African Journal of Marine Science 2005, 27(3): 567–575
Printed in South Africa — All rights reserved

AFRICAN JOURNAL OF MARINE SCIENCE
EISSN 1814–2338

Growth patterns of the pearl oyster *Pinctada margaritifera* L. in Gazi Bay, Kenya

KM Mavuti[1], EN Kimani[2]* and T Mukiama[3]

[1] *Department of Zoology, University of Nairobi, PO Box 30197, Nairobi, Kenya*
[2] *Kenya Marine and Fisheries Research Institute, PO Box 81651, Mombasa, Kenya*
[3] *Department of Botany, University of Nairobi, P O Box 30197, Nairobi, Kenya*
* *Corresponding author, e-mail: ekimani@kmfri.co.ke*

Culture of pearl oysters is rapidly increasing worldwide, including the western Indian Ocean. The oyster *Pinctada margaritifera* L., which produces the most highly valued black pearls, occurs in East Africa, and has been exploited there for the shell for many decades. The growth patterns of *P. margaritifera* from a natural population in the sheltered back-reef, and from oysters translocated to a tidal current-swept site, both sites within Gazi Bay, Kenya, are described. The growth rate in the natural population ranged from 31.3mm year^{-1} (60–65mm size-class) to 7.6mm year^{-1} (105–110mm size-class). The von Bertalanffy growth coefficient (K), calculated with a fixed L_∞ of 127.2mm, was 0.30 for the natural population and 0.38 for the translocated oysters. The mean growth rate during the north-east monsoon season was approximately double that for during the south-east monsoon season. The daily rate of nacre deposition ranged from 1.3µm to 5.9µm (mean 3.45µm); it declined with the size of oysters and was marginally higher at the high-energy current site. At that rate, it would take approximately two years to produce a marketable cultured half pearl with a 2.5mm layer of nacre. The results of the study are relevant to the understanding of the influence of the environment on growth, and are applicable to the optimisation of growth rate of pearl oysters in the inshore region along the east coast of Africa.

Keywords: growth rate, Kenya, monsoon seasons, nacre deposition, *Pinctada margaritifera*, tidal currents

Introduction

Pinctada margaritifera L. is the second largest pearl oyster and has the widest Indo-Pacific distribution. The western Indian Ocean, from the coast of Tanzania in the south to the Red Sea in the north, is the western limit of the global distribution of the species (Sims 1993). It is harvested for its shell, known as 'Mother of Pearl' (MOP), and it produces the highly valued cultured black pearl. The history of the shell trade in the western Indian Ocean before the 19th century is poorly known, although there is evidence of shell trade from Zanzibar (Middleton 1992). It is likely that East Africa was a source of MOP since the 17th century, when shell buttons became fashionable in Japan (Marshall *et al*. 2001). The main Kenyan markets for commercial shells (principally MOP) are Japan, South Korea, Singapore, Taiwan and Hong Kong, but the value is difficult to quantify because the available data mostly provide an amalgamation of products (Wood and Wells 1995). Cultured pearls from *P. margaritifera* have been commercially produced in the Seychelles since the mid-1990s, the first batch being harvested in 1995. A community-based pearl oyster culture trial project, under the Eastern Africa Marine Ecoregion initiative in the Mafia Island Marine Park, Tanzania, harvested the first batch of hemispherical pearls (known as 'mabe') in 2004. The United Nations Development Program initiated a project on pearl production in the Maldives, which introduced techniques of collecting seed and rearing pearl oysters to the local community in Vaavu atoll in 2003.

The growth of the pearl culture industry has motivated extensive studies on the biology and ecology of the pearl oysters, particularly in the South Pacific and Australia where culturing pearls is of substantial economic importance. Studies include those on larval growth and nutrition (Hayashi and Seko 1986, Numaguchi 1999), seed collection and juvenile growth (Rose and Baker 1994, Southgate and Beer 2000), hatchery and nursery culture (Southgate and Beer 1997), population genetics (Durand *et al*. 1993, Benzie and Ballment 1994, Wada and Komaru 1994) and ecological modelling (Hawkins *et al*. 1998, Pouvreau *et al*. 2000). Growth patterns in pearl oysters have been reported mainly from important pearl-producing areas (Nasr 1984, Elnaeim 1984, Sims 1994, Rodgers *et al*. 2000), and it was demonstrated that their growth performance shows high specific and intra-specific variation (Pouvreau *et al*. 2000). Therefore, the relevance of growth performance is important in determining the

suitability of the environment for culture, shell growth and deposition of nacre.

Growth performance in bivalves is determined by their genetic makeup (Wada and Komaru 1994), and is influenced by the environment — mainly food availability (Griffiths 1980, Newell and Shumway 1993). Genetic mixing is high between distant pearl oyster populations in the Indo-Pacific region (Durand *et al*. 1993, Benzie and Ballment 1994). Hydrodynamics also influence growth in bivalves through the response of the filter-feeding process to current flow (Wildish and Kristmanson 1988). Water flow supplies food particles, re-suspends poor quality sediments leading to the dilution of organic matter in the water column, and also physically influences the retention of food particles in the gills of bivalves.

Dominant features of the inshore regions of East Africa are the seasonal monsoons and tidal currents. They determine seasonal fluctuations in water temperature, salinity, suspended matter and primary productivity. The large tidal amplitude, of up to 3.5m during maximum spring tides, generates strong tidal currents through reef channels into and out of the shallow bays and lagoons during flood and ebb tides respectively. Therefore, the shallow lagoons that are available and easily accessible for oyster culture experience a wide range of tidal current velocities (Kitheka *et al*. 1996). However, information on the influence of water flow on the growth rate of pearl oysters is scarce. Furthermore, except for a few studies in the Red Sea (Nasr 1984, Elnaeim 1984), little is known about growth patterns of pearl oysters from the western Indian Ocean, despite the growing interest in that resource.

The aims of this study are to determine the growth performance of *P. margaritifera*, and to investigate the influence of the monsoon seasons and tidal currents on their growth rates in the inshore regions off Kenya. Growth patterns and nacre deposition of *P. margaritifera* from a sheltered back-reef and from a high current-flow area in Gazi Bay, Kenya, are compared.

Material and Methods

Study area

The study was conducted in Gazi Bay (4°25'S, 39°30'E), a shallow tropical system with a mean depth of 5m and an area of about 5km^2. The bay is protected by the Chale Peninsula, Chale Island and a fringing reef to the north, and it opens to the Indian Ocean through a relatively wide (3.5km) channel to the south (Figure 1). The hydrodynamics within the bay are dominated by semi-diurnal tides, of up to 3.5m amplitude, which generate strong tidal currents. The ebb tide lasts 7–8h, whereas the flood tide lasts 4–5h (Hemminga *et al.* 1994). Two tidal creeks, Kidongoweni and Kinondo, measuring about 5km and 2.5km respectively, drain water from the intertidal flats into the bay (Figure 1). The Kidongoweni River feeds the Kindongoweni Creek at a water discharge rate of around 700m^3 day^{-1} during the dry season and 1.19 x 10^{5}m^3 day^{-1} during wet season (Kitheka 1996). One sampling site (Site 1) was located in front of the two channels that drain the

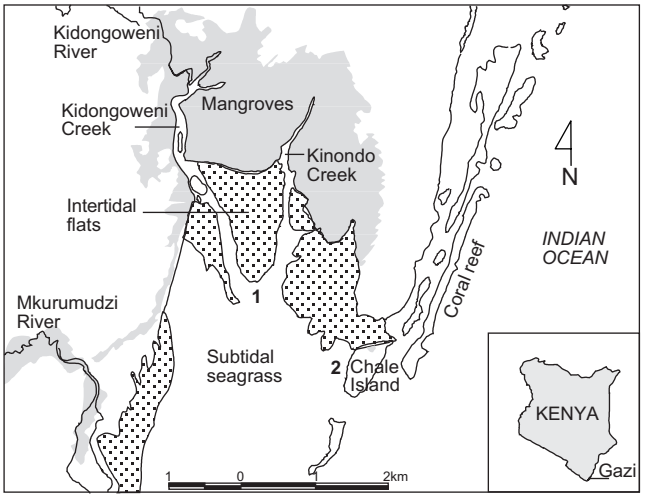

Figure 1: Map of Gazi Bay showing the positions of Site 1 and Site 2 and locations mentioned in the text

intertidal areas. The other site (Site 2) was located west of Chale Island, which is sheltered by a fringing reef. The two sites were 2–2.5km apart and both relatively shallow, with depths of about 0.5m at spring low tide. The sites were selected for this study because they are relatively close to each other, so minimising differences in environmental factors, the natural abundance of pearl oysters and the potential of the bay for oyster culture.

Physical environment

The abiotic environment at the two sites was monitored monthly between April 2002 and March 2003. Sea surface temperature (SST) and salinity were recorded around mid-day using a hand-held mercury thermometer (±0.1°C) and a refractometer respectively. Three 1-l replicate water samples were taken to determine total suspended matter (TSM) and the organic matter content (OC). The water samples were filtered using 4.5cm diameter pre-ashed GF/C filters of 1.2µm, dried at 70°C for 48h, then ashed at 450°C to obtain the organic matter of the water. The 'clod card' technique (Jokiel and Morrissey 1993) was used to estimate the relative intensity of water motion in the study sites using 'plaster of Paris' blocks. The blocks, weighing between 31g and 37g, were dried at 70°C and weighed using an electronic balance (±0.1g). Ten blocks were suspended 15cm above the bottom, on bamboo sticks that were randomly placed onto the substrate at the two sites, for 24h. Five control blocks were placed in 25-l seawater containers during the same period. The relative intensity of water motion, i.e. the diffusion factor (DF), for each block was calculated as follows:

$$DF = 100 \times ((FIDW - FFDW / FIDW) - (CIDW - CFDW / CIDW))$$

where FIDW (field initial dry weight) = dry weight of the blocks before deployment in the sea;

FFDW (field final dry weight) = dry weight of blocks after recovery from the sea and drying at 70°C for 48h;
CIDW (control initial dry weight) = dry weight of control blocks before placing in 25-l seawater containers for 24h;
and CFDW (control final dry weight) = weight of the control blocks after drying at 70°C for 48h.

The experiments were done during the maximum spring tide (18–19 December 2002; 0m low tide) and neap tide (10–11 March 2003; 1.4m low tide). DF values were expressed as percentage weight loss per 24h. The seasons and site environment data were compared using the Student's t-test and the Kruskal-Wallis test, where the conditions for parametric analysis were not met. Test for normality of the data was done using Shapiro-Wilks' W-test, and the homogeneity of variances was tested using Levene's test.

Growth rates

The growth rate of *P. margaritifera* was determined at the two study areas, using the measure and re-measure method, between February 2002 and February 2003. Because too few *P. margaritifera* were found at Site 1, additional pearl oysters were relocated to that site so that effective comparisons of growth rate could be made between sites. Pearl oysters were collected by means of snorkeling at low tide at various times between February and October 2002. Six pearl oysters were collected and marked at Site 1 on 1 February, 18 more were collected from Site 2 and translocated to Site 1 on 14 February, and 10 were collected in a random search all over the bay and translocated to Site 1 on 17 July 2002. At Site 2, 29 pearl oysters were marked on 1 February, four on 14 February, 15 on 17 July and eight were marked on 24 October 2002.

The oysters were tagged using a piece of numbered plastic dymo-tape tied on a fishing line and passed through a hole drilled posteriorly to the umbo side of the shell using a hand-drill fitted with a 0.3mm diameter bit. The shell diameter of the oysters was measured, and termed the dorsoventral measurement (DVM; Figure 2), to ±0.1mm using calipers, as described by Sims (1994). The oysters were then tied onto small bamboo stakes, which were stuck in the substrate, as close as possible to the bottom to simulate natural situations. The sites were visited monthly and the oysters were re-measured. From the oysters marked at Site 1, three were recovered dead and four were not recovered at the end of the experiment. At Site 2, five oysters were recovered dead and nine were lost. A total of 108 and 124 measurements were obtained from Site 1 and Site 2 respectively. The growth rates within the study sites and during the north-east and south-east monsoon seasons were compared using analysis of covariance (ANCOVA). Growth rate was measured using the von Bertalanffy growth parameters:

$$L_t = L_\infty \left(1 - e^{\left(-K\left(t - t_0 \right) \right)} \right)$$

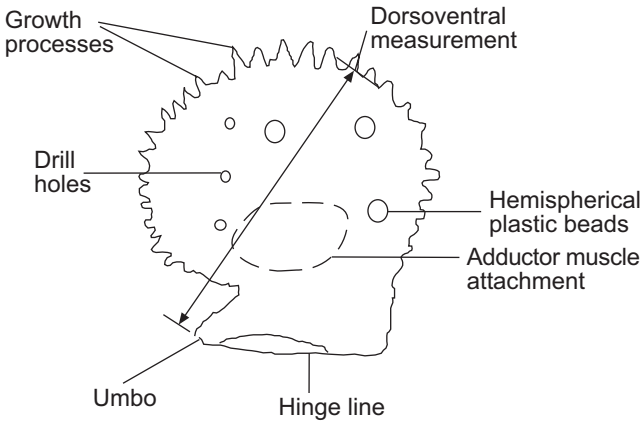

Figure 2: Dimension (dorsoventral measurement) used for measurement of growth rate, and positions of drill holes and hemispherical plastic beads

where L_∞ is the asymptotic length, K the growth constant, t the age and t_0 is the age at zero length. The growth parameters were estimated according to Fabens (1965), by fitting the measured and re-measured data into the following von Bertalanffy function:

$$L_2 = L_1 + \left(L_\infty - L_1 \right) \left(-e^{\left(-K\left(t_2 - t_1 \right) \right)} \right)$$

where L_1 is the length at the beginning and L_2 the length at the end of the time at large, and $t_2 - t_1$ is the time interval, using FISAT software (Gayanilo *et al*. 1995).

Growth performance (Φ) was calculated as: $\Phi = \log_{10}(K) + 2\log_{10}(L_\infty)$, according to Munro and Pauly (1983).

Nacre deposition

Two methods were used to determine the rate of nacre deposition between July and October 2003. The first method involved drilling holes in the shell 20mm, 40mm and 60mm away from — and perpendicular to — the hinge line, between the umbo and the adductor muscle (Figure 2). In the second method, hemispherical plastic beads of between 2.3mm and 2.7mm in height were glued on the right shell, similar to the method used in the culturing of hemispherical pearls. The oysters were then labelled with dymo-tape as done in the growth study. After recovery, the oysters were dissected to remove the flesh, and the shell was cut along the line of the holes and along the diameter of the blisters on the plastic beads using a fine saw blade. The width of the nacre over the drill holes and the plastic beads was measured using a caliper, and was recorded relative to the distance from the hinge line. Regression analyses of the width of nacre layer deposited, position of drill hole or bead, and shell growth, were used to determine the relationships between the deposition rate of nacre and other growth parameters. ANOVA was used to compare nacre deposition between the study sites.

Results

Environmental parameters

Variation in SST and salinity at the two sites is shown in Figure 3, and Table 1 shows the means and statistical comparisons of the environmental variables during the north-east monsoon (NEM) and south-east monsoon (SEM) seasons. The variances at the two sites were homogenous ($F = 0.257$, $p = 0.614$; $F = 0.088$, $p = 0.766$; $F = 0.0005$, $p = 0.980$; $F = 0.007$, $p = 0.932$ for SST, salinity, total suspended matter [TSM] and percentage organic matter [%OC] respectively), and the distributions were normal ($W = 0.941$, $p = 0.042$; $W = 0.972$, $p = 0.434$; $W = 0.971$, $p = 0.404$ for salinity, TSM and %OC data respectively). The parametric Student's t-test was used for all comparisons, except for SST, which was not normally distributed ($W = 0.882$, $p << 0.01$). SST was therefore compared using the equivalent non-parametric test, the Kruskal-Wallis ANOVA by median test. SST was similar between April–July, October, January and February at the two sites, but higher at Site 1 during the other months (Figure 2). SST did not differ significantly ($p < 0.05$) between the monsoon seasons at Site 1, but was significantly higher during the NEM season at Site 2. The pooled data for both sites showed significantly higher SST during the NEM season than the SEM season ($\chi^2 = 6.269$, $p = 0.012$). Mean SST at the two sites was not significantly different during SEM season ($\chi^2 = 2.201$, $p = 0.130$), the NEM season ($\chi^2 = 2.014$, $p = 0.155$), as well as the pooled annual data ($\chi^2 = 2.157$, $p = 0.141$). Annual salinity ranged from 31.5 to 37.0, and was lower at Site 1 from April to September and higher at Site 1 between October and March (except in January). Salinity did not differ significantly between sites and monsoon seasons ($p < 0.05$).

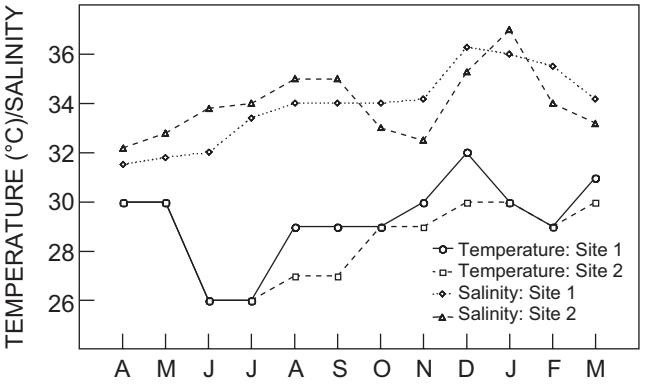

Figure 3: Monthly sea surface temperatures and salinities at Sites 1 and 2 between April 2001 and March 2002

The range in TSM was higher during the SEM season (7.7–36.0µg l^{-1}) than the NEM season (8.8–29.4µg l^{-1}), and was also higher at Site 1 (10.4–36.0µg l^{-1}) than at Site 2 (7.7–28.9µg l^{-1}). The mean TSM was highest at Site 1 during both monsoon seasons, and the overall mean TSM was higher at Site 1 by approximately 8.3%. The overall mean %OC was similar between sites (14.7 ± 3.8% and 14.6 ± 4.2% at Site 1 and Site 2 respectively), but higher at Site 2 during the NEM season than the SEM season. The mean percentage DF of the plaster of Paris blocks was significantly higher at Site 1 than at Site 2 during both the neap and the spring tides. The mean DF at Site 1 was 59% and 38% higher than at Site 2 during the spring tide and neap tide respectively.

Growth of oysters

The size range of the marked oyster population was 51.9–127.2mm DVM (mean 85.8 ± 13.04mm). The relationship between shell size (DVM, mm) and weight (shell + dry

Table 1: Mean (±SD) temperature, salinity, total suspended matter, organic content and diffusion factor of plaster of Paris blocks at Sites 1 and 2 in Gazi Bay

Site	SEM	NEM	Test statistic	p	Annual mean
		Temperature (°C)			
Site 1	28.7 ± 1.7	30.1 ± 1.1	$\chi^2 = 1.227$	0.267	29.2 ± 1.6
Site 2	27.9 ± 1.7	29.5 ± 0.4	$\chi^2 = 4.150$	0.041	28.5 ± 1.6
		Salinity			
Site 1	33.3 ± 1.1	34.4 ± 2.6	t = 1.38	0.17	33.9 ± 1.5
Site 2	34.0 ± 1.2	34.4 ± 2.6	t = 0.46	0.64	34.2 ± 1.4
		Total suspended matter (mg l^{-1})			
Site 1	19.4 ± 0.8	18.3 ± 0.6	t = 0.362	0.719	19.2 ± 7.8
Site 2	17.8 ± 0.6	17.1 ± 0.7	t = 0.247	0.806	17.6 ± 0.6
		Organic content (%)			
Site 1	13.5 ± 3.9	16.9 ± 2.8	t = 1.177	0.249	14.7 ± 3.8
Site 2	14.5 ± 4.1	14.9 ± 4.8	t = 0.077	0.939	14.6 ± 4.2
		Diffusion factor (%)			
	Site 1	*Site 2*			
Spring tide	42.6 ± 3.41	17.28 ± 2.4	t = 12.015	0.00002	
Neap tide	18.2 ± 1.3	11.4 ± 1.4	t = 3.128	0.020	

flesh weight, g) for *P. margaritifera* was weight = $-2.57DVM^{3.048}$ ($r^2 = 0.812$). The period between measure and re-measure ranged between 41 to 134 days. The highest mean growth rate of 0.086 ± 0.001mm day^{-1} (31.3mm $year^{-1}$) and lowest growth rate of 0.021 ± 0.021 day^{-1} (7.7mm $year^{-1}$) were obtained in the 60–65mm and 95–100mm size-classes respectively (Table 2). Mean growth rates were higher at Site 1 than at Site 2 for most size-classes, exceptions being the 55–60mm size-class (only one individual) and the 70–75mm and 80–85mm size-classes.

Size-classes >110mm were poorly represented in the population, so they were excluded from the dataset during subsequent analysis. The correlation between growth rate and mean size were weak, but significant, for both sites (r = 0.252 and p = 0.008, r = 0.480 and p = 0.001 for Sites 1 and 2 respectively, Figure 4). The overall growth rate at Site 1 (0.040mm day^{-1}) was significantly higher than at Site 2 (0.035mm day^{-1}; ANCOVA, F = 5.999, p = 0.015). The size-adjusted growth rate for Site 1 (0.042mm day^{-1}) was 21.4% higher than the size-adjusted growth rate (0.033mm day^{-1}) for Site 2.

Growth parameters obtained using Feben's (1965) method were K = 0.32 and L_∞ = 131.7mm for Site 1, and K = 0.58 and L_∞ = 106.6mm for Site 2. L_∞ predicted by Feben's method for Site 2 was lower than the largest individual observed in the oyster population under study (i.e. 127.2mm), whereas the L_∞ predicted from growth data at Site 1 was higher than the observed maximum size in the population. Therefore, K was underestimated at Site 1 and overestimated at Site 2. K was estimated using L_∞ fixed at 127.2mm, using Gulland and Holt routine in FISAT, which gave values of 0.38 for Site 1 and 0.30 for Site 2. Using these values in the growth equations, the age of the majority of the oysters in Gazi Bay (60–110mm) would range between 2 and 6 years old (Figure 5). The growth performance (Φ) of the oysters at Site 1 (3.788) was slightly higher than at Site 2 (3.686).

Growth during the monsoon seasons

The NEM season was assumed to be between October and March, and the SEM season between April and September. Measured and re-measured data that overlapped seasons were not included in the comparison. The growth rate and mean oyster size regressions for the sites and seasons are shown in Figure 6. Growth rate was significantly higher during the NEM season than during the SEM season at both sites (ANCOVA; F = 47.9, p << 0.05 and F = 14.8, p = 0.0003 for Sites 1 and 2 respectively). The mean daily growth rate at Site 1 was 0.056 ± 0.031mm and 0.020 ± 0.018mm during the NEM and SEM seasons respectively. The mean size-adjusted growth rate of 0.056mm day^{-1} during the NEM season was more than double the rate during the SEM season (0.022mm day^{-1}). The mean growth rate at Site 2 was 0.038 ± 0.030mm day^{-1} and 0.024 ± 0.021mm day^{-1} during the NEM and SEM seasons respectively. The mean size-adjusted growth rate at Site 2 during the NEM season (0.040mm day^{-1}) was less than that at Site 1, whereas the mean growth rate of 0.022mm day^{-1} during the SEM season was similar to that at Site 1. The

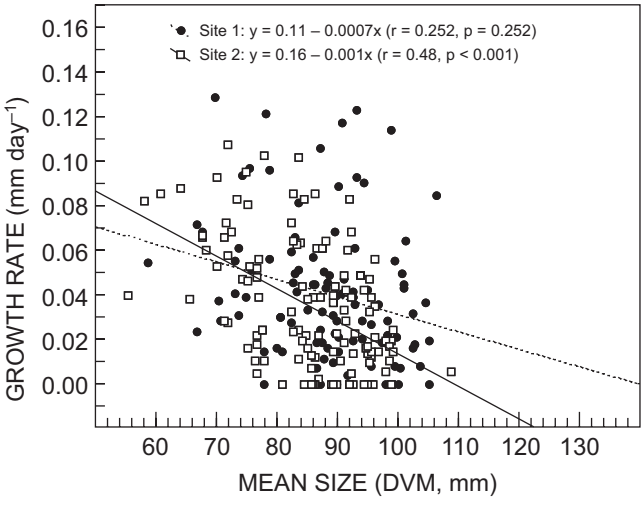

Figure 4: Gulland and Holt-type plot of growth rate of *P. margaritifera* at Sites 1 and 2. Regression equations for each site are given

Table 2: Mean and pooled growth rates (±SD) of *P. margaritifera* in 5-mm size-classes at Sites 1 and 2, and pooled growth rate in Gazi Bay. Numbers of samples are given in parenthesis

	Growth rate (mm day^{-1})		
Size-class (mm)	Site 1	Site 2	Pooled
55–60	0.054(1)	0.060 ± 0.029 (2)	0.058 ± 0.021 (3)
60–65	–	0.086 ± 0.001 (2)	0.086 ± 0.001 (2)
65–70	0.072 ± 0.043 (4)	0.057 ± 0.013 (4)	0.065 ± 0.030 (8)
70–75	0.049 ± 0.043 (7)	0.063 ± 0.024 (11)	0.058 ± 0.024 (18)
75–80	0.059 ± 0.042 (8)	0.041 ± 0.029 (17)	0.046 ± 0.034 (25)
80–85	0.042 ± 0.020 (12)	0.044 ± 0.032 (16)	0.043 ± 0.027 (28)
85–90	0.032 ± 0.024 (25)	0.026 ± 0.025 (27)	0.029 ± 0.024 (52)
90–95	0.042 ± 0.035 (24)	0.028 ± 0.024 (21)	0.036 ± 0.031 (45)
95–100	0.030 ± 0.029 (13)	0.016 ± 0.015 (24)	0.021 ± 0.021 (37)
100–105	0.037 ± 0.029 (11)	–	0.037 ± 0.029 (11)
105–110	0.034 ± 0.044 (3)	0.005 (1)	0.027 ± 0.038 (4)
115–120	–	0.024 (1)	0.024 (1)
125–130	–	0.032 (1)	0.032 (1)

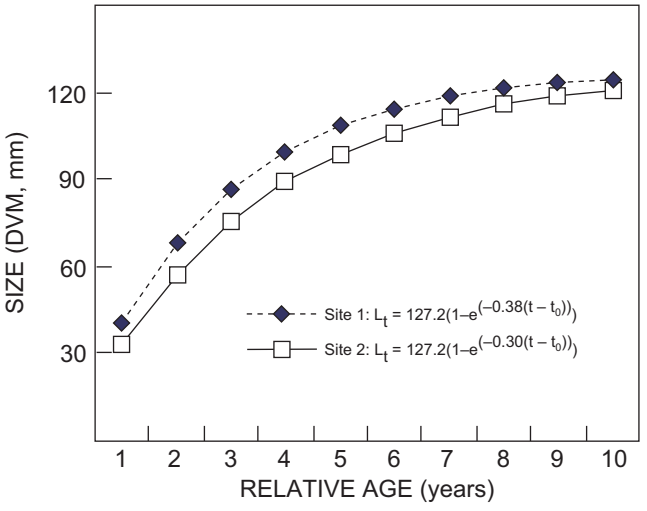

Figure 5: Growth curves of the von Bertallanffy growth function of *P. margaritifera* at Site 1 and Site 2.

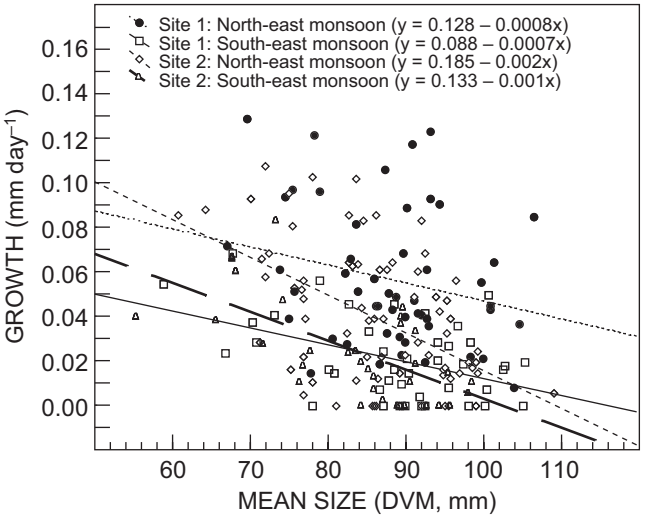

Figure 6: Relationship between size and growth rate of *P. margaritifera* at Sites 1 and 2 between April and September (south-east monsoon) and October and March (north-east monsoon). Regression equations are given

growth rate during the NEM season was higher at Site 1 than at Site 2 ($F = 16.4$, $p < 0.001$). However, growth was similar at both sites during the SEM season ($F = 0.092$, $p = 0.761$). The observed difference in growth rate between the two sites reflects the significantly higher growth rate at Site 1 during the NEM season.

Nacre deposition rate

Nacre deposition rate ranged between 1.3µm day^{-1} and 5.3µm day^{-1} on the plastic beads, and between 2.3µm day^{-1} to 5.9µm day^{-1} over the drill holes. The mean rate of nacre deposition over the drill holes was 3.4 ± 0.9µm day^{-1}, 3.0 ± 1.0µm day^{-1} and 3.7 ± 1.2µm day^{-1} for holes 20mm, 40mm

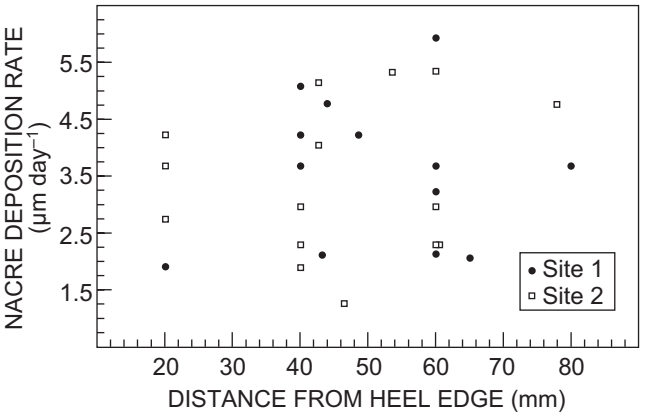

Figure 7: Nacre deposition rate of *P. margaritifera* in Gazi Bay, over drilled holes 20mm, 40mm and 60mm from the hinge edge of the shell, and over 10 hemispherical plastic beads glued between 40mm and 80mm from the hinge edge

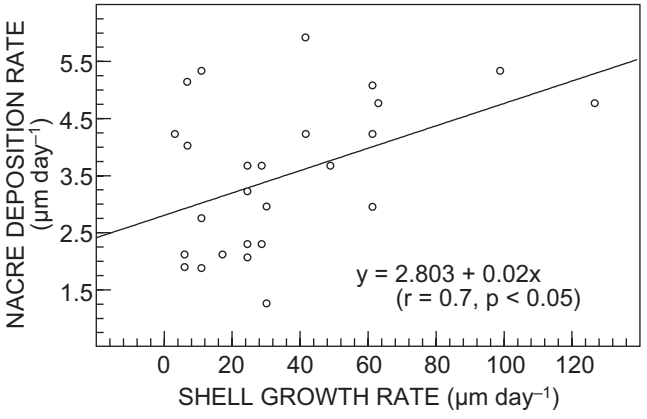

Figure 8: Relationship between shell growth and nacre deposition rates of *P. margaritifera* in Gazi Bay

and 60mm from the heel edge respectively, and 3.5 ± 1.4µm day^{-1} on the plastic beads. Mean nacre deposition rates over the drill holes and on the plastic beads were similar (ANOVA, $F = 0.365$, $p > 0.05$). Also, the rate of deposition was independent of the position from the heel of the shell (Figure 7). There was no significant difference ($F = 0.057$, $p = 0.812$) in the mean of the pooled nacre deposition rates over the drill holes and on the plastic beads between Site 1 (0.0035 ± 0.0011mm day^{-1}) and Site 2 (0.0034 ± 0.0013mm day^{-1}). The deposition of nacre was significantly correlated with shell size growth rate ($r = 0.700$, $F = 28.9$, $p < 0.05$; Figure 8).

Discussion

The environment

The seasonality exhibited in SST and salinity during the study period was typical of inshore lagoons in Kenya (McClanahan and Young 1996). SST was higher during the

NEM season (October–March) than the SEM season (April–September) and salinity was lower during the SEM season than the NEM season. The SST at Site 1 was slightly higher on account of the influx of water from the shallow mud flats and channels within the mangrove forest during ebb tide. Increased flow of freshwater into Gazi Bay during the SEM season (Kitheka 1996) lowered the salinity at Site 1. Freshwater flow from the river is less during the NEM season, and evaporation in the intertidal zone overrides the freshwater influx causing higher salinity at Site 1. However, the overall annual mean salinity at the two sites was similar. Mean TSM and %OC at Site 1 were higher during the SEM season, which may be attributable to the higher river discharge during that period. The percentage DF (intensity of water motion) was higher at Site 1. The difference between the sites was less during the neap tide, on account of the higher tidal amplitude during spring tide, which results in higher tidal currents.

Growth rate

There were large variations in growth rates between the oysters under study, indicated by the low correlation between the sizes of oysters and growth rates (Figure 4). This is a common feature in pearl oysters (Sims 1994, Pouvreau *et al*. 2000, Urban 2000). For instance, Urban (2000) reported a regression coefficient of 0.376 between the growth and size of *P. imbricata*, and Rajagopal *et al*. (1998) suggested uncoupling between shell and weight growth as an explanation for the high variability. Oysters commonly show no change or decrease in shell size over time because of the breakage of the shell margin, known as sloughing (Sims 1994). Growth rates in pearl oysters have a genetic basis (Wada and Komaru 1994), and large interspecific variation in growth rates are useful in selective breeding to enhance the growth performance of cultured stock (Pearson and Munro 1991).

Growth rate is an important indicator of the overall suitability of a habitat for a particular species. Growth rate in oysters depends on a wide range of factors including their age, availability of food, depth of water and water currents. Few studies on pearl oysters have investigated environmental variables with growth rates, and most of the reported growth rates are for midwater cultured pearl oysters (e.g. Nasr 1984, Pouvereau *et al*. 2000). Therefore, direct comparisons of growth rates between cultured and natural populations are inappropriate. For natural oyster populations, Sims (1994) found growth rates ranging from 5mm year^{-1} to 23mm year^{-1} for oysters 80–139mm in size, in depths between 5m and 35m in the Mahihiki atoll lagoon in the Cook Islands. The von Bertalanffy growth parameters reported by Sims (1994) ranged from K = 0.16 and L_∞ = 170.7mm to K = 0.45 and L_∞ = 151.1mm. Off Hawaii, the mean growth rate of *P. margaritifera* of the size range 116–154mm was 8.7mm year^{-1} (Rodgers *et al*. 2000), a rate similar to that of oysters of between 110mm and 135mm in the present study. Growth rates of oysters are generally higher in midwater structures compared with natural growth rates on the seabed. Annual growth rates of 1–3-year-old cultured oysters that were suspended in midwater were 23–52mm (Elnaeim 1984), 40–50mm (Nasr 1984) in the Red Sea, 10–40mm (Coeroli *et al*. 1984) and 8–33mm (Pouvreau *et al*. 2000) in French Polynesia. Values of K = 0.25 and L_∞ = 309.7 and K = 0.52 and L_∞ = 155.5 were obtained for oysters in various experimental culture structures in the Cook Islands (Sims 1994). Leduc (1997), cited by Pouvreau *et al*. (2000), obtained values of K between 0.37 and 0.42 and values of L_∞ ranging from 175.1mm to 177.6mm for oysters in culture in the Cook Islands. Values of K = 0.66 and L_∞ = 160.5mm were obtained in longline suspended culture in French Polynesia (Pouvreau *et al.* 2000). In the same region, Coeroli *et al.* (1984) reported a higher K-value of 0.76 (L_∞ = 148.9mm) than those obtained in the above studies, and Nasr (1984) reported an even higher K-value of 1.24 (L_∞ = 125.5mm) in the Red Sea. The growth performance of 3.7 estimated in this study is within the range 3.6–4.3 reported by Sims (1994) for *P. margaritifera* in the Cook Islands.

Growth rate within study sites and seasons

The growth rate of oysters was higher in the tidal current-swept site (Site 1) than in the sheltered back-reef site (Site 2). Various studies have reported a significant effect of hydrodynamics on the growth of bivalves, which appear to be species specific. For example, high current velocities have been shown to stimulate growth in the scallop *Placopecten magellanicus* (Wildish and Kristmanson 1988), the mussel *Mytilus edulis* (Walne 1972) and the hard clam *Mercenaria mercenaria* (Grizzle *et al.* 1992). Low current-flow speeds (1cm s^{-1}) reduce growth in the oyster *Crassostrea virginica* (Grizzle *et al.* 1992). Currents influence growth rate of bivalves by replenishing suspended food particles. The decline in growth rate in low current-flow habitats can be attributable to the depletion of suspended particles in such environments, whereas higher current velocities reduce growth by physically interfering with the filtration process in bivalves (Wildish and Kristmanson 1988).

Apart from differences in the current regime, factors such as salinity, water temperature, suspended matter and the organic content of the suspended matter were quite similar between the two study sites, most likely because of the close proximity of the sites. An explanation for higher growth rates at Site 1 is the increased food fluxes driven by the tidal currents there. Suspended particles would be lower at Site 2, because of settlement at the bottom and uptake by filter-feeders, particularly during spring low tide periods when water depth is shallow (<0.5m). The suspended organic matter content was higher during the NEM season than during the SEM season at both sites. Phytoplankton productivity in the inshore habitats is low (Bryceson 1982, Kasyi 1994), and wave turbulence is higher as a result of high velocity winds during the SEM season (McClanahan and Young in press). Strong waves would re-suspend the organic matter-poor bottom sediments, as demonstrated by the higher levels of suspended matter recorded during the SEM season. High levels of suspended matter, with low

organic content, would reduce the quality of suspended food particles in the water column during the SEM season. The combination of low primary productivity and re-suspension of sediments likely resulted in lower growth rates of *P. margaritifera* during the SEM season. Growth of oysters was therefore highest during the NEM season as well as in the tidal current-swept habitat.

Nacre deposition

Deposition of nacre by the mantle tissue continues throughout the life of pearl oysters. The present results show that the rate of nacre deposition on drilled holes on the shell was similar to that on plastic beads. Therefore, the drilled-hole method can be used with some degree of confidence to determine the potential rate of nacre deposition in the production of hemispherical pearls. The rate of nacre deposition was inversely related to shell growth rate in the oysters under study, which concurs with the findings of Coeroli and Mizuno (1985). However, the quality of the pearls increases with declining nacre deposition rate (P Southgate, James Cook University, Australia, pers. comm.). The mean rate of nacre deposition on the shell of 3.0–3.4mm day^{-1} is similar to the mean rate of 3.1mm day^{-1} observed by Pouvreau *et al*. (2000) for 4-year-old *P. margaritifera* in suspension culture. At a nacre deposition rate estimated in this study, it would take approximately two years to produce hemispherical pearls with 2.5mm layer of nacre, the optimum thickness required for the commercial market.

Acknowledgements — The director of Kenya Marine and Fisheries Research Institute (KMFRI) is thanked for allowing ENK study leave to conduct this work. Special thanks go to Mr Masudi Juma (KMFRI) for his valuable help in the field during the study. We thank Prof. Paul Southgate for very constructive comments on an earlier version of the manuscript. The focus and readability of this paper benefited immensely from his suggestions. This work was supported by a VLIR-IUC-UoN staff development and training project of the University of Nairobi, and the International Fund for Science Sweden project A/3360-01 to ENK. KMFRI provided personnel and logistics for the fieldwork.

References

BENZIE, J. A. H. and E. BALLMENT 1994 — Genetic difference among black-lipped pearl oyster (*Pinctada margaritifera*) populations in the western Pacific. *Aquaculture* **127**: 145–156.

BRYCESON, I. 1982 — The seasonality of oceanographic conditions and phytoplankton in Dar es Salaam waters. *Univ. Sci. J.*, *Dar es Salaam* **8**: 66–76.

COEROLI, M., DE GAILLANDE, D. and J. P. LANDRET 1984 — Recent innovations in the cultivation of molluscs in French Polynesia. *Aquaculture* **39**: 45–67.

COEROLI, M. and K. MIZUNO 1985 — Study of different factors having an influence on pearl production of black lip pearl oyster. *Proceedings of the Fifth International Coral Reef Symposium* **5**: 551–557.

DURAND, P., WADA, T. K. T. and F. BLANC 1993 — Genetic variation in wild and hatchery stocks of the black pearl oyster, *Pinctada margaritifera,* from Japan. *Aquaculture* **110**: 27–40.

ELNAEIM, A. G. 1984 — Variability in growth of the mother of pearl oyster (*Pinctada margaritifera*) in the Red Sea, Sudan. Ph.D. thesis, Dalhouse University: 120 pp.

FABENS, A. J. 1965 — Properties and fitting of the Von Bertalanffy growth curve. *Growth* **29**: 265–289.

GAYANILO, F. C., SPARRE, P. and D. PAULY 1995 — *The FiSAT User's Guide. FAO Computerised Information Series Fisheries* 99; Rome. ICLARM, DIFMAR: 265 pp.

GRIFFITHS, R. J. 1980 — Natural food availability and assimilation in the bivalve *Choromytilus meridionalis. Mar. Ecol. Prog. Ser.* **3**(2): 151–156.

GRIZZLE, R. E., LANGAN, R. W. and H. HOWELL 1992 — Growth responses of filter feeding bivalve molluscs to changes in water flow: difference between siphonate and nonsiphonate taxa. *J. expl mar. Biol. Ecol*. **162**: 213–228.

HAWKINS, A. J. S., SMITH, R. F. M., TAN, S. H. and Z. B. YASIN 1998 — Suspension-feeding behaviour in tropical bivalve molluscs: *Perna viridis, Crassostrea belcheri, Crassostrea iraderi, Saccostrea cucculata* and *Pictada margaritifera. Mar. Ecol. Prog. Ser.* **166**: 173–185.

HAYASHI, M. and K. SEKO 1986 — Practical technique for artificial propagation of Japanese pearl oyster (*Pinctada fucuta*). *Bull. Fish. Res. Inst. Mie* **1**: 36–68.

HEMMINGA, M. A., SLIM, F. J., KAZUNGU, J., GANSSEN, G. M., NIEUMENHUIZE, J. and N. M. KRUYT 1994 — Carbon outwelling from a mangrove forest with adjacent seagrass beds and coral reefs (Gazi Bay, Kenya). *Mar. Ecol. Prog. Ser.* **106**: 291–301.

JOKIEL, P. L. and J. I. MORRISSEY 1993 — Water motion on coral reefs: evaluation of the 'clod card' technique. *Mar. Ecol. Prog. Ser.* **93**: 175–181.

KASYI, J. N. 1994 — Relationship between nutrient levels, phytoplankton biomass and zooplankton composition, abundance and composition in Tudor creek Mombasa, Kenya. M.Sc. thesis, University of Nairobi: 112 pp.

KITHEKA, J. U. 1996 — Water circulation and coastal trapping of brackish water in tropical mangrove dominated bay in Kenya. *Limnol. Oceangr*. **41**: 169–176.

KITHEKA, J. U., OHOWA, B. O., MWASHOTE, B. M., SHIBIRA, W. S., MWALUMA, J. M. and J. M. KAZUNGU 1996 — Water circulation dynamics, water column nutrients and plankton productivity in a well-flushed tropical bay in Kenya. *J. Sea Res.* **35**(4): 257–268.

MARSHALL, N., MILLEDGE, S. A. H. and P. S. AFONSO 2001 — *Trade in Sea Cucumbers, Seashells and Lobsters in Kenya, Tanzania and Mozambique*. Nairobi, Kenya; TRAFFIC East and South Africa: 132 pp.

McCLANAHAN, T. R. and P. T. YOUNG 1996 — *East African Ecosystems and their Conservation*. New York; Oxford University Press: 480 pp.

MIDDLETON, J. 1992 — *The World of the Swahili*. An African Mercantile Civilization. New Haven; Yale University press: 254 pp.

MUNRO, J. L. and D. PAULY 1983 — A simple method for comparing the growth of fishes and invertebrates. *Fishbyte* **1**: 5–6.

NASR, D. H. 1984 — Feeding and growth of the pearl oyster *Pinctada margaritifera* (L.) in Dongonab Bay, Red Sea. *Hydrobiologia* **110**: 241–245.

NEWELL, C. R. and E. SHUMWAY 1993 — Grazing of natural particles by bivalve molluscs: a spatial and temporal perspective. *NATO ASI Series* **G 33**: 85–148.

NUMAGUCHI, K. 1999 — Effective feeding concentration of the microalgae *Pavlova lutheri* for growth of early spat of the oyster *Pinctada fucuta martensii. J. World Aqua. Soc*. **30**: 90–292.

PEARSON, R. G. and J. L. MUNRO 1991 — Growth, mortality and recruitment rates of giant clams, *Tridacna gigas and T. derasa,* at Michaelmas reef, central Great Barrier Reef, Australia. *J. mar. Freshwat. Res.* **42**: 242–62.

POUVRAEU, S., TIAPARI, J., GANGNERY, A., LAGARDE, F., GARNIER, M., TEISSIER, H., HAUMANI, G., BUESTEL, D. and A. BODOY 2000 — Growth of the blacklip pearl oyster, *Pinctada*

margaritifera in suspended culture under hydrobiological conditions of Takapoto lagoon (French Polynesia). *Aquaculture* **184**: 133–154.

RAJAGOPAL, S., VENUGOPALAN, V. P., NAIR, K. V. K., VELDE, G., JENNER, G. H. A. and C. DEN HORTOG 1998 — Reproduction, growth rate, and culture potential of the green mussel, *Perna viridis* (L.) in Edaiyur backwater, east coast of India. *Aquaculture* **162**: 187–202.

RODGERS, S. K., SIMS, N. A., SARVER, D. J. and E. F. COX 2000 — Distribution, recruitment and growth of the blacklip pearl oyster, *Pictada margaritifera*, in Kane'ohe Bay, O' ahu, Hawai'i. *Pac. Sci.* **54**(1): 31–38.

ROSE, R. A. and S. B. BAKER 1994 — Larval and spat culture of the western Australia silver or gold lip pearl oyster, *Pinctada maxima* Jameson (Mollusca: Pteriidae). *Aquaculture* **126**: 35–50.

SIMS, N. A. 1993 — Pearl oysters. In *Nearshore Resources of the South Pacific. Honiara (Solomon Islands), Suva (Fiji)*. Wright, A. and A. Hill (Eds). Forum Fisheries Agency (FFA) Institute of Pacific Studies (IPS). Singapore National Printers: 409–430.

SIMS, N. A. 1994 — Growth of wild and cultured black-lip pearl oysters, *Pinctada margaritifera* (L.) (Pteriidae; Bivalvia), in the Cook Islands. *Aquaculture* **122**: 181–191.

SOUTHGATE, C. P. and A. C. BEER 1997 — Hatchery and early nursery culture of the blacklip pearl oyster (*Pinctada margaritifera* L). *J Shellfish Res*. **16**(2): 561–567.

SOUTHGATE, C. P. and A. C. BEER 2000 — Growth of blacklip pearl oyster (*Pinctada margaritifera*) juveniles using different nursery culture techniques. *Aquaculture* **187**: 97–104.

URBAN, H. J. 2000 — Culture potential of the pearl oyster (*Pinctada imbrica*) from the Caribbean. I. Gametogenic activity, growth, mortality and production of a natural population. *Aquaculture* **189**: 361–373.

WADA, T. K. and A. KOMARU 1994 — Effect of selection for shell coloration on growth rate and mortality in the Japanese pearl oyster, *Pinctada fucuta martensii*. *Aquaculture* **125**: 59–65.

WALNE, P. R. 1972 — The influence of current speed, body size and water temperature on the filtration rate of five species of bivalves. *J. Mar. Biol. Assoc*. U.K. **52**: 345–374.

WILDISH, D. J. and D. D. KRISTMANSON 1988 — Growth response of giant scallops to periodicity of flow. *Mar. Ecol. Prog. Ser.* **42**: 163–169.

WOOD. E. and S. M. WELLS 1995 — The shell trade: a case for sustainable utilization in East Africa. In *The Conservation Biology of Molluscs*. Kay, E. A. (Ed.). Occasional paper of the IUCN species survival commission IUCN, Gland, Switzerland: **9**: 41–52.

Manuscript received December 2004; accepted July 2005