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The reproductive activity of the pearl oyster *Pinctada imbricata* Röding 1798 (Pteriidae) in Gazi Bay, Kenya

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This paper describes the reproductive activity of the pearl oyster *Pinctada imbricata* Röding 1798 in two adjacent areas in Gazi Bay, Kenya, exposed to different tidal current velocity. The annual mean temperature, salinity, suspended matter and organic content of the suspended matter were similar in the two areas. Gonad activity and spawning of the oyster population occurred throughout the year. Male sex expression was higher than female sex expression, and also higher in the current swept area (m:f = 1:0.72) than in the sheltered area (m:f = 1:0.81). The developing gonad stages were more abundant during the southeast monsoon period between July and October, while spent stages were more abundant between May and July and between November and February. The condition index indicated similar gonad development patterns at the two sites and was higher in the current swept site during most of the year.

KEY WORDS: *Pinctada imbricata*, reproduction, condition index, gamete production, hydrodynamism, Kenya.

INTRODUCTION

The reproductive activity of temperate bivalves is determined by seasonal factors such as temperature and food availability (Bayne 1976, Mann 1979). Their cycles have been described as "conservative" when gamete production occurs during autumn/winter using energy stored during summer, and "opportunistic" when gamete production occurs in spring/summer when food is sufficient (Bayne 1976). Reproductive activity of invertebrates is generally continuous in the tropics and in deep-sea environments with no sharp seasonal trends (Sastry 1976). In the tropics, temperature is ineffective in the regulation of reproduction of bivalves (Lasiak 1986, Fournier 1992, Frenkiel et al. 1992), which show less distinct reproductive cycles and continuous spawning (Garcia-Dominguez et al. 1996, Pouvreau et al. 2000, Urban 2000).

Instead, the role of food availability has been emphasized in the timing of reproductive activity in bivalves living in these regions (Himmelman 1980, Bayne et al. 1983, MacDonald & Thompson 1986, Shafee 1989). In areas where phytoplankton productivity is strongly affected by the seasonal monsoon dynamics, such as inshore environments in East Africa, primary production is higher during the Northeast Monsoon (NEM) when sea surface temperatures are high and the winds are calmer than during the Southeast Monsoon (SEM) (Bryceson 1982, McClanahan 1988, Kasyi 1994). Invertebrates living in this area show reproductive activities and recruitment patterns with strong seasonal trends (Van Someren & Whitehead 1961, Ruwa & Polk 1994, Muthiga 1996).

In addition to food availability per se, some local site-specific factors, such as currents, waves and other forms of water movement, influence the food supply through the replenishment of suspended particles caused by re-suspension of sediments poor in organic matter (Wildish et al. 1987, Cahalan et al. 1989, Wildish & Miyares 1990, Grizzle et al. 1992). However, excessive water movement exerts physical pressure on the gills inhibiting the filtration process (Femme et al. 1986). Therefore, hydrodynamism can directly affect the processes of feeding, energy allocation, maintenance and reproduction. Moreover, bivalves change their reproductive strategies (Lubert & Mann 1987) and sex expression (Charnov 1987) according to environmental conditions. Environmental stress, such as crowding and water pollution, favour male sex expression while optimal conditions favour female sex expression (Dolgov 1991, Pouvreau et al. 2000).

The reproductive biology of pearl oysters (family Pteriidae) in tropical and sub-tropical areas has attracted increasing attention recently due to the rapid expansion of oyster farming for pearl production (e.g. Saucedo & Monteforte 1997, Pouvreau et al. 2000, Saucedo et al. 2002). Pearl oyster culture dates to the 1990s in Seychelles and may spread to the rest of the West Indian Ocean region. The pearl oyster *Pinctada imbricata* Röding 1798 occurs in relatively high densities in sheltered lagoons, channels, intertidal reef platforms and other habitats. Although the species is not cultured for pearl production, it is suitable for studies on the response of pearl oysters to different environmental factors. The inshore marine environments of East Africa are characterized by monsoon seasons and tidal currents, with variations of temperature, salinity, nutrients and the amounts and quality of suspended matter. The NEM season occurs between October and March and is characterized by calm weather, higher temperatures and higher marine phytoplankton productivity, whereas the SEM season occurs between April and September and is characterized by strong winds and wave action, lower temperatures and lower phytoplankton productivity (Bryceson 1982, McClanahan 1988, Kasyi 1994). Tidal currents drive water exchange between the shallow lagoons enclosed by the coral reef and bays and the open sea. The large tidal amplitude, up to 3.5 m during maximum spring tides, drives strong tidal currents into and out of shallow lagoons and bays through reef breaks and channels (Kitheka 1996).

This paper is part of research on the population biology of pearl oysters in East Africa aimed at providing information for possible use in the development of pearl oyster culture. The objective of this study is the assessment of reproductive activity in natural pearl oyster *P. imbricata* populations in a channel site, subjected to strong tidal currents, and a sheltered backreef site in Gazi Bay, Kenya.

MATERIALS AND METHODS

Study area

The study area, Gazi Bay (4°25'S, 39°30'E) on the southern Kenya coast, is a shallow tropical embayment with a mean depth of 5 m and an area of approximately 5 km^2 (Fig. 1). The bay is protected by the Chale Peninsula, Chale Island and a fringing reef to the north, and opens to the Indian Ocean through a relatively wide (3500 m) channel to the south. The hydrodynamics within the bay are dominated by the semidiurnal tides, with a 3.5 m maximum amplitude, which create strong tidal currents. The ebb tide takes 7-8 hr while the flood tide takes 4-5 hr (Hemminga et al. 1994). Two tidal creeks, namely Kidongoweni and Kinondo, measuring about 5 and 2.5 km respectively, drain water from the intertidal flats into the bay. A permanent river, Kidongoweni, discharges into the Kindongoweni creek discharging over 700 m^3 d^{-1} of water during the dry season and 1.19×10^5 m^3 d^{-1} during the wet season (Kitheka 1996). The sites were selected for this study because of their relatively close proximity, which minimizes differences in environmental factors (Kitheka et al. 1996), the abundant occurrence of pearl oysters within the bay, and the suitable conditions in the bay for oyster culture. The first site (Site 1) is located in front of the two channels that drain water into and out of the intertidal areas. The second site (Site 2) is located to the south of Chale Island and is sheltered by a fringing reef. The two sites are 2-2.5 km apart, and are about 0.5 m deep at spring low tide.

Environmental parameters

The monthly sampling of oysters and monitoring of environmental parameters was performed in the two Gazi Bay sites between April 2002 and March 2003. Sea surface temperatures were recorded around midday using a mercury thermometer to 0.1 °C and salinity was measured in Practical Salinity Units (PSU) using a salinometer. Three 1 litre replicate water samples for the determination of Total Suspended Matter (TSM) and Organic Matter Content (OC) were also collected. The water samples were filtered using 4.5 cm diameter pre-ashed GF/C filters of 1.2 µm and dried at 70 °C for 48 hr, then ashed at 450 °C to obtain the OC of the water. The 'clod card' technique (Doty 1971, Jokiel & Morrissey 1993), used to estimate the relative intensity of water motion based on the dissolution of Plaster of Paris (POP) blocks, was used to determine the relative current velocity in the two sites. The blocks, weighing between 31 and 37 g, were dried at 70 °C and weighed using an electronic balance to 0.1 g precision. Ten blocks were suspended 15 cm above the bottom on bamboo sticks randomly

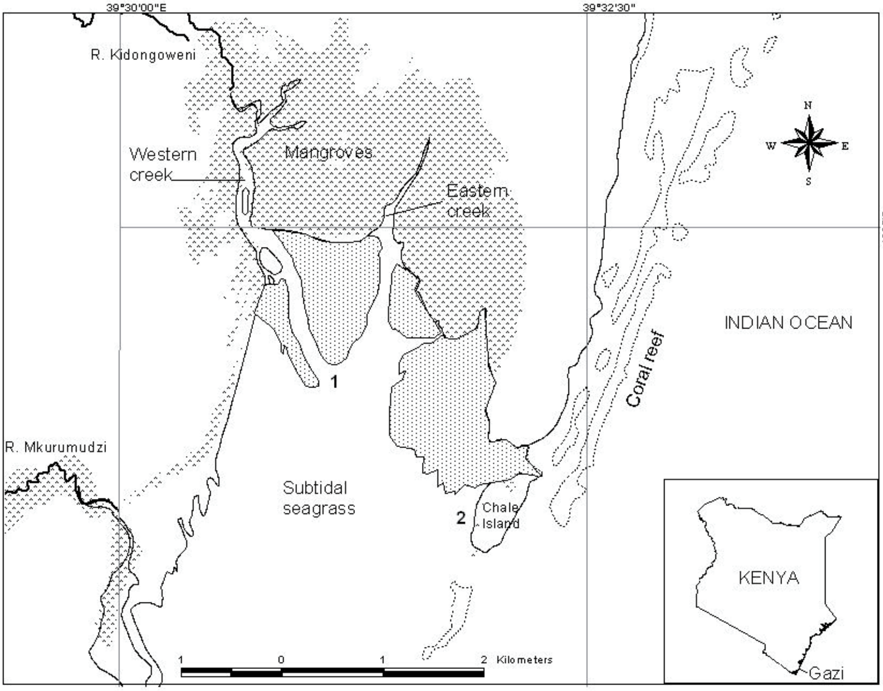

Fig. 1. — Map of the study area, Gazi Bay, Kenya. Site 1 adjacent to the two channels and Site 2 sheltered backreef.

placed on the substrate in the two study sites for 24 hr. Five control blocks were placed in 25 litre seawater containers during the same period. The relative intensity of water motion was determined as the Diffusion Factor (DF) for each block using the formula:

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

where:
FIDW (Field Initial Dry Weight) = dry weight of POP blocks before deployment in the sea,
FFDW (Field Final Dry Weight) = weight of POP blocks after recovery from the sea and drying at 70 °C for 48 hr,
CIDW (Control Initial Dry Weight) = dry weight of control POP blocks before being placed in 25 litre sea water containers for 24 hr,
CFDW (Control Final Dry Weight) = weight of the control POP blocks after drying at 70 °C for 48 hr.

This was done during the maximum spring tide (18-19 December, 0.0 m low tide) and neap tide (10-11 March, 1.4 m low tide) and the DF values were expressed as percentage weight loss per 24 hr.

Sex expression and reproductive stages

Samples of 25-30 oysters were collected monthly from the two sites for the determination of sex, gonad development stages and Condition Index (CI). The oysters were cleaned off debris and other attached material and their Dorsal-Ventral axis Measurement (DVM) was taken in mm before dissection. Sex was determined by biopsy of the gonad and observation of gametes under a light microscope: spermatozoids indicated males, oocytes indicated females, and both spermatozoids and oocytes in the same gonad indicated hermaphrodites. The gonad cell development stages were classified using the macroscopic gonad scheme (Guillou et al. 1990 in Urban 2000) for the same oyster species:

Stage 1 was undifferentiated, with no visible gonads. Two variations of this stage were recognized: (a) resting, where adults were recovering after a spawning event and (b) immature juvenile;

Stage 2 was the developing stage. Two variations of this stage were also recognized: developing (a) where gonadal tissue was visible but sexes could not be distinguished, and developing (b) where gonads were visible, sexes could be distinguished, gametes were abundant, most spermatozoids were barely moving and the oocytes were pendaculate;

Stage 3 was the ripe gonad stage, where spermatozoids were rapidly moving or spherical oocytes were seen, and spawning was imminent;

Stage 4 was the spent stage, with empty and thin gonads, with reabsorbing and mature cells.

Determination of the Condition Index (CI)

To determine the CI and PR, the flesh of the oysters was removed and dried at 70 °C in pre-weighed aluminium foil crucibles until constant weight was attained. The dry flesh weights were measured using a top loading electric balance with 0.001 precision. The CI was determined using the formula:

$$CI = (SFDWT/DVM) \times 100$$

where SFDWT is the Shell Free Dry Weight in grams and DVM (Dorsal Ventral Measurement) is the size of the shell in mm.

Data analysis

Normality of the data was assessed using the Shapiro-Wilks W test, while the homogeneity of variances was tested using the Levene test. The seasons and site environment data were compared using Student's t-test and the Kruskal-Wallis test where the conditions for parametric analysis were not met. Deviation of the m:f ratio from 1:1 was determined using the Chi-square (χ^2) test in the non-parametric module of the software "STATISTICA 6.0". The regressions of dry flesh weights and DVM of males and females and the monthly data for the two sites were compared using Analysis of Covariance (ANCOVA), with shell diameter as the covariate after $\log_{10}$ transformation as described by Zar (1974).

RESULTS

Environmental parameters

The variation of sea surface temperature and salinity at the two sites is shown in Fig. 2, while Table 1 shows the means and statistical comparisons of the environmental variables during the NEM and SEM seasons. The variances of the environmental data at the two sites were homogeneous (Levene test: temperature, F = 0.257, P = 0.614; salinity, F = 0.088, P = 0.766; TSM, F = 0.0005, P = 0.980, % OC, F = 0.007, P = 0.932) and the distributions were normal (Shapiro-Wilks test: salinity, W = 0.941, P = 0.042; TSM, W = 0.972, P = 0.434, % OC, W = 0.971, P = 0.404). The parametric Student's t-test was used for all comparisons, except temperature, whose data were not normally distributed (W = 0.882, P << 0.01); they were com-

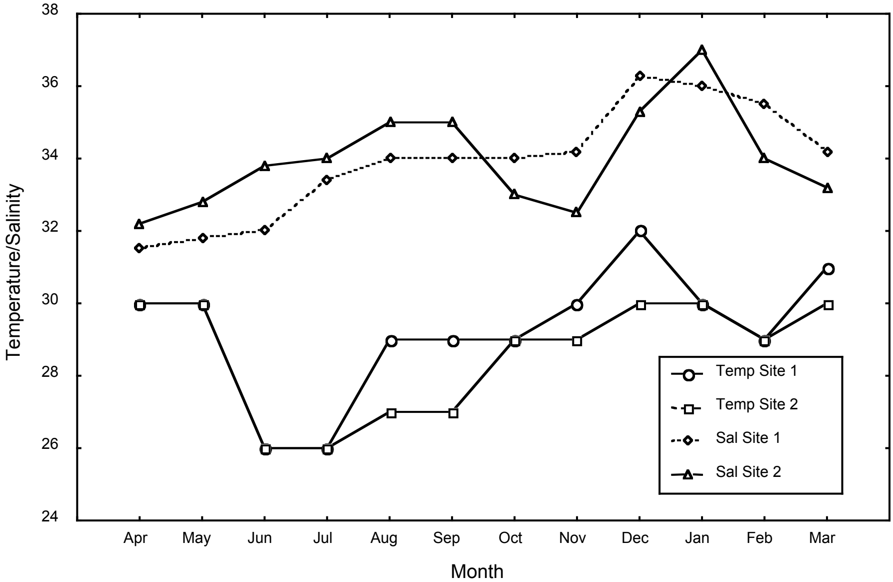

Fig. 2. — Monthly variation of sea surface temperature (°C) and salinity (PSU) in the current swept area (Site 1) and sheltered back reef area (Site 2) in Gazi Bay between April 2002 and March 2003.

Table 1.

Means (± SD) of temperature (°C), salinity (PSU), Total Suspended Matter (TSM) (mgl-), percentage Organic Matter Content (OC) and percentage Dissolution Factor (DF) of Plaster of Paris (POP) blocks at Sites 1 and 2 during the Southeast Monsoon (SEM) and Northeast Monsoon (NEM) seasons in Gazi Bay.

	SEM	NEM	Test statistic	*P*	Annual mean
Temperature					
Site 1	28.7±1.7	30.1±1.1	χ^2 = 1.227	0.267	29.2±1.6
Site 2	27.9±1.7	29.5±0.4	χ^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					
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
Percentage Organic Matter Content					
Site 1	16.9±2.8	13.5±3.9	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
Percentage Dissolution 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	

pared using the equivalent non-parametric test, the Kruskal-Wallis ANOVA by median test. Temperature showed no significant difference between the NEM and SEM seasons at Site 1, but showed a significant difference at Site 2. The pooled data for both sites showed significantly higher temperature during the NEM season than the SEM season (χ^2 = 6.269, P = 0.012). The mean temperatures at the two sites were not significantly different during the SEM (χ^2 = 2.201, P = 0.130) or NEM season (χ^2 = 2.014, P = 0.155), or with regard to the pooled annual data (χ^2 = 2.157, P = 0.141). Comparisons of the mean salinities at the sites and between seasons showed no significant difference at $P < 0.05$.

The range of TSM was higher during the SEM season (7.7-36.0 μgl^{-1}) than during the NEM season (8.8-29.4 μgL^{-1}), and was also higher at Site 1 (10.4-36.0 mgL^{-1}) than at Site 2 (7.7-28.9 μgl^{-1}). The mean TSM was higher at Site 1 during both seasons and the overall mean TSM at Site 1 was higher than at Site 2 by approximately 8.3% (Table 1). The overall site means of the OC were similar (14.7 ± 3.8% and 14.6 ± 4.2% at Sites 1 and 2 respectively) and significantly higher at Site 1 during the SEM season than during the NEM season. The mean values of percentage DF of POP were significantly higher at Site 1 than at Site 2 during both the neap and spring tides. The mean DF at Site 1 was 59% larger than at Site 2 during spring tide and 38% larger during neap tide.

Sex expression and reproductive stages

Table 2 shows the number of males and females within 10 mm size classes at the two sites. Of the 648 sexually mature oysters dissected, 353 were males and 271 were females (overall m:f ratio 1:0.76), 17 were in the gonad cell development stage 2a, 3 were hermaphrodites (0.4%) and 4 were in the resting stage. The smallest sexually active oyster was in the 10-20 mm size class and all individuals in the 30-39 mm size class were sexually active. The m:f ratio of sexually mature oysters < 60 mm was 1:0.72 in Site 1 and 1:0.81 in Site 2. The overall m:f ratio was significantly different from the 1:1 ratio in Site 1 (χ^2 = 8.90, $P < 0.002$) but not in Site 2 (χ^2 = 3.02, $P < 0.081$). Male sex expression dominated in all the size classes < 50 mm while female sex expression dominated in the 50-60 mm size class in both sites. Five of the 11 oysters > 60 mm were males and 6 were females. The Chi-square tests within size classes in both study sites were all significantly different from the m:f = 1:1 at $P < 0.05$.

Table 2.

The number of males and females of *Pinctada imbricata* in 10 mm size classes at Site 1 and Site 2 in Gazi Bay, Kenya.

	Site 1		Site 2	
Size class	m	f	m	f
10-20 mm	1	0	1	0
20-30 mm	16	4	17	4
30-40 mm	52	36	46	26
40-50 mm	94	50	73	68
50-60 mm	36	53	13	24
All	198	143	150	122

Fig. 3 shows the relative abundance of gonad cell development stages of sexually active oysters during the study period. Individuals in stage 1, which represents juvenile oysters becoming sexually active, were few in both sites, and were found in April and June in Site 1 and in March, April and September in Site 2. Oysters

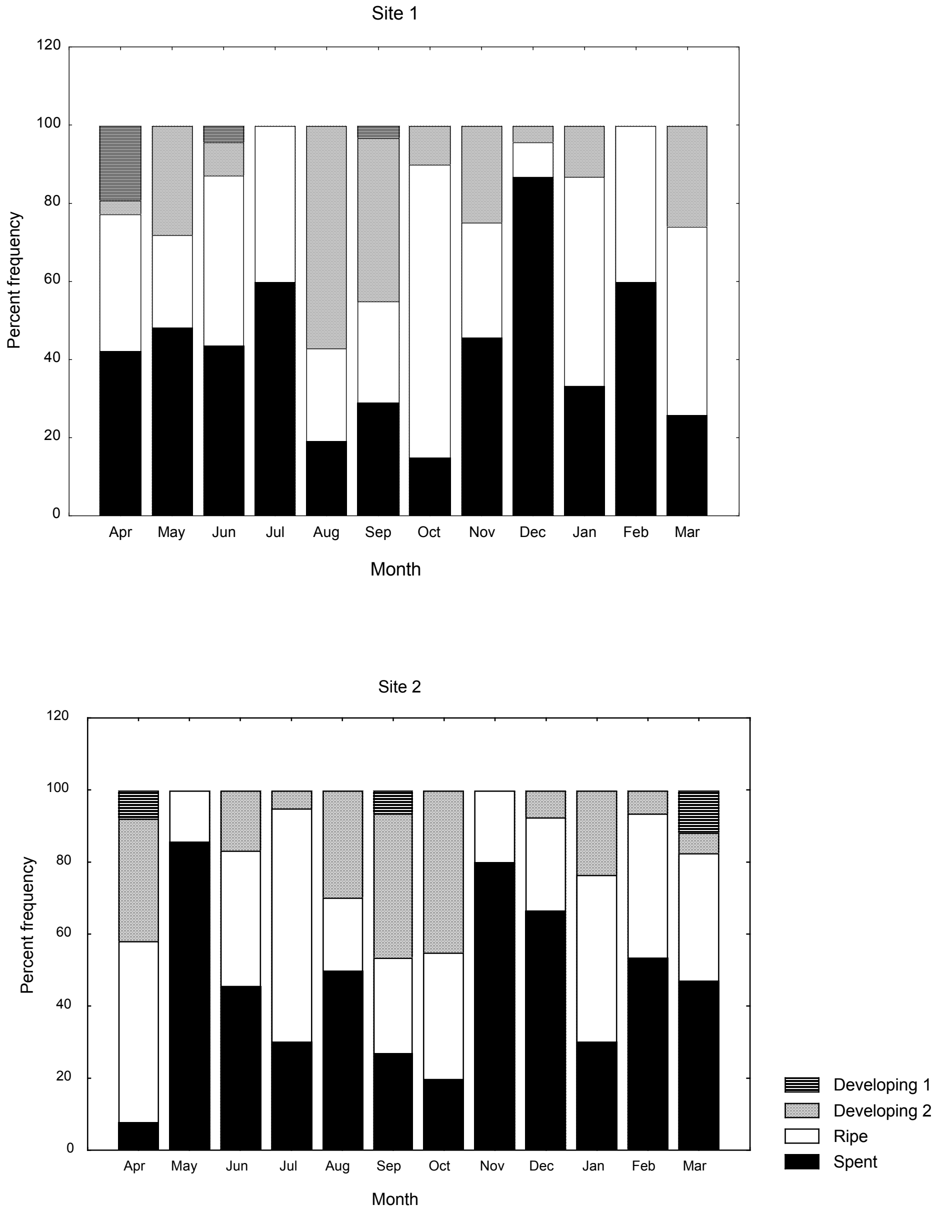

Fig. 3. — The relative occurrence of gonad development stages of mature pearl oysters *Pinctada imbricata* at Site 1 and Site 2 in Gazi Bay between April 2002 and March 2003.

in the developing, ripe and spent stages were observed throughout the sampling period. Individuals in developing b stage were observed throughout, but were most abundant during the SEM season between July and October. The spent gonad stage predominated from April to July and November to March in Site 1 and from May to June and November to December in Site 2.

Condition Index

The SFDW was between 4.8 and 13.2% (mean 7.9 ± 1.2%) of the total dry weight (SFDWT + shell weight) in Site 1, and between 4.1 and 12.9% (mean 7.7 ± 1.48%) of the total dry weight in Site 2. The mean DVM and mean SFDW of oysters from Site 1 (45.1 ± 7.7 mm and 0.286 ± 0.148 g respectively) were both higher than in Site 2 (42.3 ± 7.9 mm and 0.218 ± 0.113 g respectively). However, the differences were not significant at $P < 0.05$. ANCOVA of $\log_{10}$ transformed pooled months and sites data showed no significant difference in SFDW of males and females at $P < 0.05$ (Fig. 4). Therefore, we pooled the male and female data for the site and season comparisons.

The monthly variation of the mean CI is shown in Fig. 5. The mean monthly CI was higher at Site 1 in 10 months and higher at Site 2 in 2 months (April and June). The distribution of the CI data was not normal (Shapiro-Wilks test W = 0.966, $P < 0.001$) and the variance in the two sites was not homogeneous (Levene test F = 27.15, $P < 0.001$). Therefore, we used ANCOVA, with size as the covariate, to compare the monthly SFDWT in the sites. The regression constants 'a' and 'b' of dry flesh weight (g) and shell size (DVM mm) of the monthly data for the two sites

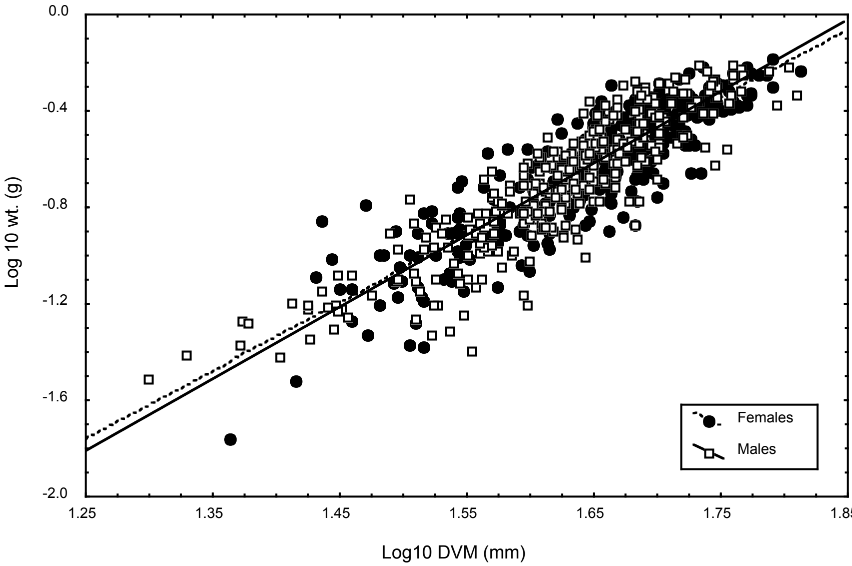

Fig. 4. — The regression of dry flesh weight (g) and size (DVM mm) of female and male pearl oysters *Pinctada imbricata* from Gazi Bay. Regression formulae: $\log_{10}$wt (g) = – 5.306 + 2.835 $\log_{10}$DVM(mm) and $\log_{10}$wt(g) = – 0.535 + 2.981 $\log_{10}$DVM(mm) for females and males respectively.

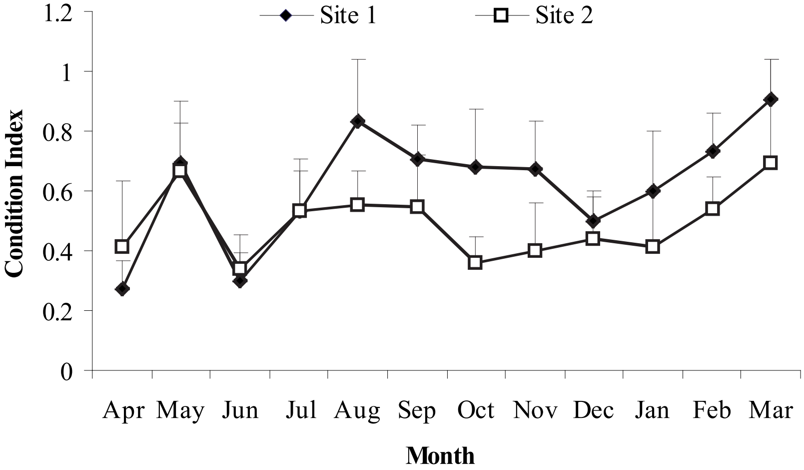

Fig. 5. — Monthly mean (+ SD) Condition Index of *Pinctada imbricata* at Sites 1 and 2 between April 2002 and March 2003.

Table 3.

The regression constants 'a' and 'b' for monthly flesh weight (g) and size (DVM mm) regression formulae of *Pinctada imbricata* from Sites 1 and 2 in Gazi Bay, showing the results of ANCOVA tests.

	Site 1		Site 2		F
Month	a	b	a	b	
April	– 5.526	2.914	– 5.240	2.939*	18.346
May	– 4.985	2.679	– 3.595	1.847	0.116
June	– 5.825	3.062	– 4.496	2.324	29.943
July	– 5.271	2.809	– 2.954	1.410	0.409
August	– 4.170	2.233*	– 4.656	2.428	28.963
September	– 2.419	1.154*	– 5.038	2.666	8.225
October	– 4.907	2.621*	– 4.668	2.379	68.664
November	– 4.721	2.505*	– 5.365	2.773	64.602
December	– 4.456	2.295	– 3.878	1.955	1.333
January	– 5.144	2.674*	– 5.872	3.101	33.989
February	– 3.844	2.012*	– 5.240	2.781	48.408
March	– 3.589	1.905*	– 4.289	2.242	50.402

* = significantly higher at $P < 0.05$.

are shown in Table 3. ANCOVA showed that the SFDWT were significantly higher at Site 1 in 7 months, higher at Site 2 in 1 month (April) and not significantly different during 4 months (May, June, July and December). The overall SFDWT was significantly higher at Site 1 than at Site 2 (ANCOVA, F = 4.643, $P < 0.0315$, Fig. 6). An a posteriori t-test showed that the regression slopes were significantly different ($t = 5.17$, $t_{\alpha}(2), 600 = 1.964$, $P = 0.05$). Therefore, relationships between shell size and SFDW at the two sites were significantly different. The regression lines indicate

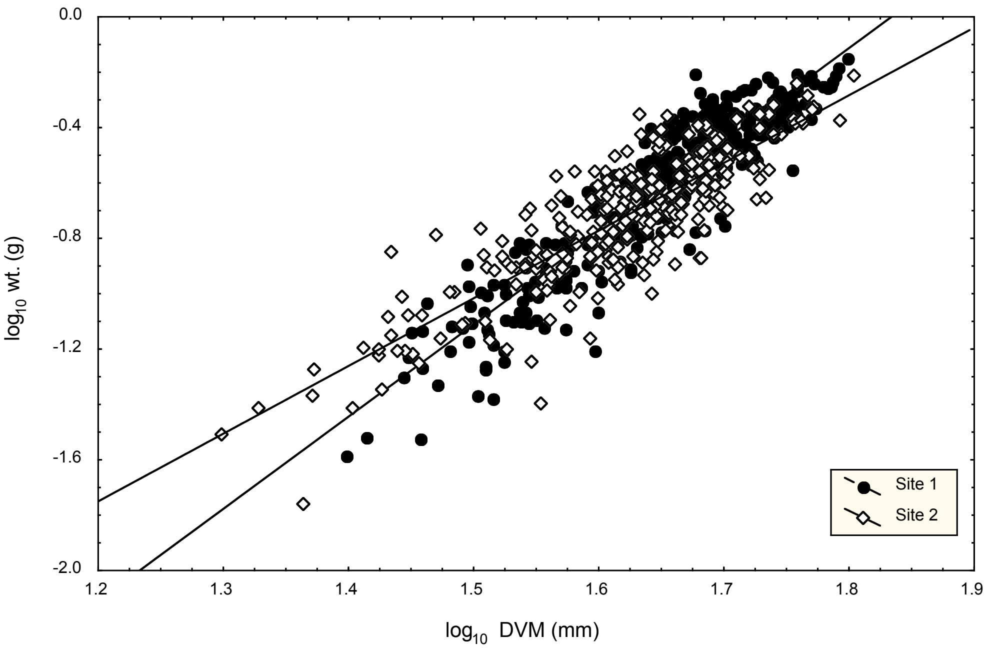

Fig. 6. — The regression of dry flesh weight (g) and size (DVM mm) of the pearl oyster *Pinctada imbricata* from the current swept area (Site 1) and sheltered area (Site 2) in Gazi Bay. Regression formulae: $\log_{10}$wt (g) = – 6.105 + 3.229 $\log_{10}$DVM and $\log_{10}$wt (g) = – 4.684 + 2.445 $\log_{10}$DVM for Site 1 and Site 2 respectively.

higher dry flesh weights for the smaller oysters at Site 2 and higher flesh weights for the larger oysters at Site 1.

Spearman correlations between the estimated SFDWT and environmental variables were not significant (salinity, R = 0.176, P = 0.432; temperature, R = – 0.009, P = 0.965, TSM, R = – 0.010, P = 0.963, % OM, R = 0.249, P = 0.262). However, the CI was lowest when water temperature declined in June, then increased with rising water temperatures between July and August. The correlations between the environmental variables and % OC were negative and not significant (salinity, R = – 0.203, P = 0.364; temperature, R = – 2.110, P = 0.345, TSM, R = – 0.001, P = 0.993). Salinity and temperature showed a positive correlation coefficient of 0.32 and P = 0.146.

The CI variation followed similar patterns in the study sites. The SFDWT declined between May and June and between August and December at Site 1. At Site 2, the decreases were between May and June, September and October, and December and January. ANCOVA conducted to compare SFDWT between sampling periods showed three significant declines at Site 1: May-June (F = 52.28, P < 0.001), August-September (F = 8.99, P = 0.004), November-December (F = 30.16, P < 0.001). There were also three significant declines at Site 2: May-June (F = 9.06, P = 0.004), September-October (F = 17.21, P < 0.001), December-January (F = 15.65, P < 0.001).

DISCUSSION

Environmental parameters

Temperature and salinity showed seasonality typical of shallow lagoons in Kenya. Both parameters were higher during the NEM season (October to March) than during the SEM season (April to September). Site 1 had slightly higher monthly temperature due to the influx of water from the shallow mud flats and channels within the mangrove forest during ebb tide. The increased flow of fresh water into the bay during the SEM season (Kitheka 1996) lowers the salinity more at Site 1 than at Site 2 due to the location of Site 1 in front of the channels. Fresh water flow from the river is less during the NEM season and evaporation overrides the fresh water influx leading to a reversal of the situation during the SEM season. The overall annual mean salinity was slightly higher at Site 2 than at Site 1. The variation of TSM and % OC of the suspended matter was high, as indicated by the high standard deviations; hence significant site or seasonal differences could not be determined from the data. The overall mean TSM and OC at Site 1 were higher during the SEM season. This can be attributed to the river discharge, which is higher during the SEM period when the long rainy season occurs. The percentage DF of the POP blocks was higher in Site 1 and the difference between the sites was less during the neap tide. This is expected because the higher tidal amplitude during spring tide results in higher tidal currents.

Sex expression

The m:f ratios show that male sex expression is predominant in *P. imbricata* populations and hermaphroditism is rare. Sex expression was size structured, with the proportion of females increasing with size. The few functional simultaneous hermaphrodites, where both the female and male acinus were equally active at the same time, was similar to the level observed in pearl oysters (usually less than 1%) (Dolgov 1991, Pouvreau et al. 2000, Saucedo et al. 2002). Reported m:f ratios of *P. margaritifera* L. 1758 were 1:0.2 in culture situation (Pouvreau et al. 2000), 1:0.6 in a natural population and 1:0.2 in the fouling of an oil drilling platform (Dolgov 1991), suggesting that male sex expression is naturally predominant in pearl oysters. However, a ratio of 1:1 was reported for a natural population of *P. mazatlantica* Hanley 1856 (Garcia-Dominguez et al. 1996), and more females than males were reported in the same population in another study (Saucedo et al. 2002). Male sex expression usually dominates in bivalve populations in less than optimal conditions, such as crowding in culture (Pouvreau et al. 2000) and polluted habitats (e.g. Dolgov 1991). Salinity and temperature stress (Rao 1956), as well as the incidence of pea crabs on the gills (Awati & Rai 1931), may also promote male sex expression in oysters. Six pea crabs were found in the 648 oysters during our study. Four of them were removed from three males and one juvenile oyster from Site 1, whereas the two pea crabs found in oysters from Site 2 were removed from male oysters. The incidence of pea crabs and environmental stress in the shallow water may have contributed to the higher level of male sex expression in the oyster population.

Gonad activity and spawning

Few gonads in the resting stage were observed, showing that gametogenesis is continuous. The few resting gonads mean that oysters rarely undergo that stage or that the resting stage is brief. This agrees with other studies showing that gonad activity and spawning in tropical and subtropical pearl oysters occur throughout the year. Examples include *Pinctada margaritifera* (POUVREAU et al. 2000), *P. mazatlantica* (GARCIA-DOMINGUEZ et al. 1996) and *P. imbricata* (URBAN 2000). However, the spawning of *P. imbricata* in the Caribbean was intensified during the upwelling season when food availability was higher (URBAN 2000). The spawning of *P. mazatlantica* was associated with high water temperature (ranging from 27 to 30 °C) in Mexico (SAUCEDO & MONTEFORTE 1997), but was also shown to occur between 21 and 31 °C (GARCIA-DOMINGUEZ et al. 1996). Ripe and spent *P. margaritifera* gonad stages were observed throughout the year, with periodic spawning intensity associated with high phytoplankton abundance (POUVREAU et al. 2000). *Pinctada radiata* Leach 1814 spawns throughout the year in Indian waters (CHELLAM 1987) and in Bahrain waters (ALMATER et al. 1993). Oysters with spent gonads in Gazi Bay were observed in all months and the mean CI was not significantly correlated with any of the environmental variables. The proportion of spent gonads and the decline of CI indicated that intensified spawning occurred in the periods September-February and April-May. These periods were also associated with increasing and declining water temperature respectively. Change in water temperature may be a cue for the spawning of the ripe oysters of the population.

Condition Index

The CI was higher at Site 1, indicating higher energy allocation to reproduction at Site 1 than at Site 2. In a related study, the biomass and density of bivalves were found to be higher at Site 1 than at Site 2. Furthermore, growth of the pearl oysters *P. imbricata* and *P. margaritifera* was also higher at Site 1 (KIMANI 2006). These results show that the conditions at Site 1 were more favourable to oysters than the conditions at Site 2. Intense hydrodynamism has been shown to improve the growth of some bivalve species by delivering suspended food particles (WILDISH et al. 1987, CAHALAN et al. 1989, WILDISH & MIYARES 1990, GRIZZLE et al. 1992). Lower gonad indices and less synchronous spawning have been shown to occur in environments with lower hydrodynamic intensity (SKERESLET & BRUN 1969, LOWE et al. 1982, NEWELL et al. 1982) and food rationing has been shown to determine the fecundity and rate of gamete development in *Placopecten magellanicus* Gmelin 1791 (MACDONALD & THOMPSON 1986) and in mussels (NEWELL et al. 1982). While it is difficult to isolate the influences of the environmental factors, the results of this study show that the gonad activity of *P. imbricata* in Kenya is relatively continuous, that spawning occurs throughout the year and that CI is higher in the current swept habitat in Gazi Bay.

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