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Population dynamics of an inarticulate brachiopod *Lingula unguis* on the intertidal flats of Kunsan, Korea

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Investigations were made on spatial and temporal variation, population structure, growth, recruitment and mortality in the intertidal flats of Kunsan (Korea, Yellow Sea) of an inarticulate brachiopod *Lingula unguis*. Statistical analysis indicates significant spatial differences and a significant relationship between density and ratio of sands to silts, suggesting that the distribution and density of this species were related to particle size. The population consisted of three year-classes, with a similar size composition each year, of which the second year-class was a major component. From estimation of parameters of growth monthly length–frequency was analysed by ELEFAN. Parameters of growth were estimated, using the modified von Bertalanffy growth function (VBGF) model incorporating seasonal variation in growth. The growth parameters are: L_∞=44.00 mm SL, K=0.88 y^{-1}, C=0.90, WP=0.48. The recruitment pattern shows two major recruitments per year. The maximum life span is estimated as 3.45 y. Total mortality (Z) by length-converted catch curve was estimated at 3.65 y^{-1}. The population mainly occurred in fine sands and exhibited patchy distribution.

INTRODUCTION

An inarticulate brachiopod, *Lingula unguis* (Linné), is one of the most common Korean brachiopods. It is locally abundant in the intertidal flats of a number of localities in coastal waters of the Yellow Sea and the East Sea (Yatsu, 1902; Kume, 1956; Black, 1970). The genus *Lingula* itself only goes back to the Ordovician, although the family is present in the early Cambrian. It has a worldwide distribution and has persisted to the present with little change. Lingulid brachiopods are of ecological importance as macrobenthic organisms as they provide suitable microhabitats for smaller infauna in the sediment due to their borrowing activity (Thayer & Steele-Petrovic, 1975; Dittmann, 1996).

Investigations of *L. unguis* have been mainly carried out on the pattern of distribution (Paine, 1970), morphology (Kawaguti, 1943; Chuang, 1959a), breeding cycles (Yatsu, 1902; Kume, 1956; Chuang, 1959b), physiology (Iijima et al., 1991) and growth (Chuang, 1961). Studies on *L. anatina* have shown that shell growth is polymodal (Kenchington & Hammond, 1978; Mahajan & Joshi, 1983), although its longevity varied with area. Growth patterns in *Lingula* spp. is considered to be analogous to that of bivalves because of regular growth lines on the outer surface of the shell (Black, 1970). Mahajan & Joshi (1983) estimated parameters of von Bertalanffy growth function for *L. anatina* without incorporating the seasonal oscillation in growth. As indicated in most fish and shellfish stocks (Pauly et al., 1984; Vakily, 1992), however, there could be seasonality in the growth of lingulid species due to factors such as water temperature and breeding season. To date there have been no studies which examine the seasonal growth of brachiopods.

The study area is extensive intertidal flats exposed for up to ~3–4 km at the lowest tide. Based on large samples we estimate parameters of revised von Bertalanffy growth, mortality and recruitment pattern from monthly length–frequency data (LFD) collected between June 1996 and August 1997. The spatial and temporal variation in density and structure of *L. unguis* populations from Kunsan intertidal flats and the influence of substrate heterogeneity on its distribution were investigated.

MATERIALS AND METHODS

Sampling

Samples of a brachiopod, *Lingula unguis*, were collected from the intertidal flats of Kunsan, Korea (Figure 1) by means of can-core sampling of five stations spaced by 50 m intervals distance on an orthogonal line to the shore. Three replicate can-core samples of 0.06558 m^2 (0.215 m in width × 0.305 m in length) were taken from each of the five stations to a depth of 12.4 cm, and such sampling was undertaken once a month at low tide during the period between April 1996 and August 1997. Each sample was sieved through a 0.1-mm mesh sieve to retain individuals of >1.0 mm shell length. This helped to remove the bias in density, within given sampling period, caused by recruitment to the sampled population. A core sample of substrate was taken adjacent to each station for analysis of particle size. Dry weight in each particle grade was measured using Sedigraph 5100. Classification of particle size and grade were adopted from Friedman & Sanders (1978).

Specimens collected were preserved in 10% neutralized seawater formalin. The maximum shell length (SL) was measured to the nearest 0.01 mm using digital Vernier

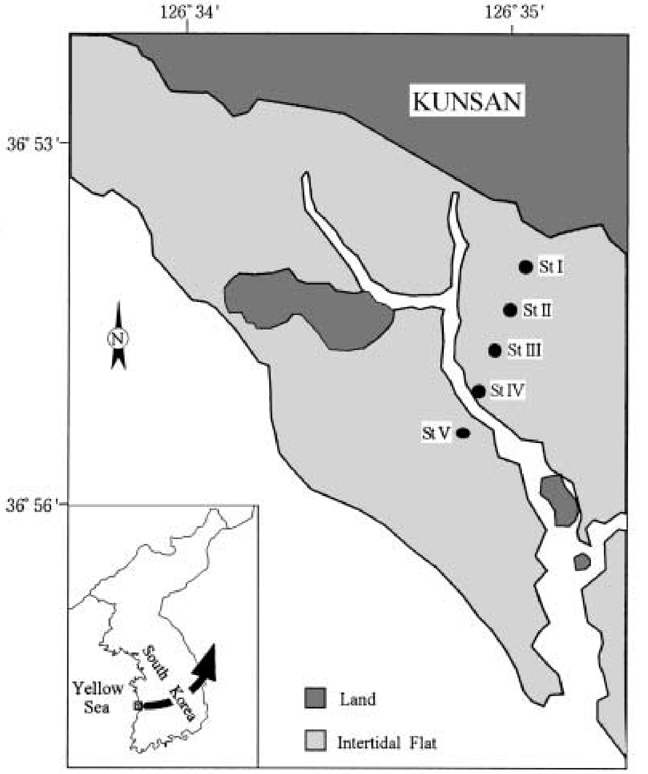

Figure 1. Map showing the location of the five sampling sites along the middle coast of western Korea.

calipers. They were blotted dry, and body wet weight (BW) determined to the nearest 0.001 g using an electronic digital balance. The regression of body weight (BW) to shell length (SL) was determined by logarithmic linear function:

$$\log_e \mathrm{BW} = a + b \log_e \mathrm{SL} \qquad (1)$$

where BW is the body weight (g), SL the shell length (mm), a the intercept, and b the slope.

Growth, mortality, and recruitment

Length–frequency distributions (LFD) were constructed using 1-mm length intervals of carapace length. Growth was described using the modified von Bertalanffy growth function (VBGF) (Pauly & Gaschütz, 1979):

$$L_t = L_\infty[(1 - \exp(-K(t - t_0) - (CK/2\pi)\sin(2\pi(t - ts)))] \qquad (2)$$

where L_∞ is the asymptotic length, K is the intrinsic growth rate, t_0 is the age which the length of animals is 0, C is the amplitude of seasonal growth oscillation, ts is the age at the beginning of growth oscillation, and WP ($=ts+0.5$) the time of year when growth is slowest. Growth curves were estimated from the length–frequency data analysis (LFDA) using the ELEFAN program (Gayanilo et al., 1995), a nonparametric method to fit the modified VBGF through modes. The Rn value gives an estimator of the goodness of fit. ELEFAN estimates the growth parameters (L_∞ K, C, and WP) without standard errors.

Comparison of growth performances was made using a growth performance index (ϕ') (Pauly & Munro, 1984).

$$\phi' = 2\log_{10} L_\infty + \log_{10} K \qquad (3)$$

When the growth can be described by the VBGF, and because the oldest specimens of a given population reach approximately 95% of their L_∞ value, $t_{\max}$ can be solved by the formula (Pauly et al., 1984):

$$t_{\max} \approx 3/K \qquad (4)$$

where K is the growth coefficient of the VBGF and $t_{\max}$ the longevity.

Mortality rate was estimated in ELEFAN using a linearized, length-converted catch curve (Pauly, 1984). Because *L. unguis* is an unexploited species in the study area, the calculated mortality rate (Z) was considered as representing only natural mortality (M).

Statistical analysis

The differences between months in density of *L. unguis* were tested by an analysis of variance (ANOVA). As there was no homogeneity of variances for both original and transformed data (Bartlett's test: $P<0.001$), the differences in density of *L. unguis* between stations were analysed by Kruskal–Wallis test and subsequent *posterior* comparisons between all pairwise stations were tested by Tukey honestly significant difference (HSD) test (Sokal & Rohlf, 1995) in SIGMASTAT version 2.0. Differences in size distribution between years and between stations were determined by Kolmogorov–Smirnov two-sample test (Sokal & Rohlf, 1995) in SYSTAT Version 7.0.

RESULTS

Spatial and temporal variation in density of Lingula unguis

Average annual density of the whole *Lingula unguis* population was 277 ind m^{-2}. It spatially ranged from 27 ind m^{-2} in station V (lowest mean density) to 687 ind m^{-2} in station II (highest mean density) (Table 1). There was a highly significant spatial difference in mean density between stations (Kruskal–Wallis test: H=45.77, df=4, $P<0.001$), with the greatest density being >96% of that at the station with the lowest mean density. Tukey HSD comparison tests revealed that significant differences were found in most, except a few comparisons (Table 2). On the other hand, there was no significant temporal variation in mean density over this period (17 months) (ANOVA: F=0.59, df=16, 60, $P>0.8$) (Table 1). There were no significant correlations between mean seawater temperature and mean density (r=0.423, $P>0.09$). Kite diagrams displayed distribution of the population relative to the profile of the Kunsan intertidal flats at the locations studied (Figure 2).

Influence of substrate heterogeneity

An analysis of particle size-class from substrate samples shows a varied composition within the study area at Kunsan intertidal flats and a variable ratio of sand to silt, dominated by fine sands (Table 3, Figure 3). In all the stations fine sands (2–4 ϕ) outweighed coarse sands

Table 1. *Mean in spatial and temporal density (m^{-2}) of* Lingula unguis *during the study period between June 1996 and August 1997 on the intertidal flats of Kunsan, Korea.*

Date	Stations (distance from shore) I (50 m)	 II (100 m)	 III (150 m)	 IV (200 m)	 V (250 m)	Mean ±SD
04/06/96	15.2	808.2	198.2	76.2	61.0	231.8 ±329.3
05/04/96	350.7	152.5	183.0	61.0	15.2	152.5 ±129.8
06/02/96	183.0	762.5	350.7	45.7	45.7	277.5 ±298.7
07/04/96	244.0	777.7	381.2	533.7	15.2	390.4 ±288.5
08/04/96	305.0	808.2	137.2	106.7	30.5	277.5 ±313.2
09/14/96	350.7	701.5	289.7	167.7	0.0	301.9 ±260.5
10/13/96	427.0	716.7	335.5	198.2	61.0	347.7 ±248.6
11/10/96	396.5	777.7	122.0	106.7	30.5	286.7 ±307.5
12/28/96	106.7	655.7	213.5	61.0	15.2	210.4 ±259.6
01/28/97	152.5	610.0	106.7	152.5	15.2	207.4 ±231.9
02/25/97	122.0	625.2	106.7	167.7	0.0	204.3 ±243.2
03/27/97	76.2	762.5	152.5	152.5	30.5	234.8 ±299.5
04/26/97	30.5	549.0	472.7	183.0	61.0	259.2 ±238.2
05/01/97	915.0	213.5	274.5	259.2	30.5	338.5 ±336.6
06/24/97	122.0	976.0	259.2	259.2	45.7	332.4 ±371.3
07/24/97	213.5	579.5	122.0	198.2	30.5	228.7 ±209.1
08/23/97	122.0	793.0	213.5	213.5	0.0	268.4 ±306.1
Mean ±SD	251.1 ±219.0	687.3 ±169.9	235.9 ±114.1	187.1 ±114.5	27.4 ±20.1	277.7 ±280.8

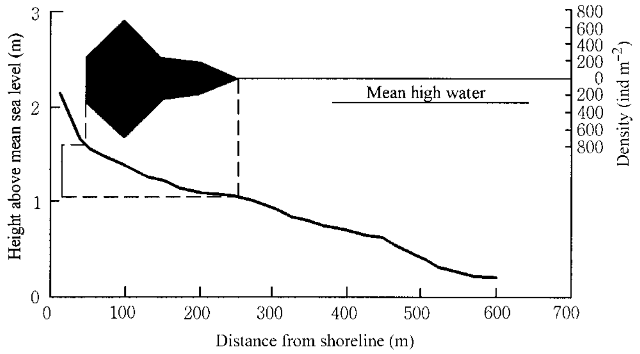

Figure 2. *Lingula unguis*: kite diagram of the distribution along a transect of the Kunsan intertidal flats superimposed upon a diagram of the intertidal area.

Table 2. *A posteriori multiple comparison for differences in mean density between the five stations.*

Stations	I	II	III	IV
I				
II	*			
III	ns	*		
IV	ns	*	ns	
V	*	**	*	*

*, $P<0.05$; **, $P<0.01$; ns, not significant.

(−1–2 ϕ). From station I through station V the percentage of sand increased, with fine sands (2–4 ϕ) outweighing coarse sands (−1–2 ϕ), while that of silt (>4 ϕ) decreased. Consequently this led to the increased ratio of sand to silt. The ratio did not appear to correspond closely with the population density of *L. unguis*.

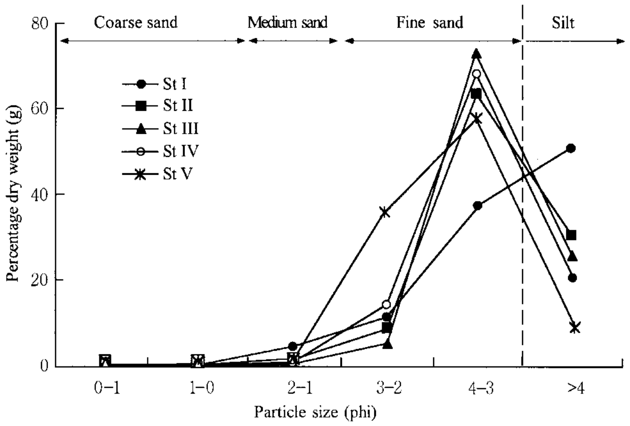

Figure 3. Spatial changes in the percentage of each particle size in the Kunsan intertidal flats.

However, when the relationship between *L. unguis* density and ratio of sand to silt was investigated, by plotting logarithm of density against ratio, a negative significant relationship was obtained (Student *t*-tests: −5.18, df=72, $P<0.001$) (Figure 4). The regression equation is:

$$\log_e \text{density} = 5.792 - 0.501(95\%\text{CL} \pm 0.193)\log_e \text{ratio} \quad (5)$$

$(N = 74,\ r^2 = 0.271,\ P<0.001)$

Population structure

The size–frequency histogram of all animals collected during the study period between June 1996 and August 1997 (Figure 5) showed that samples were not normally distributed (Anderson–Darling normality test: $P<0.001$) but skewed to the left (skewness=1.918). Although there

Table 3. *Mean percentage of each particle size group at the five stations.*

Size			Stations				
(μm)	(ϕ)	Size classification*	I	II	III	IV	V
2000–1000	−1–0	Very coarse sand	0.035 ±0.028	0.091 ±0.078	0.020	0.355 ±0.305	0.023 ±0.012
1000–500	0–1	Coarse sand	0.108 ±0.074	0.209 ±0.184	0.027 ±0.011	0.133 ±0.277	0.028 ±0.015
500–250	1–2	Medium sand	2.994 ±0.264	1.069 ±0.918	0.074 ±0.029	0.491 ±0.789	0.800 ±0.467
250–125	2–3	Fine sand	9.574 ±3.683	7.893 ±4.049	4.449 ±2.654	13.298 ±7.179	35.087 ±9.628
125–63	3–4	Very fine sand	29.088 ±8.794	61.946 ±3.924	71.363 ±6.028	66.459 ±6.623	56.421 ±8.609
<63	>4	Silt	58.225 ±7.274	28.843 ±3.233	24.108 ±5.319	18.938 ±7.800	7.664 ±2.059
Ratio (sand/silt)			0.718	2.469	3.150	4.263	12.052

*, size classification of particle is adopted from Friedman & Sanders (1979).

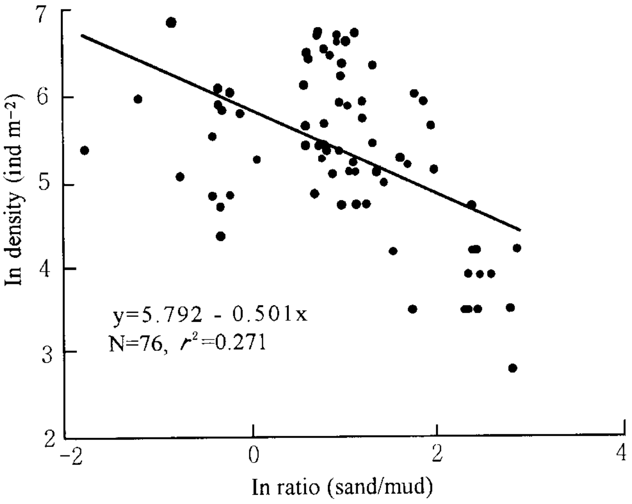

Figure 4. *Lingula unguis*: regression of $\log_e$ density on $\log_e$ median diameter (mm) of the substrate.

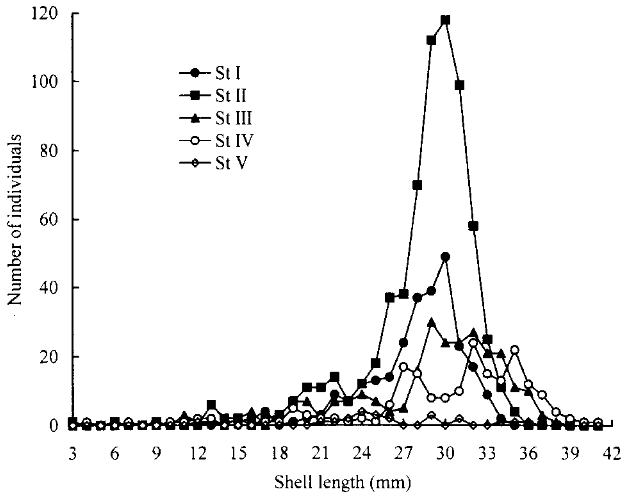

Figure 5. *Lingula unguis*: spatial size structure in the Kunsan intertidal flats.

Table 4. *Kolmogorov–Smirnov two-sample test for differences in population distribution between the five stations.*

Stations	I	II	III	IV
I				
II	ns			
III	ns	ns		
IV	ns	ns	ns	
V	*	*	***	***

*, $P<0.05$; ***, $P<0.001$; ns, not significant.

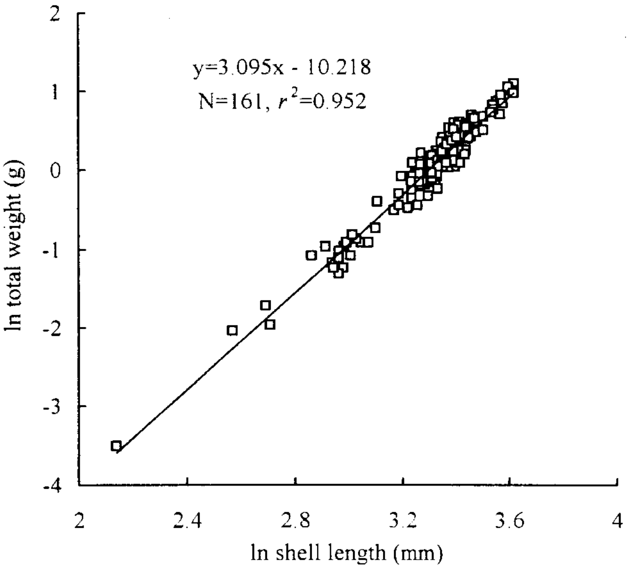

Figure 6. *Lingula unguis*: regression of $\log_e$ total weight (g) on $\log_e$ shell length (mm).

was no significant difference in size–frequency distribution between the two years (Kolmogorov–Smirnov two-sample test: $D_{max}=0.23$, $P>0.2$). The spatial population distribution pattern was not significantly different between stations I–IV, but station V, with a small number of individuals (Figure 5), found to be significantly different from the other stations (Table 4).

Growth, mortality and recruitment

The shell length (SL) of *L. unguis* ranged from 3.42 to 41.56 mm. The regression between shell length (mm) and total weight (g) was significant (ANOVA: $F=643.24$, df=1, 159, $P<0.001$), showing an isometry within a 95% confidence limit (±0.24) of slope (Figure 6).

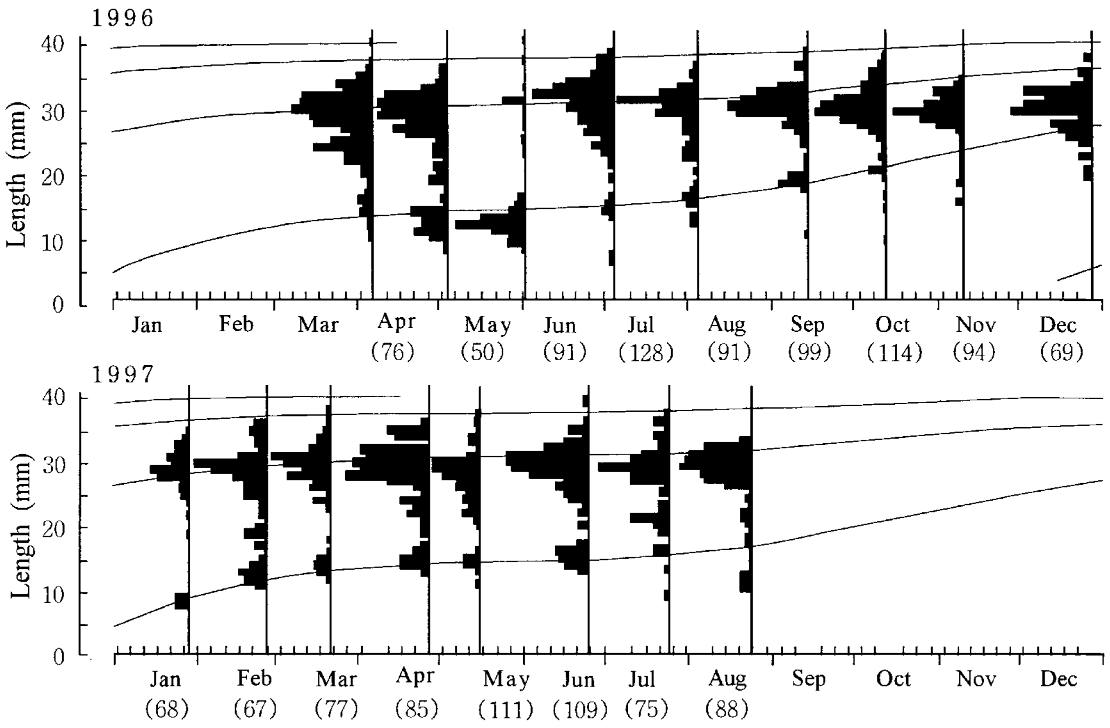

Figure 7. *Lingula unguis*: length–frequency distribution, expressed as percentage during two successive years in Kunsan intertidal flats and estimated growth curves for this population. Sample size in parentheses below months.

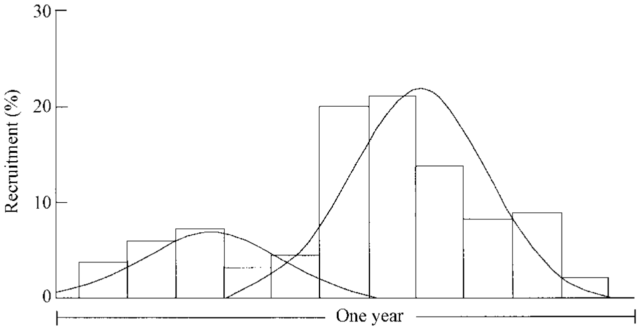

Figure 8. *Lingula unguis*: recruitment pattern identified by ELEFAN II routine.

The monthly length–frequency data used in the present analysis consisted of 1492 measurements. Modal progression analysis of 1 mm size-classes over the study period, as used in the ELEFAN program, is given in Figure 7. The best fits to the length–frequency data identified (Rn=231) and revealed that shell growth in *L. unguis* was polymodal. See Figure 5 for the VBGF estimated by ELEFAN routines. The L_∞ and K values were 44.00 mm and 0.88 y^{-1} respectively. The parameter C (the amplitude of seasonal growth oscillation) showed quite high values of 0.9. The phase of slowest growth, WP, was during the summer (May) (WP=0.48). From the best estimates of growth parameters (L_∞=44.00 mm and K=0.88), the growth performance index (ϕ') was calculated as 3.23. The animal attained a shell length of 25.7 mm, 36.4 mm and 40.9 mm at the end of 12, 24 and 36 months

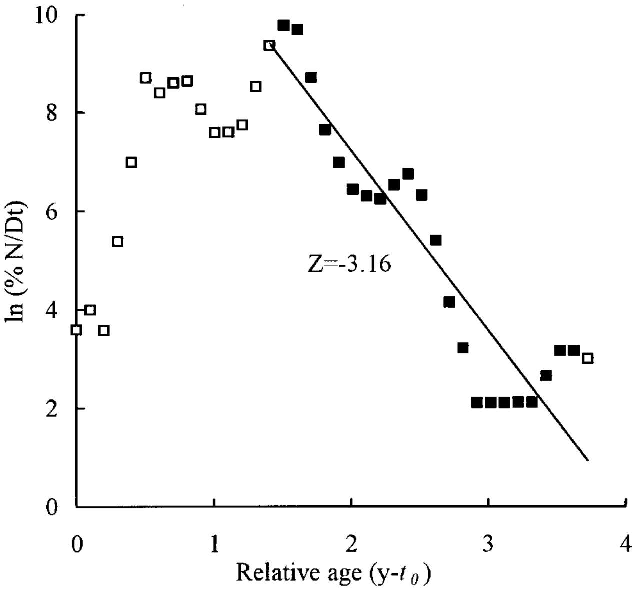

Figure 9. *Lingula unguis*: total mortality (Z) estimated by length-converted catch curve based on length-composition data.

respectively. Based on the growth coefficient (K), the maximum life span (t_{max}) of the brachiopod was estimated to be approximately 3.45 y for this study.

The structure of the recruitment pattern obtained by ELEFAN program indicated two normally distributed groups although the peaking time is unknown (Figure 8).

Mortality, calculated from the length-converted catch curves, was 3.65 (95% CL ±0.69) y^{-1} (Figure 9).

DISCUSSION

The density of population of *Lingula unguis* shows a significant spatial variation in the intertidal flats, with peak density in the Station II, while there was no significant temporal variation. In the study area *L. unguis* inhabits a wider range of substrates containing from 51–92% sand (>2.0 mm) to 8–49% silt (<0.063 mm), suggesting that the brachiopod occurred in a sediment dominated by coarse particles (Paine, 1970). These distribution patterns have been observed for *L. anatina* at Shelly Beach, Australia (Kenchington & Hammond, 1978) and *L. reevei* (Emig, 1984).

Regression analysis for *L. unguis* data indicates a significant reverse relationship between $\log_e$ ratio of sand to mud and $\log_e$ density. It suggests a preference for sandy substrates with a ratio of sands to silts below about seven. Therefore it is likely that lingulid distribution occurred predominately in sandy substrates rather than the two extremes of sediments consisting solely of sands or silts.

This study showed that *L. unguis* population has a unimodal, apparently skewed distribution of large individuals with a lack of small specimens. Similar results are found in *L. unguis* (Chuang, 1961; Kawaguti, 1943) and other lingulid species (Paine, 1963, 1969; Logan, 1975; Neall, 1970). Rudwick (1965) noted that the skewed distributional pattern occurs in a species with high pre-settlement mortality but low juvenile mortality. This pattern may be attributed to variable and patchy recruitment to the population, consequently leading to a local absence of smaller size-classes (Rudwick, 1965; Thayer, 1975).

The von Bertalanffy model successfully described the growth of *L. unguis* and our results indicate that growth curve of *L. unguis* derived from length–frequency data grew faster and reached a larger size at age than *L. anatina* (Kenchington & Hammond, 1978) and *L. reevei* (Worcester, 1969) (Figure 10). They also were consistent with its biological features. As Taylor (1958) noted for some fish stocks, older individuals usually reach 95% of the asymptotic size, which for *L. unguis* corresponds to a shell length of 41.8 mm (approximately 95% of 44.0 mm). Considering that the largest shell found during the study period measured 41.6 mm in length, the estimated growth parameters appear to be reliable. However, since no other von Bertalanffy growth curves are reported for brachiopods, no further direct comparisons can be made.

The amplitude of growth oscillation (C) and the wintering point (WP) are often related to the mean range of water temperature in the species' habitat (Pauly, 1987). In this study the tendency of high growth oscillation (C) value (0.9) indicates that *L. unguis* experiences strong seasonality in growth. However, growth oscillations in *L. unguis* appears to be correlated more with its annual reproductive cycle than with temperature. Estimated wintering point (WP=0.48) were ascribed to June, suggesting the occurrence of physiologically important events during this time. These results are supported by observations on breeding by Yatsu (1902) and Kume (1956).

Lingula unguis showed a maximum longevity of 3.45 y, which is shorter than *L. anatina* (Kenchington & Hammond, 1978; Mahajan & Joshi, 1983) and *L. reevei* (Worcester, 1969).

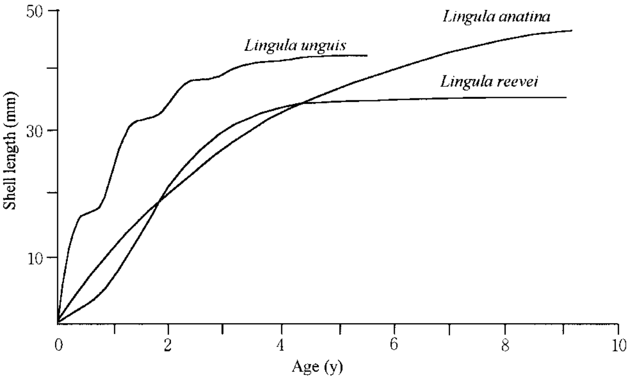

Figure 10. Average growth curves in three linguid species—*Lingula anatina* (Kenchington & Hammond, 1978), *Lingula reevei* (Worcester, 1978) and *Lingula unguis.*

Lingula unguis has two major recruitment events per year, the data from this study cannot prelude the possibility of more than two but the clear normal distribution in recruitment abundance makes this unlikely. This is in agreement with Chuang (1959b) who found year-round breeding at Singapore but does not correspond to Yatsu (1902) and Kume (1956) who suggest that the breeding season at Misaka, Japan, was limited to the two mid-summer months (July and August). As Rudwick (1970) proposed for most brachiopod species, the difference in duration of the breeding period varied with location. Therefore, it is likely that the recruitment pattern will vary according to local conditions with respect to a variety of factors.

The total mortality (Z) estimated here for *L. unguis* ($3.65\ \mathrm{y}^{-1}$) was high. As it is not an exploitable stock, this is due exclusively to natural death. This may be primarily attributed to predation, short food supply, and recruitment failure by selection of unsuitable substrate. There are few data on the causes of mortality.

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