Effects of seasonality and population density on the reproduction of the Indo-Pacific echinoid Echinometra mathaei in Kenyan coral reef lagoons

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Effects of seasonality and population density on the reproduction of the Indo-Pacific echinoid *Echinometra mathaei* in Kenyan coral reef lagoons

Abstract Reproduction in the widely distributed tropical sea urchin *Echinometra mathaei* (de Blainville) was examined in three Kenyan reef lagoons that differed in substrate cover and *E. mathaei* population density. Histological examination of the gonads and gonad index measurements for 3 years showed a seasonal reproductive cycle with gametogenesis commencing in July, when temperature and light are at their lowest, and spawning commencing in December and peaking in February to May, when temperature and light reach their annual maxima. Monthly gonad indices correlated significantly with seawater temperature and light intensity. Male urchins had mature gametes for a longer period (8 months) than females (6 months), possibly an adaptive strategy that increases the probability of fertilization. Lunar periodicity was not observed, as male and female gonads were full of gametes on all days of the lunar cycle during the period of spawning. The peak in spawning activity coincides with the peak in phytoplankton abundance, which could ensure high food availability for the planktonic larvae. Gonad weights were significantly higher relative to urchin weight at the reef having the largest mean sizes and lowest population of urchins, indicating availability of food resources for growth and reproduction. *E. mathaei* at the reef with the highest density had the smallest urchins and high relative gonad sizes, indicative of a tradeoff between growth and reproduction when food is limited.

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Introduction

Seasonality in the marine environment has been a subject of interest ever since it was recognized that many marine invertebrates reproduce during restricted periods within each year (Orton 1920; Giese and Pearse 1974). Several environmental factors that vary seasonally, including temperature (Giese and Pearse 1974), photoperiod (Pearse et al. 1986) and food availability (Pearse and Cameron 1991), have been shown to play an important role in regulating gametogenesis and spawning in marine invertebrates. Most studies have been carried out on temperate species or predominantly tropical species that occur in subtropical environments (Giese and Pearse 1974; Pearse and Barksdale 1987). The factors that control the reproduction of tropical species are less well documented (Pearse and Barksdale 1987; Lessios 1991).

Pearse and Barksdale (1987) suggested that the factors that regulate breeding patterns in tropical marine invertebrates and the mechanisms that maintain these patterns can be revealed by studies of reproduction in equatorial species, where environmental conditions are presumably less variable. The Kenyan coast occurs at the equator, without the influence of massive rivers or upwelling currents, but experiences monsoonal seasonality (northeast and southeast monsoons) with varying oceanographic conditions of temperature, light, and phytoplankton density (Bryceson 1982; McClanahan 1988a). Studies along the Kenyan coast are suitable for testing whether tropical marine environments will support marine species that breed year round or whether monsoonal seasonality will have a dominant influence on breeding patterns.

Population density has also been shown to influence the timing of spawning in some marine invertebrates. For example, Lessios (1981) showed that sea urchin species in the Caribbean in a seasonal environment synchronized their spawning, with temperature being an important factor. In the populations living in a constant

environment, however, the degree of synchrony was influenced by population density, with a tendency for tighter synchrony in sparsely populated areas, thus ensuring successful fertilization.

Echinometra mathaei (de Blainville), the world's most abundant echinoid (Palumbi and Metz 1991), is a good model for exploring these influences because it is widely distributed throughout the Indo-Pacific (Mortensen 1943; Clark and Rowe 1971) and is a common inhabitant of reef lagoons, reef flats, and back-reef rocky shores all along the East African coast (Herring 1972; Ruwa 1984; McClanahan 1988b). Previous studies on the reproductive cycles of *E. mathaei* indicate that it spawns year round throughout most of its range, with the exception of populations in Japan, the Red Sea, and the Gulf of Aqaba (Pearse 1968, 1969; Pearse and Phillips 1968).

E. mathaei plays an important role in the community structure of reefs in East Africa (McClanahan and Shafir 1990; McClanahan and Kurtis 1991; McClanahan 1998), increasing in abundance on heavily fished reefs, where the numbers of its fish predators and herbivorous competitors are low (McClanahan 1998). Overfishing has resulted in a marked increase in the population of this bio-eroder, whose feeding and excavating activities result in decreased reef topographic complexity and, ultimately, reduced species diversity (McClanahan and Kurtis 1991).

This study details the reproductive cycle of *E. mathaei* with a view to testing whether seawater temperature, light, or phytoplankton concentrations have an influence on the reproductive cycle of this urchin. Population characteristics, including body size and reproductive output, have also been analyzed to determine whether density influences the reproductive pattern as well as the magnitude of the reproductive output and, hence, reproductive success of this sea urchin on different reefs.

Materials and methods

Study sites

The study was conducted on the sheltered leeward side of three reef lagoons at Vipingo (3°47′S; 39°50′E), Kanamai (3°55′S; 39°47′E) and Diani (4°21′S; 39°34′S) along the Kenyan coast (see Muthiga 1996 for site locations). These lagoons have similar community structures, but differ markedly in population density of *Echinometra mathaei* (McClanahan and Shafir 1990). Sampling sites at each reef were homogenous in depth and benthic community structure. In Okinawa, *E. mathaei* (de Blainville) is part of a species complex distinguishable through morphology, physiology and reproduction (Arakaki and Uehara 1991, 1999). *E. mathaei* individuals are, however, morphologically very similar on the Kenyan coast, and are regarded as one species for this studies.

Annual reproductive pattern

The annual reproductive pattern was investigated by haphazardly sampling 20 urchins (ranging between 25 and 60 mm test diameter) at approximately monthly intervals from 1992 to 1994 in all three reefs. Individual urchins were measured across the longest axis of the test (test diameter), weighed and dissected. Urchins were sexed, and the gonads were removed and weighed for calculations of gonad index [GI = (wet gonad weight/total wet body weight)×100]. Additional data collected in 1986–1987 at Kanamai by the first author are also included. Temporal variation in GI at each reef and the variation between reefs each year were tested using a two-factor ANOVA, with month and reef as factors.

The seasonal pattern in the ability to spawn was investigated by inducing 20 haphazardly sampled urchins to spawn with KCl injections every month from 1993 to 1995; 0.5–1 ml of 0.5 M KCl solution was injected into the coelom. The treated urchins were inverted over a petri dish and allowed to spawn. Egg samples were washed with filtered seawater and passed through a coarse sieve to remove debris, allowed to settle and the total volume of eggs released by each individual female was measured to 0.01 ml. A correlation analysis was performed between the pooled mean monthly volume of eggs spawned after KCl injection and the pooled mean monthly GIs for all reefs.

Gametogenesis

The cellular changes that occur in the gonads of *E. mathaei* during gametogenesis were studied using standard histological techniques. The aboral tip of one gonad lobe was cut from each animal from the monthly samples and preserved in 70% alcohol, embedded in paraffin wax, sectioned (7 μm) and stained with hematoxylin and eosin (Pearse 1969; Muthiga 1996). A general examination of sections from different reefs showed a similar sequence of cellular changes; hence, pooled data from all reefs is presented.

Measurements of the thickness of the spermatogenic and sperm layers in transverse section in 10 tubules (200 μm in diameter) per male and 50 haphazardly selected oocytes (with a large nucleus and nucleolus) and ova (with nucleus) were measured from histological sections (Pearse 1969) of 10 female and 10 male gonads. Additionally, the nutritive phagocytic tissue layer of 10 individuals per month was measured in 10 gonadal tubules of each individual male and female gonad along the radius of the gonadal tubules (200 μm in diameter).

Lunar periodicity

Lunar periodicity was investigated by a comparison of the mean GI values of 20 urchins sampled at 3- to 4-day intervals at each reef in February and March, during the

peak in spawning, in 1992 and 1993 for a complete lunar period. Additionally 20 urchins were induced to spawn with KCl injections, and the proportion of urchins in the sample releasing copious gametes was calculated. A single-factor ANOVA was used to test for differences between gonad indices on different lunar days at each reef for the 2 years combined.

Temperature, light, and chlorophyll measurements

Seawater temperatures were measured monthly during low tide, and mean monthly light (MJ m^{-2} day^{-1}) data were calculated from data compiled by the Kenyan meteorological department for the Mombasa meteorological station (Muthiga 1996). The concentration of chlorophyll a in seawater was measured monthly in four 5-l samples at each reef during spring low tides following the methods of Strickland and Parsons (1972). Mean monthly temperature, light, and chlorophyll a were correlated against the pooled mean monthly GIs for the three reefs.

Population density

The population density of E. mathaei at Diani, Kanamai, and Vipingo in 1985, 1987 and 1989 was derived from McClanahan and Muthiga (1988), McClanahan and Shafir (1990) and McClanahan and Kurtis (1991). Additionally, in 1992–1994, E. mathaei density was estimated by haphazardly tossing a 1-m^2 quadrat onto the reef and counting all E. mathaei encountered in 30 quadrats per reef. The variability between reefs and between years at each reef was tested using a two-way ANOVA.

Results

Annual reproductive pattern

The sex ratios of urchins collected from Diani, Kanamai, and Vipingo did not differ significantly from a ratio of 1:1 (Table 1). The overall mean GI for all urchins in all months at Vipingo was significantly higher

($P < 0.0005$; Student's t-test) than the GI at either Kanamai or Diani, and there was no significant difference between the overall mean GI of urchins at Kanamai and Diani ($P > 0.05$) (Table 1). However, a comparison of the mean gonad indices during the peak months of reproduction (February and March 1992–1995) showed no significant difference between Vipingo and Diani, with both being significantly higher than at Kanamai (Table 1).

Correlation between GIs and urchin size (test diameter, mm) showed no significant relationship (Table 1) at Diani, Kanamai, or Vipingo. A two-factor ANOVA with sex and time as the two factors revealed no significant difference between the GI values of males and females at any of the reefs ($F = 0.19$, 0.19 and 0.07 for Diani, Kanamai and Vipingo, respectively). The mean monthly GIs pooled for male and female urchins at Kanamai for 1986–1987 and 1992–1994 (Fig. 1) and for Diani and Vipingo for 1992–1994 (Fig. 1) showed a well-defined annual cycle, with a peak in February or March followed by a sharp decrease in April or May. From a low of ~3% at all reefs in June and July, the GIs reached levels by November and December similar to those of the previous January. This pattern was remarkably similar for all reefs and years. Although gonad indices differed between sites and with time (ANOVA: P always < 0.001), the variation in the GI between months at each reef was stronger (higher F-values) than variation in the GI between the reefs.

The monthly spawning pattern of urchins induced with KCl injections at all reefs and the mean monthly volume of eggs spawned, representing the availability of eggs, also showed a seasonal cycle similar to the gonad index data (Fig. 2). There were strong correlations between the mean monthly volume of eggs released and the percent of urchins spawning each month ($r = 0.98$, $P < 0.001$) and the volume of eggs released and the mean monthly GI ($r = 0.92$, $P < 0.001$). Both the proportion of females induced to spawn and the volume of eggs released peaked in February, corresponding to the high GIs during this time. In February, females released an overall mean of 1.2 ml of eggs; 48% of females were ready to spawn by November, although they spawned only 35% of the total volume of eggs spawned during

Table 1 *Echinometra mathaei.* Morphometric characteristics calculated as the mean (± SEM) at Diani, Kanamai, and Vipingo, Kenya (sample sizes *in parentheses*). Gonad indices are calculated relative to wet weights of individual urchins. Sex ratios were tested using Chi-squared (*n.s.* not significant)

| Characteristic	Diani	Kanamai	Vipingo
Body weight (g)	35.1 ± 0.80 (117)	42.89 ± 0.66 (183)	47.1 ± 1.07 (133)
Test diameter(mm)	43.0 ± 0.44 (115)	45.8 ± 0.34 (162)	47.7 ± 0.46 (133)
Gonad index (%)			
Overall mean	6.42 ± 0.12 (751)	6.15 ± 0.12 (746)	7.82 ± 0.14 (759)
Feb–Mar 1992–1995	9.18 ± 0.16 (333)	7.83 ± 0.16 (379)	9.97 ± 0.18 (372)
Urchin density (urchins per 10 m^2)	260.0 ± 27.0 (55)	62.6 ± 6.0 (60)	28 ± 3.0 (51)
Sex ratio, F:M			
1992	1.20:1, 0.46 n.s.	1.13:1, 0.95 n.s.	1.17:1, 1.74 n.s.
1993	1.02:1, 0.01 n.s.	1.32:1, 2.35 n.s.	1.16:1, 0.98 n.s.
1994	0.88:1, 0.27 n.s.	1.09:1, 0.04 n.s.	0.97:1, 0.02 n.s.
Test diameter (mm) vs. gonad index (%)	$y = 8.35 + 2.07e^{-2x}$; $r = 0.03$	$y = 7.61 + 3.37e^{-2x}$; $r = 0.032$	$y = 3.97 + 0.12x$; $r = 0.2$
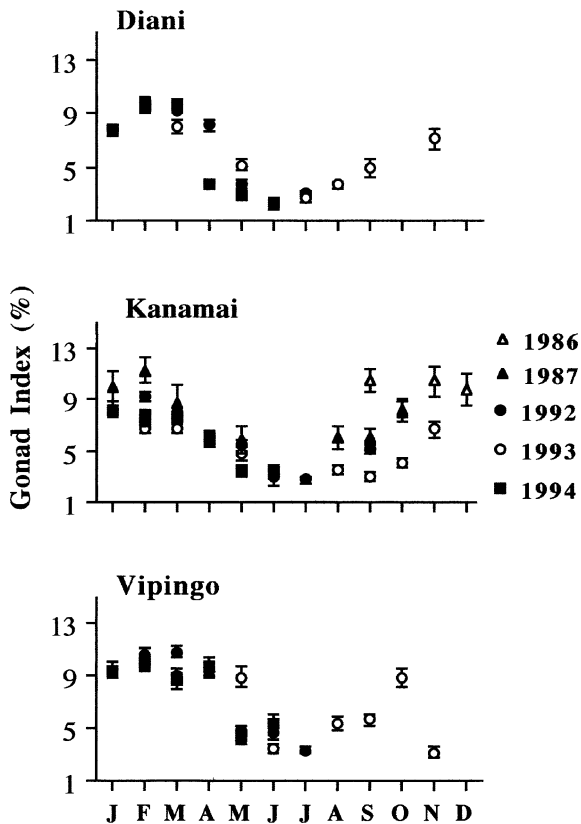
Fig. 1 *Echinometra mathaei*. Seasonal pattern of reproduction at Diani, Kanamai, and Vipingo (1992–1994) measured as the mean monthly gonad index (±SEM, *n* = 20–60). Kanamai was also sampled in 1986 and 1987 (Muthiga 1996)

the peak month of reproduction. By January, 80% of urchins that were induced released an average of 1 ml of eggs. Spawning ceased by May, since induced females spawned a negligible volume of eggs.

Gametogenesis

The monthly sequence of gross cellular events in the testis of *E. mathaei* also shows an annual cycle (Fig. 3).
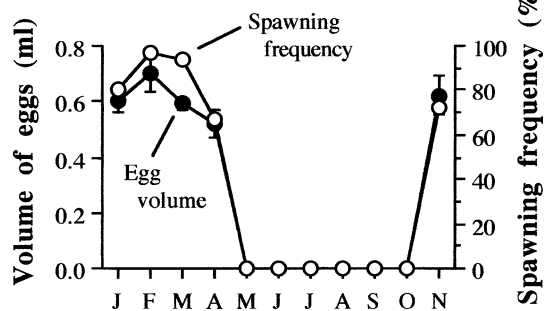

Fig. 2 *Echinometra mathaei*. Reproductive pattern at Kanamai measured as the percentage of urchins spawning copious gametes and the mean volume of eggs released after KCl injection every month in 1993 (*n* > 60 per month)

Males were considered ripe when spermatozoa filled > 50% of the lumen of the testicular tubules (Pearse 1969). A consistently high percentage (70–100%) of ripe males occurred from October to May. The quantity of spermatozoa within the tubules reached a peak in March, when the mean diameter of the spermatozoa layer was 143 μm, coinciding with the peak in GI. Most of the males were not ripe from June to September, corresponding to the period of high nutritive phagocyte development, while in July only 30% of the males had any spermatozoa. Although the spermatocytic layer was never > 17 μm, it exhibited an annual cycle, which mirrors the cycle of spermatozoa abundance.

In females, the size frequencies of oocytes and ova also followed an annual cycle (Fig. 4a). In July, the lumens of the ovarian tubules were packed with in-growing nutritive phagocytes, and, in August, a new generation of small oocytes dominated in many females. However, a mode of larger oocytes of increasing size started to form in the same month, gradually reaching a peak in February. Ova were present from October to May, and spawning was already taking place in December, when some 20% of females had partially empty lumens. Spawning continued through May, with a peak in March/April. Spent females, recognizable by large empty spaces and the presence of scattered large oocytes and ova in the lumens of the ovarian tubules, appeared in May. The thickness of the nutritive phagocytic layer increased in July, when small oocytes were present, and started decreasing at the onset of spawning (Fig. 4b). Atretic ova were still visible in 20% of females in September.

Lunar pattern

The GIs of females sampled through a complete lunar cycle during the peak spawning period, failed to show
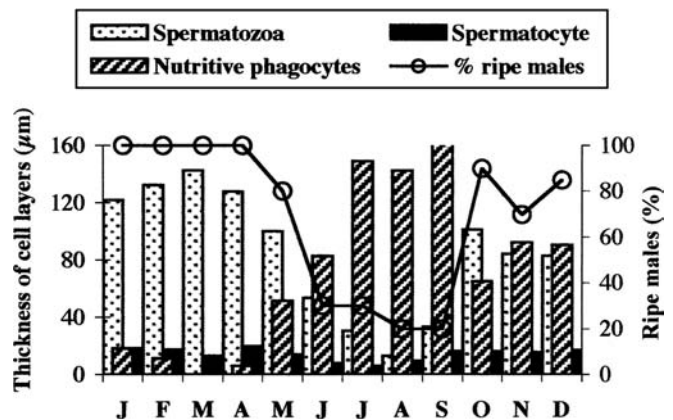

Fig. 3 *Echinometra mathaei*. Sequence of cellular changes in the testes of *E. mathaei* from Diani, Kanamai, and Vipingo measured as the mean (μm, ±SEM) monthly thickness of the layers of spermatogenic cells, spermatozoa, and nutritive phagocytes (*n* = 10 per month). The *solid line* represents the monthly percentage of males at all reefs containing mature gametes filling > 50% of the testicular lobes
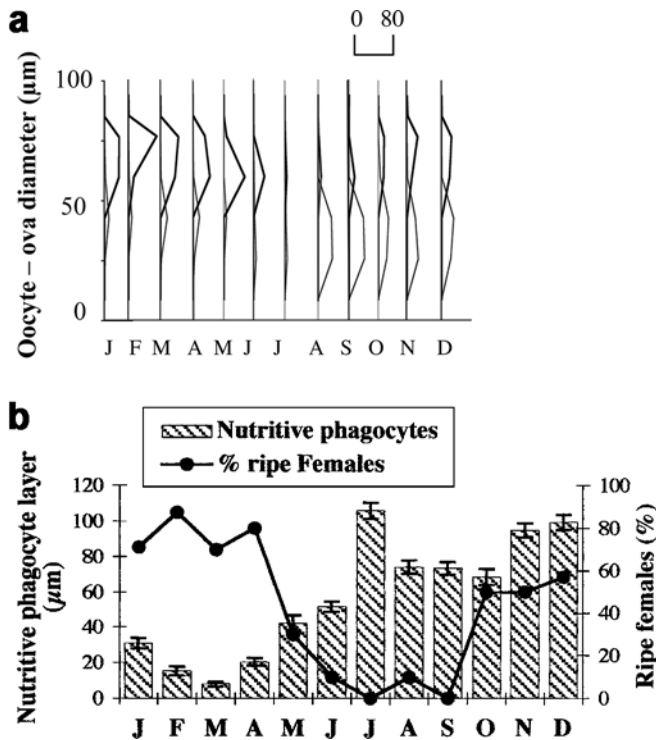
Fig. 4a, b *Echinometra mathaei.* **a** The size distribution of ova (*solid line*) and oocytes (*dashed line*) of females at Diani, Kanamai, and Vipingo collected on a monthly basis (*n* = 10 per reef per month). **b** The thickness (μm, ±SEM) of the nutritive phagocytic layer and the monthly percentage of ripe females (females containing mature gametes filling >50% of the ovarian lobes)

Fig. 5 *Echinometra mathaei.* Mean gonad index (±SEM) on different lunar days of a complete lunar cycle in February and March, 1992 and 1993 at Diani, Kanamai, and Vipingo (*n* = 20 per lunar day; new moon = day 0)

any lunar periodicity in spawning intensity (Fig. 5), and GIs were significantly different between days at all the reefs (single-factor ANOVA: *P* in all cases < 0.05). Moreover, 93% (±1.26; *n* = 16) of females spawned copious amounts of eggs when induced to spawn, showing the same absence of lunar periodicity. An examination of histological sections of both testes and ovaries sampled throughout the lunar cycle did not reveal any systematic differences between days sampled.

Temperature, light, and phytoplankton

Mean monthly seawater temperatures showed a seasonal pattern (Muthiga 1996) driven by the monsoons. Temperatures were significantly positively correlated with monthly GIs (*r* = 0.87, *P* < 0.01). In general, GIs rose with increasing temperature and decreased with decreasing temperature reaching, a minimum in July, at about the time of the temperature minima.

Light intensity also exhibited a seasonal pattern related to the monsoons (Muthiga 1996), and mean monthly radiation measurements were significantly correlated with mean monthly GIs (*r* = 0.92, *P* < 0.01). In general, GIs closely tracked light, except that GIs peaked in February, prior to the peak in light. Light measurements also decreased sharply between March
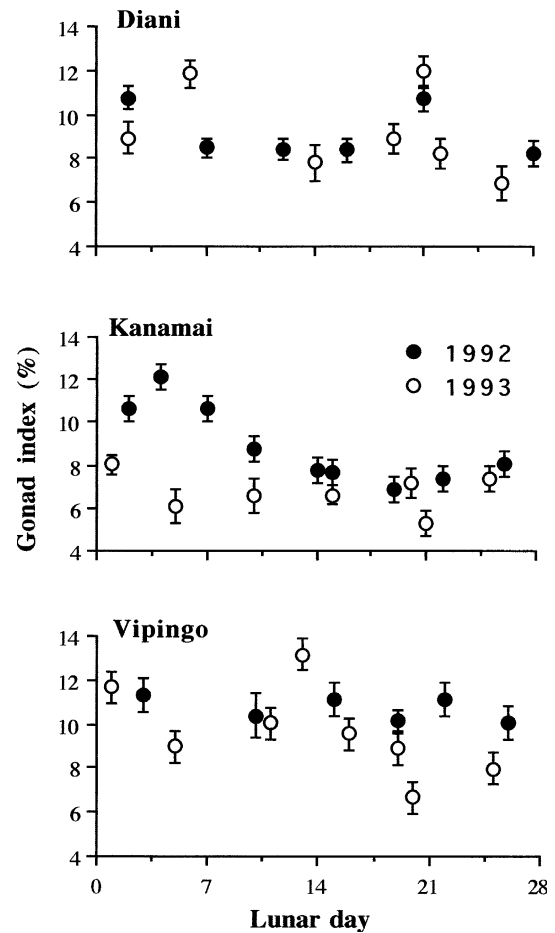
and May as did GIs, and the increase in light in August was mirrored by rising GIs.

The abundance of phytoplankton (chlorophyll *a* concentration) in 1993 and 1994 measured at all reefs on a monthly basis ranged from an average of 0.2 to 1.8 mg m^{-3}, showing a peak in March–April (Fig. 6). There was no significant correlation between mean monthly chlorophyll *a* concentrations and the concurrent mean monthly GIs for 1993–1994 (*r* = 0.44, n.s.). A correlation
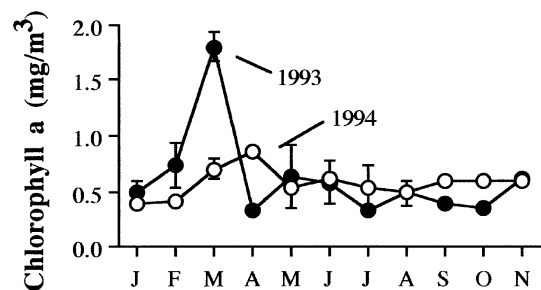

Fig. 6 Mean monthly chlorophyll *a* (mg m^{-3}, ±SEM) measurements for 1993 and 1994 at Diani, Kanamai, and Vipingo (pooled)

between the mean monthly GIs and the chlorophyll *a* concentration of the subsequent month showed, however, a significant relationship ($r = 0.78$, $P < 0.01$).

Population density

The population density of *E. mathaei* at Diani reef lagoon consistently had the highest density of urchins, ranging between 135 individuals per 10 m² in 1987 and 280 individuals per 10 m² in 1992 (Fig. 7). Vipingo reef lagoon consistently had the lowest population of urchins, ranging from 59.6 individuals per 10 m² in 1989 to 13 individuals per 10 m² in 1994, while Kanamai had intermediate densities of urchins.

A two-factor ANOVA comparison of differences in the population between reefs and between years showed a significant difference between reefs ($F = 30.9$; $df = 2, 8$; $P = 0.0001$), but not between years within each reef ($F = 0.57$; $df = 4, 8$; $P = 0.69$). There was no significant relationship between population density and potential reproductive output, as measured by GI (during the peak reproductive period February–March). Vipingo urchins had, however, mean overall GIs that were significantly higher than those of Diani and of Kanamai ($P < 0.0001$). There was no significant difference in GIs between Diani, the reef with the highest density of urchins, and Kanamai, a reef with a quarter of the population density of Diani (Table 1). Fluctuations in GI occurred from year to year during the peak period of reproduction at Kanamai and Vipingo, but not at Diani.

Discussion

The process of gametogenesis of *Echinometra mathaei* in this study was similar to that described in other studies except in the timing of growth and maturation of the gametes and changes in nutritive layers and in the size of the gonad. I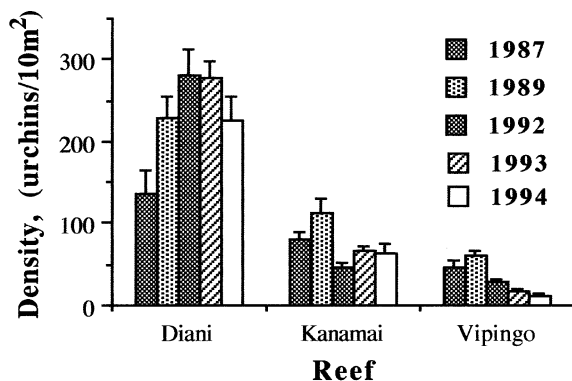n both females and males, gametogenesis starts with the growth of nutritive phagocytes between May and June. In the Gulf of Suez (Pearse 1969), the period of phagocytic growth is longer, from March to June, while in South Africa it occurs from April to September (Drummond 1995). An immediate sharp decrease (30%) in nutritive phagocytes occurs in Kenyan females in August, after the onset of oogenesis and growth of oocytes, suggesting that nutritive phagocytes provide the energy requirements for oogenesis. A similar decrease in nutritive phagocytic tissue was observed between April and July in *E. mathaei* in the Gulf of Suez (Pearse 1969).

A second period of growth of the nutritive phagocytes occurs between November and December (~30% increase), prior to the onset of spawning. The sharp decrease (60%) in the amount of nutritive phagocytes in January indicates the high demand for energy during the final stages of oocyte maturation and the onset of spawning. The gonad showed a large decrease in size after spawning similar to *E. mathaei* from South Africa (Drummond 1995). *E. mathaei* in the Gulf of Suez does not show a corresponding decrease in gonad size after spawning because the nutritive phagocytes expand and compensate for the loss of gametes (Pearse 1969).

The layer of nutritive phagocytes in testicular tubules does not decrease markedly during this time, indicating that spermatogenesis is less energetically expensive, as has been shown in other echinoids (Pearse and Cameron 1991). Male urchins also exhibit a longer spawning period (October–May) than females, an adaptive strategy to enhance fertilization success by ensuring even females that spawn late will be fertilized. *E. mathaei* males at Wadi el Dom, Gulf of Suez (Pearse 1969), also retain sperm for a long period.

Oocytes took approximately 3 months to mature to ova, similar to *E. mathaei* in the Gulf of Suez (Pearse 1969). Not all the oocytes of urchins at Wadi el Dom, mature to ova, however, since at a diameter of 20–30 μm, some oocytes continue to grow to ova, while the rest disintegrate and are phagocytosed. This allows the removal of excess oocytes, while retaining the nutrients released in this process for the growing oocytes, as has been shown in other echinoids (Pearse 1969). The smooth and continuous progression from small oocytes to large oocytes of urchins at Diani, Kanamai, and Vipingo suggests that few excess oocytes were produced; hence, gonads show a large decrease in size after spawning.

The reproductive patterns of species with a wide geographical distribution can vary considerably over their range, generally being more restricted at higher latitudes and more continuous in the tropics (Giese and Pearse 1974; Pearse and Cameron 1991). Most studies of the reproductive pattern of *E. mathaei*, a widely distributed tropical sea urchin, report different spawning patterns (Pearse and Cameron 1991). The present study shows that, contrary to expectations, populations of *E. mathaei* exhibit a seasonal reproductive cycle on the Kenyan coast, the first record for this urchin near the

Fig. 7 *Echinometra mathaei*. Population density at Diani, Kanamai, and Vipingo measured as the mean (±SEM) of 20–50 quadrats censused at each reef lagoon in 1985 (McClanahan and Muthiga 1988), 1987 (McClanahan and Shafir 1990), 1989 (McClanahan and Kurtis 1991) and 1992–1994

equator. Ntiba and Jaccarini (1990) had shown a seasonal pattern of reproduction in the rabbitfish *Siganus sutor*, though in *S. sutor* there were two spawning periods, in January /February and in May/June. These studies suggest that the generalization of year round spawning in tropical environments needs critical review.

On the Kenyan coast, gametogenesis starts in July, during the southeast monsoon season, and spawning occurs between December and May, with a peak in February/March, during the northeast monsoon season. Populations from different localities and densities (Diani, Kanamai and Vipingo) along the Kenyan coast were not in perfect synchrony, but followed the same general pattern, indicating that some large-scale environmental cue may be operating across all populations. In addition, the seasonal reproductive cycle showed a significant and positive correlation with seawater temperature levels and solar radiation, indicating that these factors could play a role in controlling the timing and length of the reproductive cycle of *E. mathaei* on the Kenyan coast.

The relative importance of temperature and light in determining the reproductive cycle of *E. mathaei* is unclear. Pearse and Phillips (1968) suggested that 18°C is the minimum temperature required for the onset of gametogenesis in *E. mathaei*; hence, spawning in Kenya would be expected to occur year round as it does at Rottnest Island, Western Australia (Pearse and Phillips 1968), where seawater temperatures range from 18°C to 22°C (Hodgkin et al. 1959). *E. mathaei* along the Kenyan coast (temperature range 24–31°C) exhibits a restricted reproductive cycle similar to populations in areas with a wider range of temperatures, including Seto and Okinawa, Japan (Onada 1936; Arakaki and Uehara 1991), Wadi el Dom, Gulf of Suez (Pearse 1969), and the eastern coast of South Africa (Drummond 1995) (Table 2). Moreover, the fact that *E. mathaei* in the northern Red Sea (closer to the equator), spawn throughout the year (Pearse 1969) makes the seasonal pattern on the Kenyan coast even more surprising. Seawater temperature, therefore, may not be the key factor in controlling reproduction in *E. mathaei* on the Kenyan coast.

The effects of light through changing day length and photoperiod play an important role in some temperate zone marine invertebrates (Giese and Pearse 1974; Pearse et al. 1986). It is unlikely, however, that the small change in day length (31 min) experienced on the Kenyan coast would act as a sufficient cue for regulating reproductive rhythms. Light intensity, however, varies seasonally and could act as a reliable cue for the onset of gametogenesis. The exact mechanism by which light intensity influences the reproduction of *E. mathaei* needs further study and could prove to be the first time light intensity is implicated in regulating reproductive rhythms in echinoids. Some species with annual cycles also exhibit monthly cycles synchronized by moonlight (Lessios 1991; Drummond 1995; Muthiga 2003). *E. mathaei* did not exhibit a lunar cycle in this study, suggesting that moonlight is not a likely cue for the onset of spawning.

Spawning in sea urchins has also been shown to coincide with the spring phytoplankton blooms in temperate environments (Himmelman 1980), thereby ensuring reproductive synchrony among conspecifics as well as adequate food and favorable environmental conditions for the larvae (Lessios 1981). Starr et al. (1990) showed that between 2 and 4 mg m^{-3} of chlorophyll *a* could induce spawning in *Strongylocentrotus droebachiensis*, and subsequent experiments provided evidence that extracellular metabolites released by various species of phytoplankton can induce spawning in sea urchins (Starr et al. 1992).

Chlorophyll *a* concentrations on the East African coast peak around February–March (0.7–1.2 mg m^{-3}), which is also the time of the light and temperature maxima (Bryceson 1982; McClanahan 1988a). *E. mathaei* spawns during this period, and this may have adaptive significance, since this ensures that young are produced when food is abundant for the extended larval period. *Diadema savignyi* on the Kenyan coast (Muthiga 2003) and *E. vanbrunti* in the Carribbean (Lessios 1981) have been reported to spawn just prior to the peak in phytoplankton concentration. Additional advantages of spawning during the peak phytoplankton period include reduced predation of young due to reduced visibility for

Table 2 *Echinometra mathaei*. Summary of the spawning periods reported throughout its geographical distribution

Latitude	Location/temperature range	Spawning period	Reference
34°40′N	Seto, Japan/15–30°C	Jul–Aug	Onada (1936)
29°26′N	Wadi el Dom, Gulf of Suez/15–31°C	Jul–Sep	Pearse (1969)
27°15′N	Al-Ghardaqa, Red Sea/15–30°C	Peak spawning Jul–Aug, ripe individuals found year round	Pearse (1969)
26°38′N	Sesoko Island, Japan/20–30°C	Sep–Oct	Arakaki and Uehara (1991)
04°00′S	Diani, Kanamai, Vipingo, Kenya/24–31°C	Feb–May	Present study
30°50′S	Ramsgate, S. Africa/19–25°C	Jan–Apr	Drummond (1995)
32°00′S	Rottnest Island, Australia/18–22°C	Throughout the year	Pearse and Phillips (1968)

predators and satiation of predators due to high larval abundance from multispecies spawning (Himmelman 1999).

Several marine invertebrate species on the Kenyan coast have been reported to settle after the peak phytoplankton period, including the urchins *D. savignyi*, *D. setosum*, and *Tripneustes gratilla* (Muthiga 2003), the oyster *Crassostrea cucullata*, the barnacle *Balanus amphitrite* (Ruwa and Polk 1994) and the mollusk *Pinctada implicata* (Kimani, personal communication), indicating that this is a common reproductive strategy. The results of this study indicate that a combination of factors related to monsoonal seasonality, including light intensity and phytoplankton, regulate the reproduction of *E. mathaei* on the East African coast. Further experimental study on the exact mechanisms by which light intensity and phytoplankton control reproduction in *E. mathaei* are required.

Population density has been shown to influence the timing of spawning in some marine invertebrates (Lessios 1981). This was not the case in this study, since populations of *E. mathaei* from different reefs followed the same general pattern. Population density, however, can influence the reproductive success of an animal through control of body size. According to Levitan (1991), there is usually a tradeoff between maternal size and population density with sea urchins either: (1) developing large maternal size with higher gamete production at low population density or (2) small maternal size with lower gamete production at higher population densities. *E. mathaei* at Vipingo fit the former model, since individuals are large, produce large gonads and have the lowest population density compared to urchins at Kanamai and Diani.

Urchins at Diani were food limited, as indicated by smaller body sizes and relatively larger jaws (McClanahan and Kurtis 1991); however, their gonads were as large as individuals at Kanamai, indicating a higher potential reproductive output despite the high population density. This suggests that *E. mathaei* at Diani allocates a higher proportion of available energy to the production of gametes, probably at the expense of growth, hence, the smaller body sizes. The allocation of resources to reproduction at the expense of growth is a common adaptive strategy shown in many marine organisms in response to food limitation (Thompson 1982; Levitan 1988).

Population density can also influence reproductive success, because the distance between the sources of gametes has an effect on the success of fertilization (Pennington 1985). Although high population densities may increase competition for food and space, the tradeoff for non-aggregating or asynchronous animals may be increased fertilization success due to increased proximity of potential mates. *E. mathaei* on the Kenyan coast spawn asynchronously during the extended spawning period; hence, reproductive success will depend to some degree on the success of fertilization, which, in turn, depends on the mean distance between

spawning individuals. This implies that *E. mathaei* at Diani may be as reproductively successful as sea urchins at the other reefs, because the high population density at Diani will enhance the success of fertilization. This hypothesis, however, needs testing through further studies of fecundity and fertilization success at these sites.

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