition of the intertidal bivalve *Phacosoma japonicum* from Seto Inland Sea, west Japan, and Tokyo Bay, central Japan. Sclerochronological analyses of microgrowth patterns in marked-and-recovered specimens indicate that a pair of 2 etch-sensitive increments and 2 etch-resistant lines is formed every lunar day (duration 24.8 h). The accretionary pattern of the lunar day growth increments (LDGIs) reflects tidal cycles. Prominent growth lines were formed during spring tides, when the bivalves were subaerially exposed, and weak ones were deposited during neap tides, when they were continuously submerged. The bivalves stop secreting shell carbonate during winter and early spring. The time interval encompassed by the winter break in the specimens from Tokyo Bay lengthened as the shells grew older. Although seawater temperature is the main controlling factor for shell growth, a number of mutually related environmental factors such as salinity and food availability also affect shell growth. In Tokyo Bay, the broadest LDGIs were deposited between temperatures of 21 and 24°C. Our findings provide a basis for the interpretation of the temporal changes in shell microgrowth patterns in terms of environmental conditions of extant and fossil *P. japonicum* specimens.

KEY WORDS: Sclerochronology · Bivalve mollusk · Shell growth · Tidal cycle · Seawater temperature

INTRODUCTION

Reconstruction of environmental conditions and life-history traits of modern and extinct organisms is an important subject in ecology and paleoecology. Mollusks are perfectly suited for such studies, because (1) they are distributed in a variety of geographic, bathymetric and environmental settings, ranging from tropical to polar realms, from intertidal to deep-sea environments and from freshwater to marine environments; (2) their shells have a high preservation potential as fossils; and (3) they can record environmental changes in chronological order and with extremely high temporal resolution (days).

Most existing paleoenvironmental reconstructions using bivalve shells have focused on geochemical data (e.g. Takesue & van Geen 2004, Gillikin et al. 2005) and used internal shell growth patterns as time gauges. Only a few studies have made use of variable shell growth rates (sclerochronology) as proxies for environmental conditions such as daily water temperature (e.g. Schöne et al. 2002, 2003, 2006). One of the main problems for the latter approach is that many different, complexly interacting environmental and physiological processes may exert control over shell growth rates. For example, temperature (Piditch & Grant 1999), food supply (e.g. Grant 1996, Carmichael et al. 2004), primary production and temperature (Witbaard et al. 1999) have been examined in terms of their impact on the growth of bivalves.

Disentangling the various environmental controls on shell growth is a tedious and time-consuming task that can be achieved, for example, through an analysis of shell growth patterns of many marked-and-recovered

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specimens combined with high-resolution environmental data that are likely to affect shell growth. However, most existing studies of this kind have employed only a few specimens and environmental data that are either not representative of the specific habitat in which the shells grew or only a single environmental factor.

The venerid bivalve *Phacosoma japonicum* treated in this paper is an ideal species to use for the comparison of exact growth records with environmental background data based on high-resolution sclerochronological analyses for a number of reasons. Firstly, the life-history traits, such as absolute growth rate, sexual maturation and reproductive cycles, of this species are well recorded in shell microgrowth patterns (Tanabe 1988b, Sato 1994, 1995, 1997). Secondly, environmental and genetic control on these life-history traits has been well studied over a broad geographic range along Japanese coasts (Tanabe & Oba 1988, Sato 1997, Schöne et al. 2003). Thirdly, this species occurs very abundantly in the Pliocene and younger shallow-marine deposits of the Japanese Islands (Chinzei 1980), enabling a detailed examination of the ecological response of the life-history traits to the Quaternary warming and cooling events in the northwestern Pacific.

In the present study, we tested the assumption of Schöne et al. (2003) that a couplet of 2 microgrowth lines and 2 microgrowth increments of *Phacosoma japonicum* shell were formed on a regular, i.e. lunar daily (duration 24.8 h) basis. Our re-investigation is based on mark-and-recovered specimens. A high-resolution sclerochronological analysis was performed on shells of 34 specimens collected alive. In order to elucidate the environmental factors controlling the shell growth of *P. japonicum*, we compared the sclerochronological data with environmental parameters of the habitat in which the bivalves lived. Confirmation of the periodic nature of microgrowth patterns requires careful examination by means of tag-and-recovery experiments (Tanabe 1988b).

MATERIALS AND METHODS

Sample material and environmental data. *Phacosoma japonicum* is an infaunal suspension feeder living at about 10 to 20 cm below the sediment surface. It is widely distributed in intertidal and shallow subtidal marine settings along the coasts of Japan, China (Yellow Sea) and Korea, as well as along the western Japan Sea coast of Far East Russia. The present study is based on 2 sample batches; 1 consisted of 8 specimens collected alive from the intertidal zone at Kawarazu, Seto Inland Sea (Fig. 1, inset A), which were previously used by Tanabe (1988a,b) for short-term mark-and-recovery experiments. These specimens were stained alive for 10 min with ca. 5% alizarin red solution on May 7, 1986, returned to the substratum, and recovered on June 4, 1986. We re-examined these specimens to reconfirm the timing and periodic nature of shell growth.

The other sample batch consisted of 26 specimens that were recovered between April 19, 2003 and December 13, 2003 from the intertidal flats of Nojima,

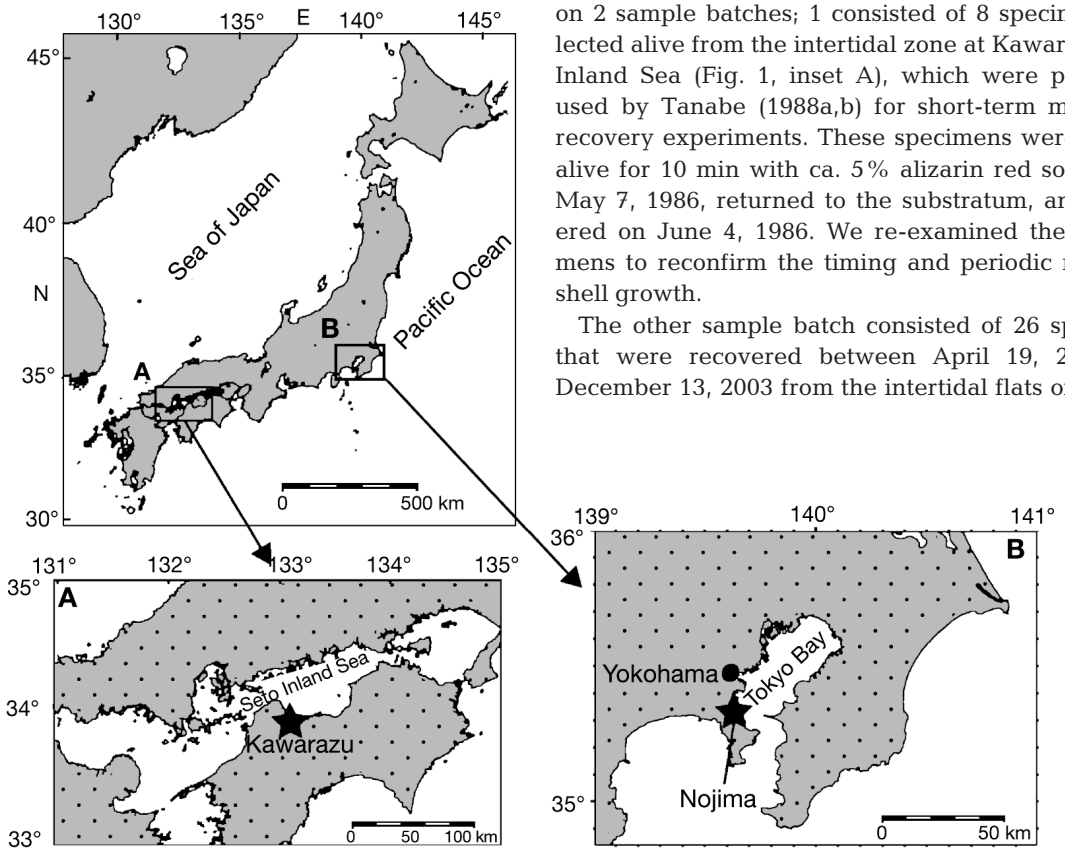

Fig. 1. *Phacosoma japonicum.* Sampling locations: (A) Kawarazu, Seto Inland Sea, and (B) Nojima, Tokyo Bay

Yokohama City, on the western side of Tokyo Bay, central Japan (Fig. 1, inset B; Table 1). The shells were collected at low tide during spring tides from ca. 55 cm above mean low-tide level. During neap tides, the sample site was continuously immersed. Of the 26 specimens recovered from Tokyo Bay, 2 specimens (Nos. 121303TB1 and 121303TB2) collected on December 13, 2003 were excluded from further analysis, because growth cessation marks were observed in their microincremental sequence formed in 2003. In order to evaluate which environmental factors control shell growth, microgrowth patterns and microincrement widths of these specimens were compared with meteorological data. For cross-calibration with shell microgrowth data, the following environmental data were obtained from nearby meteorological stations (35°33′54″N, 140°2′54″E) and kindly provided from the Japan Oceanographic Data Center of the Japanese Maritime Peace Board: sea surface temperature (SST) in 1 m water depth, chlorophyll *a* concentration (chl *a*), salinity (S) and dissolved oxygen levels (DO). Tidal data near the sample locality were obtained with TIDE for WIN (Ver. 2.11) software.

The life-history characteristics of *Phacosoma japonicum* at this locality have been extensively studied (Sato 1994, 1995, 1997, 1999, Schöne et al. 2003). According to Sato (1995), *P. japonicum* reaches sexual maturity after Age 3 yr. Spawning breaks were observed in specimens larger than 4 cm in shell height. In order to avoid complications from spawning breaks and ensure that the shells grew without extra, non-environmentally triggered interruptions during the entire growing period represented by the shell portion between adjacent winter lines, we focused on immature specimens smaller than 4 cm shell height.

Sample preparation. After removing the soft tissue, 1 valve of each specimen was partly covered with epoxy resin and cut along the axis of maximum growth from the umbo to the ventral margin using a low-speed saw (Buehler Isomet) (Fig. 2). The sectioned surface was polished and etched with 5% acetic acid solution for ca. 12 min. The etched surfaces were carefully rinsed with distilled water, air-dried, sputter-coated with a 300 Å thick platinum layer and observed under a SEM (Hitachi S-2400). The widths of the microgrowth increments were measured from the last formed winter break toward the ventral margin using image analysis software (Win Roof, Ver. 1; Mitani Corporation).

Statistical analyses. In order to empirically determine the likely effect of each environmental factor on shell growth, we first identified the lunar day growth increments (LDGIs) in the shell microgrowth sequence of the specimens examined (see section

Table 1. *Phacosoma japonicum.* Date and surface seawater temperature (SST) when shell growth started in 2003 and the length of growing periods (lunar days) (= number of lunar day growth increments since the winter break) for 24 specimens collected alive from Tokyo Bay

Specimen No.	Age (yr)	Date of collection	Starting date of shell growth	SST (°C)	Length of growing period (lunar days)
190403TB2	2	April 19, 2003	April 10, 2003	13.3	9
030503TB2	2	May 3, 2003	April 12, 2003	13.6	21
190403TB3	3	April 19, 2003	April 12, 2003	13.5	7
030503TB3	3	May 3, 2003	April 10, 2003	13.3	23
030603TB3-1	3	June 3, 2003	March 31, 2003	13.5	59
030603TB3-2	3	June 3, 2003	April 14, 2003	14.5	47
150603TB3	3	June 15, 2003	May 31, 2003	21.0	13
010703TB3	3	July 1, 2003	May 17, 2003	18.0	43
150703TB3	3	July 15, 2003	May 13, 2003	18.3	59
310703TB3	3	July 31, 2003	April 13, 2003	13.6	103
280803TB3	3	August 28, 2003	April 19, 2003	15.5	123
100903TB3	3	September 10, 2003	March 23, 2003	12.3	160
250903TB3	3	September 25, 2003	May 11, 2003	18.8	109
081003TB3-1	3	October 8, 2003	April 17, 2003	14.0	164
081003TB3-2	3	October 8, 2003	March 8, 2003	10.2	202
190403TB4-1	4	April 19, 2003	No growth	–	0
190403TB4-2	4	April 19, 2003	No growth	–	0
030503TB4	4	May 3, 2003	No growth	–	0
150603TB4	4	June 15, 2003	May 24, 2003	18.4	21
190403TB5	5	April 19, 2003	No growth	–	0
190403TB5	5	April 19, 2003	No growth	–	0
030503TB5-1	5	May 3, 2003	No growth	–	0
030503TB5-2	5	May 3, 2003	No growth	–	0
030503TB6	6	May 3, 2003	No growth	–	0

'Ontogenetic ages and timing of shell microgrowth' for detailed procedure). After this inspection, LDGI width data were compared to the tidal cycle, SST, chl *a*, S and DO. We exclusively used specimens belonging to Age Class 3 yr (13 specimens); the complicated correction of age-related growth trends was thus not required. First, the temporally aligned LDGI time series of all specimens were arithmetically averaged. Then, spectral analysis (Singular Spectrum Analysis; Fast Fourier Transformation, Welch method) was performed to identify a likely effect of the forthnightly tidal cycle on shell growth rates. This tidal effect was removed from the LDGI time series by means of band pass filtering.

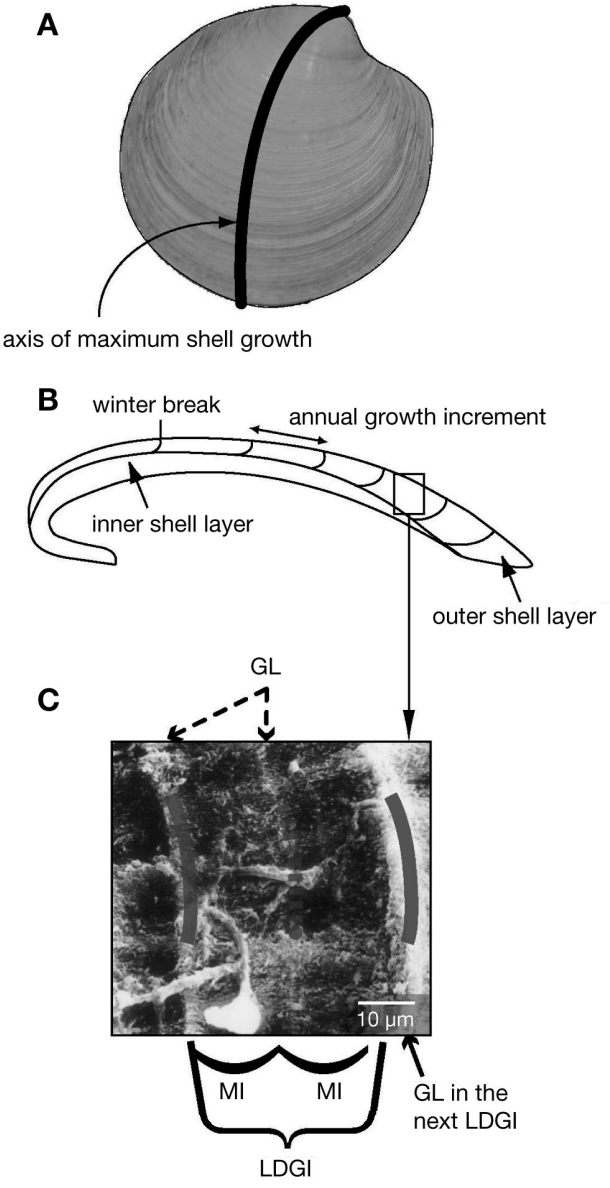

Fig. 2. *Phacosoma japonicum*. (A) Lateral external view of the right valve. (B) Shell cross-section along the axis of maximum growth, with structural details. (C) SEM of part of the outer shell layer, showing a lunar day growth increment (LDGI, bordered by grey bars) consisting of a couplet of narrower growth lines (GL) and broader microgrowth increments (MI)

We applied the Arrhenius model to describe the effects of temperature on whole-animal physiological processes (Clarke & Johnston 1999, Heilmayer et al. 2004). Model parameters are estimated by linear regression. According to this model, metabolic rate (Y) and overall growth performance (OGP) are given by the following equations: $\ln(Y) = a_1 + b_1 \times 1/T$ and $\ln(\mathrm{OGP}) = a_2 + b_2 \times 1/T$, where T is temperature in Kelvin, a_1 and a_2 are constants, and b_1 and b_2 are the slopes of the equivalent equations. Following the Arrhenius model, the tide-corrected LDGI chronologies ($\mathrm{LDGI_f}$) were logarithmically (natural logarithm) transformed and plotted versus inverted surface seawater temperature in Kelvin ($\mathrm{SST^{-1}}$). Prior to regression analyses, a test for linearity (runs test) was conducted for $\ln(\mathrm{LDGI_f}) - \mathrm{SST^{-1}}$ plot to see if shell growth and the respective SST are linearly or nonlinearly correlated. Then, single and multiple regression analyses were performed to evaluate the statistical relationship between shell growth and SST.

RESULTS

Ontogenetic ages and timing of shell microgrowth

According to the number of winter breaks (Tanabe 1988b) visible in etched cross-sections under low magnification (10×), ontogenetic ages of the 8 marked-and-recovered specimens from Seto Inland Sea varied from 5 to 7 yr. Shells from Tokyo Bay were from 2 to 6 yr old when sacrificed (Table 1).

At higher magnification (100× to 200×), cross-sectioned and etched shells revealed a sequence of alternating narrow etch-resistant 'lines' (i.e. microgrowth lines, 10 to 50 µm wide) and broad etch-sensitive 'bands' (i.e. microgrowth increments, several 10s to ~100 µm wide) in the outer aragonitic shell layer (composite prismatic microstructure; Fig. 2C). Vital staining produced a weak growth cessation mark in 3 specimens. In these specimens, microgrowth increments were densely arranged near the break, but the increment width rapidly recovered after the break (Fig. 3C; Tanabe 1988b). During the 28 solar day period (= 27 lunar days; May 7 to June 4, 1986) between Alizarin red staining and recovery of the shells, 7 out of 8 specimens (<4 yr of age) had formed 27 distinct couplets of 2 microgrowth increments and 2 microgrowth lines, i.e. 27 LDGIs. The remaining 7 yr old specimen, however, had formed only 14 LDGIs during the same interval. Shell microgrowth patterns

were well correlated with the tidal cycle that occurred during this time interval (Fig. 3A,B). Broader LDGIs were formed during neap tides. Growth lines deposited during spring tide were more prominent than those formed during neap tides when the bivalves remained continuously immersed (Fig. 3C).

Onset of shell growth after the winter break

Based on the analysis of shell microgrowth patterns between the last formed winter break and the ventral margin, we estimated the starting dates of shell growth for 24 specimens collected alive from Tokyo Bay between April 19 and October 8, 2003 (Table 1). Two specimens of ontogenetic Age 2 yr collected on April 19 and May 3, 2003 began to secrete shell carbonate in early April. The estimated starting dates of shell growth for the 13 specimens of Age 3 yr recovered from April 19 to October 8, 2003 fell between early April and middle May. In the 9 specimens older than 4 yr (recovered during late April to middle June 2003), excluding the 4 yr old specimen collected on June 15, 2003 (150603TB4), no shell secretion was recognized after the last formed winter break.

In the 3 yr old specimen collected on July 31, 2003 (310703TB3), we recognized a newly formed winter break in the LDGI sequence, showing partial dissolution of LDGIs (Fig. 4A). In both 3 yr old specimens collected on December 13, 2003 (131203TB1 and 131203TB2), 2 small growth cessation marks were identified near the ventral shell margin, but no sign of the winter break was observed (Fig. 4B).

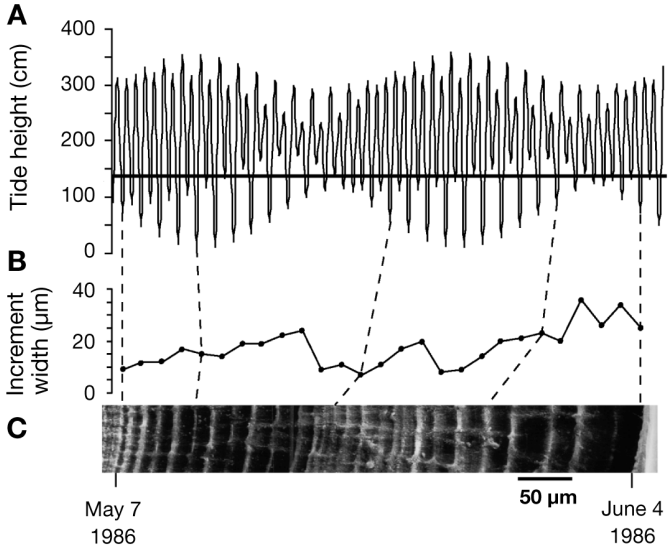

Fig. 3. (A) Local tidal regime and (B,C) microgrowth sequence formed between May 7, 1986 and June 4, 1986 in 2 yr old *Phacosoma japonicum* specimen from Kawarazu, Seto Inland Sea. Line in (A) is mean low-tide level

Estimation of tidal effect on shell growth

Fast Fourier Transformation of the average LDGI time series revealed a cluster at a frequency of ca. 0.077 corresponding to 12.99 LDGIs (Fig. 5B). This signal, however, is not significant at the 95% confidence level. For further comparison with other environmental parameters, we applied a band-pass filter and removed the forthnightly period from the LDGI time series. According to eigenvalue decomposition (Singular Spectrum Analysis) of the average LDGI time series of 3 yr old *Phacosoma japonicum* specimens

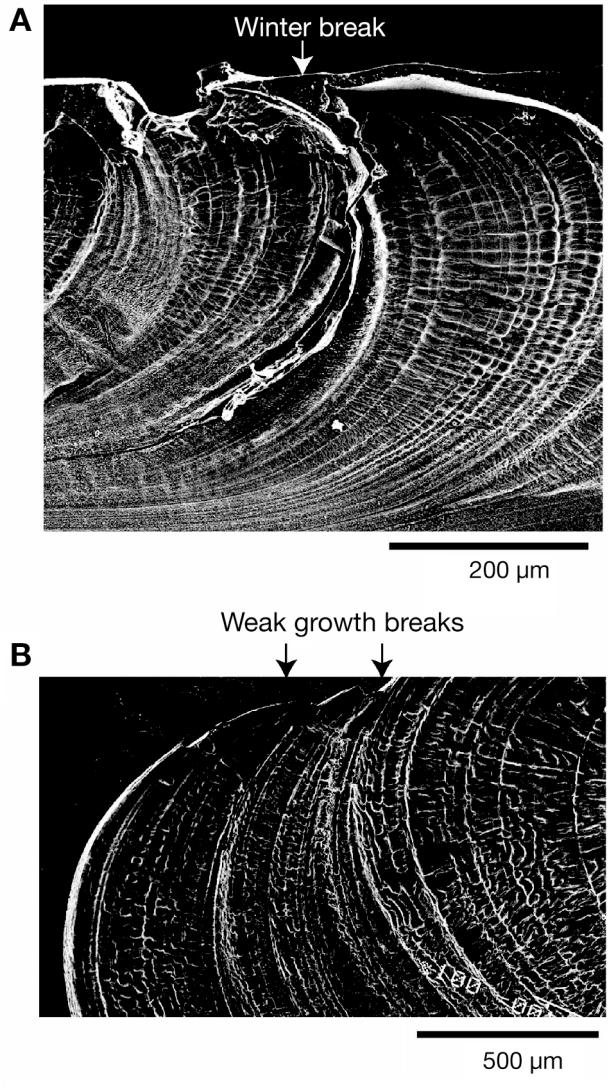

Fig. 4. *Phacosoma japonicum.* SEMs of microgrowth patterns near the ventral margin. (A) Lunar day growth incremental sequence with a clear winter break near the ventral shell margin. Specimen (No. 310703TB3) collected alive on July 31, 2003 from Nojima, Tokyo Bay. (B) Lunar day growth incremental sequence exhibiting 2 weak breaks. Specimen (No. 131203TB1) collected alive on December 13, 2003 from Nojima, Tokyo Bay

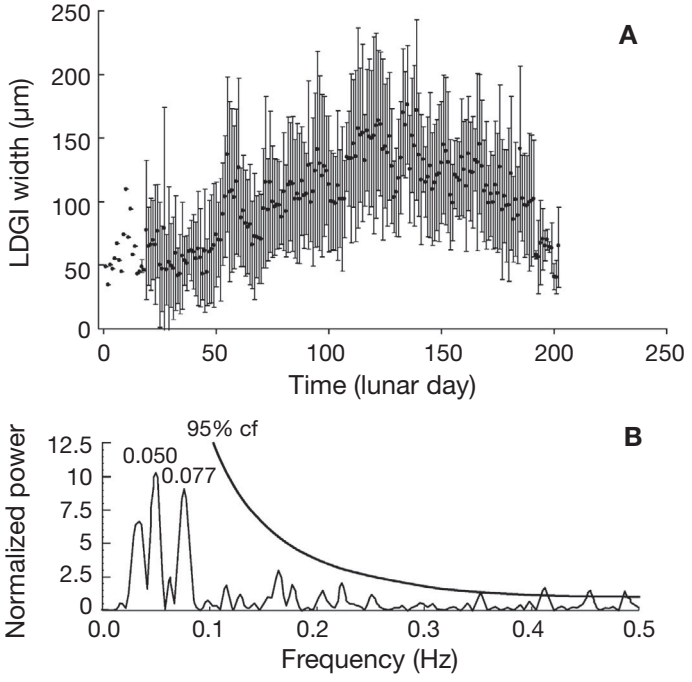

Fig. 5. *Phacosoma japonicum.* (A) Time-series change of the averaged lunar day growth increment (LDGI) widths of 13 specimens of Age 3 yr from Tokyo Bay collected in 2003. Means and 1 SE are indicated. (B) Fourier Transform of the mean LDGI width series shown in (A). The low frequency cluster at 0.077 Hz roughly corresponds to 13 LDGIs (95% cf: 95% confidence interval)

(Fig. 5A), only 2.7% (eigenvalues 7 and 8) of the variability of shell growth is explained by the tidal cycle, indicating that the effect of the forthnightly tidal cycle on shell growth is relatively weak.

Environmental factors controlling shell microgrowth patterns

Seasonal change in the mean tide-corrected LDGI width of the 13 specimens of Age 3 yr from March to October 2003 was compared with that of SST, DO, S and chl *a* near the sampling location in Tokyo Bay, after the latter data were converted to the lunar day scale (Fig. 6). According to linearity tests, shell growth is non-linearly correlated with SST ($p < 0.0001$) and S ($p < 0.0001$), but linearly with chl *a* ($p = 0.06$) and DO ($p = 0.17$). Single regression analysis based on the linear model shows that the tide-corrected LDGI width is strongly positively correlated with SST ($R = 0.72$, $R^2 = 0.52$, $p < 0.0001$), but much more weakly correlated with other environmental parameters (Fig. 7A, D to F, Table 2). The tide-corrected LDGI width is significantly related to SST (Arrhenius model; Fig. 7B,C), indicating that the relationship is non-linear. The ln-transformed, tide-corrected LDGI width plotted versus 1/SST is better expressed by the third-degree polynominals (Fig. 7C) ($R = 0.79$, $R^2 = 0.62$, $p < 0.0001$) than by the linear regression (Fig. 7B) ($R = 0.75$, $R^2 = 0.56$, $p < 0.0001$), and this suggests the presence of the upper SST tolerance limit of this species at approximately 24 to 25°C.

DISCUSSION

Lunar day cycles of microincrement growth

High-resolution sclerochronogical analyses of vitally stained specimens of *Phacosoma japonicum* from the intertidal zone of Seto Inland Sea, west Japan, support the conclusion of Schöne et al. (2003) that shell growth of this species is controlled by the tides. In the seven, 2 to 4 yr old specimens, each couplet of 2 microgrowth increments and 2 microgrowth lines was formed during 1 lunar day. LDGI widths fluctuate on a fortnightly basis, namely, broader increments were formed during neap tides, whereas narrower ones were formed during spring tides. The reason why the 7 yr old specimen from Seto Inland Sea secreted a fewer number of distinct couplets during the observation period of 27 lunar days (May 7 to June 4, 1986) is still unresolved, but it is presumably due to the

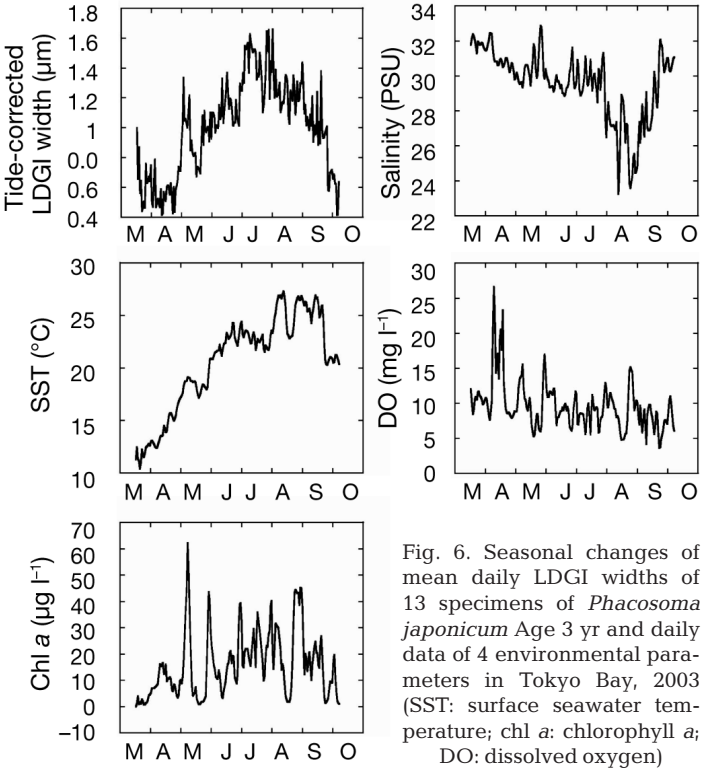

Fig. 6. Seasonal changes of mean daily LDGI widths of 13 specimens of *Phacosoma japonicum* Age 3 yr and daily data of 4 environmental parameters in Tokyo Bay, 2003 (SST: surface seawater temperature; chl *a*: chlorophyll *a*; DO: dissolved oxygen)

Table 2. Correlation matrix and partial correlation for the tide-detrended mean lunar day growth increment width (LDGI), surface seawater temperature (SST), dissolved oxygen (DO), salinity (S) and chlorophyll *a* concentration (chl *a*)

	Correlation matrix					Partial correlation				
	LDGI	SST	Chl *a*	S	DO	LDGI	SST	Chl *a*	S	DO
LDGI	1.00	0.72	0.51	−0.49	−0.27		0.40	0.37	0.13	−0.22
SST	0.72	1.00	0.47	−0.76	−0.34	0.40		0.26	−0.69	−0.50
Chl *a*	0.51	0.47	1.00	−0.53	0.36	0.37	0.26		−0.06	0.62
S	−0.49	−0.76	−0.53	1.00	0.00	0.13	−0.69	−0.06		−0.29
DO	−0.27	−0.34	0.36	0.00	1.00	−0.22	−0.50	0.62	−0.29	

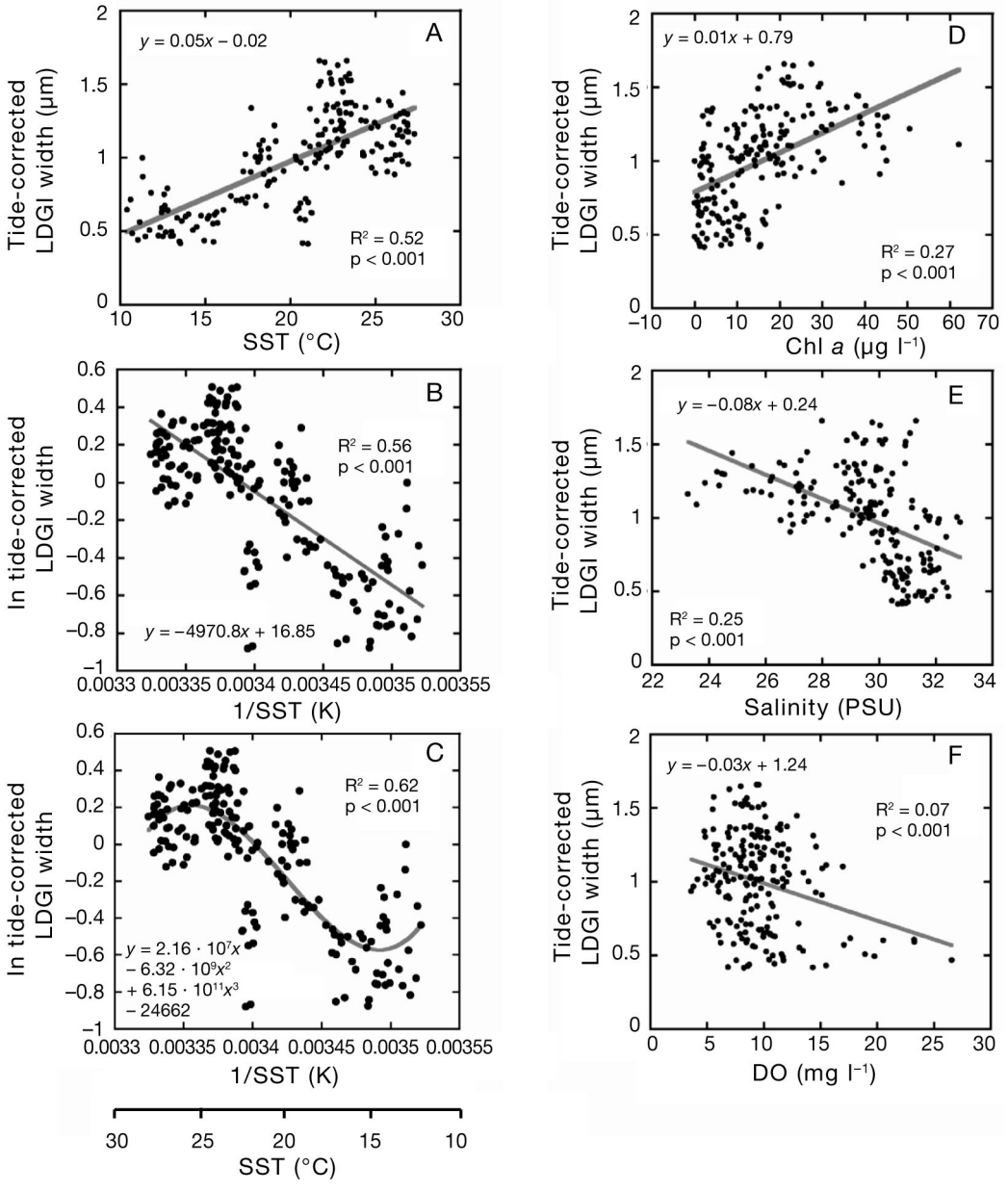

Fig. 7. *Phacosoma japonicum*. (A, D to F) Scatter plot of averaged tide-corrected lunar day growth increment (LDGI) widths of the 13 specimens of Age 3 yr versus daily surface seawater temperature (SST), chlorophyll *a* concentration (Chl *a*), salinity and dissolved oxygen (DO) in 2003 in Tokyo Bay. Regression line by least-squares fit for (A) and (D to F). (B,C) Linear (B) and third-degree polynomial approximation (C) between logarithmically transformed, tide-corrected LDGI width and SST (Arrhenius model)

delayed recovery after the physiological shock caused by vital staining. Another explanation may be that May 7 is too early in the year for the specimen to commence shell growth.

Tidally controlled shell growth has been recognized in many intertidal and subtidal bivalve species, such as *Mercenaria mercenaria* (see Rhoads & Pannella 1970, Ohno 1985), *Cardium* (*Cerastoderma*) *edule* (see Farrow 1972, Ohno 1983, 1985), *Mya arenaria* (see Cerrato et al. 1991) and *Spisula subtruncata* (see Richardson 1988a) from North Atlantic coasts, and *Clinocardium nuttalli* (see Evans 1972), *Tridacna* spp. (see Pannella & MacClintock 1968, Ohno 1985), *Fragum unedo* (see Ohno 1985), *Fruvia mutica* (see Ohno 1985) and *Scapharca broughtoni* (see Ohno 1985) from North Pacific coasts.

Evans (1972) and Ohno (1983, 1985) postulated that paired broad growth bands and narrow growth lines within each LDGI are secreted during intervals of immersion (high tide) and subaerial exposure (low tide), respectively. This prediction was confirmed by the sclerochronological analyses of cultured specimens of *Ruditapes phillipinarum* (see Richardson 1988b) and *Mytilus edulis* (see Richardson 1989). Fortnightly and seasonal tidal fluctuations within the habitat strongly affect the relative strength and appearance of the narrow growth lines and the width of LDGIs in bivalves (Ohno 1983, 1985).

A weak, etch-resistant growth line within each LDGI has been described as an organic-rich growth line (Pannella 1975), and, in *Phacosoma japonicum*, this portion is enriched in sulfur and phosphorus (Tanabe 1988b). Laboratory experiments have shown that the formation of growth lines and increments is controlled by biological clocks (e.g. Richardson et al. 1980, Richardson 1988a, b, Kim et al. 1999, 2003). Circalunidian rhythms have been found in shell gaping and siphon extension of *Chione stutchburyi* (Williams et al. 1993) and in the oxygen consumption of *Ruditapes phillipinarum* (Kim et al. 1999).

Age-related changes in the length of the growing period

Shell growth rates vary throughout the year and eventually cease (Kennish 1980, Jones 1985). Growth cessation marks can be formed episodically as a response to physical shocks (e.g. excavation of infaunal bivalves by storms; Rhoads & Pannella 1970), but in most cases they are formed regularly during the reproductive season (spawning break), during the hot summer season (summer break), or during the cold winter season (winter break) (see Sato 1995 for the complete list of species for which these annual breaks have been reported).

Winter breaks commonly occur in *Phacosoma japonicum* along Japanese coasts (Tanabe & Oba 1988). This study indicated that the starting date of shell growth tends to be delayed with increasing ontogenetic age, especially in mature specimens exceeding the age of 4 yr (Table 1). Sato (1994) discussed the relationship between shell growth and sexual maturity in *P. japonicum*. According to his observations, juvenile specimens spend most of their energy resources on somatic growth, so that they secrete calcium carbonate at high rates. However, after attaining sexual maturity, shell growth rate rapidly declines because most energy resources are devoted to reproduction. In Tokyo Bay, *P. japonicum* attains full sexual maturity at Age 4 yr. At this age, the starting date of the seasonal growth period is significantly delayed and, consequently, the number of LDGIs per annual increment is sharply reduced. Our observations substantiate Sato's (1994) interpretation.

Trade-off relationships between somatic and shell growth and gonad development observed in *Phacosoma japonicum* have been widely recognized among many marine bivalves (e.g. *Actina equine*, Navarro et al. 1981; *Mytilus edulis*, Sukhotin & Pörtner 2001).

Environmental parameters controlling the shell microgrowth pattern

The growth rate of a bivalve mollusk shell may be controlled by a number of mutually related environmental factors. Of these factors, seawater temperature of the habitat has been regarded as the most important control on shell growth (e.g. Kennish 1980, Jones et al. 1989, Goodwin et al. 2001, Schöne et al. 2002). Our study confirms that the duration of the shell growing season and the lunar day shell growth rate of *Phacosoma japonicum* in Tokyo Bay are primarily controlled by seawater temperature (Schöne et al. 2003). However, our study also shows that the seawater temperature at which shell growth starts varies markedly among specimens of the same age, and that the seawater temperature at which shell growth ceases appears to be higher than that at which the shell growth starts (Fig. 6). These findings suggest that the shell growth of this species is not constrained by seawater temperature alone.

The optimum seawater temperature range for lunar day shell growth of *Phacosoma japonicum* in Tokyo Bay (21 to 24°C; see Figs. 6 & 8) observed in the present study is slightly lower than that estimated by Schöne et al. (2003, their Table 1; 24.8 to 25.5°C), who used the seawater temperature data at Tateyama, outside of Tokyo Bay, where the influence of the warm Kuroshio Current is stronger than in Tokyo Bay. We,

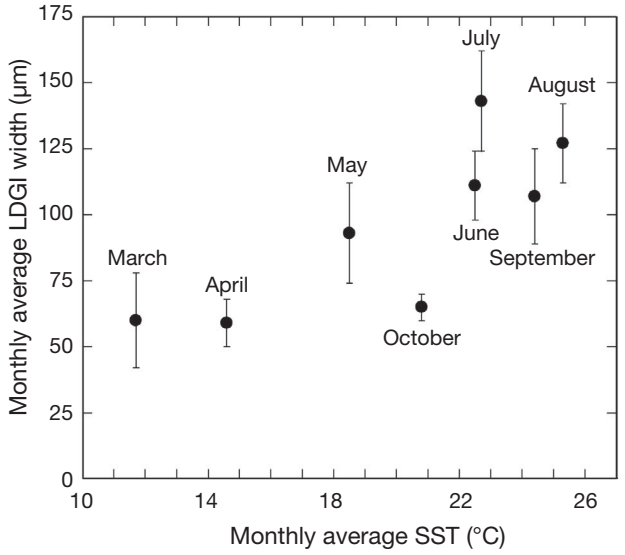

Fig. 8. Monthly averaged lunar day growth increment (LDGI) width for 15 specimens of Ages 2 and 3 yr collected alive from Nojima, Tokyo Bay, in 2003 versus monthly averaged surface seawater temperature (SST). Means and 1 SE are indicated

therefore, conclude that the true optimal growth temperature is lower than the estimate produced by Schöne et al. (2003) because of inappropriate application of the temperature data at Tateyama to the habitat of *P. japonicum* in Tokyo Bay.

In Tokyo Bay, the mean lunar day shell growth rate gradually declined in August and September, when the seawater temperature exceeded 24°C. This finding is well expressed in the relationship between the ln-transformed, tide-corrected LDGI width and 1/SST (Fig. 7C). In October, the mean seawater temperature declined rapidly to 20°C, but the lunar day shell growth rate did not return to the high rates of early summer, rather it continued to decrease (Fig. 8).

Two other environmental factors, i.e. salinity and food availability, might contribute to the decline of the lunar day shell growth rate after August, namely, a marked decline of salinity in August and early September due to the influx of large amounts of freshwater into Tokyo Bay from typhoons (Fig. 6) and a decrease in phytoplankton abundance (expressed by chl *a* concentration) in October (Fig. 6). Previous work has suggested that food availability greatly influences shell growth rates of bivalve mollusks (Sato 1997, Lorrain et al. 2000, Carmichael et al. 2004, Schöne et al. 2005).

CONCLUSIONS

The main findings of the present study are as follows. (1) Shell growth of *Phacosoma japonicum* is controlled by the tidal cycle. The shells form LDGIs, which fluctuate in width on a fortnightly basis. (2) Shell growth of *P. japonicum* depends on 3 different parameters: (a) variable environmental conditions throughout the growing season, (b) reproduction and (c) ontogenetic age. (3) Shell growth of *P. japonicum* is primarily controlled by seawater temperature. Optimum growth rates occur between 21 and 24°C. Above and below these temperatures, shell growth is reduced. (4) Aside from temperature, shell growth of this species is controlled by food availability and salinity. Lower salinity and phytoplankton concentrations result in lower shell growth rates.

Results of our study suggest that a combined analysis of high resolution (i.e. daily) sclerochronology and environmental parameters of the habitat is useful to elucidate the response of marine organisms to present and past environmental changes.

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LITERATURE CITED

Carmichael RH, Shriver AC, Valiela I (2004) Changes in shell and soft tissue growth, tissue composition, and survival of quahogs, *Mercenaria mercenaria*, and softshell clams, *Mya arenaria*, in response to eutrophic-driven changes in food supply and habitat. J Exp Mar Biol Ecol 313:75–104

Cerrato RM, Wallace HVE, Lightfoot KG (1991) Tidal and seasonal patterns in the chondrophore of the soft-shell clam *Mya arenaria*. Biol Bull (Woods Hole) 181:307–311

Chinzei K (1980) Molluscan fauna of the Plio-Pleistocene Kakegawa Group; its composition and horizontal distribution (in Japanese with English abstract). Mem Natl Sci Mus (Tokyo) 13:15–20

Clarke A, Johnston NM (1999) Scaling of metabolic rate with body mass and temperature in teleost fish. J Anim Ecol 68: 893–905

Evans JW (1972) Tidal growth increments in the cockle *Clinocardium nuttalli*. Science 176:416–417

Farrow GE (1972) Periodicity structure in the bivalve shell: analysis of stunting in *Cerastoderma edule* from the Burry Inlet (South Wales). Palaeontology 15:61–72

Gillikin DP, Lorrain A, Naves J, Taylor JW, André L, Keppens E, Baeyens W, Dehairs F (2005) Strong biological controls on Sr/Ca rations in aragonitic marine bivalve shells. Geochim Geophys Geosyst 6:1–16

Goodwin DH, Flessa KW, Schöne BR, Dettman DL (2001) Crosscalibration of daily growth increments, stable isotope variation, and temperature in the Gulf of California bivalve mollusk *Chione cortezi*: implications for paleoenvironmental analysis. Palaios 16:387–398

Grant J (1996) The relationship of biogenetics and the environment to the field growth of cultured bivalves. J Exp Mar Biol Ecol 200: 239–256

Heilmayer O, Brey T, Pörtner HO (2004) Growth efficiency and temperature in scallops: a comparative analysis of species adapted to different temperatures. Funct Ecol 18: 641–647

Jones DS (1985) Growth increments and geochemical variations in the molluscan shell. In: Broadhead TW (ed) Mollusks. Studies in Geology 13, University of Tennessee Department of Geological Sciences, Knoxville, TN, p 72–87

Jones DS, Arthur MA, Allard DJ (1989) Sclerochronological records of temperature and growth form shells of *Mercenaria mercenaria* from Narragansett Bay, Rhode Island. Mar Biol 102:225–234

Kennish MJ (1980) Shell microgrowth analysis: *Mercenaria mercenaria* as a type example for research in population dynamics. In: Rhoads DC, Lutz RA (eds) Skeletal growth of aquatic organisms. Plenum Press, New York, p 255–294

Kim WS, Huh HT, Lee JH, Rumohr H, Koh CH (1999) Endogenous circatidal rhythm in the Manila clam *Ruditapes phillippinarum* (Bivalvia: Veneridae). Mar Biol 134:107–112

Kim WS, Huh HT, Je JG, Ham KN (2003) Evidence of two-clock control of endogenous rhythm in the Washington clam, *Saxidomus purpuratus*. Mar Biol 142:305–309

Lorrain A, Paulet YM, Chauvaud L, Savoye N, Nezan E, Guerin L (2000) Growth anomalies in *Pecten maximus* from coastal waters (Bay of Brest, France): relationship with diatom blooms. J Mar Biol Assoc UK 80:667–673

Navarro E, Ortega MM, Madariaga JM (1981) Effect of body size, temperature and shore level on aquatic and aerial respiration of *Actinia equine* (L.) (Anthozoa). J Exp Mar Biol Ecol 53:153–162

Ohno T (1983) A note on the variability of growth increment formation in the shell of the common cockle *Cerastoderma edule*. In: Brosche P, Sünderman J (eds) Tidal friction and the earth's rotation. Springer, Berlin, p 222–228

Ohno T (1985) Experimentale Analysen zur Rhythmik des Schalenwachstums einiger Bivalven und ihre paleobiologische Bedeutung. Palaeontographica 189:63–123

Pannella G (1975) Paleontological clocks and the history of the Earth's rotation. In: Rosenberg GD, Runcorn SK (eds) Growth rhythms and the history of the Earth's rotation. John Wiley & Sons, London, p 253–284

Pannella G, MacClintock C (1968) Biological and environmental rhythms reflected in molluscan shell growth. J Paleontol 42:64–80

Pilditch CA, Grant J (1999) Effect of temperature fluctuations and food supply on the growth and metabolism of juvenile sea scallops (*Placopecten magellanicus*). Mar Biol 134: 248–253

Rhoads DC, Pannella G (1970) The use of molluscan shell growth patterns in ecology and paleoecology. Lethaia 3: 143–161

Richardson CA (1988a) Tidally produced growth bands in the subtidal bivalves *Spisula subtruncata* (da Costa). J Mollusc Stud 54:71–82

Richardson CA (1988b) Exogenous and endogenous rhythms of band formation on the shell of the clam *Tapes philippinarum* (Adams & Reeve, 1850). J Exp Mar Biol Ecol 122: 105–126

Richardson CA (1989) An analysis of the growth bands in the shell of the common mussel *Mytilus edulis*. J Mar Biol Assoc UK 69:477–491

Richardson CA, Crisp DJ, Runham NW (1980) An endogenous rhythm in shell deposition in *Cerastoderma edule*. J Mar Biol Assoc UK 60:991–1007

Sato S (1994) Analysis of the relationship between growth and sexual maturation in *Phacosoma japonicum* (Bivalvia: Veneridae). Mar Biol 118:663–672

Sato S (1995) Spawning periodicity and shell microgrowth patterns of the venerid bivalve *Phacosoma japonicum* (Reeve). Veliger 38:61–72

Sato S (1997) Shell microgrowth patterns of bivalves reflecting seasonal change of phytoplankton abundance. Paleontol Res 1:260–266

Sato S (1999) Genetic and environmental control of growth and reproduction of *Phacosoma japonicum* (Bivalvia: Veneridae). Veliger 42:54–61

Schöne BR, Lega J, Flessa KW, Goodwin DH, Dettman DL (2002) Reconstructing daily temperatures from growth rates of the intertidal bivalve mollusk *Chione cortezi* (northern Gulf of California, Mexico). Palaeogeogr Palaeoclimatol Palaeoecol 184:131–146

Schöne BR, Tanabe K, Dettman DL, Sato S (2003) Environmental controls on shell growth rates and $\delta^{18}O$ of the shallow marine bivalve mollusk *Phacosoma japonicum* in Japan. Mar Biol 142:473–485

Schöne BR, Houk SD, Freyre Castro AD, Fiebig J, Kröncke I, Dreyer W, Oschmann W (2005) Daily growth rates in shells of *Arctica islandica*: assessing sub-seasonal environmental controls on long-lived bivalve mollusks. Palaios 20: 78–92

Schöne BR, Rodland DL, Fiebig J, Oschmann W, Goodwin D, Flessa KW, Dettman D (2006) Reliability of multitaxon, multiproxy reconstructions of environmental conditions from accretionary biogenic skeletons. J Geol 114:267–285

Sukhotin AA, Pörtner HO (2001) Age-dependence of metabolism in mussels *Mytilus edulis* (L.) from the White Sea. J Exp Mar Biol Ecol 257:53–72

Takesue RK, van Geen A (2004) Mg/Ca, Sr/Ca, and stable isotopes in modern and Holocene *Protothaca ataminea* shells from a northern Calfornia coastal upwelling region. Geochim Cosmochim Acta 68:3845–3861

Tanabe K (1988a) An attempt for age estimation of bivalves, using shell growth lines (in Japanese with English abstract). Benthos Res 32:12–17

Tanabe K (1988b) Age and growth rate determinations of an intertidal bivalve, *Phacosoma japonicum*, using internal shell increments. Lethaia 21:231–241

Tanabe K, Oba T (1988) Latitudinal variation in shell growth patterns of *Phacosoma japonicum* (Bivalvia: Veneridae) from the Japanese coast. Mar Ecol Prog Ser 47:75–82

Williams BG, Palmer JG, Hutchinson DN (1993) Comparative studies of tidal rhythms. VIII. Is a clam clock similar to those of other intertidal animals? Mar Behav Physiol 24:1–14

Witbaard R, Duineveld GCA, de Wilde PAWJ (1999) Geographical difference in growth rates of *Arctica islandica* (Mollusca: Bivalvia) from the North Sea and adjacent waters. J Mar Biol Assoc UK 79: 907–915

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