

## Growth of *Crassostrea cucullata* Born (Bivalvia) at different levels in the intertidal zone

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(Accepted 26 October 1989)

### ABSTRACT

Ruwa, R.K., 1990. Growth of *Crassostrea cucullata* Born (Bivalvia) at different levels in the intertidal zone. *Aquaculture*, 88: 303–312.

The growth patterns of *Crassostrea cucullata* Born at different levels in the intertidal zone were studied using empirical equations based on size at age data in the exponential growth phase which occurred in the first 10 months after the spat settled. The growth rate was related to height of shore level and decreased in an upward direction. The faster growth occurred below mean tide level. Oysters translocated from higher levels to lower levels showed an increase in growth rate. Conversely, those translocated from lower levels to higher levels showed reduction in growth rate.

### INTRODUCTION

The oyster *Crassostrea cucullata* Born, whose maximum shell length in wild specimens is 65 mm (Van Someren and Whitehead, 1961), is an intertidal oyster found in brackishwater marine environments where it cements onto mangroves, rocks and other hard substrates. In a macrotidal coast like that of Kenya, where the tidal range is 4 m (Brakel, 1982), the distributional range of this oyster on rocky shores is up to 2.7 m wide (Ruwa, 1984). Following the shore terminology of Lewis (1964) and Hartnoll (1976), these oysters are abundant in the upper eulittoral zone.

There are various documentations (e.g. Seed, 1968) about bivalves growing faster at lower levels of the shore, and even fastest subtidally (Sumner, 1981). Van Someren and Whitehead (1961) stated that the growth of *Crassostrea cucullata* was fastest at lower levels of the shore although they did not conduct quantitative studies at various levels across the vertical range of the intertidal zone. Okemwa et al. (1986) established an upward shore decrease in the mean shell lengths of *Crassostrea cucullata* on a rocky cliff but the individuals were of unknown ages. Because the ages of the oysters in the latter study were unknown, and the growth patterns of *Crassostrea cucullata* at var-

ious levels across the intertidal zone have not been studied, the present work was carried out to study the growth of oysters of known ages.

#### MATERIALS AND METHODS

The study was carried out at the Gazi Oyster Culture Station in Southern Kenya using oyster spat that settled on cemented coconut shells, the strings being coded as B, B1 and C for ease of reference. The strings were tied and hung vertically from an oyster rack in the intertidal zone in a mangrove creek such that the coconut shells were positioned at 1.1, 1.5, 2.5 and 2.9 m above datum (Fig. 1). They were calibrated in relation to the Kilindini harbour datum using Kenya Ports Authority (1986) tide tables during very calm water periods around neap tide days.

Strings B and B1 (Fig. 1) were tied in the intertidal zone in April 1986 to coincide with the occurrence of the long rains when the peak spatfall occurs (Van Someren and Whitehead, 1961). Measurement of the maximum shell lengths of all the oysters on each coconut shell, using vernier calipers, was started from the time recruitment began on each shell and was done at monthly intervals. The oyster spat were said to be recruited on a coconut shell when they reached a size which could be seen with the naked eye. After 2 months, the sequence of the coconut shells of string B was reversed as shown in string B2 of Fig. 1. At the time of reversing B, string C was tied in the intertidal zone. Measurements of oysters on the coconut shells of string B2 were continued monthly. Likewise, when the oyster spat settled on the coconut shells of string C, their measurements were taken monthly. The study was terminated after about 18 months. The day when spatfall was first detected on each coconut shell was recorded. The age of the oysters was determined by counting from the first day that spatfall occurred on each coconut shell.

From the data obtained at various levels, plots of size against age were made.

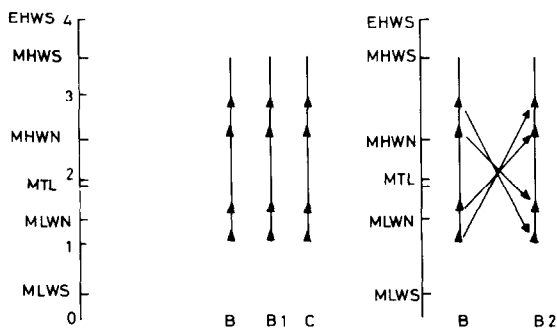


Fig. 1. Positions of the cemented coconut shells in relation to the Kilindini (Mombasa) harbour datum. The shells were positioned at 1.1, 1.5, 2.5 and 2.9 m shore level above datum. The shells of string B were translocated to new positions shown in string B2.

A comparison of the mean shell lengths computed from 100% and 50% of the total number of oysters on each coconut shell was made using a paired *t*-test. In the case of the 50%, it was the larger sized individuals which formed half of the total number of oysters that were used. It was necessary to calculate the mean shell lengths based on 50% because it is known that a decrease effect in the mean shell lengths based on 100% of the population may occur due to continuous recruitment and mortality (Ricker, 1975), and overcrowding.

The growth patterns across the intertidal levels were studied by comparing the values of the gradients *b* (=the growth rate) of the regression equations during the exponential growth phase which in this oyster occurs in the first 10 months from settlement of spat (Ruwa, 1988). The Student–Newman–Keuls (SNK) multiple range test was used in the comparisons to test the differences in the growth rates after an analysis of covariance (ANCOVAR) as described by Zar (1974).

## RESULTS

The plot (Fig. 2) of size against age at 1.1 m above datum over the period of nearly 18 months showed that the fastest growth occurred within the first 10 months. The biggest size of oyster measured during this period was 34.2 mm (at age 9.5 months). The mean shell lengths based on 50% larger sized oysters were significantly bigger than the mean shell lengths based on 100% of the oysters (paired *t*-test,  $P < 0.001$ ).

Continuous recruitment occurred from April to October 1986 (Fig. 3). The highest total number of oysters that settled on the coconut shell was 85. After this peak recruitment, it was observed that there was: (i) rapid mortality at

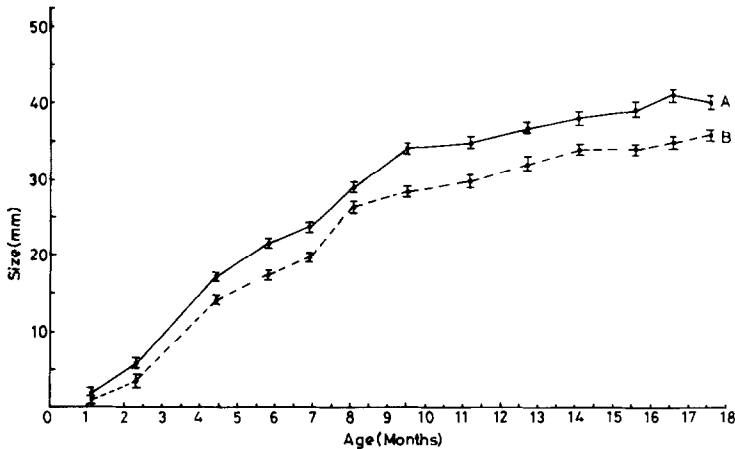


Fig. 2. Plots of size against age for *Crassostrea cucullata* Born at 1.1 m above datum. A, based on 50% larger sized oysters; B, based on 100% of the oysters.

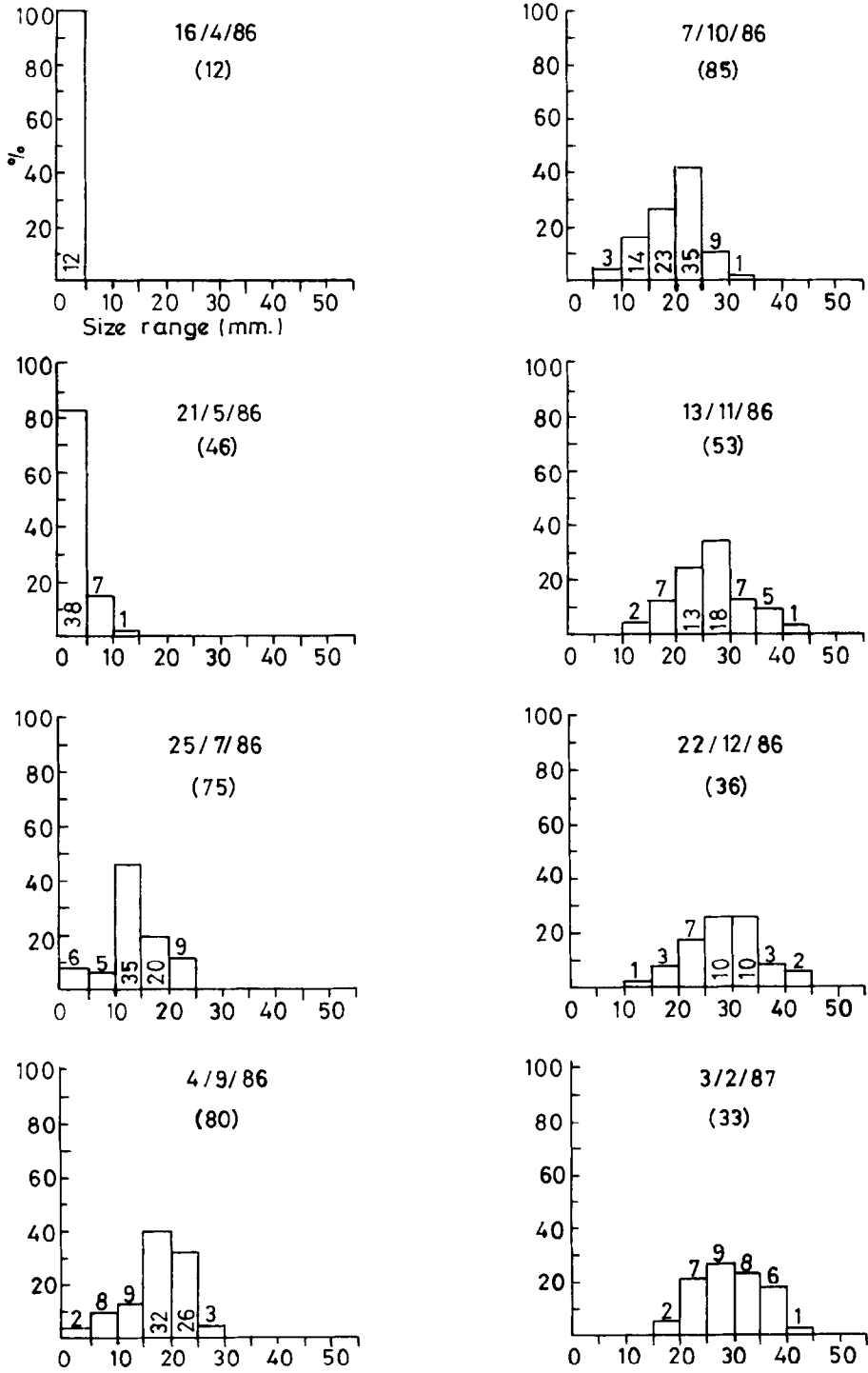


Fig. 3. Settlement of *Crassostrea cucullata* Born from April 1986 to August 1987.

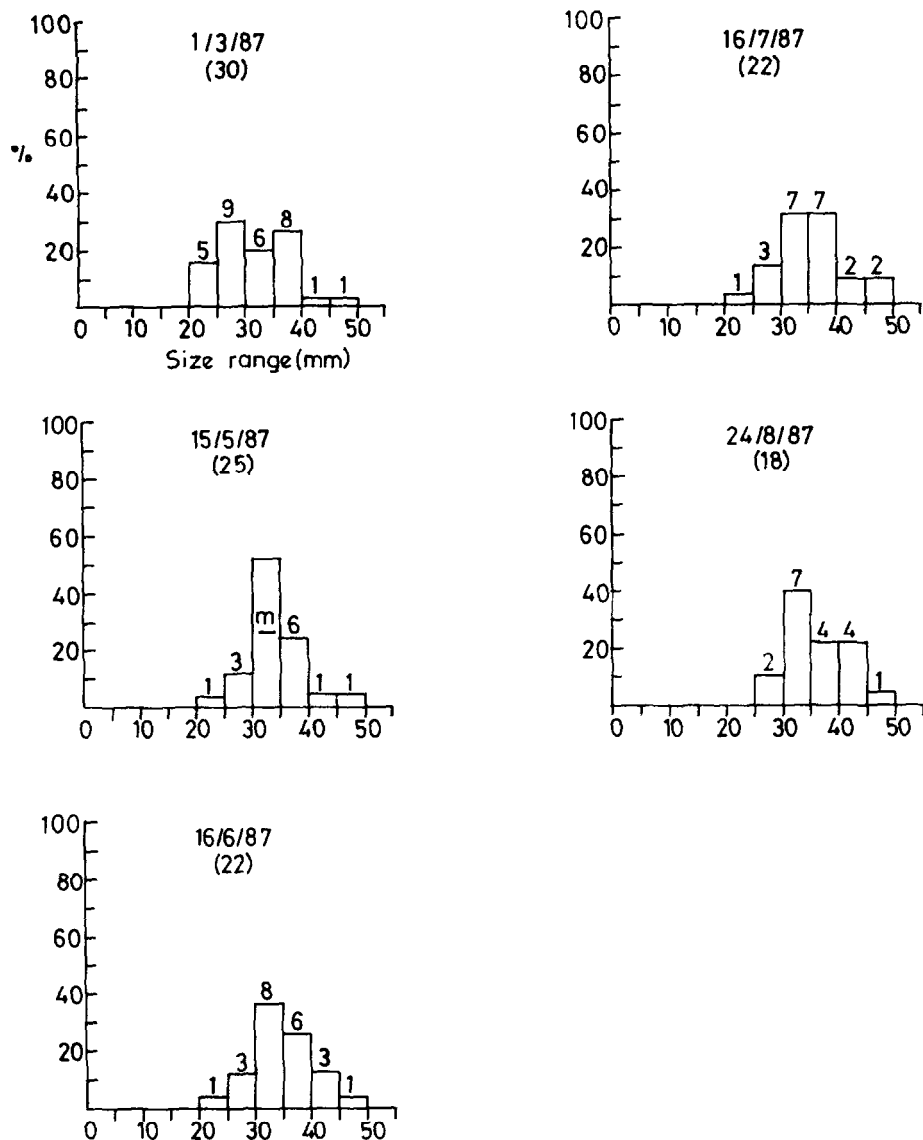


Fig. 3 (continued).

the ages between 8 and 10 months, in November and December. During this period 57.6% of the 85 oysters died, 37.6% in November and 20% in December; (ii) thereafter the monthly mortality was very low and ranged from 0 to 5.8%. At the time of termination of the investigation 78.8% of the 85 oysters had died.

The regression equations describing the relationships of the size against age

on the coconut shells at different levels of strings C, B1 and B2 are shown in Table 1. The results from oysters on strings C and B1 showed that the growth rates of the oysters decreased in an upward shore direction. The growth rates at the different levels from 2.5 m and below were not significantly different. However, the growth rates at 1.1- and 1.5-m levels were significantly higher than the growth rate at 2.9 m (SNK test,  $P < 0.05$ ). This indicated that significant differences in growth rates occurred when the oysters grew at widely different levels of the shore.

The growth rate of the oysters translocated from 1.1 to 2.9 m (string B2) was compared with growth rates at 2.9 m (string C), 1.1 m (string C) and 1.1 m (string B1). The growth rates at 1.1 m (string B1) and 1.1 m (string C) were significantly higher than the growth rate of the oysters at 2.9 m (string B2) (SNK test,  $P < 0.001$ ). However, the growth rates at 1.1 m (string C) and 1.1 m (string B1) were not significantly different. Likewise, the growth rates at 2.9 m (string C) and 2.9 m (string B2) were not significantly different.

Other comparisons of the growth rates at 1.5 m (string C), 1.5 m (string B1), 2.5 m (string C), 1.5 and 2.5 m (string B2) showed that growth rates at 1.5 m (strings C and B1) were significantly higher than: (i) at 1.5 m (string B2) which had been translocated from 2.5 m (SNK test,  $P < 0.01$ ), and (ii)

TABLE 1

Regression equations ( $y = bx + a$ ), with 95% confidence limits of  $b$ , for size ( $y$ ) against age ( $x$ ) of oysters growing on coconut shells at different levels. The coconut shells of strings B1 and C were not translocated whereas those of string B2 were translocated from different levels as shown in brackets. The correlation coefficient,  $r$ , was significant at  $P < 0.001$  in all cases.

Level (m)	$a$	$b$	$r$
<b>String B1</b>			
1.1	-1.509	$3.896 \pm 0.605$	0.988
1.5	-2.239	$3.965 \pm 0.503$	0.982
2.5	2.293	$2.512 \pm 0.734$	0.960
2.9	No settlement of oyster spat		
<b>String B2</b>			
1.1 (from 2.9)	No settlement of oyster spat at 2.9 m		
1.5 (from 2.5)	4.031	$2.454 \pm 0.753$	0.966
2.5 (from 1.5)	2.700	$2.626 \pm 0.892$	0.959
2.9 (from 1.1)	3.657	$2.131 \pm 0.721$	0.947
<b>String C</b>			
1.1	2.408	$4.026 \pm 1.031$	0.976
1.5	-0.838	$4.397 \pm 1.039$	0.980
2.5	-0.715	$3.572 \pm 0.892$	0.969
2.9	-1.046	$2.881 \pm 0.595$	0.984

at 2.5 m (string B2) which had been translocated from 1.5 m (SNK, test  $P < 0.01$ ). This indicated that the translocation of the oysters upset their growth and therefore in undisturbed conditions the growth rates at the same levels were higher. The comparisons again showed that the growth rates of oysters which are at the same levels were not significantly different. The growth rates of the non-translocated oysters at 1.5 m (string B1) and 2.5 m (string C) were again not significantly different. Similarly, the growth rates of the translocated oysters at 1.5 and 2.5 m (string B2) were not significantly different.

Observations on recruitment and mortality across the vertical range of the intertidal zone (Table 2) showed that recruitment occurred first and profusely on the lower level coconut shells but the spatfall became scanty in an upward shore direction, occurring much later at higher shore levels. Mortality (Table 2) was correspondingly higher at lower levels and decreased in an upward shore direction. The mortality of oysters translocated from lower (1.1 m) to higher (2.9 m) levels was lower than that of oysters maintained at the lower level, 1.1 m above datum. It was observed that a living oyster does not extend and grow over another living oyster. When living oysters meet, both right and left valves of the shells grow upward forming wings, giving an impression of formation of fences. However, the right surfaces of the valves of the large living oysters may support oyster spat.

TABLE 2

Recruitment and mortality of oysters at various height levels in the intertidal zone on cemented coconut shells. PN stands for peak number of settled oysters and LON for numbers of live oysters at the end of the 10th month which marked the end of the asymptotic growth phase

Level (m)	PN	LON	Mortality (%)
String B1			
1.1	85	33	61.2
1.5	39	24	38.5
2.5	34	25	26.5
2.9	0	0	0
String B2			
1.1 (from 2.9)	33	33	0
1.5 (from 2.5)	42	24	42.9
2.5 (from 1.5)	37	24	35.1
2.9 (from 1.1)	82	44	46.3
String C			
1.1	45	18	60.0
1.5	9	6	33.3
2.5	9	5	44.5
2.9	8	6	25.0

## DISCUSSION

Growth is under the influence of various biotic and abiotic factors which influence each other, and the effect of a single factor could therefore be overshadowed and difficult to demonstrate (e.g. Malouf and Breese, 1977). Against this background it is therefore necessary to be cautious when considering whether a single given factor may significantly control growth when other factors have not been controlled, as in this study.

The present study was done under natural field conditions. It can be argued that the influence of shore level on growth has been demonstrated in this study for three reasons. (1) There was a decrease in the rate of growth in an upward shore direction. (2) When low level oysters were translocated to higher levels, their growth rate was reduced and was significantly lower than that of oysters maintained at lower levels. (3) Conversely, when higher level oysters were translocated to lower levels, their growth rate increased and was significantly higher than that of their counterparts which were maintained at higher levels. However, it is important to note that such significant differences in growth rates occurred conspicuously when the oysters grew at widely different levels of the shore.

Ruwa (1988) found that the settlement of oyster spat occurs much earlier and abundantly at lower levels of the shore, and especially below mean tide level. From the observed pattern of settlement it could be inferred that the difference in size between the higher and lower level oysters on rocky shores is a function of age. However, the evidence from this study indicates, indeed, that the factor that affects the growth rate, other than age, is height of shore level and these interact and explain the size gradients described by Okemwa et al. (1986). Since young oysters which were still within the exponential growth phase when translocated from lower to higher levels exhibited lower growth rates than their counterparts maintained at lower levels, and similar to the oyster spat which settled much later at the lower level, it follows that oysters at higher levels will be comparatively smaller than those at lower levels at any given age.

The faster growth at lower than at higher levels has been attributed to longer feeding hours for the lower level oysters because the immersion times at the lower levels are longer (Morton, 1977). In a macrotidal shore like that at the Kenyan coast, large differences in immersion times across the intertidal zone occur and consequently differences in growth rates of low level and high level oysters are not unexpected.

The seasonality in recruitment of the oysters (Van Someren and Whitehead, 1961) did not appear in this study (Fig. 3). This could be explained by the fact that, with time, the surface available for settlement was used up because various benthic organisms settled on the surfaces. This cut off further settlement and therefore overshadowed the seasonality. Thus, from Fig. 3, it



can be seen that the conspicuous abundant recruitment in May to September/October 1986 was not observed in the same period in 1987.

The mortality was higher at lower levels of the shore and during the first 10 months in the exponential growth phase. It is commonly observed that mortality in oysters is highest during their early stages after settlement but later becomes very low, showing that it is size and age dependent (Walne, 1974). The high mortality at low shore levels could be caused by high biological competition with other benthic species which was clearly evident from the profuse settlement of spirobids, serpulids, bryozoans and hydrozoans. The gregarious nature of the oyster spatfall at the lower levels may also have contributed to their own mortality due to intraspecific competition.

#### ACKNOWLEDGEMENTS

I am greatly indebted to Prof. P. Polk, Free University of Brussels, Belgium, who is the Director of the Kenyan–Belgian Project in Marine Sciences, for various discussions and suggestions he put forward, and to Mr. S.O. Allela, Director of the Kenya Marine and Fisheries Research Institute, for his cooperation.

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