GROWTH DETERMINATION OF TROPICAL LIMPET *Cellana testudinaria* (Linnaeus, 1758) LIVING ON THE ROCKY SHORE OF OHOIWAIT, SOUTHEAST MOLUCCAS, INDONESIA

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ABSTRACT

Monthly shell-length frequency distributions were used to analyse the size and age structure of the limpet population inhabiting the rocky shore of Ohoiwait, Southeast Moluccas. The lengths of the collected specimens ranged from 8.0 to 31.8 mm. The analysis of the successive frequency distributions suggested that the population consisted of 4 to 5 distinct age groups (cohorts) at any given time, and that two new cohorts recruited during the one-year investigation period. An analysis to determine growth pattern using FiSAT software showed that the longevity of C. testudinaria extended up to 2 years. The values of von Bertalanffy growth parameters (L_∞, K and t_0), estimated from size-frequency distributions, were 33.1 mm, 1.4 yr^{-1}, and 0.09, respectively. The highest growth increments were 25% and 18% of the asymptotic length during the first 3 and 6 months, respectively. The effects of environmental variables on the growth rates showed important seasonal variations, with the highest increment of 2.6 mm/month during dry season. Here, growth parameter of C. testudinaria limpet shows the same value as other tropical limpets and depends on environmental variables.

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INTRODUCTION

The tropical limpet *C. testudinaria* is reasonably well known from systematic and geographical distribution aspects (Wilson, 1993; Attrill et al., 2001), but there are little published studies regarding its growth or other aspects of its biology. Many investigations about growth rates of various Patellacea have been carried out focusing on several factors affecting growth, such as tidal height (Takada, 1997; Williams et al., 1999), water temperature (William & Morritt, 1995; Saad, 1997), seasonal changes and food availability (Brêthes et al., 1994; Ruiz Sebastián et al., 2002).

A burst of theoretical contributions regarding estimation of growth parameters from growth data (Lotze, 1998; Khouw, 2002) has led to the clarification of the concept of the effects of environmental variables on the growth of limpets (William & Morritt, 1995; Liu & Morton, 1998). Iwasaki (1998) examined growth rates of some tropical gastropods in an attempt to determine whether life spans were under primary temperature control as suggested by

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Levins (1968) or whether some other features of the milieu of these animals determined their longevity. In a review of the physiological variation among intertidal molluscs, Dunmore & Schiel (2000) concluded that on the whole southern hemispheres, species have shorter life span and attain smaller final size than northern ones. The evidence from the north Atlantic and Pacific coasts of North America indicated that this generalization also holds within species with broad latitudinal distribution (Dunmore & Schiel, 2000). These findings imply that differences of growth parameters between limpets in different regions can be explained either by a single primary environmental effect or may result from a combination of interaction between environmental and other factors.

C. testudinaria is an excellent species to study growth, as they are present in high numbers, range freely on all rocky substrata, and the shells of these animals show distinct dimensions, suggesting a possibility for determining growth. The notion that environmental stress is generally an important factor which directly or indirectly influences the population dynamics of common intertidal animals (Lohse, 1993; Delany et al., 1998; Brey, 2003; Clarke et. al., 2004) has led this study to further examine the same hypothesis.

Therefore, this research would present information on the growth rates of *C. testudinarai* and some factors presumably affecting them. Moreover, the results are compared it with those of similar limpets from temperate regions.

MATERIALS AND METHODS

Study site

The study was carried out monthly on the intertidal rocky shore of Ohoiwait (latitude $5^0 45'15"$ S, longitude $132^0 57'20"$ E), Big Kai Island, Southeast Mollucas, Indonesia **(Fig. 1)** from October 2001 to September 2002. The intertidal region investigated is about 0.25 km^2 (1 km long and 0.25 km wide). Thus, it is small enough that atmospheric conditions may be assumed, for most purposes, to be uniform over the whole area. The shore consisted of shingles, pebbles, medium and big boulders of about 90% of covering substrate. The physical conditions in the tidal zones are quite different; the higher shore is wetted almost exclusively by tidal sea level rise, but the lower shore receives considerable wave action.
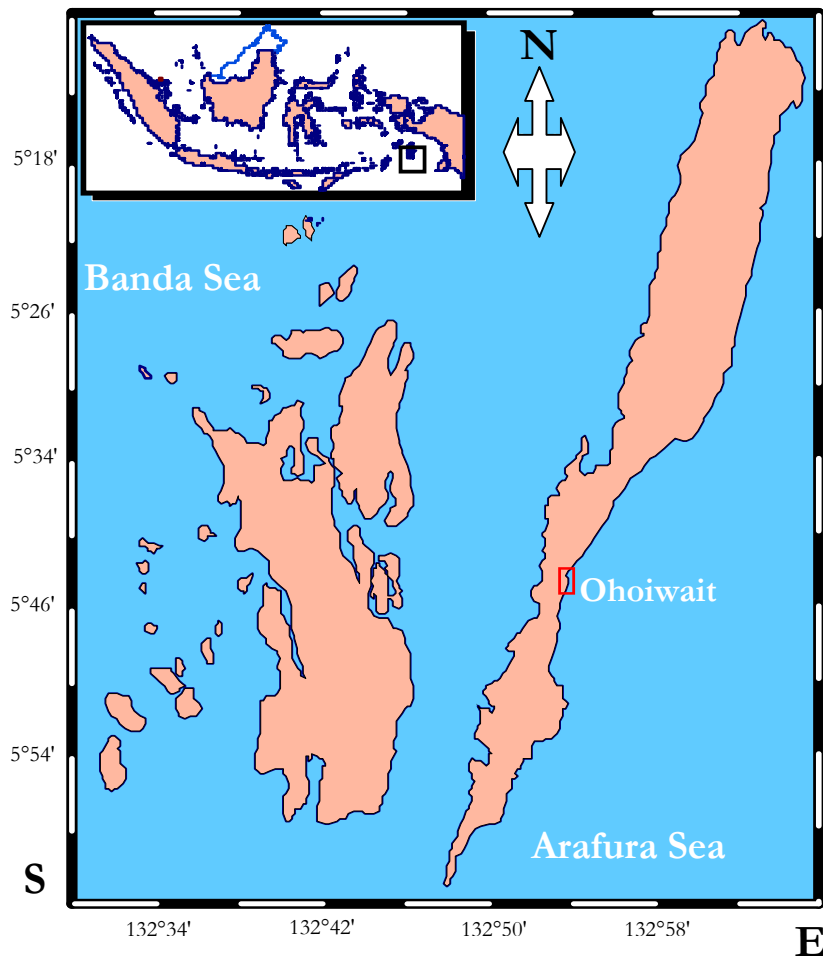
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Fig 1. Map of study site of Ohoiwait located at the Big Kai Island.

Growth measurements

The population of *C. testudinaria* was sampled periodically and the mean size of the individuals within distinct age cohorts was calculated from polymodal size-frequency distributions (Tablado et. al., 1994; Turon et al., 1995; Murray, 2002). Age classes were defined through analysis of length frequency distributions to decompose monthly size-frequency into their component normal curves (Brêthes et al., 1994). The estimate of growth used the monthly size of frequency data, whereby the mean sizes of cohorts were followed through time.

Analyses

Population structure. The population structure of *C. testudinaria* was analysed using the Modal class Progression Analysis, MPA (Gayanillo et al., 1996) by the aid of FiSAT software (Sparre & Venema, 1998). This methodology infers growth from the apparent shift of the modes or means in a time series of length frequency samples. It was then applied to the

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frequency histograms of the limpets' shell lengths to divide them into distinctive cohorts.

Growth. The growth of limpets was analysed by using the most widely used being that developed by von Bertalanffy (1938) that has been known as the Bertalanffy equation: $L_t = L_\infty [1 - e^{-K(t - to)}]$ where L_t is the length at age t, L_∞ is the asymptotic length (representing the maximum theoretical length of animal), K the growth coefficient (describing the rate of growth of the animal to its maximum size), and t_o the theoretical age at length 0 (the start of growth of the settled larva); the intercept between the curve and the t axis.

Statistical analysis. Seasonal variation in the growth of cohorts was assumed to be negligible in the present study, because growth rates calculated at different times could confound an analysis of seasonal variability. As a consequence, I proceeded with the comparison of regression lines resulting from the relationships between shell length and the number of months, using an analysis of covariance ANCOVA (Sokal & Rohlf, 1995). This test determines the level of similarity between the samples, and, in case of heterogeneous relationships, obtained the nature of the source of the differences (Baxter, 1983).

Bartlett's test (Sokal & Rohlf, 1995) was used to check the assumption of homogeneity of the residual variances before using ANCOVA.

RESULTS AND DISCUSSION

Population structure

The size structure of the population of *C. testudinaria* was examined through the analysis of percentage size frequency distribution **(Fig. 2)**. The overall specimen sizes ranged from 8.0 to 31.8 mm, representing 6 cohorts. The first cohort consists of juvenile limpets with an average length of < 10.5 mm, representing 13 % of the total population. The second cohort encompasses the limpets with lengths of 10.5 – 15.5 mm, accounting for 48 % of the total population. This sub-population generally presents the group of limpets with the highest growth rates. The remaining cohorts consist of limpets with an average length of 15.5 – 20.5 mm, 20.5 – 25.5 mm, 25.5 – 30.5 mm, and > 30.5 mm, accounting for 22 %, 9 %, 7 %, and 1 % of the total population, respectively.
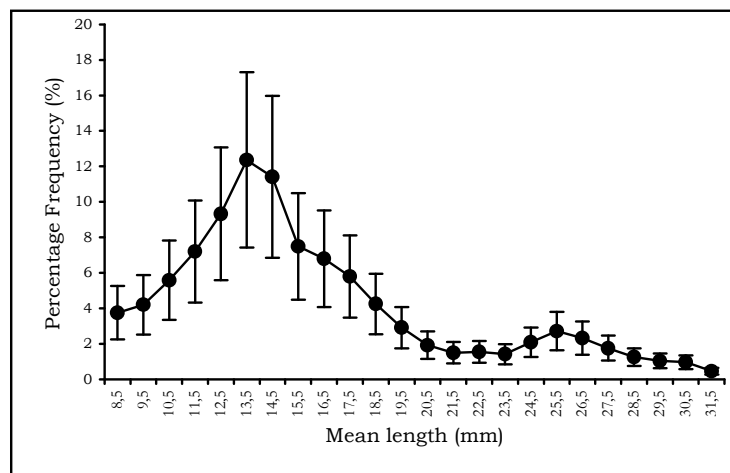

Fig 2. *Cellana testudinaria*. Mean percentage frequency of each size class category. Vertical lines represent standard deviation (SD).

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Growth

All monthly size-frequency histograms are polymodal; 4 modes were found in October, March, July, August and September, and 5 modes in the remaining months **(Fig. 3)**. The presence of several modes in the frequency distributions indicates that more than one age classes appear likely present in the population. The overall size-class distribution ranged from 8.5 mm to 31.5 mm and the smallest limpets (8.5 – 10.5 mm) are assumed having settled 2 months before being sampled **(Fig. 3)**. Overall eight distinct cohorts were identified (using the Bhattacharya method implemented in the FISAT software) throughout the 1-year study period. For each cohort, mean length, its standard deviation, and its percentages have of the total population been calculated **(Table 1).**
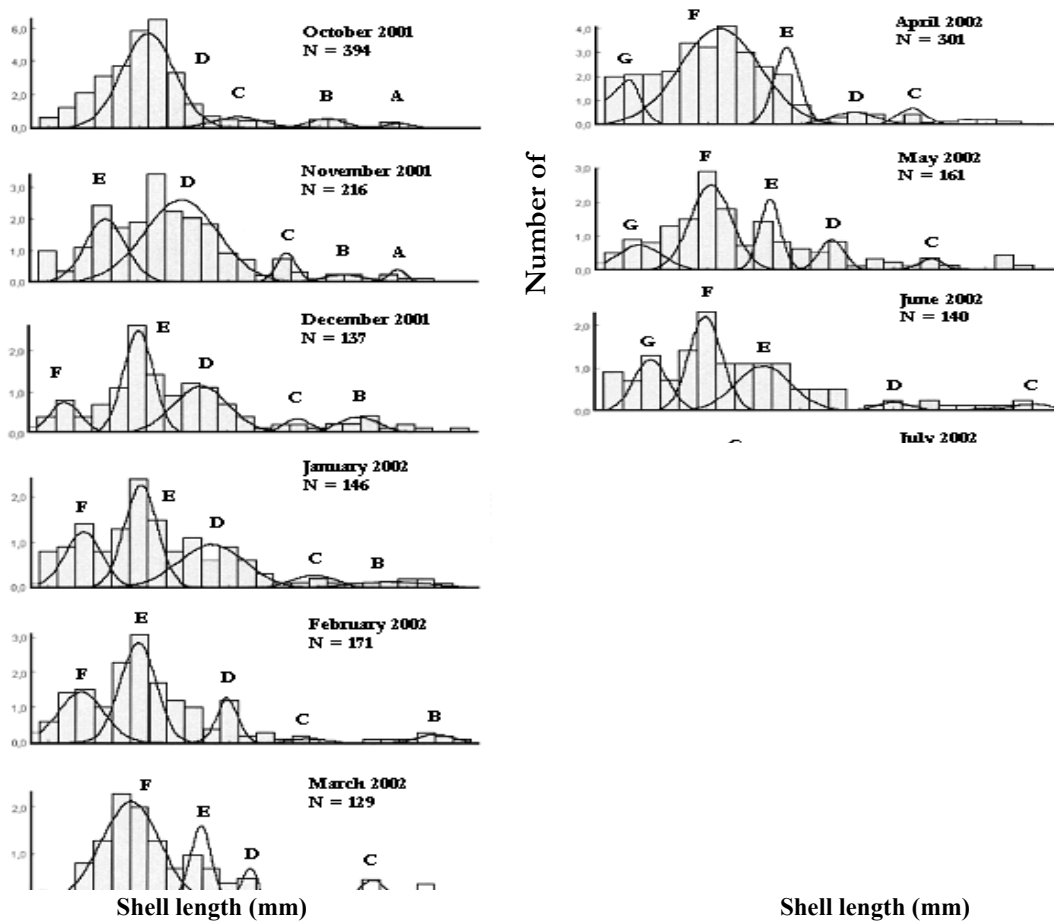
Fig 3. Monthly size-frequency histograms of *Cellana testudinaria*. Curves show estimated modal sizes. Alphabets A – H refer to cohorts. Analyses used the Bhattacharya method by the FiSAT software.

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Table 1. Size cohorts of *Cellana testudinaria* summarised from **Fig3.** *SD*- standard deviation.

Month	Cohort	Mean length (mm) ± SD	% population
October '01	D	13.98 ± 1.46	84.49
	C	18.91 ± 1.42	8.57
	B	23.89 ± 0.94	5.31
	A	28.00 ± 0.90	1.63
November '01	E	11.70 ± 1.10	26.44
	D	15.89 ± 2.03	62.98
	C	21.77 ± 0.50	5.77
	B	25.02 ± 1.19	2.88
	A	27.91 ± 0.40	1.92
December '01	F	9.50 ± 0.85	12.60
	E	13.58 ± 0.82	40.16
	D	17.06 ± 1.52	34.65
	C	22.45 ± 0.70	4.72
	B	25.81 ± 1.07	7.87
January '02	F	10.44 ± 1.00	21.83
	E	13.62 ± 0.91	36.62
	D	17.57 ± 1.84	30.99
	C	23.25 ± 1.18	5.63
	B	27.68 ± 2.19	4.93
February '02	F	10.27 ± 1.26	31.25
	E	13.42 ± 0.99	49.31
	D	18.38 ± 0.59	12.50
	C	23.00 ± 1.20	2.08
	B	30.00 ± 1.06	4.86
March '02	F	13.04 ± 1.61	66.15
	E	16.94 ± 0.58	18.46
	D	19.25 ± 0.91	8.46
	C	26.51 ± 0.73	6.92
April '02	G	10.31 ± 1.94	10.23
	F	14.13 ± 2.14	62.56
	E	17.71 ± 0.68	18.71
	D	21.35 ± 1.21	5.10
	C	28.04 ± 2.24	3.40
May '02	G	9.83 ± 1.19	15.83
	F	16.85 ± 0.55	20.86
	E	20.18 ± 0.63	10.07
	D	25.50 ± 0.67	3.60
	C	29.54 ± 0.56	49.46
June '02	G	13.44 ± 0.87	40.00
	F	18.40 ± 1.47	31.67
	E	23.50 ± 0.85	3.33
	D	27.00 ± 0.90	22.5
	C	31.00 ± 1.20	2.50
July '02	G	14.58 ± 2.05	78.21
	F	19.82 ± 1.19	4.49
	E	24.34 ± 1.18	11.54
	D	27.81 ± 1.23	5.77
August '02	G	18.55 ± 1.60	65.33
	F	21.75 ± 0.65	16.00
	E	25.59 ± 1.14	17.33
	D	30.00 ± 1.40	1.33
September '02	H ?	11.38 ± 0.53	26.13
	G	21.03 ± 1.24	10.05
	F	25.72 ± 1.09	46.73
	E	30.59 ± 0.77	17.09

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A total of 8 distinct cohorts were identified using the modal progression technique. By following these patterns on a monthly basis, the growth of each cohort could be assessed through regression lines of the growth curves **(Fig. 3).** It was found that the cohort-G grew at the rate of 2.45 mm/month, whereas the cohort-B grew at the rate of 1.49 mm/month **(Table 2).** Moreover, ANCOVA showed that the rates of growth might vary from year to year for cohorts of corresponding age ($F =$ 135.71, $P < 0.05$).

In October 2001, 4 cohorts were identified with average estimated lengths of 13.98 mm, 18.91 mm, 23.89 mm and 28 mm, respectively. Off these cohorts, the majority were 84 % of the total population, belonged to the smallest age group, which is referred to as cohort-D. It probably consists of individuals, which have settled during the second of the two recruitment events of the year 2000. This cohort remained in the study area until August 2002 when they reached a maximum length of about 30 mm. The older cohorts (A, B and C) accounted for only 2 – 9 % of the total population examined during this study and remained for only 1 – 8 months before they completely disappeared. They probably encompassed limpets, which recruited in the first half of 2000 or joined the population during two recruitment peaks in 1999. In November 2001, a new age group appeared in the samples, attaining a quite high average length of 11.70 mm. It was referred to as cohort-E and consisted probably of limpets settled during the first recruitment event in 2001. Smaller (and probably younger) specimens were not found in the regular collections and were presumably because of incomplete sampling. Limpets of less than 10 mm in length including those of size ranges between 4 – 5 mm in length were occasionally encountered during free collections on the shore, but such small size ranges were distinctly rare. During samples collected in December 2001 limpets of < 10 mm length appeared. They were quite probably only a few months old and represented cohort-F recruited in the second event in 2001. This cohort attained the majority of the population in March 2002 as much as 66.15%. They grew very rapidly and required only 3 months to reach a mean length of 13 mm. A new cohort appeared in April 2002 (the mode of 9.32 mm) and was referred to as cohort-G, encompassing the first recruits of the year 2002. After three months, which was in July 2002, it has attained a mean size of 14.6 mm and accounted for the majority of the population (65.33%). In September 2002, an eight cohort emerged, probably representing the settlers of the second recruitment event in 2002. Specimens of this age group were comparatively large (with mean shell length of 11.4 mm).

Growth curves **(Fig. 4)** were estimated from the pattern of the modes in the histograms. The oldest cohort-A decreased from a mean size of 28.00 (± 0.90 SD) mm in October 2001 to 27.91 (± 0.40 SD) mm in November 2001. Thus, it was not possible to calculate the growth of this cohort, as there was no increase in the mean size during the period of investigation. The next oldest cohort-B grew at a steady rate of 1.49 mm/month from October 2001 to February 2002 and disappeared from the study area in March 2002. Limpets of cohort-C had virtually disappeared from the population by June 2002, with the few remaining individuals presumably having merged with cohort-D. The growth of cohort-E and cohort-F could be followed throughout the period of sampling. Cohort-E increased from a mean size of 11.70 (± 1.10 SD) mm in November 2001 to 30.59 (± 0.77 SD) mm in September 2002, equivalent to an average growth of 1.8 mm/month. Cohort-F grew at 1.77 mm/month during the period between December 2001 and September 2002. The youngest cohort-G entered the population in April 2002 and grew at 2.45 mm/month.

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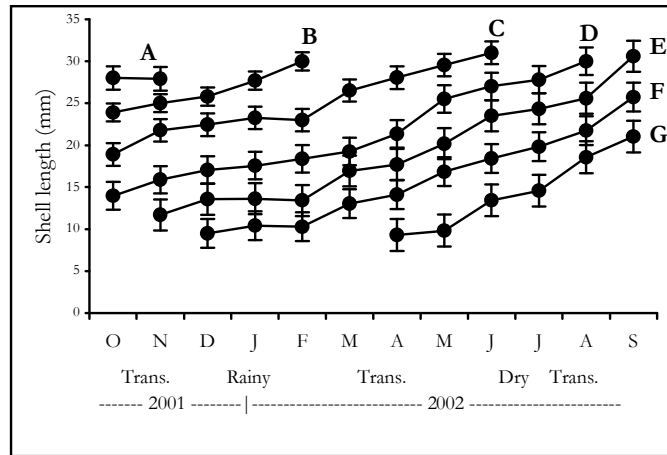
Fig 4. Growth curves of *Cellana testudinaria* estimated from monthly size-frequency histograms **(Fig. 1).** Standard error (vertical bars) of the estimated normal distributions of each cohort are shown.

Statistical analyses

For growth comparison of the various cohorts, regression lines were fitted to the growth curves **(Table 2).** The residual variances of the regressions were found to be homogeneous when compared using Bartlett's test **(Table 3),** indicating that there was no difference on the rate of growth of the cohorts ($\chi^2 = 10.22$, $P > 0.05$). ANCOVA results **(Table 4)** show that there is a highly significant difference between the slopes ($F_{5,51} = 135.71$, $P < 0.05$), indicating that young cohorts grow faster than old ones.

Table 2. *Cellana testudinaria*. The regression equations of the relationship between the shell increment and time. Y is the shell length; X is the numbers of year.

Cohort	Equation	r
B	Y = 1.4880 X + 22.016	0.98
C	Y = 1.4352 X + 17.165	0.98
D	Y = 1.6039 X + 11.630	0.98
E	Y = 1.8005 X + 8.395	0.97
F	Y = 1.7679 X + 6.269	0.98
G	Y = 2.4529 X + 5.873	0.98

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Table 3. *Cellana testudinaria*. Bartlett's test on the rate of growth of the cohorts. *df*-degree of freedom; S^2-variance.

Sources	df	S^2	$\ln S^2$	$df * \ln S^2$	$1/df$	$df * S^2$
Cohort-B	4	5.78	1.75	7.02	0.25	23.12
Cohort-C	8	16.15	2.78	22.26	0.13	129.20
Cohort-D	10	29.56	3.39	33.86	0.10	295.60
Cohort-E	10	37.61	3.63	36.27	0.10	376.10
Cohort-F	9	29.65	3.39	30.51	0.11	266.85
Cohort-G	5	21.76	3.08	15.40	0.20	108.80
Total	**46**			**145.32**	**0.885**	**1199.67**

$$\text{Mean } S^2 = \Sigma \, df * S^2 / \Sigma \, df$$
$$= 1199.67/46$$
$$= 26.08$$

Y $= \Sigma \, df * \ln(\text{Mean } S^2)$
$= 46 * 3.26$
$= 150.01$

M $= 2.3026 * (Y - \Sigma \, df * \ln S^2)$
$= 2.3026 * (150.01 - 145.32)$
$= 10.81$

C $= 1.058$

Corrected test statistic (*M/C*) = **10.22**
Tabulated $\chi^2_{0.05(5)}$ = 11.1

Table 4. *Cellana testudinaria*. Analysis of covariance on the relationships of cohorts B – G together with the ANOVA test. *F*-values that are relevant for the interpretation of the results are shown. *df*-degrees of freedom; *SS*-sum of squares; *MS*-mean square

Sources	df	SSy	SPxy	SSx	by.x	SSy'	df	SSy.x	MSy.x
Cohort-B	4	23.12	14.88	10	1.4880	22.14	3	0.98	0.33
Cohort-C	8	129.19	86.11	60	1.4352	123.58	7	5.61	0.80
Cohort-D	10	295.65	176.43	110	1.6039	282.98	9	12.67	1.41
Cohort-E	10	376.14	198.05	110	1.8005	356.58	9	19.56	2.17
Cohort-F	9	266.86	145.85	82.50	1.7679	257.85	8	9.02	1.13
Cohort-G	5	108.81	42.92	17.50	2.4529	105.26	4	3.55	0.89
Sum of groups							40	51.39	1.2848
Among b's							5	17.07	3.4140
Pooled within	46	1199.78	664.24	390	*1.7032*	1131.32	*45*	*68.46*	*1.5213*
Adjusted means							*5*	*1032.23*	*206.45*
Total	51	1997.35	632.93	446.77			50	1100.69	
Groups	5	797.57	- 1.31	56.77	- 0.55	17.27	4	780.30	195.08

Anova of covariance

Source of variation	df	SS	MS	F	$F_{tabulated}$
Ajusted means (among a's)	5	1032.23	206.45	135.71***	2.42 (P < 0.05)
Error (deviation from a common slope)	45	68.46	1.52		3.44 (P < 0.01)

- *The rate of growth differ very significantly among months*
- *There is significant heterogeneity of the means around their regression slopes.*

From the growth equations **(Table 2)**, it has been fully confirmed that the rate of growth decreased as the limpet grows older. For example, cohort-G grew at a steady rate of 2.45 mm/month while cohort-B at 1.48 mm/month. However in order to gain a precise knowledge of the pattern, it is necessary to discount the possible influence of time of year and environmental variables upon the rate of growth. This has been done by taking the growth increments of the shell length for the periods of dry season and rainy season into account **(Figure 4).** During the period between June and August (dry season)

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limpets grew more quickly (at an average of 2.61 mm/month) than during the period between December and February (rainy season) (growth at an average of 0.66 mm/month). In the periods of transition, the growth rate was about 1.10 mm/month.

The theoretical growth parameters, K and L_∞ for *C. testudinaria* estimated from size-frequency data using ELEFAN I of the FiSAT software (Sparre & Venema, 1998) was 1.4 and 33.08 mm, respectively. These two parameters were substituted into the Bertalanffy equation with $L_c = 4$ mm (based on the length of the smallest limpets obtained by free collection during the period of study)

to give the value of $t_o = 0.09$ year. The growth can be described by the following von Bertalanffy equation: $L_t = 33.08 [1 - e^{-1.4(t + 0.09)}]$. By using the observed increases in size of cohorts B to G, growth for this population was estimated for 22.8 months (1.9 years). The continuous growth curve generated by this method was compared with the curve constructed from the estimate of shell growth based on von Bertalanffy equation. The line fitted approximately to the growth curve was then superimposed on the von Bertalanffy growth curve to show that both curves gave very similar results, which suggests that either estimate was reliable **(Figure. 5).**
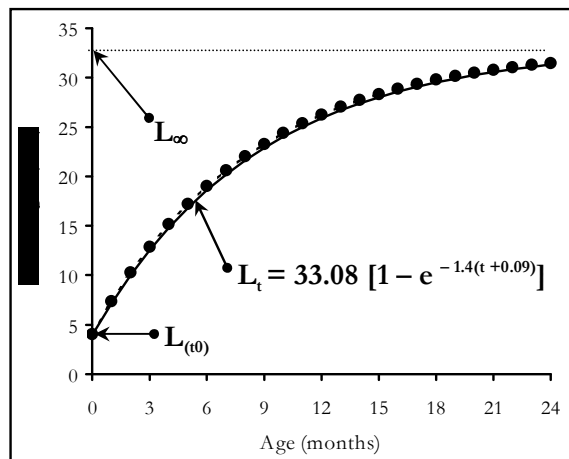
Fig 5. *Cellana testudinaria*. Growth model as estimated from the increase in shell length of age cohorts. The points represent the modes defined by the size distributions; the solid line corresponds to the von Bertalanffy growth curve and the dashed line represents the theoretical maximum length (L_∞). Only the sizes considered in the growth curve calculation are represented.

Growth continued at a relatively constant rate for further 6 months, and the maximum size of 31.43 mm (computed as $L_{max} = 0.95\ L_\infty$, according to Taylor, 1965) was attained after about 25 months. L_{max} was only a bit shorter than the actual maximum length, 31.8 mm, measured during the period of study. Therefore, it is reasonable to estimate longevity (t_{max}) as $3/K$, resulting in a value of 25.71 months (2.1 years), which is

very similar to the maximum age derived from the analysis of the size distributions.

Discussion

Size-frequency distribution data as shown in **Fig. 3**, which is composed to the continuous growth curve in **Fig. 5**, showed that the smallest *C. testudinaria* grew more rapidly at

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the first 4 months than those 18 to 24 months old. The relationship is curvilinear, since large limpets grow more slowly than is predicted by extrapolating from growth rates of juveniles. Monthly increments in shell length begin decreasing after the first year. It is clear from the estimated lengths at different age that in fact the Bertalanffy equation could describe sufficiently the growth of *C. testudinaria* over the whole range of its growth. This is interesting as many sedentary invertebrates such as limpets show a sigmoid pattern of growth ((Tablado et. al., 1994; Turon et al., 1995; Saad, 1997; Murray, 2002).

For *C. testudinaria*, the calculated L_∞ = 33.08 mm is reasonable, as it is quite close to the length of the largest shells recorded, L_{max} = 31.8 mm. It should be noted, however, that Khouw (2002) collected some specimens of *C. testudinaria* as long as 40 mm in the same area. For comparison, the asymptotic length, L_∞ of other limpet species obtained by previous works is presented in **Table 5.**

Table 5. Comparison of L_∞ (mm) values of *Cellana testudinaria* with values reported for other species.

Species	L_∞	Locality	Authors
Cellana testudinaria	33.1	Ohoiwait, Southeast Molluccas, Indonesia	This study
Cellana eucosmia	44.1	Ain Soukhna, Gulf of Suez	Saad, 1997
Cellana radiata	54.0	Gulf of Aqaba, Red Sea	Ismail & Elkarmi, 1999
Nacella delesserti	61.8	Marion Island, Sub-Antarctic	Blankley & Branch, 1985
Patelloida alticostata	48.0	New South Wales, Australia	Fletcher, 1987
Patelloida alticostata	22.3	New South Wales, Australia	Creese, 1981
Patelloida latistrigata	15.1	New South Wales, Australia	Creese, 1981
Montfortula rugosa	22.0	New South Wales, Australia	Creese, 1981
Notoacmea petterdi	19.9	New South Wales, Australia	Creese, 1981
Siphonaria denticulate	21.8	New South Wales, Australia	Creese, 1981
Siphonaria virgulata	18.0	New South Wales, Australia	Creese, 1981
Fissurella barbadensis	33.9	Barbados Island	Ward, 1967
Nacella (Patinigera) concinna	71.4	Esperanza Bay, Antarctic Peninsula	Brêthes et al., 1994
Nacella (Patinigera) concinna	41.0	Signy Island, South Orkney Islands	Picken, 1980

The L_∞ value estimated for *C. testudinaria* seems realistic, since limpets in the tropical regions grow more quickly but usually reach a smaller maximum size and have a shorter life span than limpets living in temperate or polar region (Dunmore & Schiel, 2000; Clarke et. al., 2004). Moreover, it has been known for some gastropods individuals living in the southern hemisphere tend to be smaller than those in the northern hemisphere (Delany et. al., 1998; Dunmore & Schiel, 2000; Clarke et. al., 2004). This has been considered maybe due to higher water temperatures in the southern habitat. Beside this by geographical variations, it appears that technical aspects may also have some constribution. Ismail & Elkarmi (1999) demonstrated that it is generally more precise

using growth annuli deposit in shell than modal progression analysis to estimate absolute ages.

The continuous growth curve **(Fig. 5)** indicates that *C. testudinaria* reaches a length of about 26.9 mm in its first year. This is slightly less than the first-year length attained by *Cellana eucosmia*, 27 mm, in the Gulf of Suez (Saad, 1997), but more than that of *Cellana radiata* (10 mm) in the Gulf of Aqaba (Ismail & Elkarmi, 1999). On the other hand, the Antarctic limpet *Nacella concinna* reaches only 5 mm in length during its first year (Clarke et. al., 2004). **Table 6** shows some *K* values of comparable species reported from different regions. It is evident that limpets in the tropical regions grow more rapidly than in temperate and polar region

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Table 6. Comparison of *K* values of *Cellana testudinaria* with values for other limpets.

Species	K	Locality	Authors
Cellana testudinaria	1.4	Ohoiwait, Southeast Molluccas, Indonesia	This study
Cellana eucosmia	0.69	Ain Soukhna, Gulf of Suez	Saad, 1997
Cellana radiata	0.19	Gulf of Aqaba, Red Sea	Ismail & Elkarmi, 1999
Patelloida alticostata	0.72 - 0.86	New South Wales, Australia	Fletcher, 1987
Fissurella barbadensis	0.126	Barbados Island	Ward, 1967
Nacella (Patinigera) concinna	0.077	Esperanza Bay, Antarctic Peninsula	Brêthes et al., 1994
Nacella (Patinigera) concinna	0.072	Signy Island, South Orkney Islands	Picken, 1980
Nacella delesserti	0.074	Marion Island, Sub-Antarctic	Blankley & Branch, 1985

Observations of newly settled *C. testudinaria* in the field would suggest that t_0 is negligible, i.e. it is unlikely to be greater than 1 month. However, such low t_0 value seems unrealistic because this estimate was based on a minimum length of 4 mm (the size of smallest limpets obtained by free collection during the study) and it was not possible to find living limpets with shell length < 0.2 mm. Therefore, it is reasonable to estimate the longevity or life span of *C. testudinaria* to

be 2 years. In general, limpets in tropical regions have shorter life spans than those in temperate and polar region **(Table 7).** This is probably also due to the different intertidal habitats, which these animals occupy. Several authors noted that the nature of the habitat in the intertidal range and, hence, the exposure to wave action, might influence the growth and shell form of limpets (Branch & Odendaal, 2003; Navarro et. al., 2005; Weber & Hawkins, 2006; Lima et. al., 2006).

Table 7. Comparison of longevity of *Cellana testudinaria* with values for other limpets.

Species	Longevity (yr)	Locality	Authors
Cellana testudinaria	2	Ohoiwait, Indonesia	This study
Cellana eucosmia	5	Ain Soukhna, Gulf of Suez	Saad, 1997
Cellana radiata	5	Gulf of Aqaba, Red Sea	Ismail & Elkarmi, 1999
Patelloida alticostata	6 - 7	New South Wales, Australia	Fletcher, 1987
Patelloida alticostata	5 - 6	New South Wales, Australia	Creese, 1981
Patelloida latistrigata	3	New South Wales, Australia	Creese, 1981
Montfortula rugosa	> 3	New South Wales, Australia	Creese, 1981
Notoacmea petterdi	> 10	New South Wales, Australia	Creese, 1981
Siphonaria denticulate	> 6	New South Wales, Australia	Creese, 1981
Siphonaria virgulata	2 - 3	New South Wales, Australia	Creese, 1981
Patella vulgata	10 - 20	Millport, United Kingdom	Russell, 1909
Nacella (Patinigera) concinna	63	Esperanza Bay, Antarctic Peninsula	Brêthes et al., 1994
Nacella (Patinigera) concinna	30 - 40	Signy Island, South Orkney Islands	Picken, 1980

CONCLUSION

It is clear that the growth rate of *C. testudinaria* was strongly related to environmental conditions. Despite the general problems of data interpretation due to inadequate sampling, a slight seasonal variation in temperature is discernible for the seawater and air at the intertidal of Ohoiwait. During dry season when seawater and air

temperatures were on average 29 ^{0}C and 26.5 ^{0}C, respectively, the limpets grew faster. This growth acceleration occurred in August, i.e. later than it would be expected if the limpet responded immediately to an increase in temperature. In general, the limpet grew more quickly between September and November than during other times. This suggests that there is an increase in growth in response to water temperature. This has been demonstrated for many limpets in temperate regions where seasonal variations in

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temperature are far more pronounced than in the tropics (McGrath, 1992; Takada, 1997). Beside temperature, the availability of food is known to regulate growth. Brêthes et. al. (1994), Jenkins & Hartnoll (2001), and Zhao et. al. (2003) suggested that an increase in growth of temperate limpet, during summer is related to an increased food supply. Unfortunately this data is unavailable during this study leaving water temperature to be considered as a leading factor affecting the growth rates of limpet in the study area.

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