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Variability in age and growth of common rock oyster *Saccostrea cucullata* (Bivalvia) in Ascension Island (central-east Atlantic)

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Common rock oysters Saccostrea cucullata *(Bivalvia) were sampled from intertidal volcanic rocks at five sites around Ascension Island (central-east Atlantic) in austral winter 2012–2014. Their left valves were sectioned to reveal annual growth increments. Their periodicity was validated by the presence of specific growth marks in the increment sequence visible in consecutive years of sampling. No significant differences in shell height-weight relationships were revealed between sites. Marginal analysis of the increment width showed that* S. cucullata *accelerated their growth in cooler winter months and decelerated the growth in warmer summer months. Rock oysters in Ascension Island lived up to 14–16 years with maximum age of 26 years. Young oysters (1–5 years old) had the same growth rates both in shell height and weight in all sites. However, their starting point (size and weight of 1-year-old animals) was different in various sites, with largest animals occurring in the most protected site Northeast Bay with sheltered inlets and smallest animals inhabiting exposed to surf site of Letterbox. Growth in shell height was best described by von Bertalanffy growth function with the largest* L_∞ *in animals inhabiting the windward side and smallest animals occurring in the leeward side of the Island. In summary,* S. cucullata *around Ascension Island lived longer but had slower growth than those from tropical regions of Southwest Asia probably due to comparatively low productivity observed in the central part of the equatorial tropical Atlantic.*

Keywords: *Saccostrea cucullata*, rock oyster, growth, Ascension Island

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INTRODUCTION

Ascension Island is located in the open waters of the Atlantic Ocean approximately midway between South America and Africa. This small tropical island (about 90 km^2) is an exposed part of a solitary volcanic sea mount situated just to the west of the Mid-Atlantic Ridge, approximately 8° (~ 900 km) south of the equator (Irving, 2013). The closest oceanic island is St. Helena, situated about 1130 km to the south-east. Ascension Island has a typical arid oceanic climate with slight seasonal variability in mean air temperatures from 24°C in austral winter to 27°C in austral summer. Precipitation varies seasonally from 18–33 mm of rainfall per month in March–May to just 4 mm per month in November–January. The island is surrounded by the Tropical Surface Waters with high temperatures (24–28°C) and salinities (35.5–36) carried by the equatorial branch of the westward flowing South Equatorial Current (Stramma & England, 1999; Stramma & Schott, 1999). Surface water temperatures nearshore are subject to seasonal variation ranging from 24°C in austral winter to 28°C in austral summer (Brewin & Laptikhovsky, 2013). Predominant south-westerly trade winds create a strong swell (Gordon & Bosley, 1991) that affects mainly the south-eastern and eastern coasts with a relatively quiet western leeway part of Ascension Island.

The rugged coastline of Ascension Island interchanges yellow sandy beaches and volcanic black rock outcrops. In some places, the ridges of black rocks create deep inlets protected from ocean swells. The intertidal parts of these ridges are inhabited by naturally grown common rock oyster *Saccostrea cucullata* Born, 1778. This relatively small tropical oyster (shell height usually does not exceed 10 cm) is widely distributed in the tropical Indo-West Pacific, occurring also in the southern tropical Atlantic along the western African coast (Yonge, 1960). In many parts of its area, these oysters are harvested by artisanal fisheries (Davenport & Wong, 1992). In northern Australia, Thailand, China and India *S. cucullata* are cultivated in aquaculture, being quite popular in local markets because of their strong iodine taste (Jarayabhand & Thavornyutikarn, 1995; Nell, 2001).

Growth rates of oysters are highly variable and strongly depend on environmental parameters such as temperatures, food availability, and amount of epibiontic growth as well as intrinsic biotic factors such as genetic variation (Singh & Zouros, 1978; Chiu, 1997). In the Hong Kong area, the fastest growth in *S. cucullata* was observed during first year of ontogeny with gradually decreasing growth rates with age. The growth was seasonal with maximum growth in summer and its practical cessation in winter when temperatures fell below 20°C (Morton, 1990; Chiu, 1997). *Saccostrea cucullata* have a short life cycle especially in the peripheries

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of their ranges, with the majority of animals living just over two years (Morton, 1990; Chiu, 1997). However, there are reports that *S. cucullata* may live up to 26 years (South Africa, Dye, 1990). It has been suggested that such a short life cycle in *S. cucullata* is usually a result of harsh environmental conditions with exposure to high temperatures and pollution in nearshore areas (Krishnakumari *et al.*, 1990; Davenport & Wong, 1992; Mtanga & Machiwa, 2007).

The main aim of the present study is to investigate age and growth patterns of common rock oysters from various intertidal sites around Ascension Island and to identify possible ecological cues that determine variability in growth rates and lifespan of these bivalves in one of the remote and pristine oceanic locations.

MATERIALS AND METHODS

Sampling

Random samples of approximately 100 rock oysters each were collected from intertidal rocks at five sites located around the Ascension Island in August 2012. The following areas were sampled (Figure 1A). On the lee side of the island the oysters were taken from the fishing pier in Georgetown (exposed without sheltered inlets, Figure 1C) and PanAm Bay (semi-exposed without shelter) and on the windward side of the island from Shelly Beach (semi-exposed, Figure 1D), Letterbox (very exposed) and Northeast Bay (with deep rocky sheltered inlets, Figure 1B). The right valve of oysters was cemented to porous volcanic rock (Harper, 1997) making it impossible to detach intact. Therefore, the bivalves were broken from the rocks using a chisel and hammer paying attention that the left (flat) valve with umbo attachment area was not damaged. Oysters were brought to the lab and put into boiling water for a few minutes to open the valves. The valves were separated by cutting the adductor muscle and detaching the umbo area. For each left valve, the maximum shell height from the hinge to the growth edge was measured to the nearest 1 mm. The surface of the shell valves was usually clean, but whenever the epifauna was found it was gently removed (Figure 2A). The inner surface of the left valve with intact umbo area was cleaned from the adductor, dried and then weighed to the nearest 0.1 g.

Additional control random samples of 30 oysters were collected from Northeast Bay in June 2013 and June 2014 for age validation analysis.

Ageing

The shells were kept dry until further analysis in the laboratory of the Fisheries Department in the Falkland Islands. All intact left valves sampled were cut with Buehler 1000 Isomet precision saw. Each valve was cut longitudinally from the hinge to the growing edge across the adductor muscle scar (AMS, Figure 2B). The halved valve was then ground using 600-grit waterproof sandpaper and polished using 1200-grit sandpaper with running water on Buehler Metaserve 2000 grinder/polisher. To investigate the microstructure of growth lines, some valves were sectioned (0.5–1 mm thick), put on glass slides, embedded into clear casting resin and covered with a cover slip.

Growth increments were examined and counted on the sectioned surface of halved valves. The valves were mounted

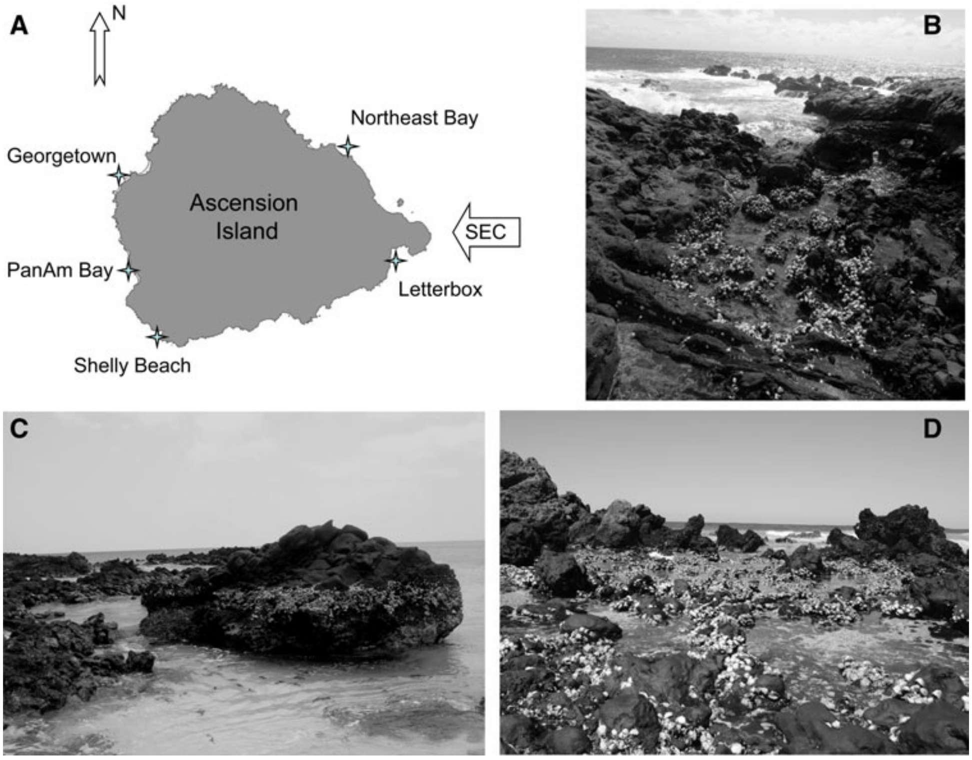

Fig. 1. (A) Locations of sampling sites of *S. cucullata* around Ascension Island. Arrow SEC shows the direction of South Equatorial Current; (B) Deep inlets with oysters sheltered from surf and breaking waves in Northeast Bay; (C) Exposed rocks with oysters in Georgetown site; (D) Semi-sheltered colony of oysters in Shelly Beach.

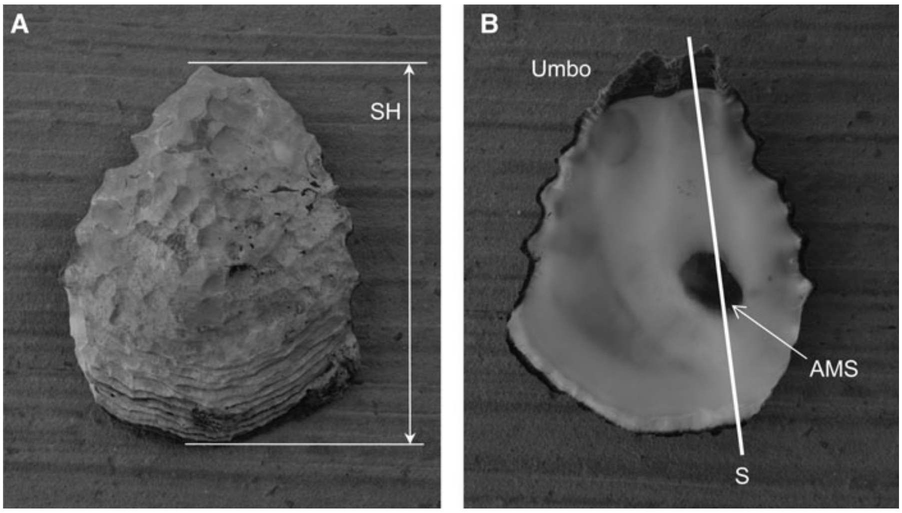

Fig. 2. General view of the left valve of *S. cucullata*. (A) Outer side without epibiontic growth, SH (shell height); (B) Inner side showing umbo area and position of adductor muscle scar (AMS). S, line of the longitudinal section through the valve.

in small trays filled with lentils, to hold the valve in place, in such a way that the sectioned surface was horizontal. The trays were then put onto the base of the Olympus SZX-12 zoom microscope. The sectioned surfaces were observed under reflected light using a powerful fibre optic light source Olympus KL-1500 at 10–20× magnification. To increase the resolution of growth increments, the section was covered with a small amount of immersion oil. Growth increments were counted in two parts of the shell section, close to the hinge and close to the AMS (Figure 3A). Growth lines that were present as continuous and uninterrupted lines in both parts of the section were considered as annual growth increments (Harding & Mann, 2006). After ascertaining that the number of growth increments in both parts of the section was the same, either part of the section was used for growth increment counts in case one of the parts had been damaged during sampling (e.g. a broken hinge area).

To validate annual growth increments, we looked for a specific pattern in shell microstructure (such as a wider band or darker line) that was present in the shells collected in three consecutive years of sampling in one site. The number of growth increments between that pattern and growing edge of the shell was compared in shells collected in 2012–2014 for possible validation of growth increment deposition.

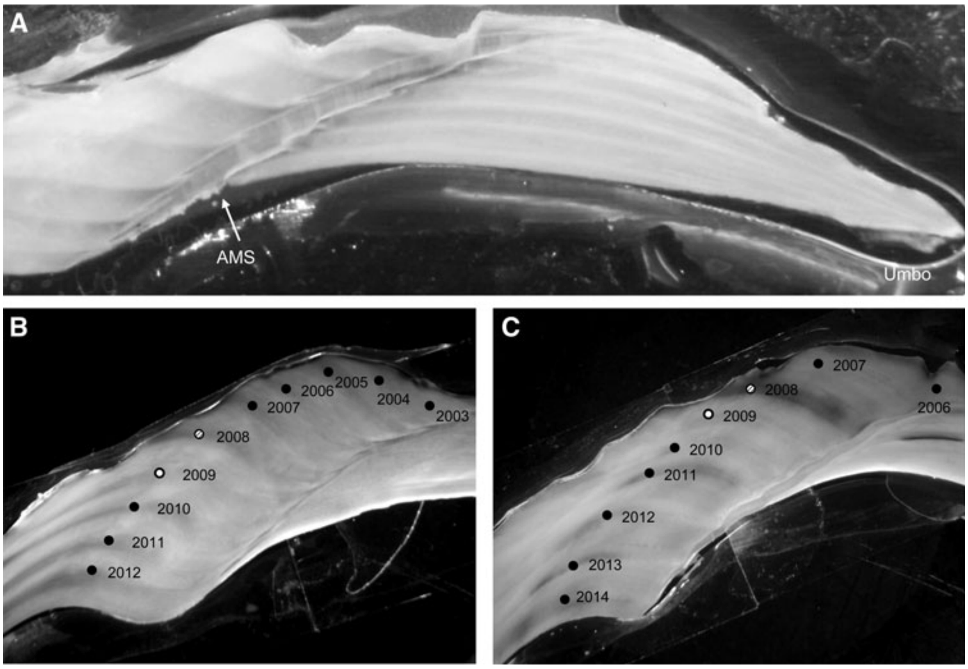

Fig. 3. Sectioned valves of *S. cucullata*. (A) General view with distinct growth increments both in the outer and inner areas to the adductor muscle scar (AMS); (B) location of weak (white circle) and very strong (hatched circle) austral summer marks of decreased growth in an oyster collected in August 2012 (11 years old); (C) location of weak (white circle) and very strong (hatched circle) summer marks of decreased growth in an oyster collected in June 2014 (10 years old). Years of increments formation are labelled.

Statistical methods

The power function was used to describe the shell height (L) – weight (W) relationship of the left valve of the oysters. Both sides of the power equation were log transformed to be able to estimate the parameters by linear regression as

$$\log(W_{i,j}) = \log(A_j) + B_j \times \log(L_{i,j}) + \varepsilon_{i,j}$$

where A_j and B_j are the parameters of the power function for each sampling site j and $\epsilon_{i,j}$ are the residuals. Parameters $\log(A_j)$ and B_j were estimated using the linear model function 'lm' in R statistical software (R Core Team, 2014). Statistical comparisons of parameters $\log(A_j)$ and B_j from different sampling sites were performed by the analysis of covariance (Dalgaard, 2008).

Preliminary analysis showed various range of age distributions in sampling sites. To compare the growth of oysters at different sites, it was decided to restrict the analysis to age classes between 1 and 5 years old, as these classes were present in all sites. Then, shell height-at-age and weight-at-age relationships were fitted by linear regressions to analyse whether the differences in slopes and intercepts were significant between sampling sites. The linear model function 'lm' in R statistical software (R Core Team, 2014) was used to fit regressions of various log transformations of shell height and weight as response variables of age. The residuals of the resultant linear models were tested for normality. The P value derived from the Shapiro–Wilk test was used as the criterion to choose the most suitable model (with the highest P value). An analysis of covariance was then performed by adding an interaction between age and sampling site as independent variables (Dalgaard, 2008). The best fit was obtained with log-transformed dependent variables shell height ($L_{i,j}$) and weight ($W_{i,j}$) explained by age ($\mathrm{Age}_{i,j}$) of the oyster i sampled in site j and modelled as

$$\log(L_{i,j}) = a_j + b_j \times Age_{i,j} + \varphi_{i,j}$$

Or

$$\log(W_{i,j}) = c_j + d_j \times Age_{i,j} + \phi_{i,j}$$

where a_j and c_j were the intercepts and b_j and d_j were the slopes for shell height-at-age and weight-at-age relationships respectively, sampled at the site j. $\phi_{i,j}$ and $\varphi_{i,j}$ were the residuals of each linear model.

Growth curves of oysters at each sampling site and for the pooled data were constructed by fitting the shell height-at-age data with the von Bertalanffy growth model (Beverton and Holt, 1957; Hilborn and Walters, 1992) as

$$L_i = L_\infty(1 - e^{-K(t_i - t_o)}) + \xi_i$$

where L_i was observed shell height of oysters i at age t_i; L_∞ was asymptotic average shell height, K was the Brody growth coefficient, t_o was the shell height at age 0 and ξ_i were the residuals for oysters i. These three parameters were estimated using nls function of the R package nlstools (Baty *et al.*, 2014). Confidence interval of each parameter was estimated by bootstrapping residuals following the methodology implemented in nlsBoot function of the same package. Asymptotic average shell height (L_∞) and Brody growth coefficient (K) were plotted with 95% confidence intervals for graphical comparisons.

RESULTS

Time of formation and validation of increments

The growth increments were well-resolved in both parts of the shell sections, close to the hinge and close to AMS (Figure 3A). The shell microstructure revealed periodic growth indicated by formation of the narrower and darker growth band as compared with the adjacent wider and lighter growth band. In samples studied, the last light growth band started to form before June. Oysters collected in June had their last increment already formed as a narrow band. In oysters collected in August, the last increment was about half the width of the penultimate light growth band.

Shells sampled from the Northeast Bay were used for validation of growth increments. The fourth increment of about 20% of large shells collected in 2012 from the end of the sequence (dated for 2009) was much paler than the rest of the brownish increments, and the 5th increment (dated for 2008) was much darker that the rest of the increments (Figure 3B). Unfortunately, none of the shells from the 2013 subsample from the Northeast Bay had this paler increment, probably due to smaller shell size. However, three shells from the 25 shells sampled in 2014 had the sixth increment (dated for 2009) paler than the rest, and the 7th increment much darker than the rest of the sequence (Figure 3C). Therefore, annual periodicity of the growth increments in *S. cucullata* was confirmed. It is notable that those 'paler' increments were not observed in all shells sampled. Probably, it appeared in shells at specific locations in the colony, which were not possible to recognise during sampling.

Shell height–weight

The shell height–weight relationships were analysed separately for every sampling site. The estimated values of intercepts of the log-transformed power function (A_j) varied from 1.26e-04 (PanAm Bay) to 3.37e-04 (Georgetown). The estimated values of the power parameter B_j ranged from 2.65 (Georgetown) to 2.85 (Northeast Bay) (Table 1). The analysis of covariance did not reveal any significant differences between intercepts and slopes between any of the five sampling sites.

Age and growth

The maximum age of oysters in various sampling sites around Ascension Island differed. Oysters were the youngest in Georgetown, with maximum age of 7 years, and the majority of oysters attaining age of 5 years (Figure 4). That represented a natural phenomenon as there is no oyster harvesting by the local population. The oldest oyster was collected in Letterbox site – a 26-year-old animal with a shell height of 49 mm and left valve weight of 17 g. Most of the animals were younger than 10 years old. Both the largest (137 mm SH, 11 years) and the heaviest (152 g LVW) oysters were sampled in the Northeast Bay (Figure 4).

Table 1. Results of the linear model fitted between log-transformed weight and log-transformed length

	George town	Letterbox	Northeast Bay	PanAm Bay	Shelly Beach
A_j	3.37e-04	1.78e-04	1.65e-04	1.26e-04	1.80e-04
A_j SE	1.85e-04	1.10e-04	0.93e-04	0.60-04	0.80e-04
B_j	2.65	2.80	2.85	2.83	2.79
B_j SE	0.11	0.12	0.11	0.10	0.09
Georgetown		0.33	0.26	0.09	0.27
Letterbox	0.36		0.91	0.58	0.99
Northeast Bay	0.20	0.77		0.65	0.88
PanAm Bay	0.23	0.83	0.92		0.50
Shelly Beach	0.32	0.97	0.71	0.78	

A_j (intercepts) and B_j (slopes) values associated with their standard errors (SE) are presented in the upper part of the table. *P* values of multiple comparisons of intercept (above the diagonal) and slopes (below the diagonal) are presented in the second part of the table.

Among animals ≤ 5 years old, shell height–age analysis (Table 2) showed that slopes of log-transformed exponential curves ranged from 0.157 (Northeast Bay) to 0.197 (PanAm Bay) and were not significantly different from one site to another. The intercepts ranged from 3.05 (Letterbox) to 3.55 (Northeast Bay). Multiple comparisons between sites revealed that the intercept of PanAm Bay sample was significantly lower than intercepts of Georgetown and Northeast Bay. The latter was also significantly higher than that of Letterbox.

Weight-at-age relationships of oysters ≤ 5 years old was best described by the exponential function, similar to that of SH-at-age relationships. The intercepts of the log-transformed functions ranged from -0.422 (Letterbox) to 1.075 (Northeast Bay). Multiple comparisons of intercepts revealed that PanAm Bay and Letterbox intercepts were significantly lower than the intercepts of Georgetown and Northeast Bay samples. The intercept of the Letterbox sample was also significantly lower than that of the Georgetown sample. Slopes varied between 0.480 (Georgetown) and 0.613 (Letterbox). No significant differences between them were revealed (Table 3).

Growth in shell height of oysters pooled from all sampling sites (population growth) was described by the von Bertalanffy growth model. The population asymptotic average shell height L_∞ was 86.06 mm (SE $\pm$ 4.04), the Brody growth coefficient $K = 0.234$ (SE $\pm$ 0.037) and shell height at $t_0 = -0.69$ (SE $\pm$ 0.33). Graphical comparisons of L_∞ (Figure 5A) of each sampling site revealed that oysters from PanAm Bay and Shelly Beach had the lowest L_∞ with narrow confidence intervals. Georgetown and Letterbox samples had intermediate L_∞ values, but the former sample had the widest confidence interval probably due to a narrow age range. The Northeast Bay oysters have the highest L_∞ with intermediate confidence interval (Figure 5A). The Brody growth coefficients K were the lowest both in Northeast Bay and Georgetown samples, intermediate values in the Letterbox sample and highest values in PanAm Bay and Shelly Beach samples. Confidence intervals of the K coefficients were quite similar in all sampling sites and overlapped one another (Figure 5B).

DISCUSSION

Saccostrea cucullata exhibit a seasonal periodical growth of the shell which resulted in the appearance of well-defined growth increments. Our validation experiment showed that these increments were laid down with annual periodicity, similar to the other oysters (*Ostrea edulis*; Richardson *et al.*, 1993; *Crassostrea virginica*; Kraeuter *et al.*, 2007). Growth of temperate species of oysters practically ceases during cold winter months, forming the sharp 'winter' line (Richardson *et al.*, 1993). Despite relatively low variation in water temperatures nearshore (24–28°C, Brewin & Laptikhovsky, 2013), tropical *S. cucullata* had periodical growth of their shells. The results of the present study showed that *S. cucullata* accelerated their growth in cooler winter months and decelerated the growth in warmer summer months of the southern hemisphere. It is known that the heat tolerance of *S. cucullata* is high (43°C) and these oysters do not take any oxygen from the air because of the risk of desiccation (Davenport and Wong, 1992). However, their body temperature is taken from the rock (Davenport and Wong, 1992) that might be heated >40°C during tidal exposure. Thus, increased sun radiation in summer months could depress the growth of oysters, forming a seasonal mark in the shell microstructure.

The results of our study showed that pristine water conditions around the Ascension Island favoured long lifespans and relatively fast growth rates in intertidal common rock oysters *S. cucullata* despite oligotrophic conditions typical to the tropical part of the open Atlantic Ocean (Gordon and Bosley, 1991; Stramma and England, 1999). Overall, *S. cucullata* in Ascension Island lived much longer (up to 14–16 years) than in either polluted or eutrophic inshore waters of Southern Asia (2–4 years, Morton, 1990; Chiu, 1997). The maximum age of *S. cucullata* revealed from our samples on Ascension Island (26 years) was similar to that observed in South African coasts (Dye, 1990).

It was revealed that the level of heterozygosity might be one of the possible reasons for high variation in shell size in oysters of the same age, with positive correlation between individual heterozygosity and body weight (Singh and Zouros, 1978). Marine predation by muricid drilling gastropods on molluscs was another factor influencing the development of thicker valves in *Crassostrea* oysters living in shallow marine and estuarine environments in Tertiary and Quaternary (Kirby, 2001). The small size of Ascension Island should favour interbreeding at the dispersal planktonic stage thus providing genetic homogeneity of the local population of *S. cucullata*. Therefore, variability in ecological conditions such as food availability and shelter from surf and breaking waves were

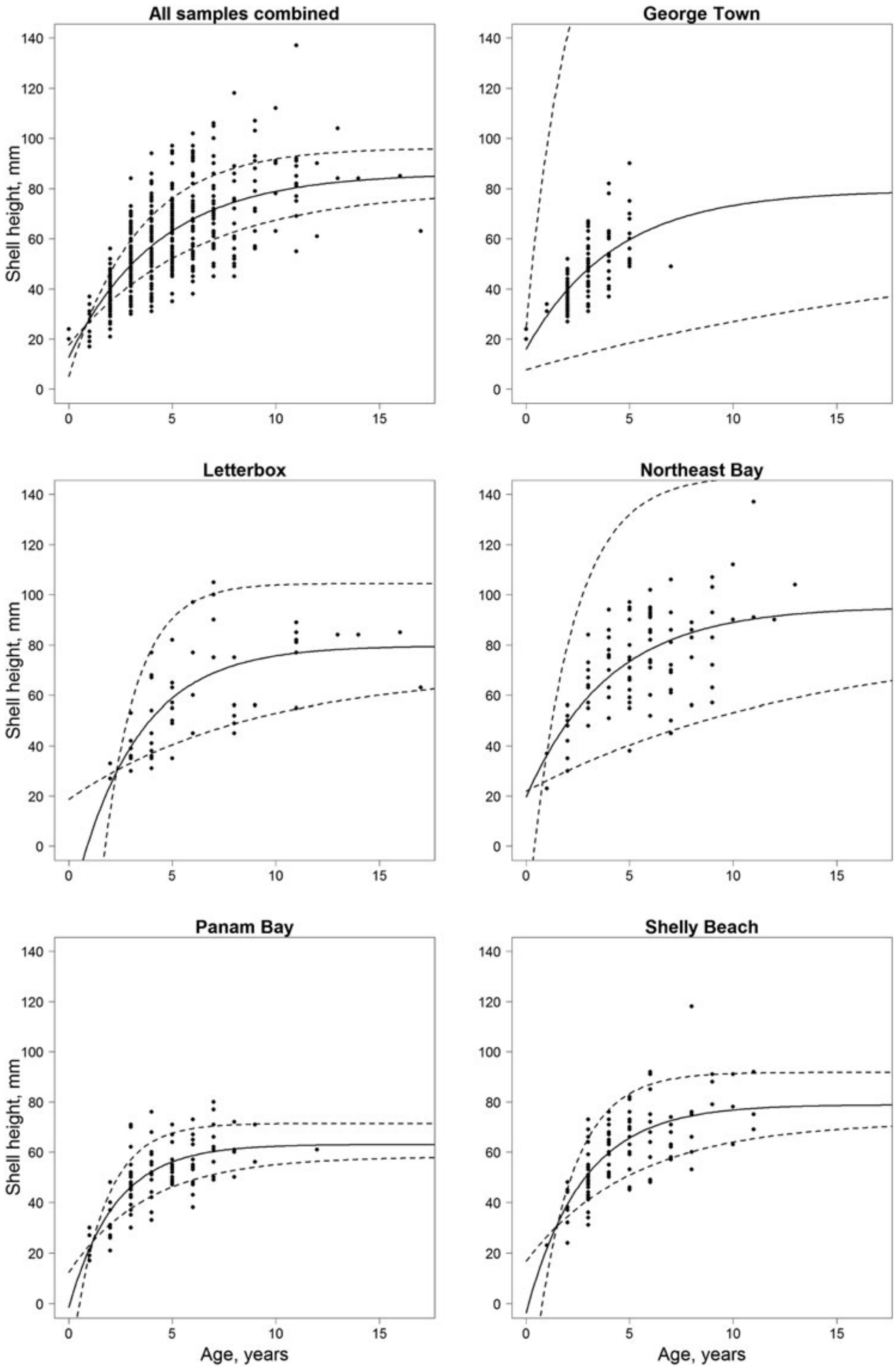

Fig. 4. Shell height at age scatterplots and fitted von Bertalanffy growth curves with 95% confidence intervals for *S. cucullata* at various sampling sites around Ascension Island.

probably the main drivers of diversity both in lifespan and growth rates at various sites around Ascension Island.

Among all five sites studied, oysters that lived in the windward area of the island displayed maximum variability both in shell height and weight. Among them, bivalves that inhabited deep inlets of the Northeast Bay and were therefore most protected from the impact of surf and breaking waves were the largest (in terms of L_∞), whereas those from exposed enclosures of Letterbox had medium L_∞. These animals had also the longest lifespans (up to 14 and 26 years, respectively) as compared with other sites. Oysters that lived in leeward side of the Island on the rocks facing the shore (Shelly Beach and PanAm Bay) but exposed to surf had smaller variability in shell size of the same-aged animals, shorter lifespans and smaller sizes (in terms of L_∞). And, oysters which lived on exposed rocks of the leeward part of the Island

Table 2. Results of the linear model fitted between log-transformed length and age

	George town	**Letterbox**	**Northeast Bay**	**PanAm Bay**	**Shelly Beach**
Intercept	3.34	3.05	3.55	3.13	3.32
Intercept SE	0.07	0.18	0.09	0.08	0.09
Slope	0.162	0.195	0.157	0.197	0.187
Slope SE	0.021	0.045	0.024	0.021	0.022
Georgetown		0.14	0.056	0.042	0.84
Letterbox	0.50		0.01	0.68	0.19
Northeast Bay	0.87	0.45		4.65e-04	0.06
PanAm Bay	0.24	0.98	0.21		0.12
Shelly Beach	0.43	0.87	0.38	0.76	

Intercept and slope values associated with their standard errors (SE) are presented in the upper part of the table. *P* values of multiple comparisons of intercept (above the diagonal) and slopes (below the diagonal) are presented in the second part of the table. Values in bold represent differences at 5% significance level.

Table 3. Results of the linear model fitted between log-transformed weight and age

	George town	**Letterbox**	**Northeast Bay**	**PanAm Bay**	**Shelly Beach**
Intercept	0.700	−0.422	1.075	−0.345	0.575
Intercept SE	0.171	0.473	0.237	0.198	0.234
Slope	0.480	0.613	0.502	0.609	0.529
Slope SE	0.053	0.117	0.063	0.055	0.064
Georgetown		**0.03**	0.20	**8.34e-05**	0.67
Letterbox	0.30		**4.97e-03**	0.88	0.06
Northeast Bay	0.79	0.41		**6.33e-06**	0.13
PanAm Bay	0.09	0.97	0.20		**2.96e-03**
Shelly Beach	0.55	0.53	0.76	0.35	

Intercept and slope values associated with their standard errors (SE) are presented in the upper part of the table. *P* values of multiple comparisons of intercept (above the diagonal) and slopes (below the diagonal) are presented in the second part of the table. Values in bold represent differences at 5% significance level.

(Georgetown) had the shortest lifespan but medium L_∞. The rate of attaining L_∞ (Brody growth coefficient, K) was the highest in semi-sheltered sites of the leeward side of the island and smallest in oysters living in the windward side of the Island. The bivalves in the exposed part of the Georgetown site died before attaining their L_∞, therefore their calculated value of K was not reliable.

Interestingly, young oysters (1–5-year-old) had the same growth rates both in shell height and weight in all sites studied expressed in terms of the slope of their exponential growth curves. However, their starting point (size and weight of 1-year-old animals as indicated by intercept of the growth curves) was different in various sites, with largest animals occurring in the protected Northeast Bay and smallest animals inhabiting exposed Letterbox site. Different starting point of growth at the age of 1 year resulted in corresponding differences both in size and weight of the oysters at the age of 5 years.

The growth rates of the Ascension populations of *S. cucullata* were lower than those from tropical regions of Southeast Asia, where 2-year-old oysters attained 46–50 mm SH (Krishnakumari *et al.*, 1990). Probably, relatively low productivity of the equatorial tropical Atlantic (Stramma & England, 1999) was the main factor of slower growth of *S. cucullata* as compared with those inhabiting the productive eutrophic inshore waters of Indian coasts. The sizes of adult common rock oysters *S. cucullata* around Ascension Island were smaller than those of commercial Pacific oysters *Crassostrea gigas* both in the Atlantic (Cardoso *et al.*, 2007) and Pacific (Harding & Mann, 2006). However, the ability of common rock oysters to survive high temperatures in the tropics and their specific taste make them popular in artisanal fisheries and aquaculture in tropical areas of the Indo-West Pacific (Nell, 2001).

A relatively long lifespan and clear seasonal periodicity in growth rates of the shell can make rock oysters from Ascension Island suitable ‘recorders’ of environmental changes by comparing stable isotope and trace element concentrations in shell growth increments, as well as the increment thickness with interannual fluctuations in oceanographic parameters and precipitation in the central tropical Atlantic.

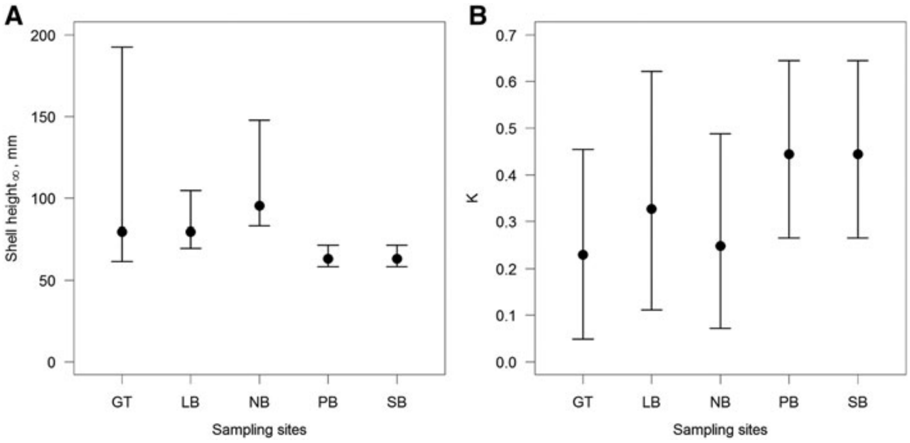

Fig. 5. Asymptotic shell height (A) and Brody growth coefficient (B) of von Bertalanffy growth curves with 95% confidence intervals for *S. cucullata* at various sampling sites around Ascension Island. GT, Georgetown; LB, Letterbox; NB, Northeast Bay; PB, PanAm Bay; SB, Shelly Beach.

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