AN ALLOMETRIC ANALYSIS OF JUVENILE FLUTED GIANT CLAM SHELLS (*TRIDACNA SQUAMOSA* L.)

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Abstract *To explore potential allometric relationships in juvenile giant clams,* Tridacna squamosa, *log-transformed shell dimensions were regressed against the logarithm of shell length. Results indicate that shell height and vertical shell height are negatively allometric; possibly a strategy to enhance stability in high water energy environments. Anterior length also exhibits negative allometry; in this case growth may be constrained by contact with the substrate. Shell width, right-valve width, posterior length, scute length and scute width show positive allometry, and could contribute to increased survival as both greater overall width and larger scutes are known to reduce predation.*

Keywords *Allometry, Giant clam, Morphometrics,* Tridacna

INTRODUCTION

As the shape of a mollusc's shell directly reflects its mode of life, much can be learnt from examining shell morphology (Lauzon-Guay, Hamilton & Barbeau, 2005). Growth is usually estimated by measuring shell length and height (Ross & Lima, 1994) whereas ratios of shell length, shell width and shell height are often used as parameters of three-dimensional shell shape (e.g. Seed & Brown, 1978; Gaspar, Santos, Vasconcelos & Monteiro, 2002). In bivalves, most morphometric characters are positively correlated with each other and different shell dimensions increase simultaneously with shell length (Klingenberg, 1996). However, when bivalve characters grow at different rates to shell length, the morphology of a larger specimen will be different to a smaller one, i.e. the mollusc has undergone allometric growth (Cock, 1966). Establishing allometric relationships in bivalves can help answer fundamental ecological questions as well as identify the effects of changing external environmental conditions (Innes & Bates, 1999; Gimin, Mohan, Thinh & Griffiths, 2004).

Tridacna squamosa are found throughout the Indo-Pacific, from the Red Sea in the west to Tonga and Pitcairn Island in the east. They live in shallow, well-lit tropical waters where they are adapted to high levels of sunlight, ultraviolet light, desiccation, infrared heating and nutrient-poor water (Rosewater, 1965; Lucas, 1988). Photosynthesis by symbiotic zooxanthellae living in the mantle of giant clams produces a ready source of inorganic and organic nutrients in oligotrophic reef waters (Yonge, 1936). To maximise exposure of the mantle to sunlight, giant clams have undergone an evolutionary rotation of structures about the foot, such that the dorsal hinge and umbo of the ancestral bivalve is now ventral (Yonge, 1936, 1975; Stasek, 1962). *Tridacna squamosa* has an elongate shell, with shell length considerably larger than shell width. They are equivalve, possessing valves that interlock with one another and are almost equilateral, with posterior length similar to anterior length. The valves posses ridges and flutes; and from the ridges protrude distinct rows of scutes, sharp fingernail-shaped calcareous protrusions (Yonge, 1936, 1975; Stasek, 1962).

To our knowledge, no morphometric research has been published on the fluted giant clam *T. squamosa*. Here, the morphology of *T. squamosa* is examined for allometric relationships. The study is exploratory but we predict that there exists allometric growth in various shell dimensions of *T. squamosa* with respect to shell length.

MATERIALS AND METHODS

Tridacna squamosa right-valves (n = 28) ranging from shell length of 18.15mm to 89.88mm (mean 54.16mm, S.D. 17.0mm) were analysed. Valves originated from *T. squamosa* raised in an aquarium environment (a natural seawater flow-through system in large outdoor tanks

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Table 1 *Tridacna squamosa* morphometric measurements and descriptions with number of shells tested and the mean (± SE) dimensions. The number of T. squamosa used for ScW and ScL are lower due to scutes missing or damaged on some shells.

Abbreviation	Description	n	Mean (mm)	SE
SL	Shell length: Maximum antero-posterior dimension of the shell.	128	54.26	1.47
SH	Shell height: Maximum dorsal-ventral dimension of the shell, measured perpendicular to SL.	128	35.10	0.93
VSH	Vertical shell height: Height of shell measured perpendicular to its anterior axis.	128	33.33	0.93
RVW	Right valve width: Height of right valve when inside surface is lying on a flat surface (scutes excluded).	128	27.41	0.91
AL	Anterior length: Maximum dimension of the shell along the anterior axis.	128	30.58	0.79
PL	Posterior length: Maximum dimension of the shell along the posterior axis.	128	27.48	0.83
ScL	Scute length: How far the 2nd row (from ventral margin) scute protrudes from the 3rd (i.e. centre) ridge.	76	7.19	0.28
ScW	Scute width: Maximum dimension of the 2nd row, 3rd ridge scute measured perpendicular to mid-length ScL.	66	5.73	0.31

Table 2 Allometric relationships of shell dimensions with respect to shell length. n represents the number of *T. squamosa* used to study the relationship, a is the initial index and b is the allometry coefficient with the associated standard error (SE). r^2 indicates the goodness of fit.

Relationship	n	a	b ± SE	r^2	p-value	Type
SH vs SL	128	1.079	0.911 ± 0.0160	0.963	<0.001	–
VSH vs SL	128	0.715	0.962 ± 0.0158	0.967	<0.05	–
RVW vs SL	128	0.150	1.120 ± 0.0243	0.944	<0.001	+
AL vs SL	128	0.819	0.907 ± 0.0158	0.963	<0.001	–
PL vs SL	128	0.411	1.051 ± 0.0191	0.960	<0.01	+
ScW vs SL	76	0.098	1.04 ± 0.0633	0.789	>0.05	+
ScL vs SL	65	0.009	1.572 ± 0.0949	0.813	<0.001	+

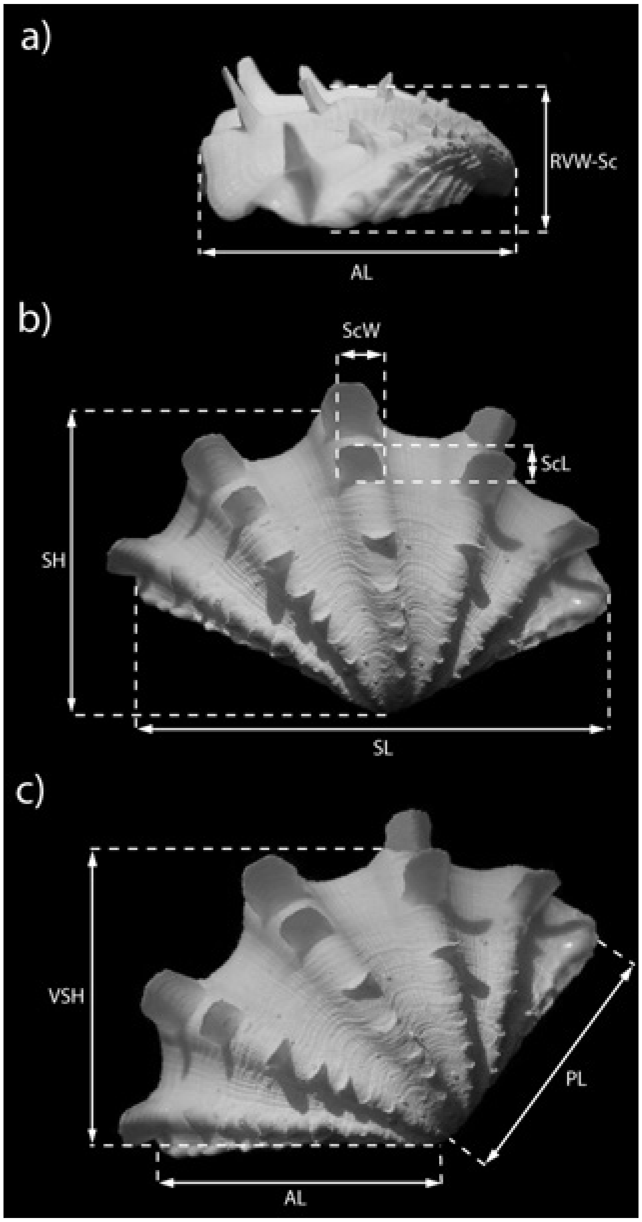

Fig. 1 The morphometric measurements of *T. squamosa* used for allometric analysis.

under 50% shade netting) at the Tropical Marine Science Institute, Singapore; parental origins were *T. squamosa* from Singapore's reefs. Due to the rarity of *T. squamosa* around Singapore (Guest, Todd, Goh, Reddy & Sivalonganathan 2007) wild populations could not be tested. The morphometric variables measured are listed in Table 1 and illustrated in Fig. 1. To avoid bias due to measuring procedures, the same researcher (K. R. Chan) took all the readings to the nearest 0.01mm using digital Vernier calipers. As double valve shells were limited, right-hand valves were used for all analyses.

Regression analysis was used to compare the interrelation among nine *T. squamosa* morphometric measurements. Huxley's (1932) allometry formula was applied, i.e. $y = ax^b$ or, in log-transformed notation, $\log y = \log a + b \log x$, where 'x' and 'y' are the dimensions of interest, 'b' is the allometric coefficient, and 'a' is the proportionality coefficient between two variables and corresponds to the value of y when $x = 1$.

When $b = 1$ the growth is described as isometric, indicating a direct proportionality between x and y. When $b > 1$ there exists positive allometry, that is, the relative rate of growth of y is faster than that of x, whereas the opposite is true when $b < 1$. To determine the value of allometric coefficients, the morphometric variables were first logarithmically transformed to better satisfy the assumptions of regression analysis. All statistical analyses were conducted using JMP IN software.

RESULTS AND DISCUSSION

The mean measurements and standard errors of the eight morphometric characters are presented in Table 1. The relationships of these variables to shell length (after log-log transformations) are described in Table 2. By comparing r^2, the goodness of fit, we can see that the simple allometry equation can be used to explain all characters other than scute width (Table 2). The morphological features of *Tridacna squamosa* measured show both positive and negative ontogenetic allometry. For example, scute length and width, and right-valve width increase relative to shell length (positive allometry) whereas shell height and vertical shell height decrease (negative allometry).

Tridacna squamosa anterior length exhibits negative allometry whereas the posterior length exhibits positive allometry. Physical constraints are known to affect bivalve morphology (Newell & Hidu, 1982; Lauzon-Guay, Hamilton & Barbeau, 2005) and, as the anterior length of the shell is attached to the substrate, it may be in some way constricted by its mode of attachment, i.e. foot and byssal threads, and therefore does not grow at the same rate as the posterior length. Negative allometry is also exhibited by shell height and vertical shell height, contrary to the findings for many other bivalves (Gaspar, Santos, Vasconcelos & Monteiro, 2002). The particularly upright and vertical orientation of *T. squamosa* could make it more vulnerable to the influence of water currents. Some marine bivalves exhibit plastic responses to increased hydraulic energy (Harger, 1970) and water flow is known to be a factor threatening dislodgement in larger specimens of *Pinna nobilis* (Garcia-March, Perez-Rojas & Garcia-Carrascosa, 2006). Reduction of vertical height would result in less drag as the clams grow.

Positive allometry in scute length suggests scutes play a role in *T. squamosa*'s autecology, potentially as defense structures. Scutes may provide protection from crushing predators in three ways, firstly by decreasing the proportion of the predator population with a gape large enough to fit over the shell and scutes, secondly by reducing the mechanical advantage of those predators large enough to hold the clam, and thirdly by increasing injury risk to predators during handling (Ling, Todd, Chou, Yap & Sivaloganathan, 2008). The potential advantage conferred by scutes, however, should also be applicable when they are smaller. A possible explanation for this contradiction is that they do not have the resources to build large scutes at a very young age.

Shell width increases at a rate greater than shell length and therefore *T. squamosa* becomes more spherical with time, a common trend within Bivalvia (Gaspar, Santos, Vasconcelos & Monteiro, 2002). Boulding (1984) demonstrated that similar inflation in burrowing bivalves forces a change in the predatory behavior of crabs from crushing to chipping, which significantly increased handling time (Dudas, McGaw & Dower, 2005). If a greater width to height ratio is protective for *T. squamosa*, again it would likely be advantageous to the smallest clams, and therefore not show an allometric relationship. Perhaps juvenile clams are inconspicuous in their natural environment until they reach a certain age. If so, this would also help explain the positive allometry in scute growth discussed in the previous paragraph.

It should be noted for future studies that, since the various dimensions of *T. squamosa* show allometric growth, comparing ratios such as RVW:SL and SH:SL between different populations of *T. squamosa* will not be meaningful unless shell length is in some way standardised (Lajtner, Marusic, Klobucar, Maguire & Erben, 2004). These relationships could be explored and used to examine whether environmental conditions affect the growth morphology of *T. squamosa*. This could include studies of predator-induced (Trussell, 2000) or habitat-induced (Franz, 1993; Laudien, Flint, van der Bank & Brey, 2003) plastic changes as well as genetic adaptations (Brodie & Brodie, 1999).

The allometry coefficient calculated in this research may not be applicable for *T. squamosa* with shell lengths of more than ~90 mm. Furthermore, this study is cross-sectional, not longitudinal, i.e. it does not control for genotype of *T. squamosa* (although the specimens in the population we used are likely to be closely related). In order to be sure that the allometry observed is not due to differences between individuals, a longitudinal study, whereby individuals are monitored over time, should ideally be conducted. Finally, the capacity of Huxley's (1932) power function to describe relative growth has been questioned (e.g. Bervian, Fontoura & Haimovici, 2006). This is due to the fact that the allometric coefficient, b, assumed to be constant, may change during the life cycle, i.e. polyphasic allometry.

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