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Coexistence and reproductive isolation of the sympatric echinoids *Diadema savignyi* Michelin and *Diadema setosum* (Leske) on Kenyan coral reefs

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Abstract The sympatric echinoids *Diadema savignyi* and *D. setosum* coexist in shallow reef lagoons throughout East Africa. The reproductive strategies of these echinoids were studied to investigate reproductive isolation as a possible mechanism for maintaining the coexistence of these closely related species. The annual reproductive cycle and lunar periodicity were determined by gonad index measurements, histological examination of gametogenesis, and induction of spawning with injections of KCl. The peak reproductive period of *D. savignyi* coincided with the north-east monsoon period (when light and temperatures are high) as gonad indices were high (>8%) beginning in February and peaked at 9.7% in May. Gonad indices subsequently rapidly decreased (by 26%) in June at the beginning of the cooler south-east monsoon period. However, the presence of sperm and ova in most months of the year indicates continuous gametogenesis with reduced reproductive effort during the cooler months. The annual cycle for *D. setosum* showed less of a seasonal trend as gonad indices remained above 7% throughout much of the year but tended to be highest when temperatures were lower. This is the first confirmation of continuous reproduction in these two species at the equator. The reproductive patterns of both species remained consistent over 2 years of sampling. Both species exhibited a synchronized lunar spawning periodicity during the 3 months sampled, with *D. setosum* spawning on lunar days 8–10 and *D. savignyi* spawning after the full moon (lunar days 17–18). Whereas spawning in *D. savignyi* was very tightly synchronized, 20% of *D. setosum* individuals still spawned after the peak spawning period. The coexistence of these closely related species appears to be maintained by temporal reproductive isolation during the lunar

spawning period reinforced by seasonal differences in reproductive effort.

Introduction

Coral reefs are characterized by high species diversity, and the coexistence of species plays an important role in maintaining this diversity (Sale 1977, 1980; Connell 1978; Waldner and Robertson 1980; Birkeland and Neudecker 1981; Robertson and Polunin 1981; McClanahan 1988a, 1998). Coexisting species have the potential for hybridization and hence reproductive mechanisms that prevent hybridization assist the maintenance of species diversity (Hendler 1991; Lessios and Pearse 1996). For example, studies of the anemone fishes *Amphiprion clarkii* and *A. perideraion* (same host anemone) showed that these species are able to coexist because of a combination of reproduction suppression of *A. perideraion* when cohabiting with the larger *A. clarkii* and differences in settlement patterns of the juveniles possibly related to differing reproductive strategies (Hattori 1995).

Variable recruitment patterns have also been implicated in studies of the damselfish *Dascyllus* that inhabit the same coral in the Red Sea. Shpigel and Fichelson (1986) showed that *Dascyllus* species are able to coexist because of random settling of juveniles and predation pressure that limits resettlement of these fishes. Most of the studies of coexistence of closely related coral reef species have concentrated on fishes, and the factors that control the coexistence of closely related coral reef invertebrates, important components of reef communities, are not well documented (McClanahan 1988a).

In East Africa, the sea urchins *Diadema savignyi* Michelin and *D. setosum* (Leske) co-occur in large mixed groups on most shallow reefs along the coasts of Kenya and Tanzania (Herring 1972; McClanahan 1988a, 1998). These two species are also widespread on reefs in the

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Indo-Pacific (Mortensen 1940; Clark and Rowe 1971) and are the only sympatric species within the genus *Diadema* (Clark and Rowe 1971). McClanahan (1988a, 1998) attributed coexistence of these species in a guild of sea urchins including *Echinometra mathaei* to differences in the ability to utilize predator-free space. *D. savignyi* was a better competitor for small crevices whereas *D. setosum* was the superior competitor in the open.

Competition for predator-free space, although an important mechanism for enhancing coexistence, may not be the only mechanism controlling the coexistence of these two species. Because these species are so closely related and live in mixed groups, hybridization is possible, as was recently confirmed by Lessios and Pearse (1996). Reproductive mechanisms, therefore, that keep these species of *Diadema* as separate species as suggested by Pearse (1990) could cause reproductive isolation in *Diadema*, thus allowing for the maintenance of separate species.

The present research documents a comparative study of the reproductive patterns of *D. savignyi* and *D. setosum* populations along the Kenyan coast and the relationship with seawater temperature and solar radiation, to establish the factors that maintain genetic isolation and coexistence in these sympatric species of *Diadema*. Information on the reproduction of these species in East Africa will also enhance the growing body of literature on the factors that control reproductive patterns in the tropics.

Materials and methods

Morphometric characteristics

Diadema savignyi and *D. setosum* have been the subject of some taxonomic confusion. Pedicellarial shape and test color pattern are the main characteristics used to distinguish between them (Pearse 1970). In Kenya, *D. savignyi* has iridescent blue or green lines along the interambulacra and around the periproct and sometimes very pale white spots on the aboral ends of the interambulacra. *D. setosum*, on the other hand, has five bright (rarely pale) white spots on the aboral ends of the interambulacra, iridescent dotted blue lines along the interambulacra, and an orange ring along the periproct. Occasionally individuals with intermediate characteristics are encountered (McClanahan 1988a); however, in this study individuals of the two species of *Diadema* were distinguished using interambulacral and periproct color.

Reproductive patterns

The annual pattern of reproduction was studied by haphazardly collecting monthly samples of 10–20 individuals of each species at a shallow reef lagoon at Kanamai (3°55'S, 39°47'E: described in McClanahan 1988a), Kenya (Fig. 1) from June 1992 to May 1993. Individual urchins were weighed and dissected and the guts (plus contents), gonads, and jaws were removed and weighed. Organ indices were calculated (organ index = wet organ weight/wet body weight × 100) for the gonads and jaws. The seasonal feeding pattern was analyzed by measuring monthly changes in the weight of the gut contents normalized to the weight of the urchin. In addition, the organic contents of the guts were analyzed using methods developed in McClanahan and Kurtis (1991). Mean monthly gonad

indices were also calculated and correlated with time. Samples of these species collected almost monthly from September 1986 to October 1987 at Kanamai and processed as above were also used for between-year comparison. In addition, gonad samples were collected for histological preparation (as described below) and examined for the presence of mature gametes. The frequency of individuals that contained mature gametes covering more than 50% of gonadal tubules was scored and plotted against time.

The effects of environmental factors on the annual reproductive pattern was studied by correlating mean monthly gonad indices with mean monthly seawater temperatures collected at Kanamai, Vipingo, and Diani reef lagoons from 1990 to 1994. Solar radiation was compiled for the period 1992–1994 from data collected by the Kenya Meteorological Department Mombasa station (the closest weather station to Kanamai).

Lunar periodicity was investigated at Kanamai by examinations of histological preparations of gonads of ten individuals of both species collected every 2–3 days and processed using methods described in Pearse (1968). Samples were analyzed microscopically by recording measurements of oocyte and ova diameters as well as the thicknesses of spermatogonial, spermatozoa, and nutritive phagocytic layers in ten tubules per individual per sample (Pearse 1968) and plotted against the lunar day.

Lunar spawning activity was investigated at Kanamai during three consecutive lunar periods (March /April, June/July, and September/October). Ten to 20 urchins from each species were collected every 3–5 days and injected with 2 ml of 0.5 M KCl (Tyler 1949). Only urchins that spawned copious amounts of gametes within minutes of receiving the injection were scored and the frequency of spawning on each lunar day was calculated (new moon = day 0). Urchins were haphazardly sampled within an area (~100 × 50 m) and removed after treatment to minimize sampling the same animal twice.

Results

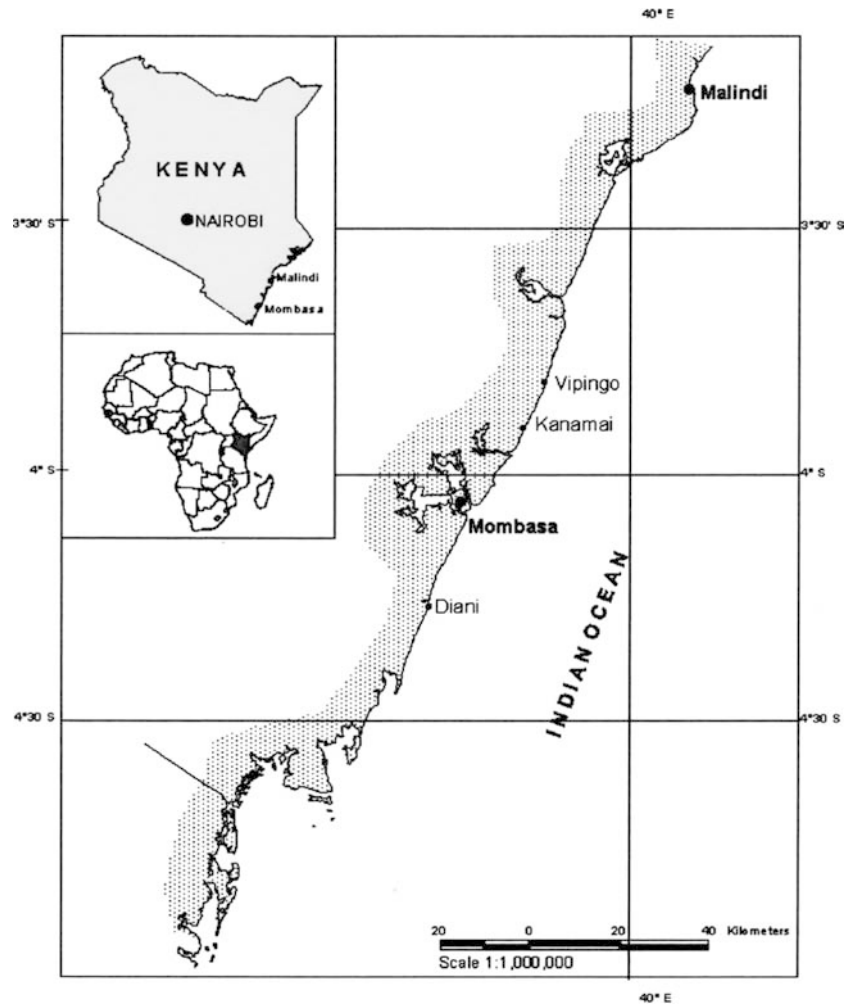
Morphological characteristics

D. savignyi and *D. setosum* could easily be distinguished by the presence of an orange ring along the periproct cone: all *D. setosum* encountered had the ring and *D. savignyi* had no orange ring (Table 1). Whereas all *D. setosum* had five bright white spots only 6 of 116 *D. savignyi* had bright white spots (Table 1), and 93 had pale white spots. In addition, *D. savignyi* had a smaller body size with significantly smaller test diameters (*t*-test, $P < 0.0005$) and weights (*t*-test, $P < 0.0005$) than *D. setosum*. (Table 1). *D. savignyi* also had statistically smaller gonads relative to body size (*t*-test, $P < 0.0005$) but statistically heavier guts with contents (*t*-test, $P < 0.0005$) than *D. setosum* although there was no significant difference in the size of the jaw relative to body size between the two species (Table 1).

Reproductive patterns

D. savignyi gonad indices showed some variation throughout the year (Fig. 2a) being on average high (> 8%) beginning in February and peaking at 9.7% in May. A 26% decrease occurred between May and June during the south-east monsoons. The gonad indices of *D. savignyi* remained low (~5%) during the later part of the year but started gradually increasing at the beginning

Fig. 1 The Kenyan coast showing the main study site Kanamai (3°55'S, 39°47'E) and Vipingo and Diani reef lagoons, which were sampled for seawater temperature measurements



of the north-east monsoons in October. The gonad indices of *D. setosum*, on the other hand, showed an opposite pattern with less monthly variation than those of *D. savignyi*, being low (~7%) between January and May and increasing gradually to 8.8–9.3% between October and December (Fig. 2b).

Comparisons of the 1992/1993 and 1986/1987 samples (Fig. 2a, b) indicated no significant differences in gonad index between years for either species. The general pattern throughout the year remained the same, despite the low monthly sample sizes in the 1986/1987 samples. Examination of monthly histological samples revealed that gonads of individuals of each species showed similar stages of development in each sample. In most cases monthly samples had more than 70% of individuals with mature gametes, consisting of large oocytes and ova in females and sperm in males filling more than 50% of gonadal tubules (Fig. 3).

Mean monthly seawater surface temperatures along the Kenyan coast (Fig. 4) showed a seasonal pattern varying from a low of 26.3°C (± 0.11 SEM) in July during the south-east monsoon period (May–October) and gradually rising to a peak of 31.6°C (± 0.24 SEM) in March during the north-east monsoon period (Novem-

ber–April). Although there was no significant correlation between mean seawater temperatures and mean monthly gonad indices for either species, there was a significant correlation when the data were offset (Table 1). High gonad indices in *D. savignyi* tended to coincide with high temperatures whereas the gonad indices of *D. setosum* track temperature to a lesser degree and the highest gonad indices coincided with the lowest temperatures (Table 1).

Mean monthly light measurements also showed a seasonal pattern similar to temperature, peaking in February–March toward the latter part of the north-east monsoon season and showing the lowest measurements in June–July during the earlier part of the south-east monsoon season (Fig. 4). Consequently there was no significant correlation between mean monthly light measurements and mean monthly gonad indices for either species (Table 1) and the relationships between light and gonad indices in both species were similar to those described for temperature.

The amount of gut contents of both species showed some variation throughout the year with *D. savignyi* showing more monthly variation than *D. setosum* (Fig. 5a). Gut contents of *D. savignyi* tended to be lower

Table 1 Morphometric characteristics of *Diadema savignyi* and *D. setosum* calculated as mean \pm SEM at Kanamai, Kenya (number of individuals in brackets). Gonad, gut, and jaw indices are calculated relative to wet weights of individual urchins. The dominant test characteristics for each species are included as well as comparisons of correlations between mean monthly seawater temperature and mean monthly solar radiation and gonad indices offset by 1 month

Characteristic	<i>D. savignyi</i>	<i>D. setosum</i>
Morphometric characteristics		
Test diameter (mm)	61.2 \pm 0.4 (240)	68.3 \pm 0.4 (256)
Weight (g)	120 \pm 2.1 (261)	172 \pm 2.8 (276)
Gonad index (%)	6.7 \pm 0.2 (260)	8.3 \pm 0.2 (276)
Aristotle's lantern index (%)	4.85 \pm 0.1 (97)	4.99 \pm 0.1 (107)
Gut index (%)	12.8 \pm 0.51 (79)	16.3 \pm 0.59 (64)
Test characteristics		
Interambulacral color		
Iridescent dotted blue lines	0	42
Iridescent plain blue lines	105	0
Iridescent plain green lines	11	0
Periproctal color		
Orange ring	0	42
No orange ring	116	0
White spots		
Bright white spots	6	42
Pale white spots	93	0
No white spots	17	0
Correlations		
Temperature vs gonad index	$y = -17.54 + 0.85x$ $r = 0.90$ (12)	$y = 25.52 - 0.61x$ $r = 0.82$ (12)
Solar radiation vs gonad index	$y = -5.72 + 0.63x$ $r = 0.86$ (12)	$y = 14.18 - 0.30x$ $r = 0.48$ (12)

when gonad indices were high and higher when gonad indices were low. The gut contents of *D. setosum*, however, closely follow the pattern of gonad indices, showing little deviation throughout the year (Fig. 5b). On average, *D. setosum* gut contents had a higher percentage of organic matter (37.6%) than that of *D. savignyi* (24.5%).

The pattern of spawning after KCl injection averaged over three lunar periods for both urchin species showed lunar periodicity (Fig. 6). *D. savignyi* had a tightly synchronized cycle, spawning a few days after the full moon (lunar days 17–18) when the frequency of spawning individuals is about 90–100%. Few *D. savignyi* release gametes when injected with KCl after this period. *D. setosum*, on the other hand, spawned approximately 2 weeks later, a few days after the new moon (lunar days 8–10). Twenty percent of *D. setosum* individuals, however, still showed some response to KCl after the peak period of spawning. Gonad smears inspected during this time indicated active live sperm and ova and large oocytes in the gonadal tubules of individual urchins.

An examination of histological preparations of gonad sections further confirms this lunar pattern. In females, numerous mature ova are found in the ovaries of *D. savignyi* only between lunar days 10 and 17; the rest of the time only mid-sized to large oocytes are present in

the ovaries with the smallest oocytes occurring a few days after spawning (Fig. 7a). A period of oocyte growth then takes place and large oocytes start accumulating in the gonad between lunar days 7 and 10 prior to spawning. In *D. setosum*, ova occur between lunar days 0 and 7, large oocytes occur just before this period, and oocytes start to grow after lunar day 7 (Fig. 7b). There are differences in the utilization of nutrients during gametogenesis, with *D. savignyi* using up a higher percentage (~50%) of the nutritive phagocytes a few days before spawnout in females (Fig. 8a). The nutritive phagocytes of *D. setosum* do not show a marked decrease until after spawnout in females (Fig. 8b). In general female gonads had more nutrients with thicker layers of nutritive phagocytes than male gonads (Fig. 8a, b).

The cycle of male *D. savignyi* was also tightly synchronized with sperm present only prior to and during the spawning period (Fig. 9a). The testicular tubules of *D. setosum* are full of sperm around lunar day 7 prior to spawning (Fig. 9b) but small amounts of sperm are present up to lunar day 25. The layer of spermatocytes tends to follow a pattern similar to the oocytes in the females, increasing in size several days after spawning and peaking before the onset of spawning in both species (Fig. 9a, b).

Discussion

Sympatric species that coexist are faced with the challenge of remaining as separate species and the development of different reproductive cycles has been suggested as a response to avoid the potential for hybridization (Hendler 1991; Lessios and Pearse 1996). Investigations of the reproductive cycles of sympatric species of *Diadema* in Kenya revealed the presence of annual reproductive as well as monthly spawning cycles with marked differences between the two species. Whereas *D. setosum* shows only a slight seasonal trend with gonad indices remaining fairly high throughout the year, *D. savignyi* shows a stronger and positive correlation with light and seawater temperature. In both species, however, mature gametes were present in all months of the year, suggesting that reproductive activity is continuous throughout the year.

Giese and Pearse (1974), in a review of the timing and reproductive patterns of marine invertebrates, suggested that species with broad latitudinal ranges would exhibit variable patterns, generally being restricted in cooler latitudes and continuous in the tropics with temperature being the main influence. Within its range of distribution, *D. setosum* spawns in the summer months at the edge of the tropics (Pearse 1970) and has continuous reproduction closer to the equator as reported in Singapore (Hori et al. 1987) and in the Philippines (Tuason and Gomez 1979). This is the first confirmation of continuous reproduction in this species so close to the equator. A closer examination of the annual cycle of

Fig. 2 Mean monthly gonad index values (mean \pm SEM) of *Diadema savignyi* (a) and *D. setosum* (b) sampled monthly in 1986/1987 and 1992/1993. Sample sizes are indicated above the month starting with the 1986/1987 samples

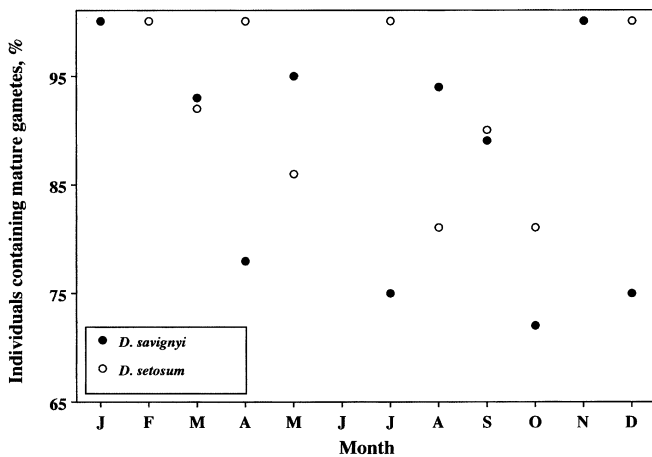
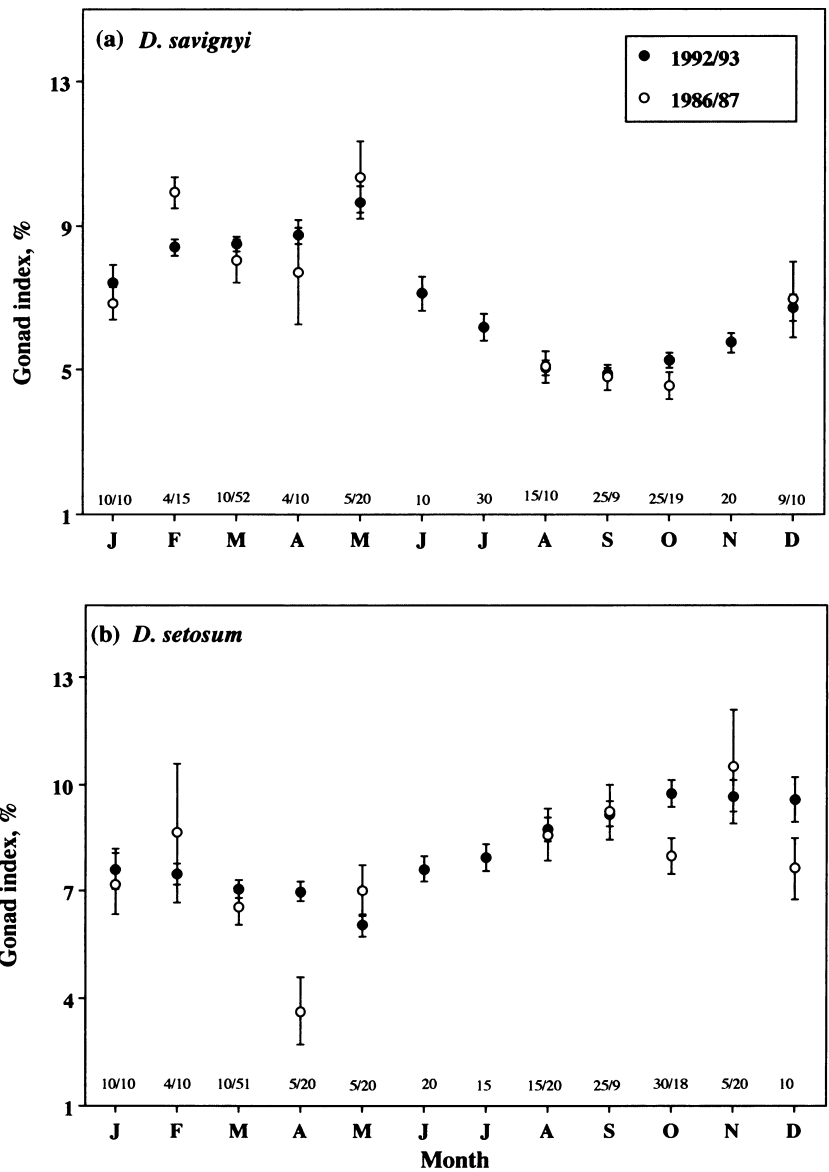


Fig. 3 Frequency of individuals of *D. savignyi* and *D. setosum* in each monthly sample with gonads containing mature gametes (ova and sperm) that filled over 50% of the gonadal tubules at Kanamai reef, Kenya in the 1992/1993 sampling period

D. setosum on the Kenyan coast, however, reveals some seasonal influence with gonad indices showing a negative correlation with temperature and light. This suggests that factors other than temperature and light might also be important in regulating the reproductive cycle of *D. setosum* on the Kenyan coast.

The seasonal pattern for *D. savignyi* showed gradual gonad growth and rapid decline with a peak north-east monsoon reproductive period. This pattern suggests that either (1) *D. savignyi* spawns continuously and that the low gonad indices (< 5%) in some months only reflect decreased reproductive output, or (2) *D. savignyi* has an annual cycle with a peak north-east monsoon spawning period and that there is storage of mature gametes during the cooler parts of the year. Drummond (1995) reported a similar pattern for *D. savignyi* on the east coast of South Africa except that ova were present only for a short period (November–January) with spawning restricted between December and March.

Fig. 4 Monthly seawater temperatures ($^{\circ}\text{C}$) and solar radiation (MJ/m^2 per day) along the Kenyan coast. Mean seawater temperatures are averaged from samples collected at Vipingo, Kanamai, and Diani reef lagoons. Solar radiation data were compiled from the Kenya Meteorological Department Mombasa station data

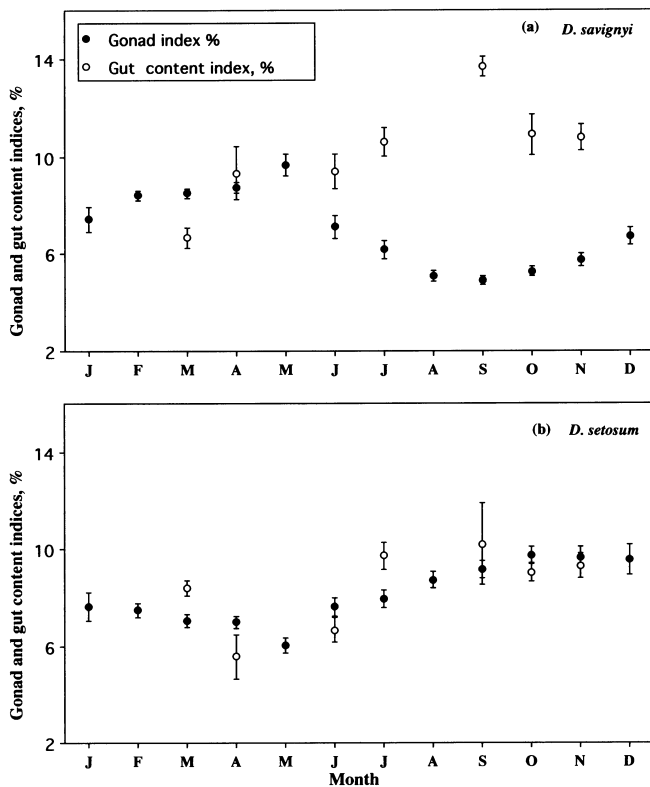
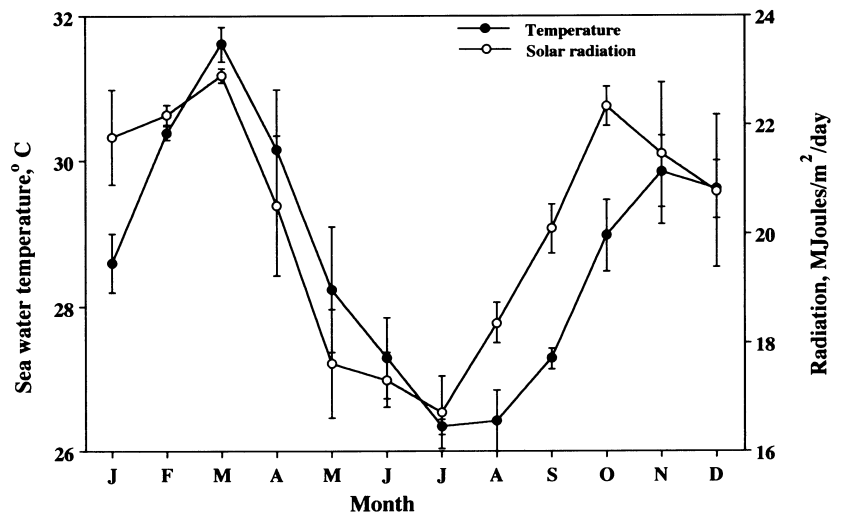


Fig. 5 Mean monthly gonad index and mean monthly gut content index for *D. savignyi* (a) and *D. setosum* (b) at Kanamai reef lagoon, Kenya

The higher reproductive output by *D. savignyi* during the north-east monsoon period is a highly adaptive strategy because this period is likely to be the most favorable time for larval survival due to higher phytoplankton concentrations (Bryceson 1982; McClanahan 1988b). Several marine invertebrate species are reported to settle just after this period in Kenya, including the sea urchins *Echinometra mathaei*, *D. setosum*, *D. savignyi*, and *Tripneustes gratilla*, starfishes, brittle stars, and sea

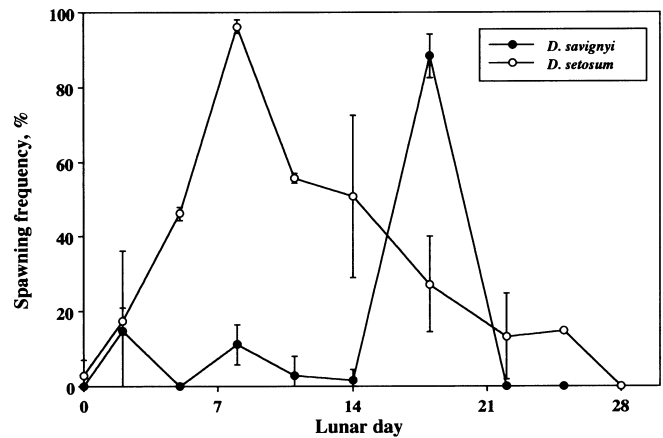


Fig. 6 The frequency of spawning after KCl injection for three lunar periods, March/April, June/July, and September/October, for *D. savignyi* and *D. setosum*. Twenty individuals of each species were induced to spawn on each sampling date. New moon corresponds to lunar day 0. Error bars are included for all samples but may be masked by the symbol

cucumbers (McClanahan and Kurtis 1991; Muthiga 1996), and oysters and barnacles (Ruwa and Polk 1994). This adds to the growing body of evidence that seasonality along the east African coast is an important influence on the reproduction of marine organisms (Bwathondi 1973; Nzioka 1979; Ntiba and Jaccarini 1990; Ruwa and Polk 1994; Muthiga 1996).

The feeding pattern in *D. savignyi* and *D. setosum* also reflects maintenance of the different reproductive strategies. *D. savignyi* exhibits seasonal changes in gut contents with higher gut contents when gonad indices are lower. This feeding periodicity may serve to allow for a period of assimilation of nutrients prior to the time of rapid gonad growth and has been shown in other echinoids including *Strongylocentrotus purpuratus* (Lawrence et al. 1965). As expected, *D. setosum* does not exhibit a feeding periodicity, suggesting a stable nutrient supply for reproduction throughout the year. Limited nutrient supply may have a

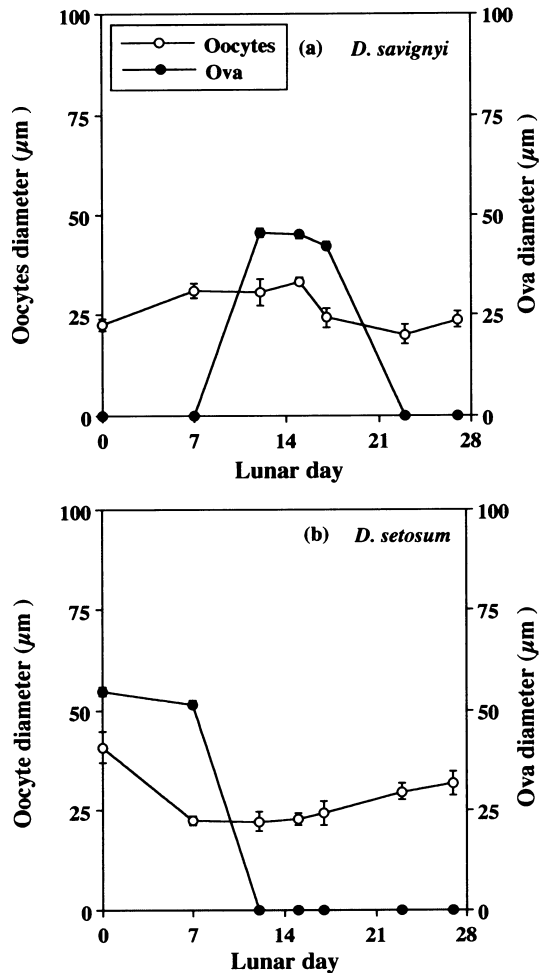


Fig. 7 The diameter (μm) of oocytes and ova for *D. savignyi* (a) and *D. setosum* (b) gonad samples in ten individuals per species collected at Kanamai reef lagoon every 2–3 days. The mean measurements for ten gonadal tubules per sample are plotted against lunar day

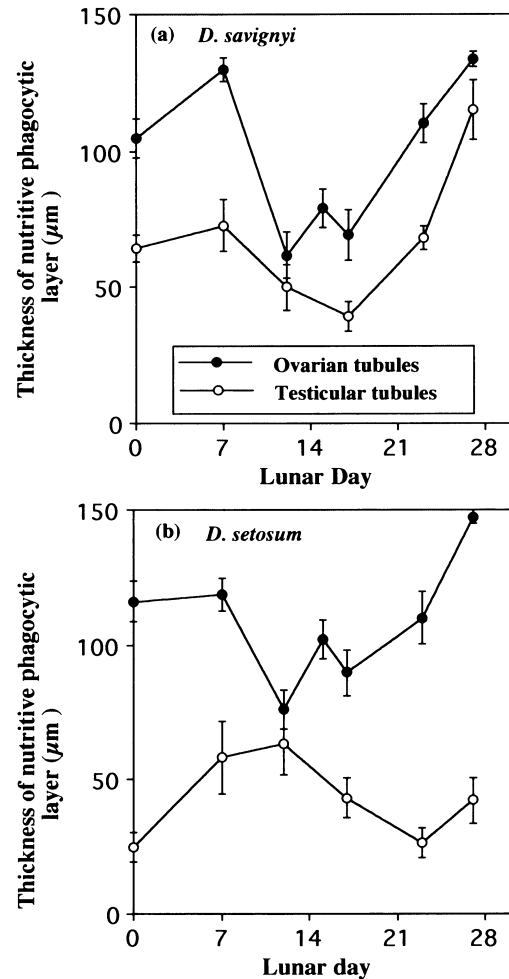


Fig. 8 The thickness of the nutritive phagocytic layer (μm) in ovarian and testicular tubules of *D. savignyi* (a) and *D. setosum* (b) in ten individuals per species collected at Kanamai reef lagoon every 2–3 days. The mean measurements for ten gonadal tubules per sample are plotted against lunar day

stronger influence on *D. savignyi* than on *D. setosum* as the latter had significantly higher organic content in the guts. *D. setosum* has been reported to feed more in the open where the supply of organic matter is presumably higher (McClanahan 1988a).

Marked differences were also observed in the monthly spawning patterns of the two species with *D. savignyi* spawning just after full moon and *D. setosum* spawning between the new moon and the last quarter. This study is the first to demonstrate monthly spawning rhythms in both *D. savignyi* and *D. setosum* on the Kenyan coast. In both species gametogenesis is tightly synchronized and commences almost immediately after spawning, as indicated by the lack of completely empty gonads in either species and the presence of small oocytes in all stages of gonadal development. Tightly synchronized gametogenesis within a population is common in Diadematidae including *D. setosum* (Pearse 1968, 1970), *D. savignyi* (Drummond 1995), and *Centrostephanus coronatus* (Kennedy and Pearse 1975).

Monthly spawning has been reported in several other urchin species (Pearse 1972; Bauer 1976; Iliffe and Pearse 1982; Lessios 1991) and is thought to be controlled by changes in moonlight and/or changes in tidal cycles (Korringa 1947; Pearse 1972). Drummond (1995), with limited samples, inferred that *D. savignyi* probably has a monthly spawning rhythm in a South African population with spawning occurring just after full moon, and Pearse (personal communication) also indicated that *D. savignyi* samples collected in Guam, Madang, Moorea, and Samoa all had sperm and ova a few days around full moon with spawning occurring a few days after full moon. The present study reinforces these findings as *D. savignyi* showed tightly synchronized spawning occurring just after the full moon, which suggests that individuals are probably responding to a common cue. Moonlight could act as a reliable cue for spawning, but experimental testing is required to elaborate the influence of moonlight on spawning activity in *D. savignyi*.

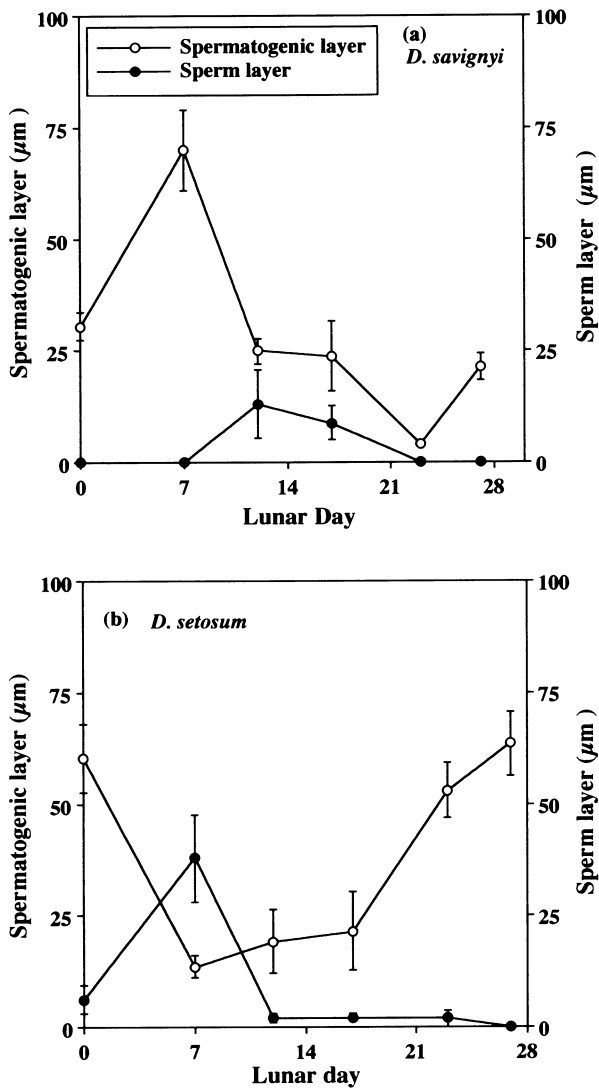


Fig. 9 The thickness (μm) of the spermatogenic layer and the sperm layer in male gonads of *D. savignyi* (a) and *D. setosum* (b) in ten individuals per species collected at Kanamai reef lagoon every 2–3 days. The mean measurements for ten gonadal tubules per sample are plotted against lunar day

The factors affecting the monthly spawning behavior of *D. setosum*, however, are less clear because it spawns at different phases of the moon (including full moon: Yoshida 1952; Pearse 1972 and both full and new moon: Fox 1924; Kobayashi and Nakumura 1967) and in some cases failed to show a lunar spawning pattern (Stephenson 1934; Mortensen 1937; Pearse 1968, 1970). Pearse (1972) suggested that reproductive patterns in *D. setosum* and *C. coronatus* could be explained by changes in tidal rhythms and this could be the case in Kenya since spawning occurred between new moon and the last quarter, which usually coincides with the switch from spring to neap tides on the Kenyan coast. This possibility has not been examined in this study, however, and the exact mechanisms remains obscure without experimentation. An alternative hypothesis would be that the presence of a sympatric species influences monthly

spawning in *D. setosum* and would require comparisons between populations that coexist and populations of single species.

D. savignyi and *D. setosum* are the only sympatric species of the genus *Diadema*. In East Africa, these species co-occur in mixed groups (McClanahan 1988a), increasing the chances of cross-fertilization. The observation of rare adults with combined features of the two species and genetic analysis that shows low levels of mixing (Lessios and Pearse 1996) suggest that hybridization is not impossible. How then do these closely related species coexist as separate species?

McClanahan (1988a) hypothesized that morphological and behavioral differences allowed the partitioning of space between these two species with *D. savignyi* being the top competitor for space. The present study demonstrates that temporal reproductive isolation is also a likely factor in maintaining these two species. Temporal separation of reproductive cycles has been reported in other marine invertebrates species including the sea urchin *D. mexicanum* (Lessios 1984) and the brittlestars *Amphiura chiajei* and *A. filiformis* (Thorson 1946). Additionally, the two species have peak reproductive outputs at different times of the year, which further decreases the chances of cross-fertilization and maintains isolation between these sympatric species. Other pre- or post-zygotic mechanisms may further insure against hybridization but have not been evaluated for these species.

Reproductive periodicity in marine invertebrates serves to allow individuals of a population (1) to take advantage of the best time of the year to produce young and (2) to synchronize spawning, thus increasing reproductive success (Lessios 1981). On the Kenyan coast, *D. savignyi* take advantage of both of these strategies and this may also serve to increase its success in East Africa. *D. savignyi* is the most abundant *Diadema* species in Kenya and Tanzania, and this dominance has remained over time in sites studied for more than 10 years (T.R. McClanahan, unpublished data). *D. savignyi* has a smaller body size and smaller gonad size than *D. setosum*. Body size is especially critical in echinoids because the amount of space available for gonad development is limited. Larger urchins are expected to have a higher reproductive effort and by extension a higher reproductive success than smaller urchins (Levitani 1991). However, the smaller *D. savignyi* is able to dominate possibly because it has a more successful reproductive strategy than *D. setosum*, where emphasis is on greater reproductive synchrony and high reproductive output during the period most favorable for larval development.

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