Allometric growth of a common Nassariidae (Gastropoda) in south-east Brazil

LEONARDO Q. YOKOYAMA[1,2] AND ANTONIA CECÍLIA Z. AMARAL[2]

[1]Departamento de Zoologia, Instituto de Biociências, Universidade de São Paulo (USP), São Paulo, SP, Brazil, [2]Departamento de Biologia Animal, Instituto de Biologia, Universidade Estadual de Campinas (UNICAMP), CEP: 13083-970, CP: 6109, Campinas, SP, Brazil

The allometric growth of two groups of Nassarius vibex *on beds of the bivalve* Mytella charruana *on the northern coast of the State of São Paulo, was evaluated between September 2006 and February 2007 in the bed on Camaroeiro Beach, and from March 2007 to June 2007 at Cidade Beach. The shells from Camaroeiro were longer and wider and had a smaller shell aperture than those from Cidade; a principal components analysis also confirmed different morphometric patterns between the areas. The allometric growth of the two groups showed great variation in the development of individuals. The increase of shell width and height in relation to shell length did not differ between the two areas. Shell aperture showed a contrasting growth pattern, with individuals from Camaroeiro having smaller apertures. The methodology based on Kullback–Leibler information theory and the multi-model inference showed, for* N. vibex, *that the classic linear allometric growth was not the most suitable explanation for the observed morphometric relationships. The patterns of relative growth observed in the two groups of* N. vibex *may be a consequence of different growth and variation rates, which modifies the development of the individuals. Other factors such as food resource availability and environmental parameters, which might also differ between the two areas, should also be considered.*

INTRODUCTION

The allometric or relative growth of an organism is a process that usually involves changes in the proportions of its body parts as well as in size (Rabaoui *et al.*, 2007). According to Gould (1966), the genetic control of allometric relationships is responsible for the morphological variation between populations or lineages of a species. Most studies have analysed this phenomenon by means of the classical allometric linear model ($y = ax^b$), in which the proportion of growth between the parameters, i.e. the allometric exponent b, is always a constant (Rabaoui *et al.*, 2007). However, the seasonal influence of factors such as water temperature (Moran *et al.*, 1984; Chow, 1987), food availability (Takada, 1995), and reproductive period (Moran *et al.*, 1984; Katsanevakis *et al.*, 2007) on growth is not considered by the linear model. Errors from the adoption of this methodology can occur if the relationship between the parameters is non-linear, or is due to a discontinuity in the allometric exponent (Katsanevakis *et al.*, 2007). Recently, efforts have been made to avoid such problems by means of an alternative analysis based on Kullback–Leibler (K-L) information theory and multi-model inference (MMI) (described by Burnham & Anderson, 2002). Assuming that the allometric exponent can change over time, Katsanevakis *et al.* (2007) used this alternative methodology to evaluate the best model for the allometric growth of some marine invertebrates. The authors observed that for several relationships, the linear model was not always the most appropriate to explain the data.

Usually, only the shell length is employed to evaluate growth for coiled gastropods, and is measured from the apex to the farthest point of the body whorl along the axis of coiling (Ekaratne & Crisp, 1984). For the family Nassariidae, commonly found on sand–mud beaches (Britton & Morton, 1994), the growth of some *Nassarius* species has been analysed. Shell length distribution frequencies were applied to describe the growth pattern of *Nassarius reticulatus* (Linnaeus, 1758) by Tallmark (1980) and Lambeck (1984). Barroso *et al.* (2005a), studying the same species, worked with the shell length distribution frequencies and internal and external growth rings. Mark–recapture experiments were used for *N. reticulatus* by Tallmark (1980), *Nassarius dorsatus* (Roeding, 1798) by McKillup & McKillup (1997), and *Ilyanassa obsoleta* (Say, 1822) by Curtis (1995). Recently, statolith growth rings were used successfully to evaluate the growth of *N. reticulatus* (Barroso *et al.*, 2005b; Chatzinikolaou & Richardson, 2007). However, there are no allometric growth analyses for the family.

The allometric growth of *Nassarius vibex* (Say, 1822), a common intertidal scavenger, was studied on two beaches in south-east Brazil. The species lives on sandy and muddy beaches and is sometimes associated with mussel beds, over a wide area along the east coast of South America. In this study, the allometric growth of *N. vibex* was analysed using the methodology described by Katsanevakis *et al.* (2007).

Corresponding author:
L.Q. Yokoyama
Email: lqyokoyama@gmail.com

Assuming that growth pressures might act differently over a spatial range, the two groups of N. vibex were also compared.

MATERIALS AND METHODS

Study areas

Specimens of *Nassarius vibex* were collected on two beds of *Mytella charruana* (d'Orbigny, 1842), one on Camaroeiro Beach ($23°37'28''$S $45°23'56''$W) and the other on Cidade Beach ($23°37'35''$S $45°23'51''$W), both located in northern Caraguatatuba Bay, State of São Paulo, Brazil (Figure 1). Camaroeiro Beach, with an intertidal zone 50 m wide during low tide periods, is composed of fine, poorly to moderately sorted sand (Yokoyama, 2010). The mussel bed was located parallel to the water line, and had an ellipsoid shape (40 m long and 20 m wide in its central portion) with elevated edges formed by the dense aggregations of bivalves.

Cidade Beach is composed of fine and very fine sand, with a high percentage of silt and clay and low proportions of organic matter and calcium carbonate (Arruda & Domaneschi, 2005). The width of the intertidal zone was around 60 m. The mussel bed, parallel to the water line, had an ellipsoid shape (28 m long and 18 m wide). In contrast to the Camaroeiro bed, no mussels were observed buried in the substrate.

Sampling and laboratory procedures

Individuals of *N. vibex* were collected monthly on Camaroeiro Beach from September 2006 to February 2007, and on Cidade Beach from March 2007 to June 2007. All samples were taken randomly over the full width of the beds, and individuals were hand-collected and stored in plastic bags. In the laboratory, six morphometric characters (Figure 2) were measured with a digital caliper to the nearest 0.01 mm: shell length (L), width (W), and height (H), and shell aperture length (Al) and width (Aw). The shell apical angle (Aa) was calculated based on Preston & Roberts (2007), by the equation: $Aa = 2\tan(0.5\ W/L)$, where W is the shell width and L is the shell length.

Data analysis

The normality of the data was assessed with a Shapiro–Wilk test, and the existence of differences in the mean size of the individuals between the areas was assessed for the six parameters with a Student's *t*-test. The morphometric data were submitted to a principal components analysis (PCA) to observe possible patterns in the two groups (Camaroeiro and Cidade). The data for *N. vibex* were subjected to a PCA in an attempt to find intra- and inter-group patterns because of size relationships and differences in growth. The components are usually characterized as composites of the shell parameters with the highest factor loadings, and, as suggested by Frey & Pimental (1978), were defined as larger than + or –0.6. Subsequently, the Chi-square test (χ^2) was used to evaluate the existence of differences between the eigenvalues of each principal component.

The allometric growth of W, H, Al, and Aw in relation to L, and the relationship between W/H and Al/Aw were investigated. The data were log-transformed, and for each comparison three different allometric models were used (linear, quadratic and cubic). The corresponding formulae applied to the data were the linear (*Ln*), $\log y = a_1 + b_1 \log x$, quadratic (*Qd*), $\log y = a_1 + b_1 \log x + b_2 (\log x)^2$, and cubic (*Cb*), $\log y = a_1 + b_1 \log x + b_2 (\log x)^2 + b_3 (\log x)^3$. Other models suggested by Katsanevakis *et al.* (2007), such as the broken-stick and two-segments, were discarded, since visually they did not fit the relationships.

According to Katsanevakis *et al.* (2007), the linear model assumes that allometry does not change as body size increases. The quadratic and cubic models assume that b changes continuously with increasing body size. The small-sample, bias-corrected form Akaike information criterion (AIC_c) (Hurvich & Tsai, 1989) of the AIC (Burnham & Anderson, 2002) was used for model selection according to the equation:

$$AIC_c = AIC + \frac{2k(k+1)}{n-k-1}$$

in which AIC is given by:

$$AIC = n\left(\log\left(2\pi\frac{RSS}{n}\right) + 1\right) + 2k$$

where RSS is the residual sum of squares of the regression, n is the number of observations, and k is the number of parameters of the regression plus 1. In this case, it was necessary to assume normally distributed deviations with homogeneous variances for the data. The model with the smallest AIC_c value ($AIC_{c,min}$) was selected as the 'best' among the models tested. The AIC_c differences, $\Delta_i = AIC_{c,i} - AIC_{c,min}$ were computed for all candidate models.

According to Burnham & Anderson (2002), models with $\Delta_i > 10$ have essentially no support and can be omitted from further consideration, and models with $\Delta_i < 2$ have substantial support, while there is considerably less support for models with $4 < \Delta_i < 7$. However, they did not discuss results such as $2 < \Delta_i < 4$ or $7 < \Delta_i < 10$. In the present study, we considered that all values of $\Delta_i < 2$ showed substantial support for the model. To quantify the plausibility of each model, given the data and the set of three models, the 'Akaike weight' (w_i) of each model was calculated, given by:

$$w_i = \exp(-0.5\Delta_i) / \sum_{k=1}^{3} \exp(-0.5\Delta_k)$$

The 'Akaike weight' is considered as the weight of evidence in favour of model *i* being the 'best' model of the available set of models (Akaike, 1983; Buckland *et al.*, 1997; Burnham & Anderson, 2002). 'Average' models were estimated by averaging the predicted response variable across models, using the corresponding w_i as weights (Burnham & Anderson, 2002). To aid in the visualization of the differences between the linear and the average models, a residual plot fitted with a loess function (as Katsanevakis *et al.*, 2007) was applied for each relation.
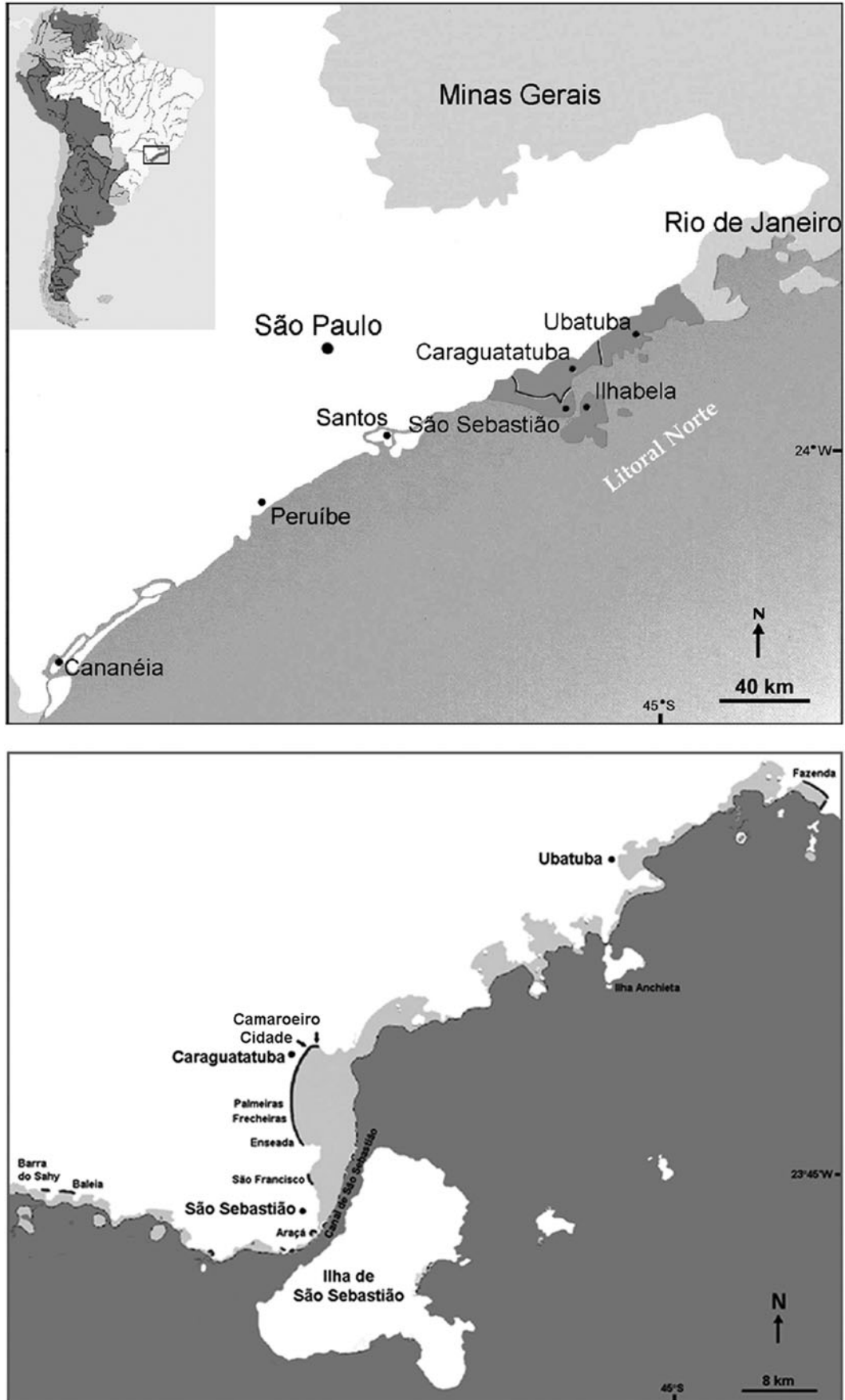
Fig. 1. Study area showing location of the Caraguatatuba Bay and the Camaroeiro and Cidade beaches on the north coast of the State of São Paulo, Brazil (maps modified from Lamparelli, 1998).
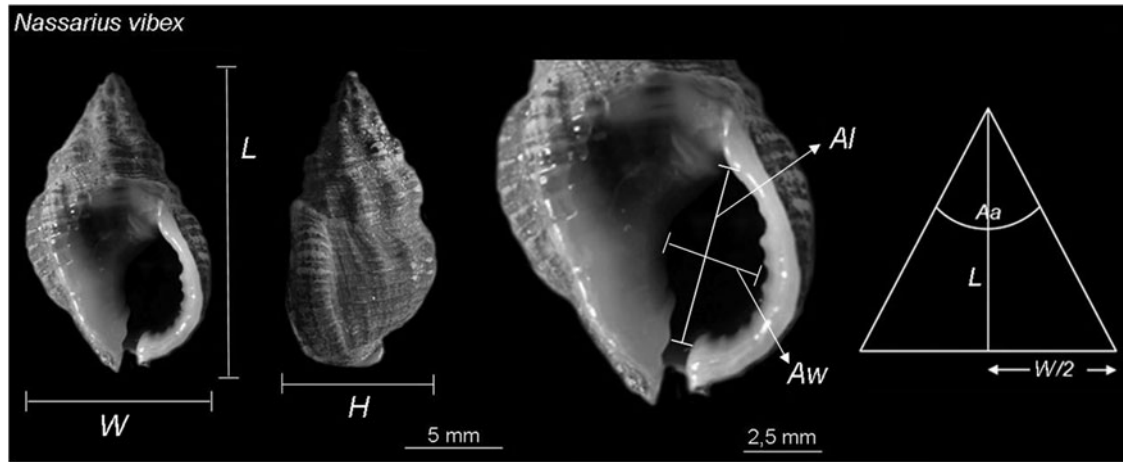
Fig. 2. Morphometric parameters measured for *Nassarius vibex*. Pictures and diagram of the shell apical angle (*Aa*) calculus. *Al*, aperture length; *Aw*, aperture width; *H*, shell height; *L*, shell length; *W*, shell width.

RESULTS

Morphometry

Comparisons between the mean values for the six morphometric parameters measured for *Nassarius vibex* showed significant differences between the areas for shell length and width, aperture length, and apical angle. Individuals from Camaroeiro had shells with greater length and width than those from Cidade (Table 1).

The PCA presented differences between the two areas with respect to the shell size (Figure 3), especially for the small individuals; as confirmed by the differences between the PCs (Table 2). In the Cidade, the very small individuals, represented by the low values of PC1, are almost restricted to the lower left quadrant of the graph (Figure 3). For the Camaroeiro, small individuals are almost equally distributed in the left quadrants of the plot. At larger sizes, represented by the positive values of PC1, most of the Camaroeiro individuals have negative PC2 values, whereas most Cidade individuals had positive values of PC2 (Figure 3).

PC1 explained 73.01% of the observed variance in the data, and was influenced by all the morphometric parameters.

The apical angle was the most notable influence in PC2, and together with PC1 corresponded to 91% of the cumulative variance in the data. The third component, in addition to its low loading value, was characterized by shell aperture parameters (*Al* and *Aw*). This PC was responsible for 5.15% of the total variance in the data, and together with the other two PCs totalled 96.75% of the total variance. When comparing each PC between the areas, significant differences were apparent. Individuals from Camaroeiro were larger ($t = 2.10$, $P < 0.05$) than those from Cidade and also had a larger apical angle ($t = 11.63$, $P < 0.05$). However, individuals from Cidade had a larger shell aperture ($t = -11.23$, $P < 0.05$), represented by PC3.

Allometric growth

The relative growth of Camaroeiro specimens varied widely during development. The cubic model was the most frequent, with high values of w_i for three of the six morphometric

Table 1. Mean values and standard deviation (SD) of the morphometric parameters measured for the individuals of *Nassarius vibex* on the Camaroeiro and Cidade beaches. The Student's *t*-test (*t*) was applied to each comparison of parameters between beaches with a significance level (α) of 0.05. Values in bold typeface indicate significant differences.

Parameter	Camaroeiro (N = 421)		Cidade (N = 427)		t	P
	Mean	SD	Mean	SD		
L	15.89	2.58	15.23	2.65	**3.66**	**<0.05**
W	9.40	1.61	8.58	1.39	**7.89**	**<0.05**
H	7.92	1.06	7.68	4.14	1.13	N.S.
Al	3.86	0.66	4.01	0.71	**−3.14**	**<0.05**
Aw	2.81	0.48	2.86	0.53	−1.24	N.S.
Aa	34.93	2.03	33.42	2.36	**9.32**	**<0.05**

Aa, apical angle; *Al*, aperture length; *Aw*, aperture width; *H*, shell height; *L*, shell length; N, number of individuals; N.S., non-significant; *W*, shell width.
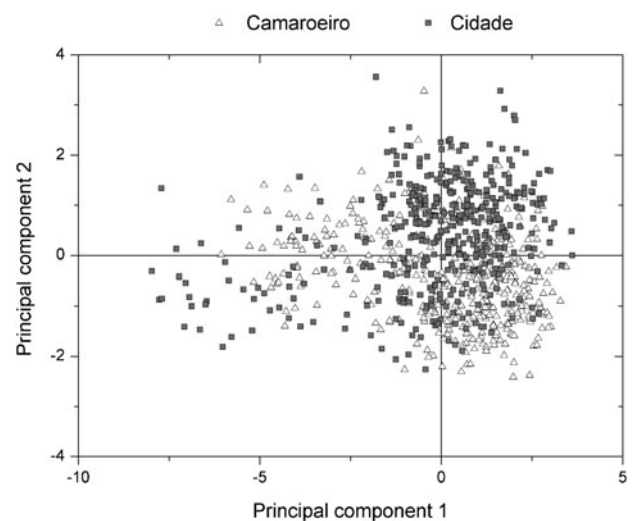

Fig. 3. Principal component analysis (PCA) for the two groups of *Nassarius vibex*. Scatter plot of the log-normalized raw data of the five measured parameters for the Camaroeiro (open triangles) and Cidade (grey quadrats) beaches.

Table 2. Principal component analysis (PCA) results. Component loadings of each morphometric parameter of *Nassarius vibex* and percentages of explained variance. High loadings are indicated in bold.

	PC1	PC2	PC3
L	**0.975**	0.01	0.197
W	**0.908**	−0.379	0.149
H	**0.957**	−0.056	0.209
Al	**0.905**	0.142	−0.309
Aw	**0.914**	0.077	−0.3
Aa	−0.195	**−0.971**	−0.137
% of explained variance	73.014	18.585	5.152
% of cumulative explained variance	73.014	91.599	96.751

Aa, apical angle; *Al*, aperture length; *Aw*, aperture width; *H*, shell height; *L*, shell length; *W*, shell width.

relationships (Table 3). The linear model was more plausible for the relationship *L/H*, whereas the relationships *L/Al* and *L/Aw* better fit the quadratic model, with the highest values of w_i (Table 3). The cubic model was also the most common for four of the six morphometric relationships for the Cidade population (Table 4). The relationships *L/Al* and *L/Aw* were better explained by the linear and quadratic models, respectively.

Both areas shared some similarities in the models tested for many of the relationships analysed (Tables 3 & 4), with the cubic and linear models being the most frequent and with the highest plausibility. Differences were observed in the relationship *L/W*, in which the linear model was the most plausible for Camaroeiro, whereas the cubic model had the highest value of w_i for the Cidade individuals. For some relationships it was difficult to isolate a single plausible model, given their low and similar Δ_i values. This was the case of *L/Aw* for Camaroeiro, where it was not possible to discard the cubic model, even though the quadratic model had a higher w_i. In these cases we opted to accept and plot, the average model, using the corresponding w_i as weights (Figure 4). The residual plots of the average models, which showed a lower dispersion of the data when compared to the linear models residuals, also indicated a differential relative growth for all of the non-linear average models (Figure 4).

The Camaroeiro individuals showed isometric growth between shell length and width (Figure 4), whereas the growth of *L* in relation to *H*, *Al*, and *Aw* varied, being described by quadratic and cubic relationships. The two relationships of shell length with aperture parameters were defined by quadratic models (Table 3; Figure 4). In the relationships *L/H* and *Al/Aw*, the cubic model showed a variation over time in the relative growth.

In the Cidade bed, the growth of shell length in relation to width and height was determined by cubic relationships, indicating variation in growth during the development of the individuals (Figure 4). Furthermore, both *W/H* and *Al/Aw* also showed variations in relative growth. The relationships *L/Al* and *L/Aw* best fit the linear and quadratic models, respectively.

The growth of shell width and height in proportion to shell length did not differ between the areas, even with different allometric models (Figure 4). The development of the shell aperture differed between the two beds: individuals from Camaroeiro had a smaller aperture than those from Cidade. There were no differences in the development patterns of allometric growth between shell width and height; however, the pattern was not the same for the relationship *Al/Aw*, where the large difference in relative growth was restricted to the small size-classes (Figure 4).

DISCUSSION

The shell size of *Nassarius vibex* was significantly different between the two areas during the period of study. Individuals from Camaroeiro had larger shell length, width, and apical angle and smaller shell aperture than those from Cidade. The data reduction by the PCA reinforced the morphometric differences between the groups. It was possible to identify patterns of size-distribution between the areas. Small individuals of Cidade are smaller than those of Camaroeiro, and there was a clear separation for the larger nassarids. The PC2 values for the larger individuals, with positive values for most of the individuals of the Cidade and negative for the Camaroeiro, indicates a morphometric variation between the two groups and reinforce our results with the non-reduced data. To the present results, PC1 represents a 'size' component, which is confirmed by the similar weights of *L*, *W*, *H*, *Al*, and *Aw*, while PC2 is considered as a 'shape' component, also confirmed by the bipolar weighting of the variables (Table 2).

Table 3. Values of Akaike information criterion (AIC_c), AIC_c differences (Δ_i), and Akaike weights (w_i) for the linear (*Ln*), quadratic (*Qd*), and cubic (*Cb*) models applied to the six morphometric relations of *Nassarius vibex* on the Camaroeiro bed. Bold percentages correspond to the most plausible models.

Model	*L/W*	*L/H*	*L/Al*	*L/Aw*	*W/H*	*Al/Aw*
AIC_c						
Ln	−1950.8	−2150.4	−1551.3	−1492.2	−1938.8	−1495.8
Qd	−1928.2	−2154.2	−1552.8	−1495.6	−1965.5	−1497.4
Cb	−1931.3	−2155.1	−1550.8	−1495.4	−1969.1	−1500.3
Δ_i						
Ln	0.0	4.7	1.5	3.4	30.3	4.6
Qd	22.6	0.9	0.0	0.0	3.6	2.9
Cb	19.5	0.0	2.0	0.2	0.0	0.0
w_i (%)						
Ln	**99.99**	5.57	26.00	8.57	0.00	7.68
Qd	0.00	36.62	**54.10**	**47.70**	14.18	17.47
Cb	0.01	**57.82**	19.90	43.73	**85.82**	**74.85**

Al, aperture length; *Aw*, aperture width; *H*, shell height; *L*, shell length; *W*, shell width.

Table 4. Values of Akaike information criterion (AIC_c), AIC_c differences (Δ_i), and Akaike weights (w_i) for the linear (Ln), quadratic (Qd), and cubic (Cb) models applied to the six morphometric relations of *Nassarius vibex* on the Cidade bed. Bold percentages correspond to the most plausible models.

Model	L/W	L/H	L/Al	L/Aw	W/H	Al/Aw
AIC_c						
Ln	−1818.0	−2169.2	−1474.0	−1478.4	−1813.9	−1521.1
Qd	−1820.9	−2130.7	−1445.0	−1479.2	−1839.9	−1512.1
Cb	−1821.4	−2174.5	−1446.1	−1477.2	−1841.8	−1524.2
Δ_i						
Ln	3.4	5.4	0.0	0.8	27.9	3.1
Qd	0.5	43.8	29.0	0.0	1.9	12.0
Cb	0.0	0.0	27.9	2.0	0.0	0.0
w_i (%)						
Ln	9.26	6.34	**99.99**	33.21	0.00	17.75
Qd	39.92	0.00	0.00	**48.83**	27.89	0.20
Cb	**50.82**	**93.66**	0.01	17.96	**72.11**	**82.05**

Al, aperture length; *Aw*, aperture width; *H*, shell height; *L*, shell length; *W*, shell width.

Thus, the size differences among *N. vibex* between the areas are a consequence of a morphometric variation within the groups, with contributions of juvenile and adult individuals. There is an early morphometric separation of the two subgroups, with the small individuals of Cidade being smaller than those of Camaroeiro. This is also confirmed by the model comparisons, in which, for some morphometric variables, there was a distinction between the growths of small nassariids. Thus, the differences in relative growth patterns between the two sub-populations are supported not only by the allometric growth analysis but also by the PCA graph.

PCs 1 and 2 explained approximately 91% of the total data variance and were strongly influenced by several shell form parameters (Table 2). These results are similar to the study of Preston & Roberts (2007) on *Calliostoma zyziphinum* (Linnaeus, 1758), who found differences in size among shells from four areas of the British Isles. According to these authors, food availability was the major component that induced the morphometric differences in *C. zyziphinum*, where individuals that occurred at locations with better resources had better growth, avoided predation, and recovered quickly from unsuccessful predation attempts. For *N. vibex*, there was no record of high percentages of predation marks on the shells, and empty shells were rare in both areas. Predatory influence cannot yet be discarded, but these results point to another hypothesis. Being a scavenger species (Demaintenon, 2001), the mussel bed and its surroundings must represent a good food resource for *N. vibex*. Studies on the condition index of the two beds of *Mytella charruana* found no differences in the quality of this possible food resource. In an evaluation of the diet of *N. vibex*, Forroni *et al.* (2008) identified algae and fragments of polychaetes and crustaceans in the stomach contents. The authors did not evaluate the availability of these resources in the areas, and therefore it is not possible to establish a relationship for the morphometric differences observed between the two groups of nassariids. Similar observations have been reported for other species, including *Nassarius pauperatus* (Lamarck, 1822) (McKillup & Butler, 1983) and *Nassarius dorsatus* (McKillup & McKillup, 1997), where small-sized individuals exposed to high food concentrations grew more rapidly than older and larger individuals.

Chilina parchappii (d'Orbigny, 1835) from the Napostá Grande stream in southern Argentina showed morphological contrasts in shell shape among four locations (Martín, 2003).

Nassarius festivus (Powys, 1838) had different mean shell lengths at three beaches in Hong Kong (Morton & Chan, 2004). Comparing the two groups of *N. vibex*, a small degree of morphological overlap was recorded, but mean shell parameters (length, width and aperture length) were significantly different. As stated by Martín (2003) for *C. parchapii*, because of the spatial proximity between the areas (approximately 500 m), genetic isolation between the two groups of *N. vibex* is improbable, and the morphological differences must consequently result from other factors.

Adopting the classical allometric model to analyse the growth of an organism, instead of selecting a specific model based on K-L information theory and MMI as described by Burnham & Anderson (2002) and Katsanevakis *et al.* (2007), may lead to false conclusions (Katsanevakis *et al.*, 2007; Protopapas *et al.*, 2007; Rabaoui *et al.*, 2007). In this case there is a high possibility of concluding that positive allometry exists when it is actually negative, or vice versa (Katsanevakis *et al.*, 2007; Protopapas *et al.*, 2007). Such errors normally are not considered in analyses of allometric growth of many organisms. Unfortunately, apart from a few studies (Katsanevakis, 2007; Katsanevakis *et al.*, 2007; Rabaoui *et al.*, 2007), information theory and multi-model inference have not been used in the study of relative growth of gastropods. Until now most studies have applied the classical approach (linear allometric model) for marine (McShane *et al.*, 1988; Tokeshi *et al.*, 2000; Tanaka & Maia, 2006), freshwater (Kemp & Bertness, 1984; Martín, 2003; Elkarmi & Ismail, 2007), and terrestrial gastropods (Shanmugan, 1997; Estebenet, 1998).

The linear allometric model, used in several allometric growth studies, was not the most common for all relationships in *N. vibex* (Tables 3 & 4). Most of the relationships were better explained by the *Cb* model, and this suggests that the proportion of growth of one parameter to another is size-dependent. Normally, small individuals of *N. vibex* showed different growth rates from those of adults, which generated a curved line in the plots (Figure 4). In the present study, the proportion of growth of the shell height differed between beaches according to the respective shell length. Young individuals from the Cidade bed increased their shell height more than the gastropods of the same size from Camaroeiro, whereas the inverse was observed for individuals with large shell lengths. The growth pattern of *Al* and *Aw* differed between the areas, with Cidade snails developing larger
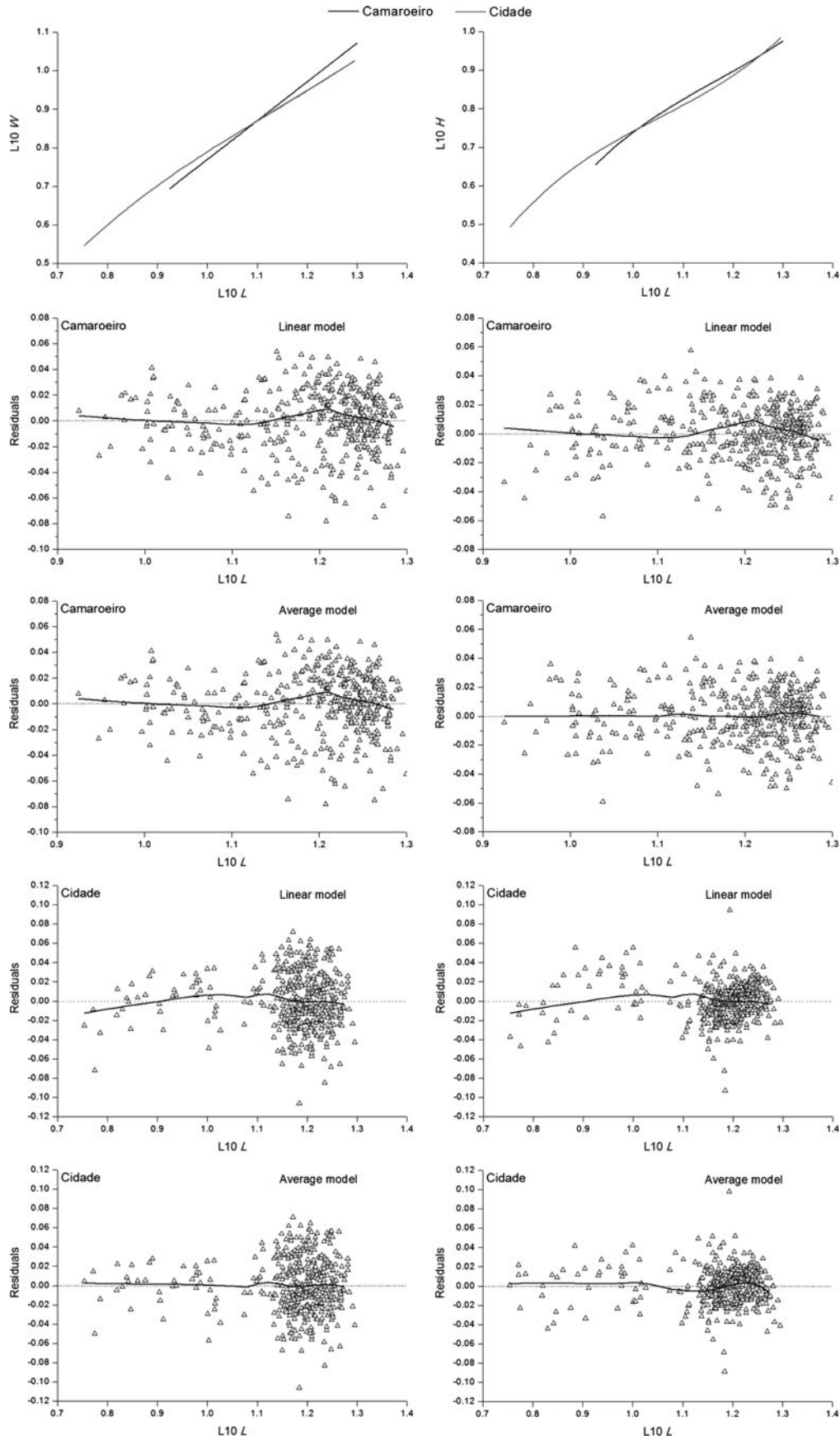
Fig. 4. Growth estimates and comparisons of the linear and average models for the six morphometric relations of *Nassarius vibex* evaluated in the Camaroeiro and Cidade beds. The curves were calculated based on the equations obtained for each average model. *Al*, aperture length; *Aw*, aperture width; *H*, shell height; *L*, shell length; *W*, shell width. Comparisons are based on a loess function fitted to the residuals of each morphometric relation.
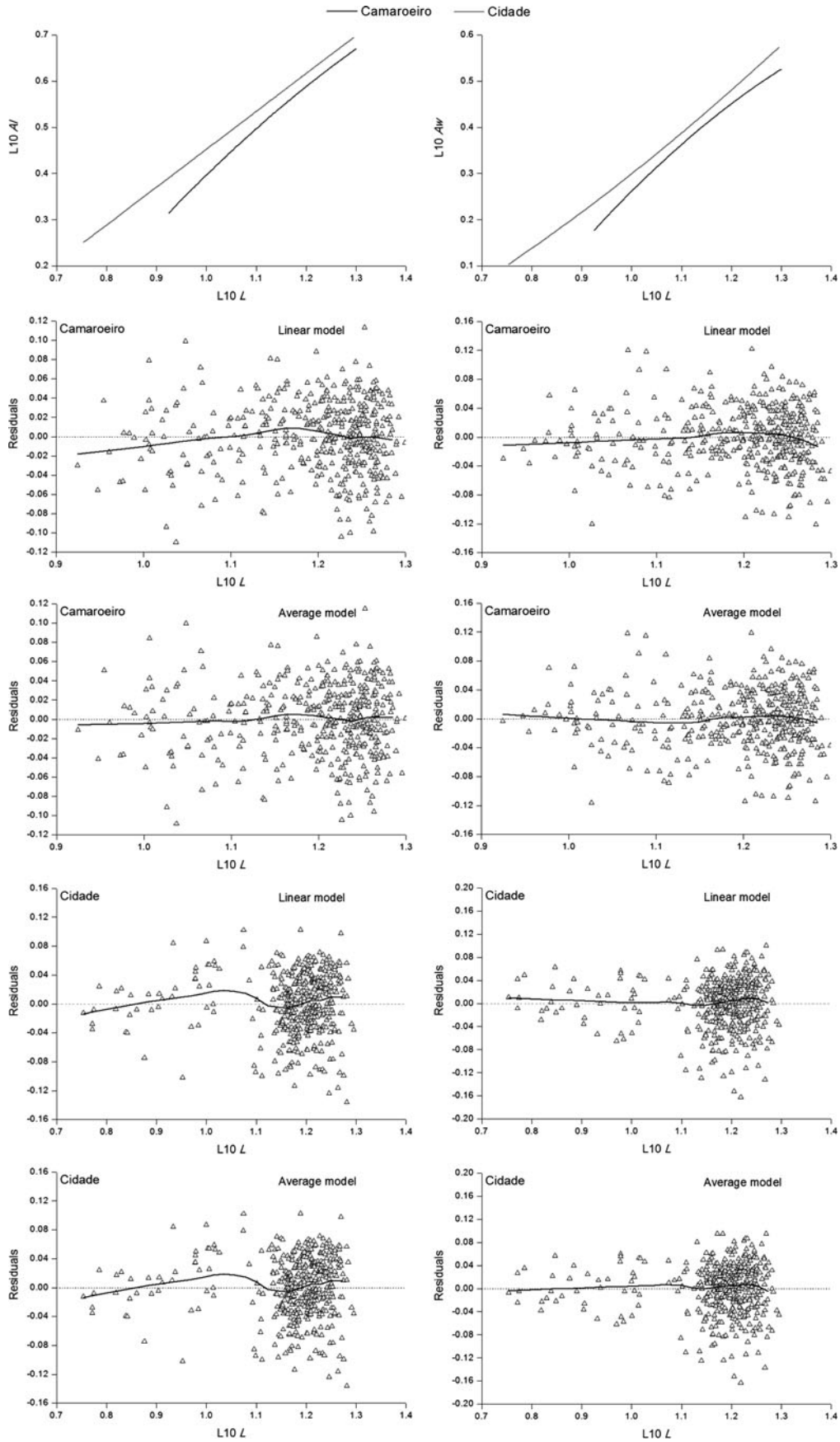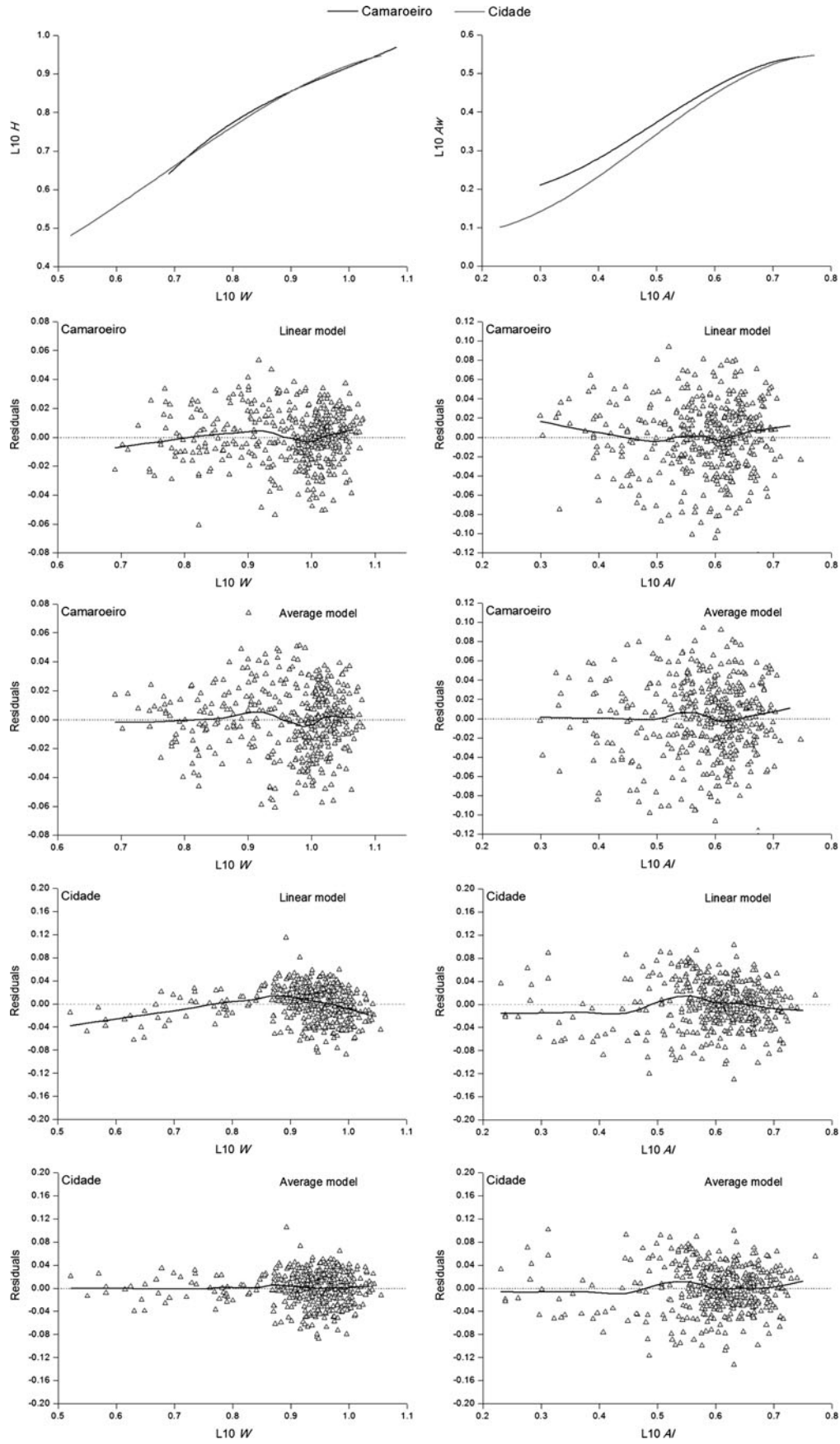
Fig. 4. *Continued.*

Fig. 4. *Continued.*

apertures than individuals from Camaroeiro. It seems that this growth pattern derived from an initial difference in growth rate in the two areas, because large individuals had the same growth curves independently of the beach. This indicates a high growth rate for the individuals from Cidade. However, a study of population dynamics in the two mussel beds (Yokoyama, 2010) found rapid growth for individuals of Camaroeiro Beach, and could explain the differences between the two areas. The significant difference in the shell aperture between the groups of *N. vibex* may reflect a differential growth rate influenced by the age of the individuals, especially for the juveniles.

In the present case, it is obvious that adopting the linear approach could result in loss of information. For gastropods such as *N. festivus* (Morton & Chan, 2004), there is a temporal variation in growth rates over the lifespan, with juveniles growing faster than adults. Such temporal modifications may be lost in the linear model ($y = ax^b$), where the allometric exponent b is always a constant. However, the allometric exponent may not always remain constant, since points of discontinuity in slope b were recognized by Huxley (1932) and can change continuously following a smooth, curvilinear trend without exhibiting marked breakpoints (Hall *et al.*, 2006; Rabaoui *et al.*, 2007). This is a consequence of differential age-class growth because of pressures including competition (Grudemo & Bohlin, 2000), food availability (Underwood, 1976; Edwards & Huebner, 1977; McKillup & McKillup, 1997), and temperature (Barroso *et al.*, 2005a).

The allometric growth of *N. vibex* is irregular, changing over the development of the individual. Even with the spatial proximity, the two groups analysed showed different growth patterns. Marked differences in growth patterns have also been reported between individuals of the same population that are subject to different environmental conditions (García-March *et al.*, 2007). The two areas (Camaroeiro and Cidade beaches) differ in the morphodynamic states and the degree of human influence. Camaroeiro is normally affected by cyclical currents that form sand beds (Farinaccio, 2000), which modifies the sediment composition and consequently reduces the population of *N. vibex*. Breakwaters present at Cidade provide better protection for this area, preventing changes in the sediment composition. However, human-caused effects are more intense than at Camaroeiro, because of the exploitation of the mussels by local fishermen. This mussel removal reduces the population of *M. charruana* and also alters the sediment composition. As stated by Katsanevakis *et al.* (2007), the present study confirms the necessity to apply a set of allometric models that assume changes in the allometry and discontinuity of the allometric exponent. These changes in the growth trajectory are an important source of information about the biology of the species, and may reflect the direct influence of processes such as sexual maturation and recruitment.

ACKNOWLEDGEMENTS

REFERENCES

Akaike H. (1983) Information measures and model selection. *Bulletin of the International Statistical Institute* 44, 277–291.

Arruda E.P. and Domaneschi O. (2005) New species of *Macoma* (Bivalvia: Tellinoidea: Tellinidae) from south-eastern Brazil, and with description of its gross anatomy. *Zootaxa* 1012, 13–22.

Barroso C.M., Moreira M.H. and Richardson C.A. (2005a) Age and growth of *Nassarius reticulatus* in the Ria de Aveiro, north-west Portugal. *Journal of the Marine Biological Association of the United Kingdom* 85, 151–156.

Barroso C.M., Nunes M., Richardson C.A. and Moreira M.H. (2005b) The gastropod statolith: a tool for determining the age of *Nassarius reticulatus*. *Marine Biology* 146, 1139–1144.

Britton J.C. and Morton B. (1994) Marine carrion and scavengers. *Oceanography and Marine Biology: an Annual Review* 32, 369–434.

Buckland S.T., Burnham K.P. and Augustin N.H. (1997) Model selection: an integral part of inference. *Biometrics* 53, 603–618.

Burnham K.P. and Anderson D.R. (2002) *Model selection and multimodel inference: a practical information-theoretic approach.* 2nd edition. New York: Springer.

Chatzinikolaou E. and Richardson C.A. (2007) Evaluating growth and age of netted whelk *Nassarius reticulatus* (Gastropoda: Nassariidae) using statolith growth rings. *Marine Ecology Progress Series* 342, 163–176.

Chow V. (1987) Patterns of growth and energy allocation in northern California populations of *Littorina* (Gastropoda: Prosobranchia). *Journal of Experimental Marine Biology and Ecology* 110, 69–89.

Curtis L.A. (1995) Growth, trematode parasitism, and longevity of a long-lived marine gastropod (*Ilyanassa obsoleta*). *Journal of the Marine Biological Association of the United Kingdom* 75, 913–925.

Demaintenon M.J. (2001) Analysis of reproductive system ontogeny and homology in *Nassarius vibex* (Gastropoda: Buccinidae: Nassariinae). *Journal of Molluscan Studies* 67, 37–49.

Edwards D.C. and Huebner J.D. (1977) Feeding and growth rates of *Polinices duplicatus* preying on *Mya arenaria* at Barnstable Harbor, Massachusetts. *Ecology* 58, 1218–1236.

Ekaratne S.U.K. and Crisp D.J. (1984) Seasonal growth studies of intertidal gastropods from shell micro-growth band measurements, including a comparison with alternative methods. *Journal of the Marine Biological Association of the United Kingdom* 64, 183–210.

Elkarmi A.Z. and Ismail N.S. (2007) Growth models and shell morphometrics of two populations of *Melanoides tuberculata* (Thiaridae) living in hot springs and freshwater pools. *Journal of Limnology* 66, 90–96.

Estebenet A.L. (1998). Allometric growth and insight on sexual dimorphism in *Pomacea canaliculata* (Gastropoda: Ampullariidae). *Malacologia* 39, 207–213.

Farinaccio A. (2000) *Alterações relacionadas à ação antrópica na dinâmica dos processos costeiros nas planícies de Praia Grande/Mongaguá e Enseada de Caraguatatuba, SP.* MSc thesis. Universidade de São Paulo, São Paulo, Brazil.

Forroni T. de O., Yokoyama L.Q. and Amaral A.C.Z. (2008) Dieta alimentar de *Nassarius vibex* (Gastropoda: Nassariidae). In *XXVII Congresso Brasileiro de Zoologia, Curitiba, Paraná*, p. 1784.

Frey D.F. and Pimental R.A. (1978) Principal component analysis and factor analysis. In Colgan P.W. (ed.) *Quantitative ethology.* New York: John Wiley and Sons, pp. 219–245.

García-March J.R., García-Carrascosa A.M., Peña Cantero A.L. and Wang Y.G. (2007) Population structure, mortality and growth of *Pinna nobilis* Linnaeus, 1758 (Mollusca: Bivalvia) at different depths in Moraira bay (Alicante, Western Mediterranean). *Marine Biology* 150, 861–871.

Gould S.J. (1966) Allometry in Pleistocene land snails from Bermuda; the influence of size upon shape. *Journal of Paleontology* 40, 1131–1141.

Grudemo J. and Bohlin T. (2000) Effects of sediment type and intra- and interspecific competition on growth rate of the marine snails *Hydrobia ulvae* and *Hydrobia ventrosa. Journal of Experimental Marine Biology and Ecology* 253, 115–127.

Hall N.G., Smith K.D., Lestang S. de and Potter I.C. (2006) Does the largest chela of the males of three crab species undergo an allometric change that can be used to determine morphometric maturity? *ICES Journal of Marine Science* 63, 140–150.

Hurvich C.M. and Tsai C.L. (1989) Regression and time series model selection in small samples. *Biometrika* 76, 297–307.

Huxley J.S. (1932) *Problems of relative growth.* London: Methuen.

Katsanevakis S. (2007) Growth and mortality rates of the fan mussel *Pinna nobilis* in Lake Vouliagmeni (Korinthiakos Gulf, Greece): a generalized additive modelling approach. *Marine Biology* 152, 1319–1331.

Katsanevakis S., Thessalou-Legaki M., Karlou-Riga C., Lefkaditou E., Dimitriou E. and Verriopoulos G. (2007) Information-theory approach to allometric growth of marine organisms. *Marine Biology* 151, 949–959.

Kemp P. and Bertness M.D. (1984) Snail shape and growth rates: evidence for plastic shell allometry in *Littorina littorea. Proceedings of the National Academy of Sciences of the United States of America* 81, 811–813.

Lambeck R.H.D. (1984) Dynamics, migration and growth of *Nassarius reticulatus* (Mollusca, Prosobranchia) colonizing saline Lake Grevelingen (SW Netherlands). *Netherlands Journal of Sea Research* 18, 395–417.

Lamparelli C.C. (1998) *Mapeamento dos ecossistemas costeiros do Estado de São Paulo.* São Paulo: CETESB.

Martín P.R. (2003) Allometric growth and inter-population morphological variation of the freshwater snail *Chilina parchappii* (Gastropoda: Chilinidae) in the Napostá Grande Stream, Southern Pampas, Argentina. *Studies on Neotropical Fauna and Environment* 38, 71–78.

McKillup S.C. and Butler A.J. (1983) The measurement of hunger as a relative estimate of food available to populations of *Nassarius pauperatus. Oecologia* 56, 16–22.

McKillup S.C. and McKillup R.V. (1997) Effect of food supplementation on the growth of an intertidal scavenger. *Marine Ecology Progress Series* 148, 109–114.

McShane P.E., Smith M.G. and Beinssen K.H.H. (1988) Growth and morphometry in abalone (*Haliotis rubra* Leach) from Victoria. *Australian Journal of Marine and Freshwater Research* 39, 161–166.

Moran M.J., Fairweather P.G. and Underwood A.J. (1984) Growth and mortality of the predatory intertidal whelk *Morula marginalba* Blainville (Muricidae): the effects of different species of prey. *Journal of Experimental Marine Biology and Ecology* 75, 1–17.

Morton B. and Chan K. (2004) The population dynamics of *Nassarius festivus* (Gastropoda: Nassaridae) on three environmentally different beaches in Hong Kong. *Journal of Molluscan Studies* 70, 329–339.

Preston S.J. and Roberts D. (2007) Variation in shell morphology of *Calliostoma zizyphinum* (Gastropoda: Trochidae). *Journal of Molluscan Studies* 73, 101–104.

Protopapas N., Katsanevakis S., Thessalou-Legaki M. and Verriopoulos G. (2007) Relative growth of the semi-terrestrial crab *Pachygrapsus marmoratus*: an information–theory approach. *Scientia Marina* 71, 383–394.

Rabaoui L., Zouari S.T., Katsanevakis S. and Hassine O.K.B. (2007) Comparison of absolute and relative growth patterns among five *Pinna nobilis* populations along the Tunisian coastline: an information theory approach. *Marine Biology* 152, 537–548.

Shanmugam A. (1997) Length–weight and allometric relationship in a pulmonate snail *Cassidula nucleus* Martyn. *Indian Journal of Marine Sciences* 26, 224–226.

Takada Y. (1995) Variation of growth rate with tidal level in the gastropod *Monodonta labio* on a boulder shore. *Marine Ecology Progress Series* 117, 103–110.

Tallmark B. (1980) Population dynamics of *Nassarius reticulatus* (Gastropoda, Prosobranchia) in Gullmar fjord, Sweden. *Marine Ecology Progress Series* 3, 51–62.

Tanaka M.O. and Maia R.C. (2006) Shell morphological variation of *Littoraria angulifera* among and within mangroves in NE Brazil. *Hydrobiologia* 559, 193–202.

Tokeshi M., Ota N. and Kawai T. (2000) A comparative study of morphometrics in shell-bearing molluscs. *Journal of Zoology* 251, 31–38.

Underwood A.J. (1976) Food competition between age-classes in the intertidal neritacean *Nerita atramentosa* Reeve (Gastropoda: Prosobranchia). *Journal of Experimental Marine Biology and Ecology* 23, 145–154.

and

Yokoyama L.Q. (2010) Nassarius vibex *(Gastropoda, Nassariidae): crescimento e reprodução em bancos de mitilídeos de substrato areno-lamoso na costa Sudeste do Brasil.* PhD thesis. Universidade de São Paulo, São Paulo, Brazil.

Correspondence should be addressed to:
L.Q. Yokoyama
Departamento de Zoologia
Instituto de Biociências
Universidade de São Paulo (USP)
São Paulo, SP, Brazil
email: lqyokoyama@gmail.com