GROWTH OF BIVALVES BASED ON ALLOMETRIC RELATIONSHIP AND A TIME SERIES OF LENGTH-FREQUENCY DATA

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Abstract: The relationship of shell length with wet, dry and shell weight of the bivalve species – *Cyclina sinensis, Gafrarium tumidum, Katelysia japonica, Psammotaea elongata, Quidnipagus palatum* and *Semele carnicolor* from Tomigusuku intertidal flat, Okinawa, Japan were measured. In *P. elongata* and *Q. palatum* (predominant species), relationship between shell length and wet weight was examined monthly. There was a significant relationship and strong correlation between the shell length and wet, dry and shell weight in all species ($p < 0.01$; $r^2 > 0.818$). The regression lines were significantly different by species (ANCOVA $p < 0.01$). Allometric growth by wet, dry and shell weight in bivalve species indicates the highest rate in *G. tumidum* and lowest in *P. elongata*. The regression lines between shell length and wet weight were significantly different by months in *P. elongata* (ANCOVA $p < 0.05$) and *Q. palatum* (ANCOVA $p < 0.01$). Growth of the bivalves *P. elongata* and *Q. palatum* on the tidal flat were measured and compared. The von Bertalanffy growth function (VBGF) was applied on a length-frequency data of the both species. The growth parameters were determined using electronic length frequency analysis (ELEFAN) module in "FiSAT" program. The maximum length recorded during sampling for *P. elongata* and *Q. palatum* were 80.1 and 54.9 mm, respectively. However, as indicated by asymptotic length, L∞ of VBGF, *P. elongata* could attained maximum growth of 81.38 mm while *Q. palatum* 56.4 mm. VBGF growth constant, *K* for *P. elongata* and *Q. palatum* were 0.65 and 0.58 year⁻¹, respectively. These indicate that on the tidal flat, *P. elongata* grows faster than *Q. palatum*.

KEYWORDS: Allometry growth, bivalve, intertidal flat, length-frequency, length-weight relationship, von Bertalanffy growth function

Introduction

Growth is one of the most-used measures of an organism's vitality in a given environment and has received considerable attention as the starting point of any comprehensive analysis of life history of individuals in a population (Stearns, 1994). In many organisms, the size is directly related to its age, and this cumulative increase in biomass with respect to time is termed "absolute growth", while the percentage increase in biomass per unit time is "relative growth" (Seed, 1976). On the other hand, growth is not a uniform phenomenon because at a certain period in an organism's life growth is more rapid.

Allometry is a relation between the size of an organism and the size or proportion of any of its parts. Allometric growth is differential growth of body parts (x and y), expressed by the equation "$y=ab^x$", where a and b are fitted constants (Lincoln et al., 1998). Allometric relations can be studied during the growth of a single organism, between different organisms within a species, or among organisms in different species. In bivalves, allometric growths have been widely studied in many species and used as one parameters to describe the trophic conditions of bivalve species in different habitats (Ross and Lima, 1994; Kuang, 2000; Park and Oh, 2002; Saxby, 2002).

Some other methods used to assess growth in bivalves are following size changes in marked individuals, measuring shell growth rings in relation to biomass and tracking size frequency distributions (Huges, 1970; Gilbert, 1973). Furthermore, numerous growth models have been developed such as monomolecular model, logistic model and Gompertz model (Yamaguchi, 1975; Tanaka, 1982; Dame, 1996). Following a particular cohort by measuring size frequency distribution through time is a common technique. In this method, growth parameters are estimated directly from the length composition of the stock, without previously translating the length scale into an age scale. The von Bertalanffy model (Bertalanffy, 1957) for example, in its general form includes all of the preceding models. This model has been favoured by biologists because of this generality and its derivation from allometric and metabolic relationships with biological meaning.

An earlier study indicates that benthic bivalves represent a substantial proportion of intertidal communities of Tomigusuku, Okinawa, Japan (Bachok, 2000). Length and weight are two basic components in the biology of species at the individual and population levels. Therefore, in order to assess bivalves that coexist on Tomigusuku intertidal flat, the study of length-weight relationship was done. In this study, six bivalve species were selected – *Cyclina sinensis, Gafraium tumidum, Katelysia japonica, Psammotaea elongata, Quidnipagus palatum* and *Semele carnicolor*. The relationships of the bivalve shell lengths with the bivalve wet weight, dry weight and shell weight were determined. Because *P. elongata* and *Q. palatum* are dominant species in the study area, enough specimens were obtained for studying monthly length-weight relationships. This study also attempts to measure and compare the growth of *P. elongata* and *Q. palatum* based on a time series of the bivalve length-frequency data. The Von Bertalanffy growth model was used to estimate the growth parameters of the bivalves. The growth parameters were determined using electronic length frequency analysis (ELEFAN) module in "FiSAT" program (Gayanilo et al., 1989).

Materials and methods

Sample collections

Six bivalve species – *Cyclina sinensis, Gafraium tumidum, Katelysia japonica, Psammotaea elongata, Quidnipagus palatum* and *Semele* were collected from 20 sampling stations on Tomigusuku intertidal flat, Okinawa, Japan (see detailed in Bachok et. al. 2006). In the laboratory, located next to the tidal flat the bivalves were kept in running filtered sea water for gut content clearance. The shell length (L), defined as the longest distance of shell (anterior to posterior) was measured to the nearest mm with vernier callipers along the anterior-posterior axis. The wet weight (W_{wet}), including shells, was taken to an accuracy of 0.01 g after shaking the specimens and wiping with dry tissue paper to remove adherent water. Bivalves were selected (small to large size) and dried in oven at 60°C to a constant weight. The dry weight (W_{dry}), including shells, was taken to an accuracy of 0.01 g and after the tissues of the bivalve was removed, shell weight (W_{shell}) was measured.

The length-weight relationships for six bivalve species was done on the samples that were collected from May to October 1999. In *P. elongata* and *Q. palatum* (predominant species) enough

specimens were obtained for studying monthly length-weight relationships from May 2000 to April 2001. The time series of length-frequency study for *P. elongata* and *Q. palatum* sampled from Tomigusuku intertidal flat was done from May 1999 to October 1999 and from May 2000 to April 2001.

Data analysis

The relationship of shell length (L) with wet weight (W_{wet}), dry weight (W_{dry}) and shell weight (W_{shell}) were calculated by using the Le Cren's equation:

$$W = a L^b$$

where a and b are constants of linear regressions, were fitted by transforming the data into logarithms and deriving the regression line by the least squares methods. Correlations were expressed by the product moment correlation coefficient, r^2. The regression lines were compared among bivalve species and months (for *P. elongata* and *Q. palatum*) using ANCOVA. The analyses were performed by using Stat View 5 software at 95% confidence intervals.

The monthly length data of *P. elongata* and *Q. palatum* was grouped into classes. Size interval was decided according to the size ranges between minimum and maximum values. A size interval of 5 mm was chosen for *P. elongata* and 2.5 mm for *Q. palatum* (16 size classes for *P. elongata* and 18 for *Q. palatum*). Then the frequencies from each length group were calculated. The growth was estimated using the ELEFAN program which is available in the "FiSAT" module (Gayanilo et al., 1996). Length-frequency data set of both species were analysed to determine the growth parameter ($L\infty$ and K) from the von Bertalanffy growth function (VBGF):

$$Lt = L\infty \left(1 - e^{-K(t-t_0)} \right)$$

where L_t is the size at time t; $L\infty$ is the asymptotic length or maximum size, K is growth constant expressing the rate at which maximum size is approached and t_0 is the "age" at zero size. ELEFAN is a routine that can be used to identify the growth curve that "best" fits a set of length-frequency data, using the value of Rn as a criterion (Gayanilo and Pauly, 1997). Data are reconstructed to generate "peaks" and "troughs", and the goodness of fit index (Rn) is define by:

$$Rn = 10ESP/ASP/10$$

where the ASP ("Available Sum of Peaks") is computed by adding the 'best' values of the available 'peak' and the ESP ("Explained Sum of Peaks") is computed by summing all the peaks and troughs "hit" by a growth curve.

Results and Discussion

Length-weight relationships of bivalve species

Because sex determinations for molluscs are often difficult and may, as in bivalves, require microscopic examination of the gonad, biological studies such as growth have seldom been determined separately for males and females. Most studies assumed that there is no sexual dimorphism e.g. those in the growth patterns. For instant, Brousseau (1979) showed that in *Mya arenaria*, this assumption is

valid. Therefore in this study, the growth of bivalves was not measured separately for males and females.

Shell length and wet/dry weight represent some of the measurements that have been commonly used to assess growth, or increase in biomass in bivalves (Walz, 1978; Smit and VanHeel, 1992; Ross, 1994; Saxby, 2002). In this study, there was a significant relationship between the shell length (L, *mm*) and wet weight (g, W_{wet}), dry weight (g, W_{dry}) and shell weight (g, W_{shell}) in all species (p <0.01). Their regression lines and the coefficients, r^2 are shown in Fig. 1. The regression lines were significantly different according to the species (ANCOVA p <0.001). Allometric growth rates by wet weight, dry weight and shell weight of all bivalve species showed similar patterns by wet, dry and shell weight (Fig. 2). The highest rate was found in *G. tumidum* and lowest in *P. elongata*.

The bivalves used in this study were collected from May 1999 to October 1999. On Tomigusuku tidal flat, based on the data collected from the same period, *P. elongata* and *Q. palatum* are predominant species, followed by *S. carnicolor, K, japonica, C. sinensis* and *G. tumidum* (Bachok, 2000). Comparison of the allometric growth rates also showed the same ranking, whereas the rate was slowest in *P. elongata* and *Q. palatum*, followed by *S. carnicolor, K, japonica* and *C. sinensis*. *G. tumidum* has the fastest rates compared to other species (Fig. 2). Crawford et al. (1996) compared the allometry growth rates of the oyster from different areas and found that the growth rate was more rapid in the area where food was more abundant. This suggests that animals with high growth rates need more food. Therefore this study might indicate that *G. tumidum* needs more nutrient supply compared to *P. elongata* and *Q. palatum* in order to survive successfully. Thus for the coexisting bivalve species that are exposed to uniform environmental condition on tidal flat, the abundance of food could be a limiting factor, that control the abundance of the bivalves on tidal flat.

Monthly length-weight relationships of P. elongata and Q. palatum

Monthly relationship between shell length and wet weight of *P. elongata* and *Q. palatum* is shown in Fig. 3. The regression lines are significantly differed by months in *P. elongata* (ANCOVA p <0.05) and *Q. palatum* (ANCOVA p <0.001). In *P. elongata*, an allometric growth rate was the highest during November 2000 and lowest during March and April 2002 (Fig. 4a). In *Q. palatum*, the growth rate was highest in May 2000 but lowest in January 2001 (Fig. 4b). These results indicate the influence of season on the allometric growth. Temperature is the major factor affecting the allometric growth rates of bivalves (Saxby, 2002). Seasonal variation of food sources in habitat also influence the energy absorption as well as the growth of bivalves (Linton and Taghon, 2000). In addition, the physiological condition of bivalves such as maturity stage may also effect the growth rate (Griffiths and King, 1979; Smit et al., 1992). Individuals of the same size may increase their weight during reproduction and then decrease in weight after their gametes have been released from their bodies (Harvey and Vincent, 1990), thus showing variability in allometric growth rate in certain months.

In this study the allometric growth rate was measured by determining the relationship between bivalve shell length and the bivalve biomass (wet and dry weight of bivalves including shell, and bivalve shell weight). The relationship between shell length and tissue weight (dry or ash free dry weight, AFDW) was not investigated in this study. Some study showed that more energy may be allocated for tissue growth than shell growth (e.g. Hilbish, 1986), and in this condition, the allometric growth of bivalve species may be different. However, it is not always feasible to obtain the tissue dry weight or AFDW, because it requires the destruction of the animal, which is not a suitable methodology for monitoring the long-term growth of a group of individuals, especially for the species that exist in low abundance in certain ecosystems.

Growth of bivalves based on the length-frequency data

Other methods used to assess growth in bivalves are measuring shell growth rings in relation to biomass and following the size changes in marked individuals. Shell rings or growth lines are defined as abrupt or repetitive changes in the character of accreting bivalve tissues (Dillon and Clark, 1980) and, depending on the circumstances, may be a post mortem indicator of growth. These lines are evident in some bivalves when they experience well-defined seasonal conditions, particularly suspended periods of shell growth (Kawai, 2000), such as extreme temperatures, wave action, or reproductive periods. However, care should be taken to check the reliability of rings in each locality because bivalves from environments with uniform conditions generally do not exhibit rings and line formation is variable both between habitats and within a habitat. On the other hand, in the marked individuals technique, the bivalves are often kept in wire or nylon cages at a particular depth or intertidal elevation (Ito et al., 2001). The cage partially protects the bivalve from predation and makes them easier to retrieve. However, Harger (1970) found that mussels kept in intertidal cages grew faster than those not in cages.

In this study, the Von Bertalanffy growth model was used to estimate the growth parameters of the bivalves, which were determined using electronic length frequency analysis (ELEFAN) module in "FiSAT" program (Gayanilo et al., 1989). Although criticised by several researchers (e.g. Frank, 1965; Knight, 1968; Yamaguchi, 1975; Sakawa and Kimura, 1976), as shown by Brousseau (1979) and Kaufmann (1981), the Von Bertalanffy growth model, gives a good approximation for measured growth rate when (1) comparing the population growth of coexisting species in natural habitat for a long term, (2) large numbers of animals are used and (3) the entire size range of the animals is considered, especially that portion when growth rate is progressively decreasing. Therefore, it remains a valuable growth model for this kind of studies.

Monthly data of mean, median, minimum and maximum length of both species is given in Table 1. In *P. elongata,* smaller size than 10 mm was recorded in May 1999, July 1999, August 1999, May 2000, August 2000, December 2000 and March 2001. In *Q. palatum* no bivalves with size smaller than 10 mm was recorded. However, bivalves with size range from 10 to 14 mm shell lengths was recorded in May 1999, May 2000 and from November 2000 to March 2001. Size range was more diverse in *P. elongata* than *Q. palatum* in all sampling periods. These were indicated by the high standard deviation values from the mean of the size distribution data of *P. elongata* compared to *Q. palatum* (Table 1).

Fig. 5 and 6 illustrate the size-frequency distributions of *P. elongata* and *Q. palatum* on Tomigusuku intertidal flat at each month. In some months, the data show the usual polymodal distributions typical of animal populations made up of several distinct age groups. In *P. elongata,* this was clearly shown especially from May to July of each year (Fig. 5). In *Q. palatum,* the distribution of animal populations did not show any clear distinct age group (Fig. 6). In the "FiSAT" module (Gayanilo et al., 1996), Bhattacharya's method of modal progression analysis (MPA) provides a method to decompose composite length-frequency distributions into their components to identify means, then "linking" the means perceived to belong to the same cohorts. In this study, this method could not be used because the mean lengths did not display a clear progression through time. However, analysis using the ELEFAN program was able to estimate and compare the growth parameters in the both bivalve species.

Growth rates within species are commonly found to increase with increasing temperature with bivalves occurring at lower latitude regions grow faster (Newell, 1964). However, Brousseau (1979) showed that the same species of bivalve reach a smaller maximum size than those living at higher latitudes. These were due to two factors, metabolic compensation and an extended growing season (Huges, 1970; Dame, 1972). In this study, the maximum size recorded during sampling

for *P. elongata* was 80.1 mm (September 1999) while for *Q. palatum* was 54.9 mm (May 1999). However, VBGF calculation of asymptotic length, $L\infty$ indicates that *P. elongata* maximum growth is 81.4 mm while 56.4 mm for *Q. palatum*. Growth curves fitted by ELEFAN program for *P. elongata* and *Q. palatum* are shows in Fig. 7. VBGF growth constant, *K* for *P. elongata* and *Q. palatum* are 0.65 and 0.58 year^{-1}, respectively. These indicate that, on the Tomigusuku tidal flat, *P. elongata* might grow faster than *Q. palatum*. As compared to other bivalve species from other habitats, e.g. *Donax serra* inhabiting highly exposed sandy beaches of South African, an asymptotic length (L_∞) of 82 mm and a growth constant (*K*) of 0.274 y^{-1} were determined (Laudien, 2002).

In surf clam *Donax serra*, the spawning season on sandy beaches lasted from August/ September until February but juveniles (2-6 mm anterior-posterior shell length) were only present for three months in the intertidal zone (Laudien et al., 2001). In this study, small sizes of *P. elongata* was recorded from June to August (6.3 to 6.9 mm) and December (4.6 mm) of the year (Table 1). In *Q. palatum*, the size below 13.6 mm was found from November to March. Therefore, the occurrence of these young individuals might suggest that the spawning seasons of *P. elongata* and *Q. palatum* on Tomigusuku intertidal flat might have occured mainly during the cold (December to January) and warm seasons (July to September).

Shell length has been demonstrated to be an important tool in estimating the growth of many marine bivalves (e.g. Rodhouse et al., 1984; Harvey and Vincent, 1990; Smit et al., 1992). Environmental parameters, population density and reproductive state can influence measurement used to estimate growth, whereas in some cases, more energy may be allocated towards tissues growth than shell growth. (Seed, 1976; Brown et al., 1976; Hibbert, 1977; Griffiths and King, 1979; Rodhouse et al., 1984; Hilbish, 1986; Harvey and Vincent, 1990; Smit and VanHeel, 1992). In this study, size and growth of bivalves are expressed in terms of a linear dimension of the shell. Other possible measures, such as weight or carbon content of meats, would probably give more meaningful indices of size and growth, particularly in inter-and intra-seasonal studies.

Acknowledgements

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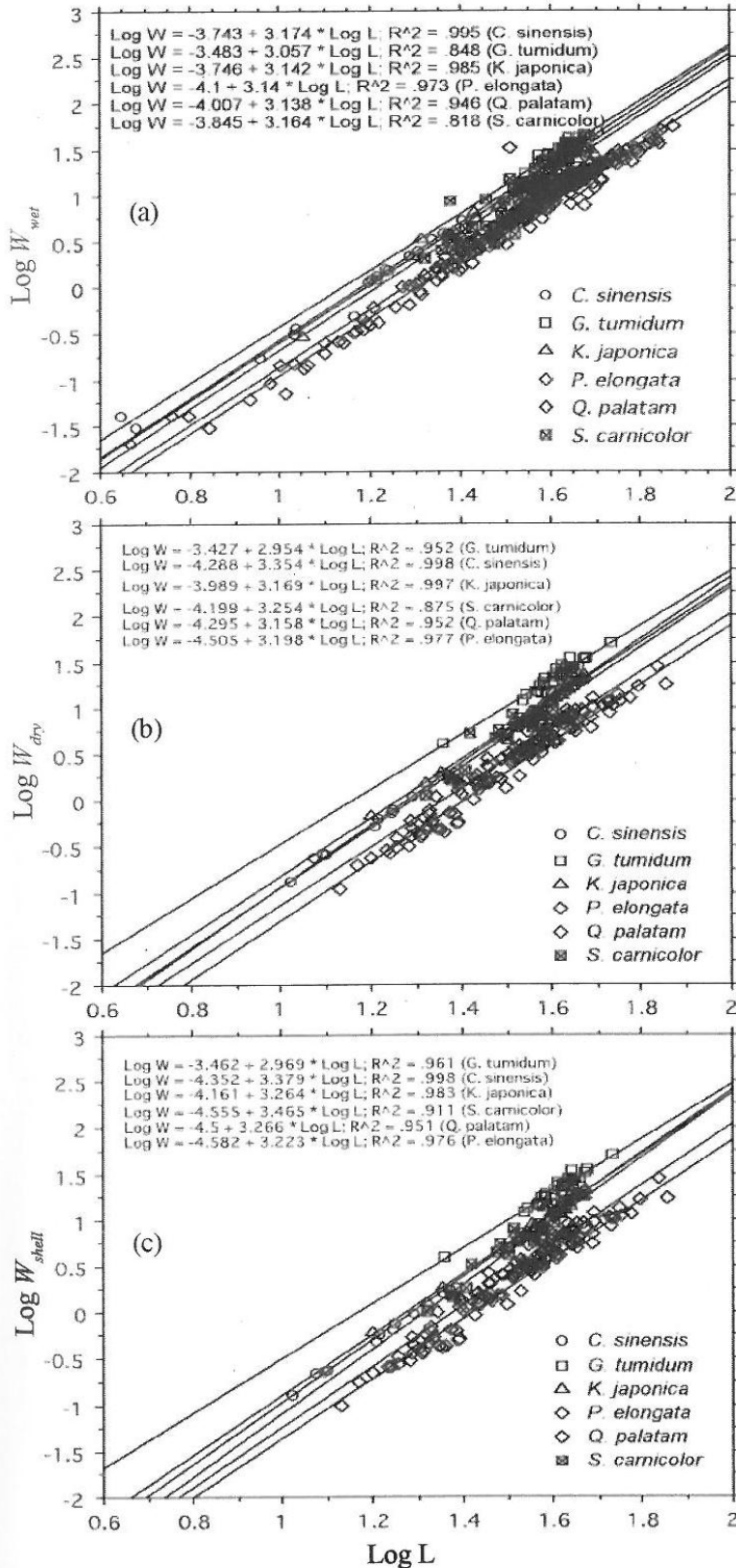
Fig. 1. Relationships of Log L (shell length) with (a) Log W_{wet} (wet weight), (b) Log W_{dry} (dry weight) and (c) Log W_{shell} (shell weight) of *Cyclina sinensis, Gafrarium tumidum, Katelysia japonica, Psammotaea elongata, Quidnipagus palatam* and *Semele carnicolor.* The regression lines are significantly different by species (ANCOVA $p<0.001$).
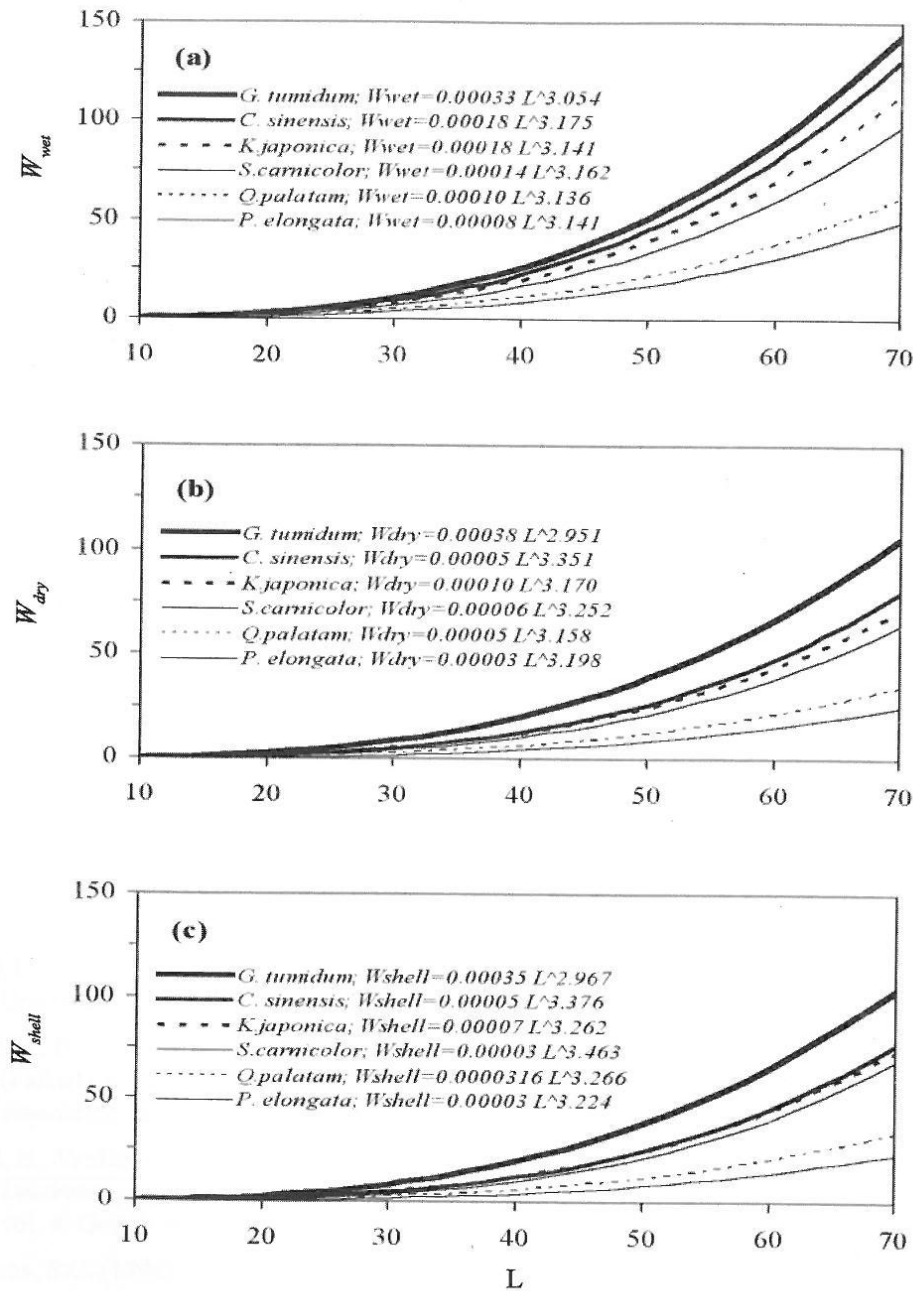
Fig. 2. Allometric growth rates by (a) wet weight (*Wwet*, gram), (b) dry weight (*Wdry*, gram), and (c) shell weight (*Wshell*, gram) of *Cyclina sinensis, Gafrarium tumidum, Katelysia japonica, Psammotaea elongata, Quidnipagus palatum* and *Semele carnicolor*. In the calculation, Le Cren's equation was used, $W = aL^b$ where a and b were constants of linear regression, which were fitted by transforming the data into logarithms and deriving the regression line by least squares method as shown in Fig. 1.
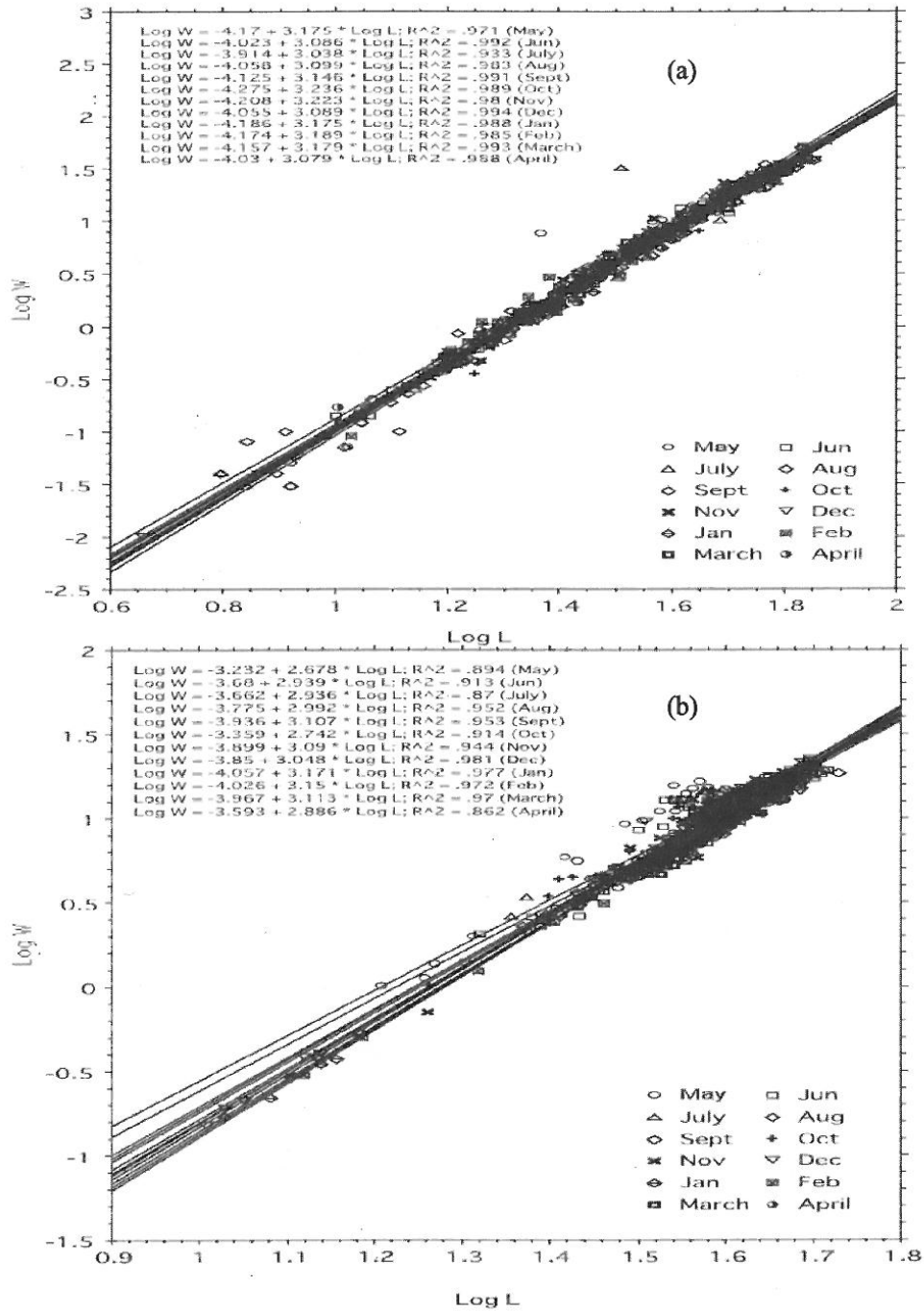
Fig. 3. Relationships between Log *L* (shell length) and Log *W* (wet weight) of (a) *Psammotaea elongata* and (b) *Quidnipagus palatum* from May 2000 to April 2001. The regression lines are significantly different by months (ANCOVA p <0.05).
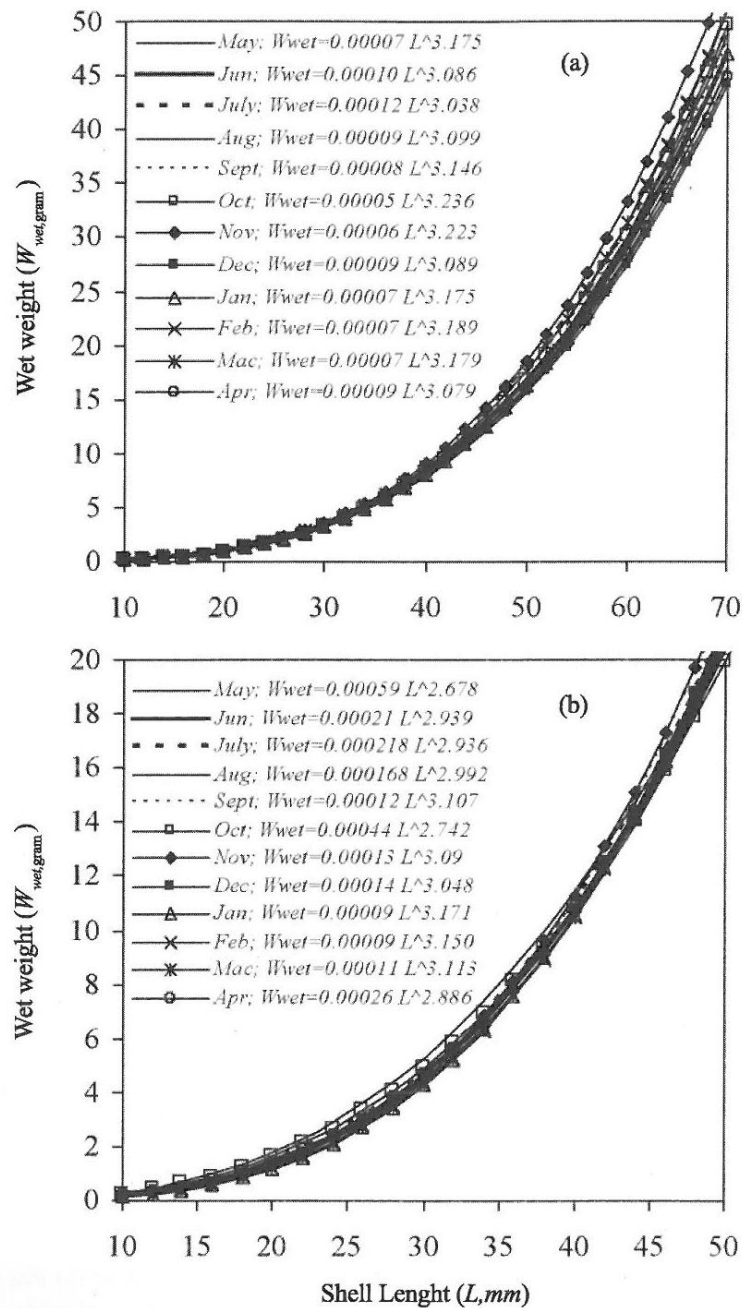
Fig. 4. Allometric growth rates of (a) *Psammotaea elongata* and (b) *Quidnipagus palatum*. In the calculation, Le Cren's equation was used, $W = aL^b$ where a and b were constants of linear regression, which were fitted by transforming the data into logarithms and deriving the regression line by least squares method as shown in Fig. 3.
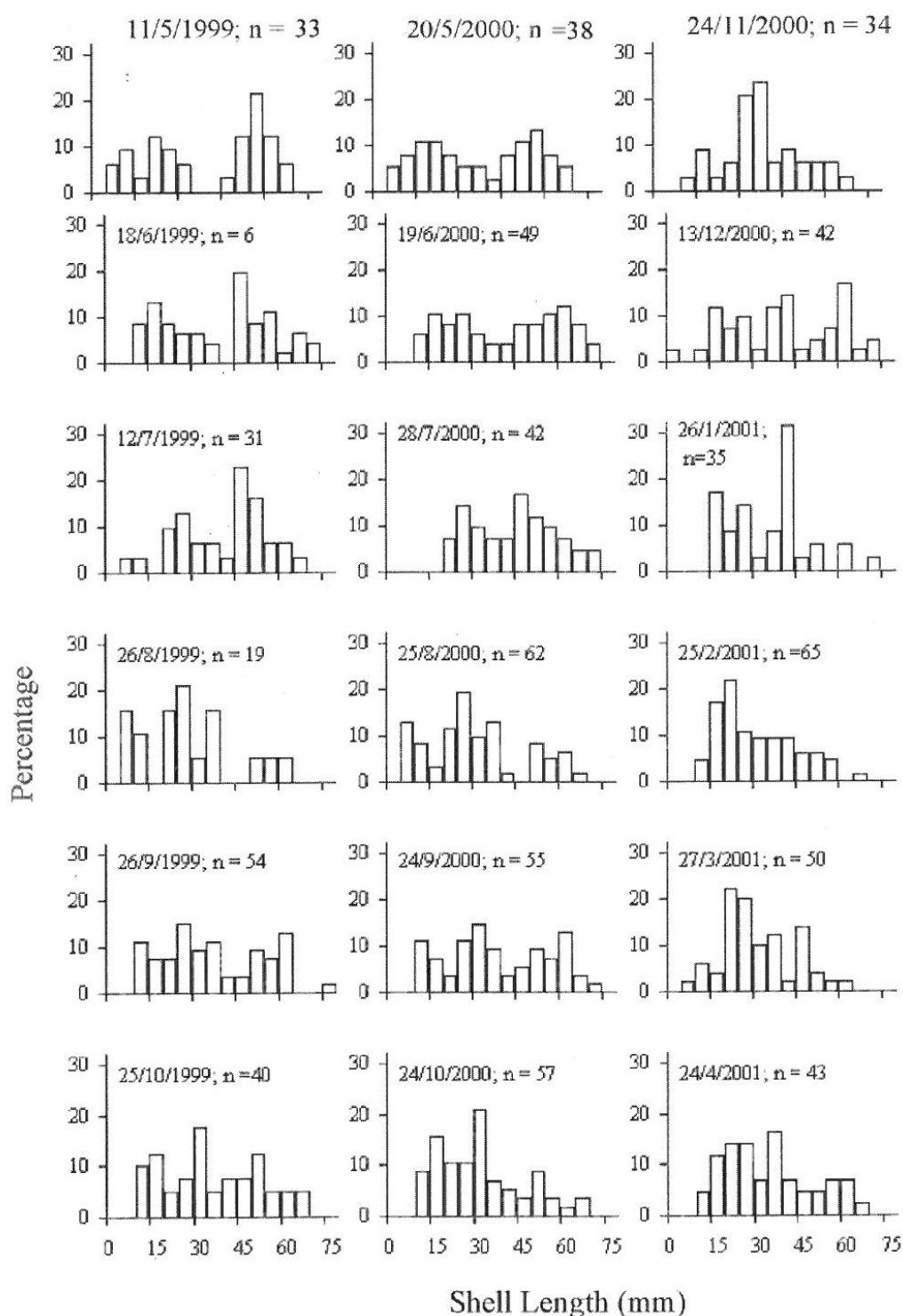
Fig. 5. Length-frequency distributions (percentage of total number measured, n) of *Psammotaea elongata*.
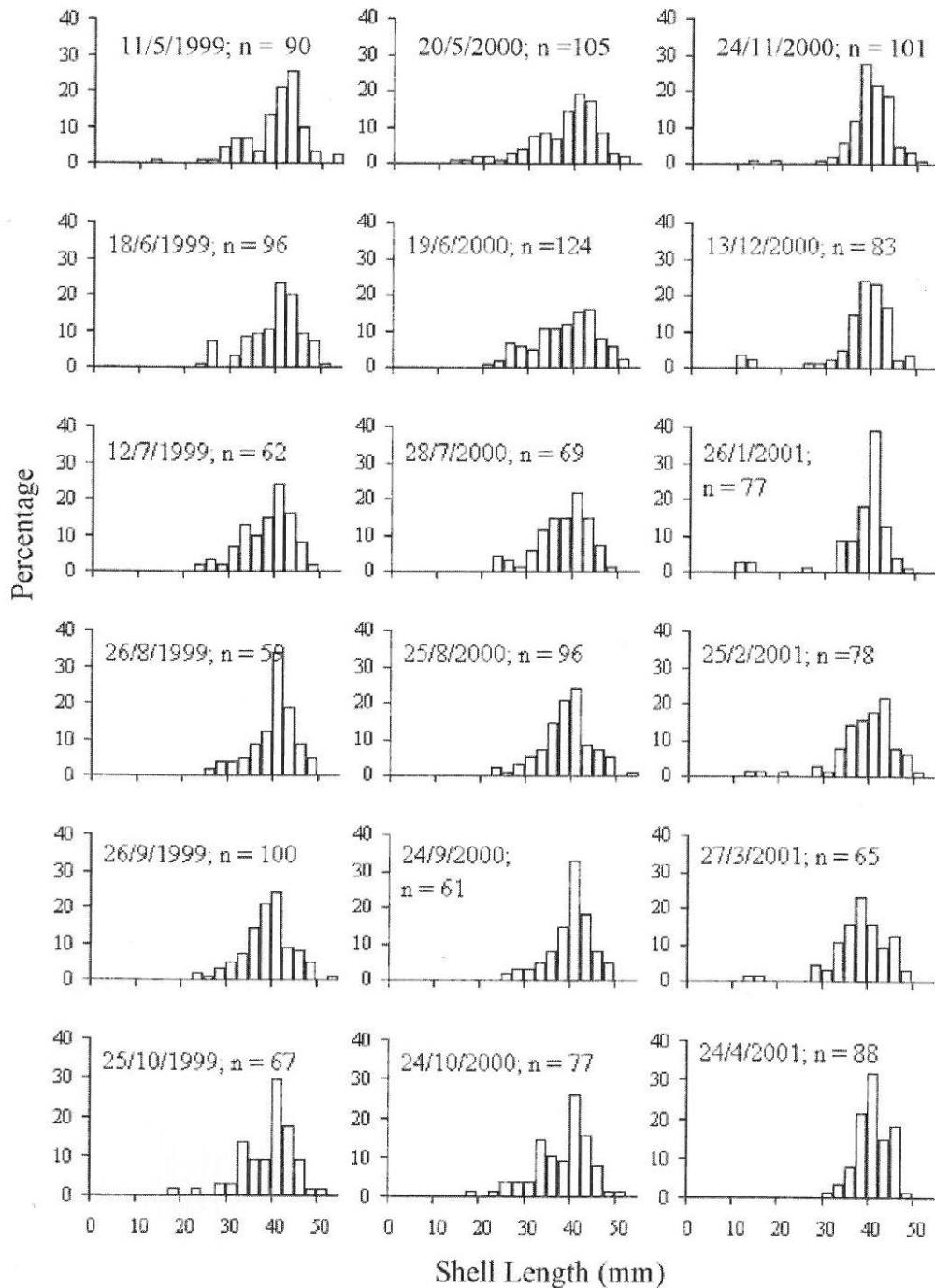
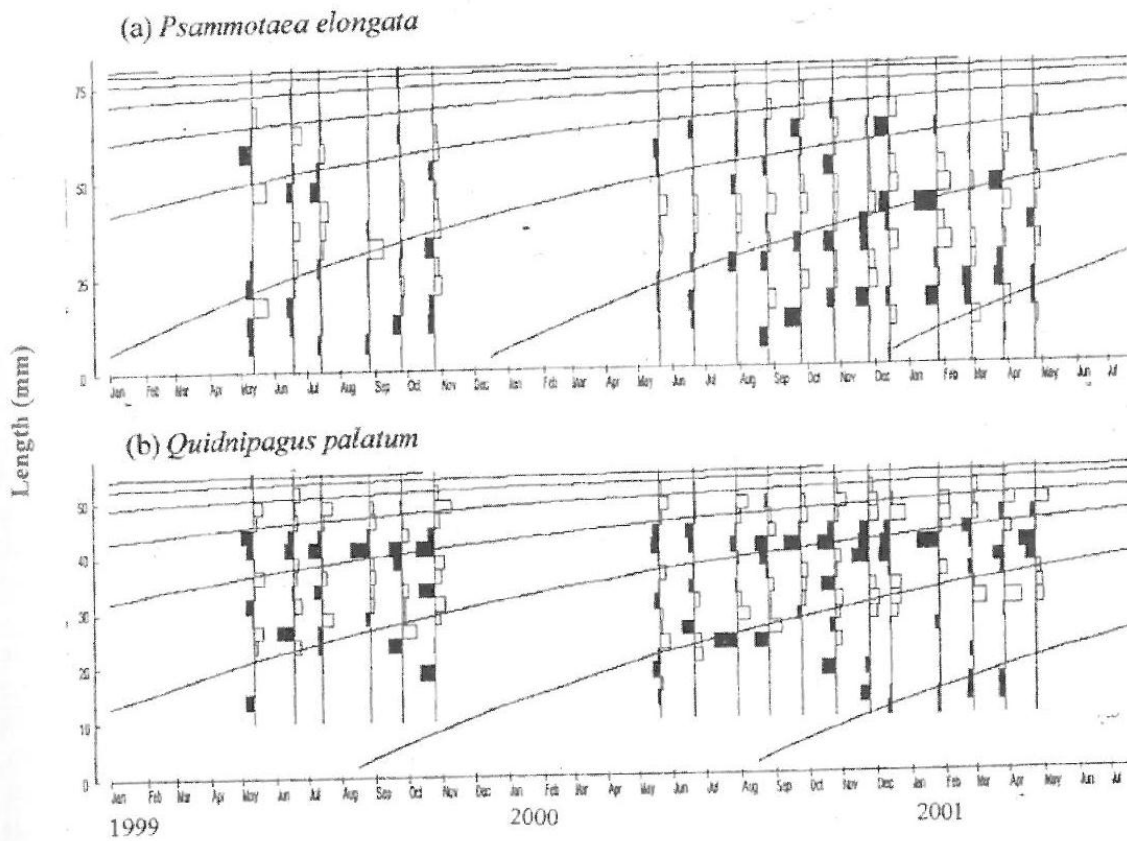Fig. 6. Length-frequency distributions (percentage of total number measured, n) of *Quidnipagus palatum.*

Fig. 7. The length-frequency with VBGF growth curves fitted by the ELEFAN. (a) *Psammotaea elongata*, $L\infty = 81.38$ mm, $K = 0.65$ year[1], and (b) *Quidnipagus palatum*, $L\infty = 54.9$ mm, $K = 0.58$ year[1].