UNIVERSITY OF NAIROBI

THE ROLE OF EARLY LIFE HISTORY STRATEGIES ON THE POPULATION DYNAMICS OF THE SEA URCHIN *ECHINOMETRA MATHAEI* (de BLAINVILLE) ON REEFS IN KENYA

By

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A DISSERTATION

Submitted to the Zoology Department, College of Biological
and Physical Sciences, University of Nairobi
in partial fulfillment of the requirements for the degree of
Doctor of Philosophy

Mombasa, Kenya June, 1996

Declaration.

I, Muthiga, Nyawira, A., do hereby declare that this dissertation is my original work and to the best of my knowledge has not been presented to any other university for any academic honours or otherwise

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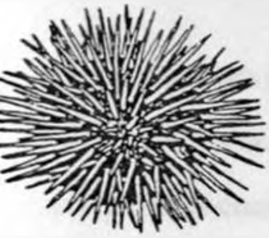
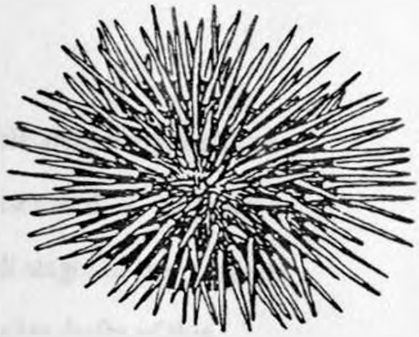
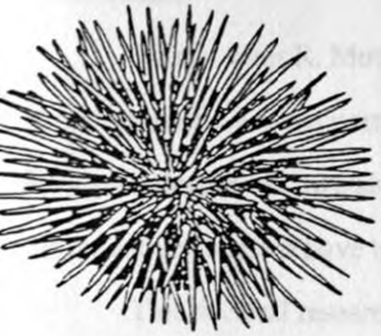
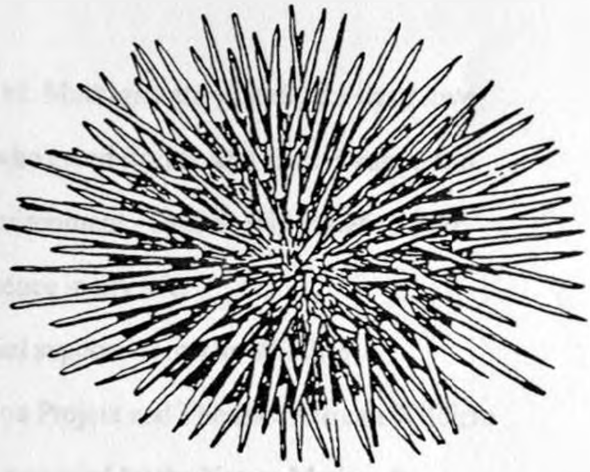


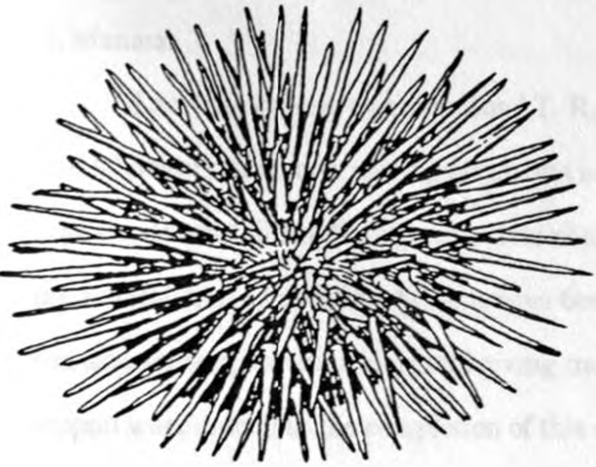
Dedication

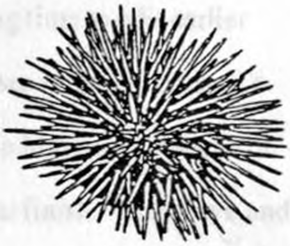


To Tim and Robert
for giving added meaning to my life









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ABSTRACT

Sea urchins are marine benthic invertebrates that are dominant grazers in a wide range of habitats in tropical and temperate environments. Their grazing activities have major biological and geological effects on coral reefs, sea grass beds, and kelp forests (Lawrence, 1975; Estes *et al.*, 1978; Lawrence and Sammarco, 1982; Carpenter, 1986; Lessios, 1988; McClanahan and Muthiga, 1988; Watanabe and Harrold, 1991). The sea urchin, *Echinometra mathaei*, the world's most abundant sea urchin, (Palumbi and Metz, 1991) is a common inhabitant of reef lagoons, reef flats and back-reef rocky shores and fringing reefs along the east African coast (Khamala, 1971; Herring, 1972; Ruwa, 1984; Muthiga and McClanahan, 1987).

Recent studies have shown that the population of *E. mathaei* is increasing on Kenya's fished reefs. The increase in *E. mathaei* is due to a reduction in the numbers of its predators as a result of overfishing (Muthiga and McClanahan, 1987; McClanahan and Shafir, 1990; McClanahan and Kurtis, 1991). Increased densities of *E. mathaei* result in increased bioerosion leading to reduced topographic complexity, reduced species diversity and decreased fisheries productivity. Understanding the factors that control the population density of *E. mathaei* is therefore crucial to the conservation and sustainable utilization of Kenyan coral reefs. This study provides information on important aspects of the population biology of *E. mathaei* including reproduction, recruitment and growth and the factors affecting these life history strategies.

The reproductive pattern of *E. mathaei* on the Kenyan coast and the influence of seasonality on this pattern is detailed in Chapter 2. The east coast of Africa experiences strong seasonality due to monsoons. This monsoonal seasonality allows for the testing of the effects of seasonally changing environmental factors on the reproductive activity of a tropical marine invertebrate. Results showed that on Kenyan reefs, *E. mathaei* has a seasonal reproductive pattern with gametogenesis beginning in July - August and spawning activity peaking in March-April. This pattern was similar to the reproductive

patterns of *E. mathaei* in Japan and the Gulf of Suez except that spawning occurred in the summer months in these areas (Pearse, 1969; Arakaki and Uehera, 1991).

The reproductive activity of *E. mathaei* on the east African coast was found to be highly correlated with temperature and light which also followed a similar seasonal pattern. Temperature however was not considered to be the important cue for the onset of gametogenesis. This is because minimum temperatures on East African reefs are above the critical temperature for the onset of gametogenesis for *E. mathaei* elsewhere in its distribution. Light may have an influence on reproduction in *E. mathaei* but the mechanism by which light controls gametogenesis in *E. mathaei* was not explored in this study.

Reproduction in *E. mathaei* also correlated significantly with chlorophyll **a** concentrations offset by one month. This suggests that spawning in *E. mathaei* is timed to occur sometime prior to the phytoplankton peak which would ensure adequate food availability for the feeding larvae. Spawning in sea urchins has previously been shown to coincide with the spring phytoplankton bloom in temperate environments (Himmelman, 1980). The results of this study indicate that although environmental parameters on the east coast of Africa may not vary with as great a range as in temperate environments, temperature, light and chlorophyll concentrations all peak near the same time of the year. The combined effects of these factors would act as an ultimate cause of seasonal reproductive behavior in this region.

The reproductive strategy of *E. mathaei* is further explored by a detailed study of the fecundity and egg sizes of different populations on Kenyan reef lagoons (Chapter 3). The results indicate that *E. mathaei* produced significantly more eggs at Vipingo, the reef with the highest food availability which is consistent with the classic allocation model (Gadgil and Bossert, 1970). Fecundity however, fluctuated from year to year probably as a response to fluctuations in food availability. Maternal size was a good predictor of parental investment at Vipingo where larger urchins tended to have a higher fecundity but not at Diani or Kanamai. Contrary to expectations, *E. mathaei* at Diani allocated more resources to reproduction despite food limitation. This was achieved at the expense of body size - an appropriate adaptation to food limitation (Thompson, 1982).

Egg size is another common parameter used to gauge parental investment. The diameter of *E. mathaei* eggs however did not show any relationship with fecundity which is contrary to life-history models that predict the production of large numbers of small eggs or small numbers of large eggs (Vance, 1972, 1973; Roff, 1992). Moreover, egg diameter showed no relationship with maternal size further indicating that egg size was not a good predictor of maternal investment in *E. mathaei*. Similar studies on other echinoderm species have shown no relationship between maternal and egg size (McEdward and Carson 1987; Lessios 1987) although George (1994) showed the opposite in a brooding starfish.

E. mathaei like most marine benthic invertebrates has a planktonic stage and a sessile benthic stage. A study of its recruitment patterns and the factors that control recruitment are key to understanding the processes that control the abundance and distribution of this widespread sea urchin. A detailed study of the recruitment of *E. mathaei* is described in Chapter 4. Results indicate that *E. mathaei* recruits to the reef on an annual basis at the end of the northeast monsoon period (April-May) on the Kenyan coast. Recruitment is closely linked to reproductive activity of the local population with the earliest recruits appearing on the substrate 1 to 2 months after the peak spawning period.

The argument is made that because other marine invertebrates (oyster, barnacles, starfish and brittle stars) have been shown to recruit during this time (van Someren and Whitehead, 1961; Ruwa and Polk, 1994), this period is an ideal time for recruitment for marine invertebrates in Kenyan waters. Moreover because similar environmental conditions occur along the east coast of Africa (except in southern Mozambique and off Somalia where upwelling occurs) it is suggested that this pattern may be a common phenomenon for *E. mathaei* all along the east African coast. The presence of *E. mathaei* larvae settling late in the season in Kenyan waters, indicates a non-local source of larvae. Although the source of this late larvae was not known, dispersal over long distances is probably the mechanism allowing *E. mathaei* to be so widely distributed.

Recruitment of *E. mathaei* was variable both temporally and spatially, showing no relationship with temperature, rainfall or fecundity of the local population. This is common in echinoderms (Ebert, 1983). Recruitment showed a significant relationship with chlorophyll **a** concentrations indicating that increased food for the larvae was an important factor in the strength of recruitment in *E. mathaei*. This has been shown in other marine invertebrates including sea urchins (Himmelman, 1980; Starr, 1990; Starr *et al.*, 1991).

Even in an exceptional recruitment year, adult population density was not affected by recruitment. This indicates that recruitment has little effect on the regulation of *E. mathaei* population. Predation on juveniles and adults were strongly correlated and had a much stronger influence on the population density of *E. mathaei* than recruitment (McClanahan and Kurtis, 1991).

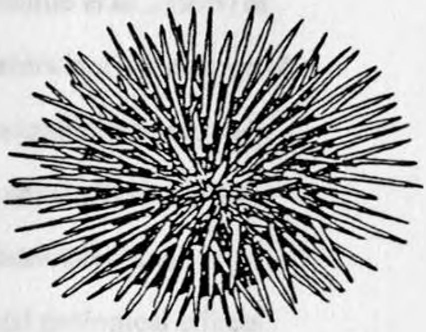
In Chapter 5, the morphology of *E. mathaei* from different populations and the allocation of resources to different body parts is described. These data will be valuable for comparative studies of *E. mathaei* in the western Indian Ocean region. *E. mathaei* appears to be well adapted to living under different conditions of food availability. When food is abundant, urchins are large, have larger stomachs and high fecundity - such as urchins at Vipingo. When food is scarce, more resources are allocated to the food gathering apparatus (by growing relatively larger jaws) - such as urchins at Diani. *E. mathaei* also allocates more resources to reproduction at the expense of body size - an appropriate adaptation under food limitation.

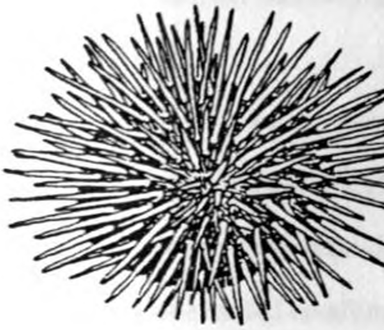
An important hypothesis in population biology is that within a species a larger body size translates to greater reproductive success (Williams, 1975; Brown 1985) thus urchins at Vipingo should be the most reproductively successful. Population density however has a strong influence on reproductive success because fertilization is dependent on a minimum distance between spawning individuals. Using Levitan's (1991) model that takes into consideration population density, maternal size and fecundity, urchins living in high population densities were estimated to produce more offspring despite smaller maternal size. Body size was therefore not a good predictor of reproductive success in *E. mathaei*. Results also indicate that *E. mathaei* in East Africa had similar growth rates to other Echinometridae in Hawaii. There are no comparative growth data for *E. mathaei* in the western Indian Ocean region.

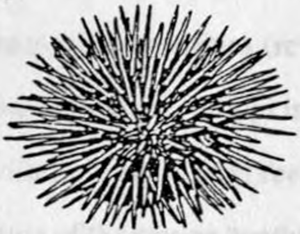
The dominance and abundance of *E. mathaei* in the reefs of Kenya and its strong population control by predatory fishes makes it an important indicator species of fishing effects and other disturbances to coral reefs. It is hoped that the information complied in this dissertation will be used by scientists, fisheries and protected areas managers to gauge the health of reefs. Symptoms of degraded reefs including low fecundity, small body sizes and relatively large jaws of *E. mathaei* should assist in developing informed fisheries and protected area management plans.

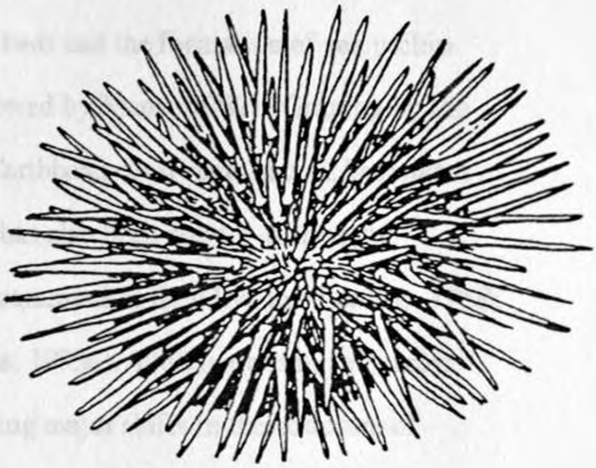
CHAPTER ONE

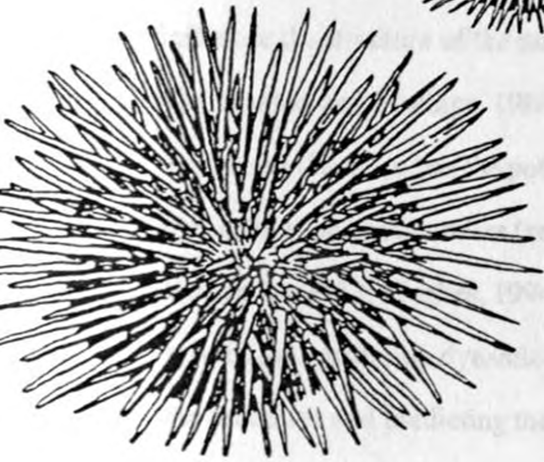
General Introduction

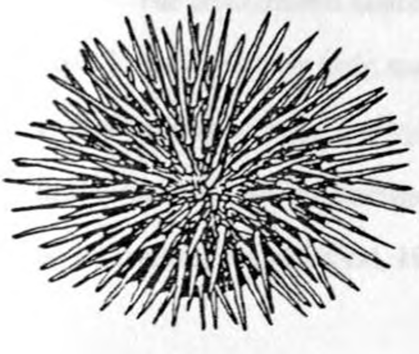


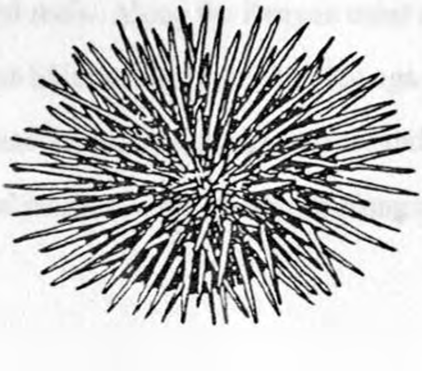












INTRODUCTION

Sea urchins belong to an ancient group (600 million years; Doolittle *et al*., 1996) of marine invertebrates the Echinoderms. They are dominant grazers in a wide range of intertidal and subtidal habitats worldwide within coral reefs, seagrass beds and kelp forests. Grazing by sea urchins has major biological and geological effects on these communities. Biological effects include an alteration of the distribution and abundance of the community structure of plants and animals and geological effects include sediment production, erosion of carbonate rock and limitation of coral reef growth.

Increases in the population of the sea urchin *Strongylocentrotus droebachiensis* (Muller) off the Atlantic coast of Nova Scotia, for example, resulted in the large-scale destructive grazing of kelp beds and the formation of sea urchin dominated coralline algal communities (reviewed by Mann, 1982). Grazing by the sea urchins *Diadema antillarum* Philippi in Caribbean coral reefs and *Echinometra mathaei* (de Blainville) in East African reefs has also been shown to strongly influence the structure of the marine benthic communites they live in (Lessios, 1988; McClanahan and Muthiga, 1988; McClanahan, 1995a). Fluctuations in sea urchin abundance therefore has the potential of causing major shifts in the structure of marine benthic communities (reviewed by Lawrence, 1975 and Lawrence and Sammarco, 1982; Hughes, 1994; McClanahan, 1995a). Elucidating the factors that control the population dynamics of sea urchins is therefore crucial to understanding the processes and predicting the changes occuring in shallow water marine benthic communities.

The predominant shallow water benthic communities along the East African coast include seagrass beds, mangroves and coral reefs. Along the Kenyan coast an extensive fringing coral reef system extends from Shimoni in the south to Kiunga in the North with breaks where large rivers (Tana and Sabaki) discharge into the Indian ocean (Hamilton and Brakel, 1984). Occassional platform reefs also occur along the coast including the patch reefs at Kisite and Malindi which have been designated Marine Protected areas. The coral reef communities of the Kenyan coast play an important role in the economy and ecology of the area by supporting an important fishery and playing a crucial role in coastal tourism ((Hamilton and Brakel, 1984; McClanahan and Obura, 1995). Kenya's coral reefs however, are vulnerable to many human impacts including overfishing.

Overfishing not only causes a reduction in fisheries productivity, but has also been implicated in the Caribbean and in Kenya in causing a shift in community structure from finfish to the sea urchin grazers, *D. antillarum* and *E. mathaei* (Hay, 1984; McClanahan and Shafir, 1990; McClanahan *et al*., 1994). Recent studies on the population structure of *E. mathaei* on Kenyan reefs, have shown that the density of this sea urchin is high on heavily fished reefs and the numbers are increasing (Muthiga and McClanahan, 1987; McClanahan and Kurtis, 1991). Studies have also shown that predation rates on *E. mathaei* are highest on protected reefs where its triggerfish predators occur in the highest numbers and the rate is lowest on heavily fished reefs (McClanahan and Shafir, 1990). Predation by finfish especially the triggerfish *Balistapus undulatus* (Park) plays an important role in the population regulation of *E. mathaei* (McClanahan and Kurtis,1991; McClanahan, 1995b). *E. mathaei* has also been shown to be the top competitor for space among the commonly occurring sea urchins (McClanahan, 1988a) allowing it to dominate if its predators and competitors are removed by fishing.

Increased densities of *E. mathaei* result in increased bioerosion which leads to decreased reef topographic complexity. This in turn results in lowered species diversity and decreased fisheries productivity. Decreased topographic complexity also results in lowered shoreline protection with the subsequent increase in beach erosion and loss of earnings from tourism. *E. mathaei* is therefore an important key species that can be used as an indicator of the health of coral reefs in East Africa.

Although predation has been shown to be an important factor in the control of *E. mathaei* population densities on Kenyan reefs, information on other aspects of its life history strategies is lacking. A key element in the understanding of population regulation is recruitment (Ebert, 1983; Connell and Keough, 1985; Roughgarden *et al.*, 1988). Patterns of growth and reproductive activity are also factors that are crucial to the understanding of the population dynamics of sea urchins. No information is available on any of these aspects for *E. mathaei* on the east African coast. Therefore in order to validate the importance of predation as the main factor controlling *E. mathaei* populations in East Africa, the influence of other factors especially recruitment, must be tested. The aim of the present work was to study aspects of the early life history strategies of *E. mathaei* including patterns of reproduction, recruitment and growth and the influence of seasonality and population density on these life history characteristics.

Distribution and Taxonomy of *Echinometra mathaei*

Echinometra mathaei is a regular sea urchin species belonging to the family *Echinometridae*. Although two species of Echinometra were originally described by de Blainville (de Blainville, 1825, in Palumbi and Metz, 1991), subsequent morphological studies of the adults and larvae led to the conclusion that only one species *E. mathaei* exists in the Indo-Pacific (Mortensen, 1943). However this species is currently under review using molecular techniques by Palumbi and Uehara (pers. Comm).

The sea urchin *E. mathaei* has been described as the world's most abundant sea urchin (Palumbi and Metz, 1991) inhabiting a wide range of intertidal and subtidal habitats including reef lagoons, reef crests, back reef and reef edge habitats worldwide. This sea urchin is one of the most widely distributed echinoids in the Indo-Pacific (Mortensen, 1943; Clark and Rowe, 1971) ranging from Mexico in the east, to East Africa and the Red sea in the west and from central Japan in the north to South Western Australia in the south (Mortensen, 1943; Clark and Rowe, 1971;

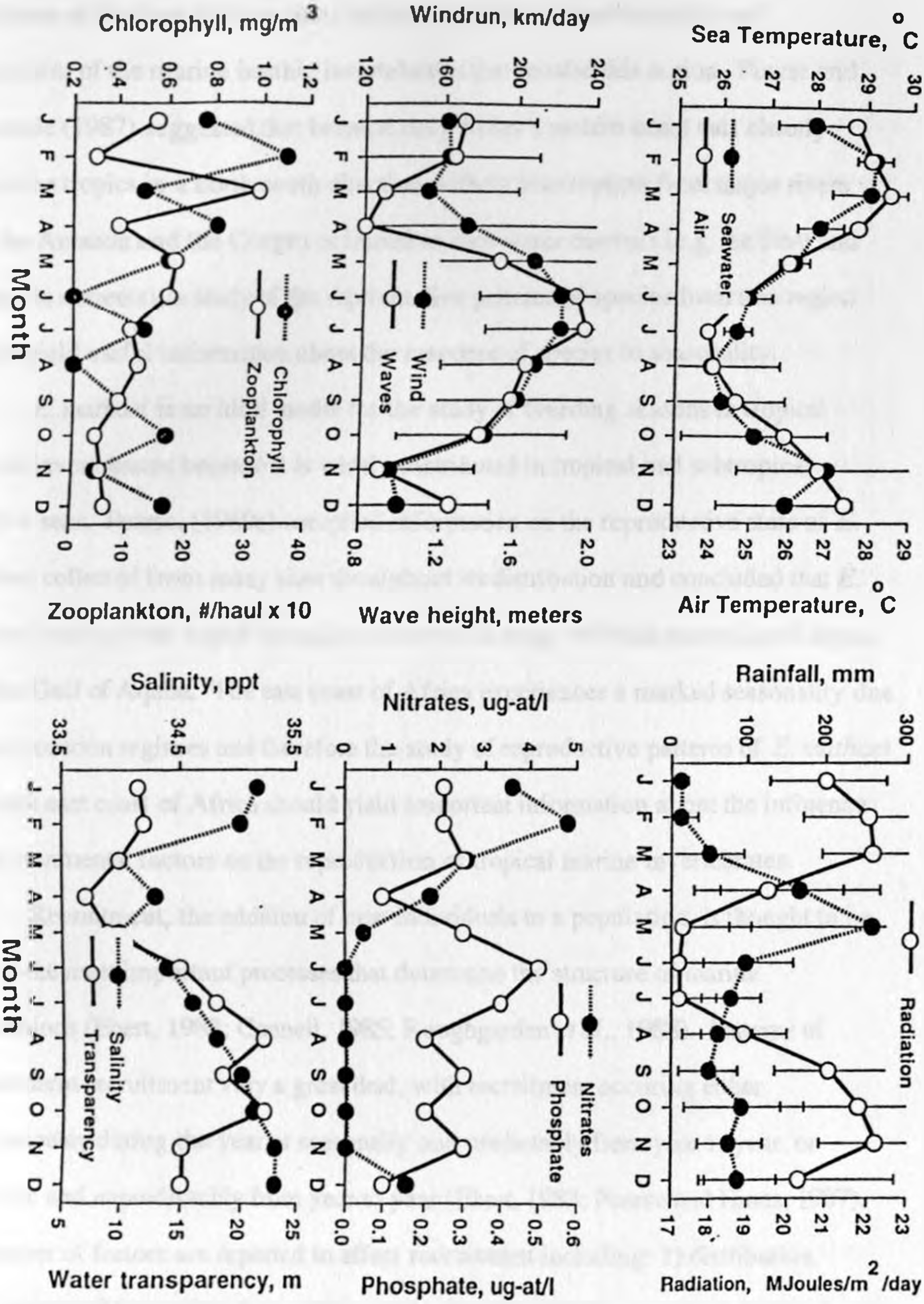
Clark, 1925 in Palumbi and Metz, 1991). *E. mathaei* is a common inhabitant of reef lagoons, reef flats, back reef rocky shores and fringing reef edges along the East African coast (Khamala, 1971; Herring 1972; Ruwa, 1984; Muthiga and McClanahan, 1987).

E. mathaei has many color variants ranging from black to pastel pink and morphological variants which in Okinawa and Hawaii are seperated into four types (Uehara *et al*., 1986). Although *E. mathaei* also has a wide range of colors in East Africa ranging from maroon to pale purple no taxonomic or morphological types have been described in this region (Clark and Rowe, 1971).

Seasonality of the East African coast

The climate and oceanographic conditions of East Africa follow a monsoonal cycle driven by the north-south migration of the Inter-tropical Convergence Zone (ITCZ). Two main seasons, the north-east monsoons (NEM) and the south-east monsoons (SEM), occur along this coast characterised by marked differences in physical and biological oceanographic conditions (Fig. 1.1). During the NEM (October to March), winds are light allowing for water column stratification; temperatures are warmer therefore productivity is higher than during the SEM (higher phytoplankton and zooplankton abundance) and lower benthic algal biomass (Bryceson, 1982, McClanahan, 1988). The inshore currents move southwards along the coast during this time. During the SEM (April - September), conditions are opposite of the NEM with high winds, lowered temperatures, reduced phytoplankton and zooplankton abundance and higher benthic algal biomass.

Figure. 1.1. Physical, chemical and biological parameters of the East African coast. Adapted from McClanahan and Young, 1996.



Sea Temperature, °C
Air Temperature, °C
Seawater
Air
Windrun, km/day
Wave height, meters
Wind
Waves
Chlorophyll, mg/m³
Zooplankton, #/haul x 10
Chlorophyll
Zooplankton
Rainfall, mm
Radiation, MJoules/m² /day
Rainfall
Radiation
Nitrates, ug-at/l
Phosphate, ug-at/l
Nitrates
Phosphate
Salinity, ppt
Water transparency, m
Salinity
Transparency
Month
J F M A M J J A S O N D

Reproduction, Recruitment and Population regulation

It is not known whether the seasonal nature of the climatic and oceanographic conditions of the East African coast influence patterns of reproduction and recruitment of the marine benthic invertebrates that inhabit this region. Pearse and Barksdale (1987) suggested that because only Africa's eastern coast cuts cleanly across the tropics in a north-south direction without interruption from major rivers (i.e. the Amazon and the Congo) or intrusive cool-water currents (e.g. the Peru and Benguela currents), a study of the reproductive patterns of species from this region would yield useful information about the response of species to seasonality.

E. mathaei is an ideal model for the study of breeding seasons in tropical marine invertebrates because it is widely distributed in tropical and subtropical shallow seas. Pearse, (1969a) compiled information on the reproductive state of *E. mathaei* collected from many sites throughout its distribution and concluded that *E. mathaei* spawns year round throughout most of its range with the exception of Japan and the Gulf of Aqaba. The east coast of Africa experiences a marked seasonality due to the monsoon regimes and therefore the study of reproductive patterns of *E. mathaei* from the east coast of Africa should yield important information about the influence of environmental factors on the reproduction of tropical marine invertebrates.

Recruitment, the addition of new individuals to a population, is thought to be one of the most important processes that determine the structure of marine populations (Ebert, 1983; Connell, 1985; Roughgarden *et al*., 1988). Patterns of echinoderm recruitment vary a great deal, with recruitment occuring either continuously during the year.or seasonally and predictably from year to year, or episodic and unpredictably from year to year (Ebert, 1983; Pearse and Hines, 1987). A number of factors are reported to affect recruitment including: 1) distribution, abundance and fecundity of sexually matur individuals, 2) the chemical, physical and biological oceaographic conditions during the planktonic larval stage and 3) larval settling preferences (Ebert, 1983, Eckman, 1983). After settlement other factors including predation and competive interactions, food availability, shelter and other resources determine the survival of the recruits (Shulman, 1985). There is little information on the patterns of recruitment and the factors that influence these patterns for marine invertebrates on the east coast of Africa.

How and whether recruitment affects the population dynamics of a population is a question of much debate among marine ecologists. One view point is that benthic populations are regulated by competition for limited resources and hence recruitment affects the extent to which resources are available (Keough, 1988). Recent studies have provided support for a second viewpoint emphasizing the importance of variable factors such as seasonal availability of larvae rather than competition or predation (Doherty, 1982, 1983; Doherty and Williams, 1988; Sale, 1988). If this is the case for *E. mathaei*, then recruitment should not show a density-dependent effect but should reflect seasonal differences in larval availability. McClanahan and Kurtis (1991) showed that recruit densities were similar at different reefs in Kenya. They argue that processes that affect recruits prior to settlement may be important in understanding the population dynamics of *E. mathaei*. Further work is therefore required to determine the contribution of settlement and post-settlement processes and their effect on sea urchin biomass and population dynamics. The fact that *E. mathaei* occurs in different densities on reefs that are similar in structure in Kenya, also allows us to test the influence of population density on recruitment and reproduction of this widespread and important species.

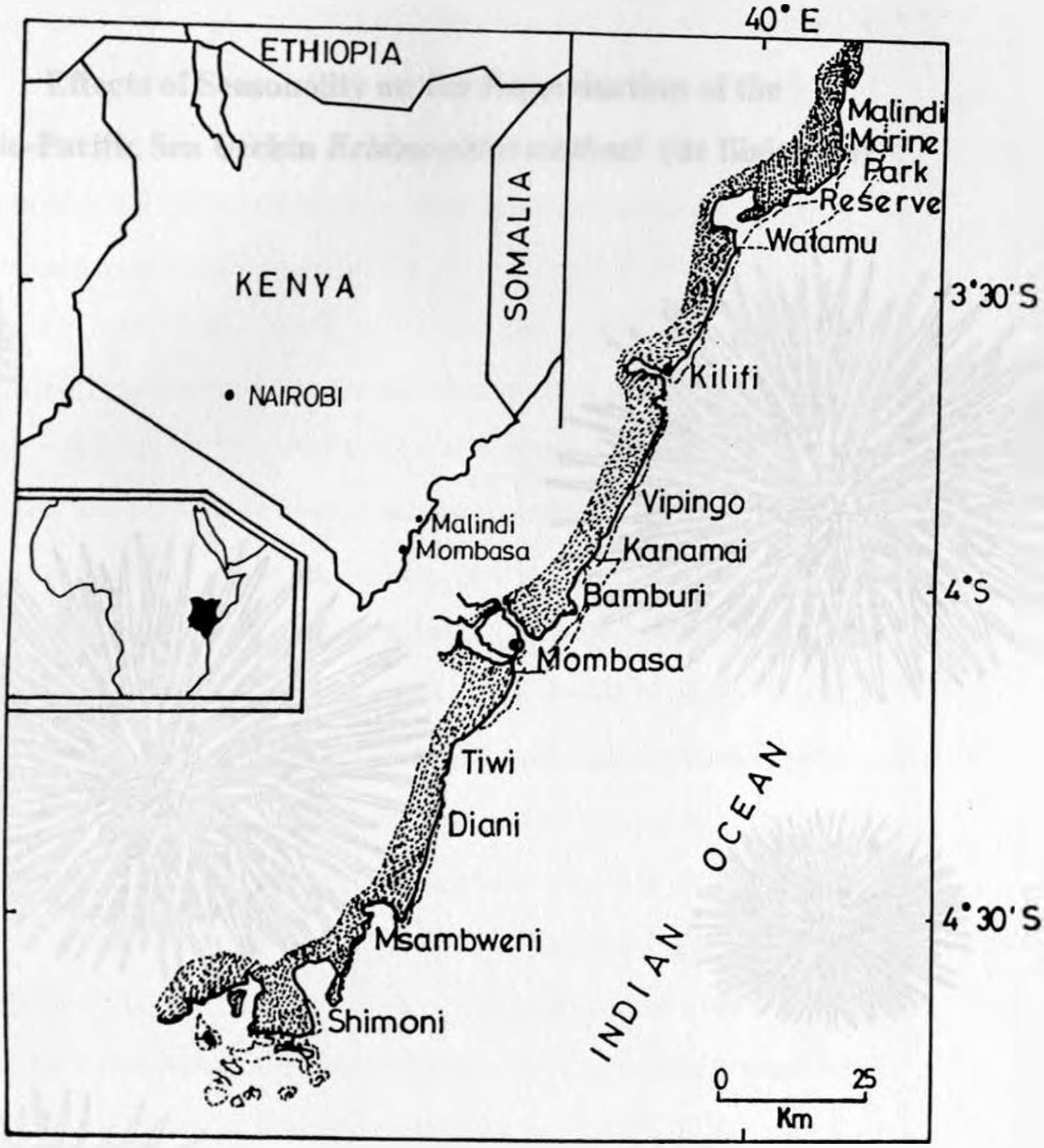
Description of the Study sites

The study was conducted at three reef, Diani, Kanamai and Vipingo on the Kenyan coast (Fig. 1.2). Previous descriptions of Kenya's coral reefs and these study sites include Khamala (1971), Hamilton and Brakel (1984), McClanahan and Muthiga (1988). The Kenyan coastline is dominated by a fringing reef system that is similar in structure and faunal composition to reefs in the central and western Indian ocean (Rosen, 1971; Hamilton and Brakel, 1984). The fringing and platform reefs have an algal covered reef crest that is usually exposed during low tides. Within the leeward lagoons, corals of the genus *Porites*, *Stylophora* and seagrass communities of the genus *Thalassia* dominate. On the windward reef edge coral cover is usually dominated by the genus *Porites* and *Acropora*.

Studies were conducted on the sheltered leeward side of the fringing reefs at Diani, Kanamai and Vipingo. These three reefs were selected because of the similarities in the topographical and community structure (McClanahan and Shafir, 1990) and also because data on population density were available from previous studies (Muthiga and McClanahan, 1987; McClanahan and Muthiga, 1988; McClanahan and Shafir, 1990; McClanahan and Kurtis, 1991). Kanamai and Vipingo lie north of the Mtwapa creek, and Diani south of the Tudor creek.

These three reefs also differ in the intensity of fishing, the density of development on the adjacent shores and the density of *E. mathaei*. Diani has the highest density of urchins followed by Kanamai and Vipingo (Muthiga and McClanahan, 1988; McClanahan and Shafir, 1990). Diani beach is also the most highly developed and is the most intensely fished.

Figure. 1.2. Map of the Kenyan coast showing the locations of the study. Study sites were situated within the reef lagoons of Diani, Kanamai and Vipingo.


40° E
ETHIOPIA
SOMALIA
KENYA
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Mombasa
Malindi
Marine
Park
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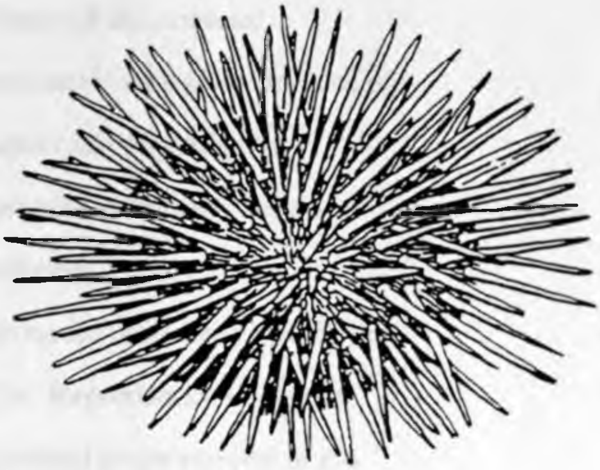
25
Km

CHAPTER TWO

Effects of Seasonality on the Reproduction of the Indo-Pacific Sea Urchin *Echinometra mathaei* (de Blainville)



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. Restricted breeding periods probably result from natural selection for times when the probability of survival of the offspring is highest (Giese and Pearse. 1974). The seasonal availability of food for the planktonic offspring of shallow water marine benthic invertebrates is therefore an ultimate cause of this seasonal reproductive behavior and is usually linked in temperate environments to times of the year (Spring and Summer) when temperatures are warmer and phytoplankton concentrations are higher. The ultimate causes of seasonal reproductive behavior have received less attention for tropical marine invertebrates.

The proximate causes of seasonal reproduction on the other hand include the specific factors that cue seasonal reproductive behavior. Reproduction in marine invertebrates involves two processes whose timing is critical to the survival of the organism. The onset of gametogenesis that starts the whole reproductive process, and the release of gametes (spawning) prior to fertilization. The timing of these two processes maybe cued by several factors acting separately or in synergy. Three main hypothesis have been suggested as explanations for the factors that regulate and control the timing of gametogenesis and spawning in marine invertebrates 1) physiological thresholds of environmental temperature 2) seasonally changing photoperiod 3) seasonal changes in pytoplankton concentration.

The environmental factor that has received a great deal of interest is sea temperature. The importance of temperature as a controlling factor in reproduction was first articulated by Orton (1920). He observed that many marine invertebrates in temperate waters have a restricted breeding and spawning period often corresponding to a particular temperature level. He proposed the idea that gametogenesis will not start below a certain level of temperature for many marine species and that this temperature appears to be a physiological constant for the species (Orton's Rule, Thorson, 1946). He went further to suggest that in thermally stable environments for example in the tropics marine organisms should breed year round.

Reviews of studies of reproductive cycles of both temperate and tropical species show that although temperature was an important factor, several exceptions and modifying factors to Orton's Rule could be found (Giese, 1959; Pearse, 1968; Giese and Pearse, 1974; and Pearse, 1974). Breeding seasons of species with wide geographical distribution, for example, could vary considerably generally being restricted in temperate regions and more continuous in the tropics, as shown in the sea urchins *Echinometra mathaei* (Pearse, 1968, 1969a), *Diadema setosum* (Leske) (Pearse, 1970) and *Tripneustes gratilla* (Linnaeus) (Chang-Po and Kun-Hsiung, 1981). In these cases, the temperature that stimulates gametogenesis may have a lower minimum threshold (in populations closer to temperate regions) but would vary in populations throughout their geographical distributions. There are also examples of tropical and deep-water species (inhabiting thermally stable environments) that have distinct breeding seasons and temperate species (inhabiting thermally variable environments) that breed continuously throughout the year (Pearse, 1968, 1969a; Giese and Pearse, 1974). Pearse *et al*. (1986) argued that gametogenesis seemed too precisely timed from place to place and year to year in many species of marine invertebrates to be determined solely by changing sea temperature.

The realization that Orton's Rule could not explain the timing of reproduction in some marine species led to the testing of other factors including photoperiod (Pearse et al. 1986). Seasonally changing photoperiod has been known to synchronize reproductive activities in terrestrial plants and animals and was suggested by Giese (1959) and Richard (1971) as a possible controlling factor in marine invertebrates. Photoperiod has a more regular and precise temporal pattern then sea temperature and hence can be a more reliable regulatory cue for synchronizing gametogenesis (Pearse et al., 1986).

On the west coast of North America where temperature changes are moderate (5-7 ^{0}C) photoperiod has been shown to regulate the timing of gametogenesis in the sea urchin *Strongylocentrotus purpuratus* (Stimpson) (Pearse *et al.*, 1986) and the sea stars *Pisaster ochraceus* (Brandt) (Pearse and Eernisse, 1982) and *Leptasterias* sp. (Pearse et al. 1986). Photoperiod has also been shown to regulate gametogenesis and pyloric caeca growth of the sea star *Asterias vulgaris* (Linnaeus) from the northeast coast of North America where temperatures range by 20 °C (Pearse and Walker, 1986).

Moreover, Pearse *et al.* (1986) argued that photoperiod may also be an important factor in other species of marine invertebrates as it was shown to regulate gametogenesis in species inhabiting environments both with highly variable and also stable temperature regimes and species with planktonic larvae (*P. ochraceus* and *A. vulgaris*) as well as a brooding species without larvae (*Leptasterias* sp.). No studies have shown a correlation between photoperiod and reproduction in the tropics. Photoperiod, however, would not be expected to be important in the tropics as daylengths show little variation throughout the year (maximum of 30 minutes).

The reproductive cycles of marine organisms culminate in spawning, and in some marine organisms, spawning may seemingly not require an external stimulus beginning spontaneously after completion of gametogenesis (Giese and Pearse, 1974). In these species the factor controlling gametogenesis is therefore the key to reproductive success. In many marine invertebrates however mature gametes are retained for a period of time before being released. In these organisms gametogenesis and spawning are probably regulated by different factors.

Many workers favour the hypothesis that physical factors such as changes in temperature, light, and turbulence are the cues that induce spawning. Evidence of spawning events in temperate and tropical environments coinciding with periods of changes of temperature, and evidence from laboratory experiments showing that sudden changes in temperature (5-10 °C) can stimulate spawning led to the conclusion that temperature was a key factor in the control of spawning (Himmelman, 1980). The correlation between such temperature changes and spawning in nature, however, has proven more difficult to establish (Giese, 1959; Himmelman, 1980).

The most recent hypothesis on the factor controlling the timing of spawning has developed from the observation that spawning in many temperate invertebrates coincides with the spring phytoplankton bloom (Himmelman, 1980). Although Thorson (1946) suggested that phytoplankton blooms might stimulate spawning in invertebrates with planktonic larvae this hypothesis has only recently been tested (Himmelman, 1980).

Himmelman (1980), Starr *et al.* (1990) and Starr *et al.* (1991) showed that phytoplankton was important in synchronizing spawning in the sea urchin *S. droebachiensis*, the chitons *Tonicella lineata* (Wood) and *T. insignis* (Linnaues) and the blue mussel *Mytilus edulis* Linnaeus. Starr *et al.*(1992) went further and extracted a substance from the diatom *Phaeodactylum tricornutum* Bohlin that induced spawning in *S. droebachiensis*. No coupling of phytoplankton and spawning has been shown for tropical species. Tropical environments, however, do not show great variability in phytoplankton concentrations and other factors may be more useful as spawning cues (Himmelman, 1980)

Other seasonal changes due to rainfall or disturbances due to storms could also lead to increased nutrients leading to increased phytoplankton and thus to spawning (Himmelman, 1980). Lessios, (1981) for example argued that spawning of *Diadema mexicanum* A Agassiz and *Echinometra vanbrunti* A. Agassiz from the Bay of Panama was timed to coincide with dry season upwelling when food was abundant for newly metamorphosed urchins rather than for larvae. The exact cue that triggers spawning to coincide with food for juveniles and not larvae is not known.

Some of the factors that control gametogenesis and spawning may act together (Giese and Pearse, 1974). Seasonal phytoplankton blooms, for example, usually correspond with warming trends (Ebert, 1983). Himmelman (1980), for example, showed that spawning was delayed by two weeks in *T. lineata* because temperatures were 1^{o}C lower at the time of the phytoplankton bloom than in previous years. He argued that the minimum temperature required for development of the larvae, or for specific processes after fertilization had not been reached by the time of the spring bloom, hence the delay in spawning. Daylength (either short days or long days) in temperate environments also corresponds to periods of low or high sea temperature and therefore may act in synergy with each other in the timing of spawning. The mechanisms involved when a number of factors act together have yet to be elucidated.

Other factors modifying the timing of spawning include population density. For example, Lessios (1981) in his study of closely related populations of sea urchins in the Bay of Panama and on the Caribbean coast, showed that the urchins in the seasonal environment synchronized their spawning with temperature being an important factor. In animals living in a constant environment, however, the intensity of synchrony was influenced by population density with a tendency for tighter synchrony in sparsely populated areas thus ensuring successful fertilization.

Most of the hypotheses about the factors controlling gametogenesis and spawning on marine invertebrates have been tested on temperate species. The paradigm that tropical environments will have organisms that breed year round is still accepted despite evidence of seasonal reproductive cycles in tropical species. As well many studies were carried out on tropical species but not in the tropics (Pearse and Barksdale, 1987). One way to explore the relationship between temperature and reproduction is to study the reproduction of a tropical species at the equator. Only the East African coast (south of the Somali upwelling region) occurs at the equator without the influence of massive rivers (e.g., the Amazon and Congo) or upwelling currents (e.g., the Peru or Benguela currents).

The East Coast of Africa has two monsoon seasons, the North East and the South East monsoons (reviewed by McClanahan, 1988) with varying oceanographic conditions of temperature, light and phytoplankton. These conditions do not vary with the magnitude of temperate latitudes and whether these have any modifying influences is not known. This area is therefore especially suitable for testing the idea that a tropical marine environment will have species that breed year round and for finding out whether the monsoon seasonality will have a modifying influence.

A good model for exploring these ideas is the sea urchin *Echinometra mathaei*. This urchin is widely distributed throughout the Indo-Pacific (described in chapter one) (Mortensen, 1943; Clark and Rowe, 1971). It is a common inhabitant of reef lagoons, reef flats, back reef rocky shores and fringing reef edges along the East African coast (Khamala, 1971; Herring 1972; Ruwa, 1984; McClanahan 1988). Pearse (1968), Pearse and Phillips (1968) and Pearse (1969a) carried out studies on reproductive cycles of *E. mathaei* and concluded that *E. mathaei* spawns year round throughout most of its range with the exception of populations in Japan, the Red Sea and the Gulf of Aqaba.

Specimen of *E. mathaei* collected at sites near the equator (Rabual, New British Islands and North East Borneo) showed no gametogenic synchrony among individuals and individual urchins matured and spawned at different times of the year (Pearse, 1968). The samples in this study (Pearse, 1968) were collected on single dates from different localities and although the results were suggestive of a continuous reproductive cycle throughout the year in some individuals at the equator, conclusive evidence of a continuous reproductive cycle in East Africa is lacking.

E. mathaei is also a useful model animal because it has been shown to have a strong influence on the community structure of reefs in East Africa (Muthiga and McClanahan, 1987; McClanahan and Kurtis, 1991). A study of the reproduction of *E. mathaei* on the Kenyan coast should provide information relevant to the reproduction of tropical species in general and the influence of seasonality on this wide ranging species in particular. Detailed analysis of the reproductive cycle of *E. mathaei* is presented in this study with a view of testing 1) whether sea temperature, light or pytoplankton concentrations have an influence on the reproductive cycle of *E. mathaei* and 2) whether other biotic factors like population density have an influence on the timing or magnitude of the reproductive output of *E. mathaei*.

MATERIALS AND METHODS

Study sites

A description of the study sites is given in Chapter 1 (Fig. 1.1). Three reef lagoons (Diani, Kanamai and Vipingo) were selected to enable a comparison of differences in reproductive behavior of *Echinometra mathaei* between populations. The three reef lagoons differ strongly in population density thereby allowing for comparisons of density dependent effects on reproduction including food availability and its influence on reproduction.

Annual maturity cycle

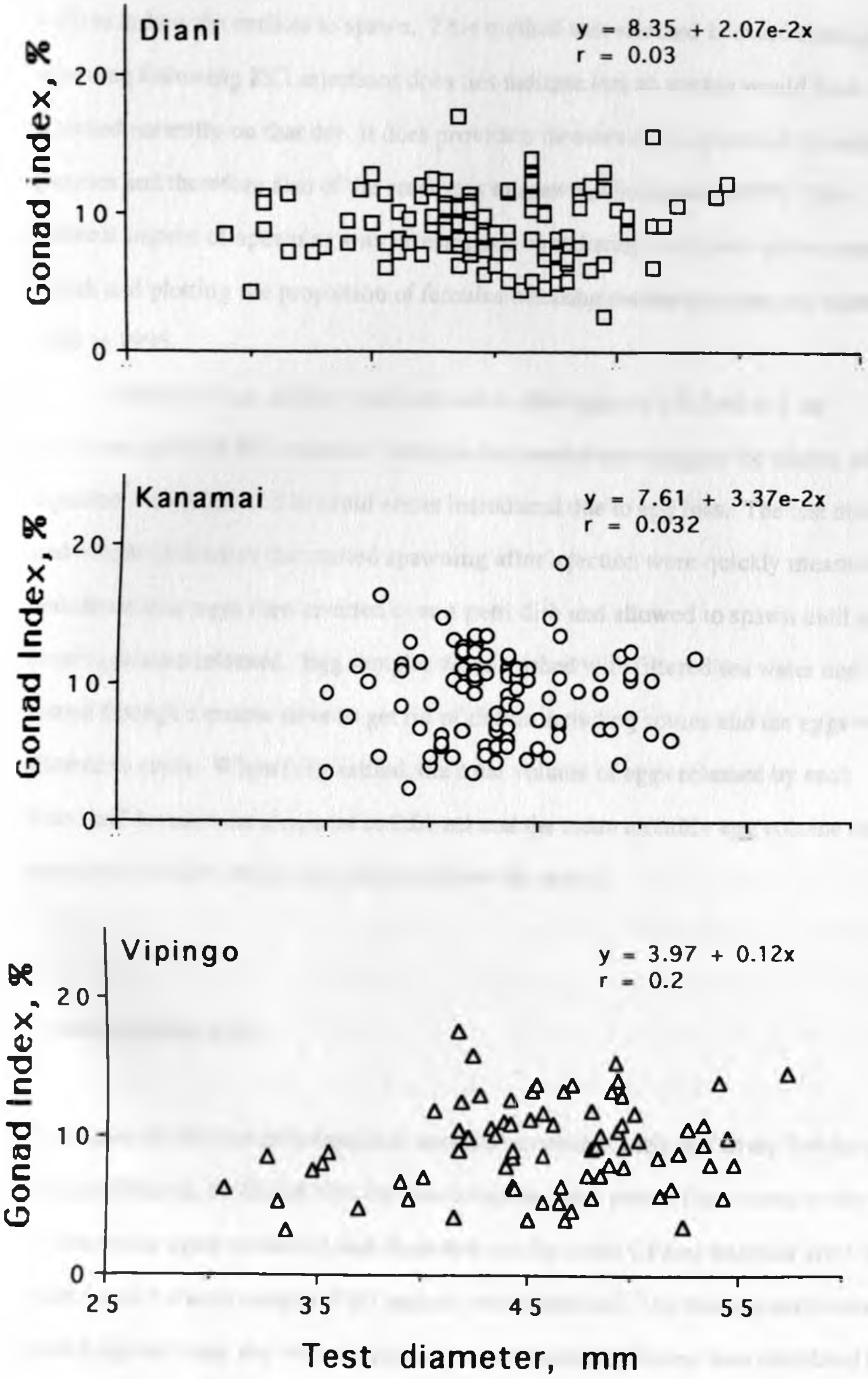
The annual reproductive pattern was investigated by haphazardly sampling 20 urchins each month from 1992 to 1994 at all three reefs. Urchins were transported to the Kenya Marine and Fisheries Research Institute (KMFRI) laboratories where they were processed in the following way: individual urchins were placed on tissue paper to drain before weighing to 0.1 gm. The test of each animal was measured with a vernier caliper to 0.1 mm across the longest and the shortest axes at the *ambitus*.. The urchins were then dissected, sexed and the perivisceral fluid allowed to drain before the gonads were removed and weighed to 0.01 gm.

Ripe male and female *E. mathaei* were easily distinguished when ripe, by the color of the gonads, males having cream colored gonads while females have orange to yellow colored gonads. Spent gonads are not easy to distinguish however since in both sexes gonads are then a uniform brown in color. Individuals with spent gonads were therefore not sexed. The Gonad Index was determined for each individual where GI = (wet gonad weight / total wet body weight) x 100. The index was used to track the reproductive state of the urchins with time. This method allows for the collection of a large amount of data with relative ease compared to histologic preparations, but has the disadvantage of yielding meaningful results only when there is no significant relationship between the GI and the size of the animal (Gonor, 1972; Grant and Tyler, 1983).

A test was therefore carried out to find out whether there was any relationship between the gonad weights and the size (using average test diameter calculated from the mean of two measurements taken at the longest and shortest axis of the test diameter) of *E. mathaei* . A correlation was calculated between the test diameter and the gonad index of 100 *E. mathaei* haphazardly selected from urchins collected on different dates at the three reefs. Plots of the gonad index of *E. mathaei* against the corresponding test diameter at each reef are shown in Fig. 2.1. There was no significant relationship between gonad index and test diameter at any of the reefs ($r = 0.03, 0.03, 0.2$; at Diani, Kanamai and Vipingo respectively, in all cases $p > 0.01$) indicating that the weight of the gonad of *E. mathaei* is not dependent on the size of the animal and is a good indicator of reproductive state and output.

The annual maturity cycle was investigated by calculating the mean monthly GI and plotting these against the month for each year at each reef. Additional data collected in 1986-87 at Kanamai by the author are also included. Temporal variation in GI at each reef was tested using a single-factor ANOVA (Sokal and Rohlf, 1981) of comparisons between years at each reef. Variation between reefs each year was tested using a two-factor ANOVA with month and reef as the factors. The magnitude of the reproductive output at each reef in different years was also tested by performing a single factor ANOVA comparison of the GI at the peak of reproductive activity between reefs in each year. The GI at the peak of reproductive activity was taken to be an indicator of the magnitude of reproductive output.

Figure. 2.1. The relationship between the test diameter and the gonad index of *Echinometra mathaei* (n = 100) sampled at the Diani, Kanamai and Vipingo reef lagoons.


Diani
y = 8.35 + 2.07e-2x
r = 0.03
Gonad index, %
20
10
0
Kanamai
y = 7.61 + 3.37e-2x
r = 0.032
Gonad Index, %
20
10
0
Vipingo
y = 3.97 + 0.12x
r = 0.2
Gonad Index, %
20
10
0
25
35
45
55
Test diameter, mm

Spawning activity was investigated by using an artificial stimulus (0.5 M KCl) to induce the urchins to spawn. This method was selected because although spawning following KCl injections does not indicate that an urchin would have spawned naturally on that day, it does provide a measure of the presence of mature gametes and therefore also of the readiness to spawn (Thompson, 1979). The seasonal pattern of spawning was investigated by inducing urchins to spawn every month and plotting the proportion of females releasing mature gametes per month in 1993 to 1995.

Individual sea urchins were induced to shed eggs by a 0.5 ml to 1 ml injections of 0.5 M KCl solution. Urchins that started spawning in the bucket prior to injection were discarded to avoid errors introduced due to egg loss. The test diameter and weight of females that started spawning after injection were quickly measured and the urchins were then inverted over a petri dish and allowed to spawn until no more eggs were released. Egg samples were washed with filtered sea water and passed through a coarse sieve to get rid of debris including spines and the eggs were allowed to settle. When fully settled, the total volume of eggs released by each individual female was measured to 0.01 ml and the mean monthly egg volume was calculated for each month and plotted against the month.

Lunar maturity cycle

Lunar periodicity was investigated in urchins sampled at each reef every 3-4 days in February/March, 1992 and 1993 for one complete lunar period (new moon = day 0). Urchins were again measured and dissected and the mean GI and standard error of the mean (sem) for each sample of 20 animals was calculated. The mean gonad index was plotted against lunar day at each reef and a correlation coefficient was calculated for each reef. Additionally, a single factor ANOVA was used to test for differences between gonad indices on different lunar days at each reef.

The presence of a lunar pattern in *E. mathaei* was also investigated by analyzing spawning activity for one full lunar cycle in February and March 1993 and 1994. Spawning was induced (as detailed above) in 20 urchins every 3-4 days for an entire lunar cycle. Urchins were injected with 0.5 M KCl and scored if copious spawning occurred. The percentage of urchins spawning on each lunar day was calculated and plotted against the lunar day.

Gametogenesis

The cellular changes that occur in the gonads of *E. mathaei* during gametogenesis were analyzed using standard histological techniques. The aboral tip of one gonad lobe was cut from each animal and preserved in 70% alcohol. No attempt was made to use other parts of the gonad as the gonad of *E. mathaei* is morphologically uniform (Pearse, 1969a). Fixed samples were imbedded in paraffin wax and sectioned at 7 um then stained with haematoxylin and eosin, after mounting on glass slides. were followed for these procedures.

The testes of *E. mathaei* like most urchins have 3 distinct layers in transverse section, a thin outer spermatogenic layer, where gametogenesis begins, a middle layer of nutritive phagocytes with the double function of nourishing developing spermatozoa and phagocytosing relic spermatozoa and a dense inner layer of mature spermatozoa (Kanatani and Nagahama, 1983). Female gonads have large ova, oocytes of various sizes and nutritive phagocytes occurring in varying amounts throughout the reproductive period. The various cell layers in the males and the sizes of the oocytes and ova in the female were used to identify the sequence of gametogenic development (Kanatani and Nagahama, 1983).

Histological samples at each reef each month were examined under a microscope and a description of the cellular events occurring during gametogenesis in *E. mathaei* were recorded using four basic stages as outlined by Fuji (1960) where:

1. Ripe: Male testicular lobes are full of spermatozoa with a thin spermatogenic and nutritive phagocytic layer. Ripe females have many large mature ova, few scattered oocytes in many size classes and a thin or absent nutritive phagocytic layer.
2. Spent: The spermatogenic cells and spermatozoa are absent and relic sperm are phagocytosed by nutritive phagocytes. Spent ovaries have empty spaces in the lumen and a few relic ova and oocytes.
3. Recovering: Nutritive phagocytes fill the gonadal lobes and gametocytes are usually very small making it difficult to distinguish the sexes.
4. Growing: In the males the spermatogenic layer increases in size almost filling the gonadal lobes and some sperm may start accumulating in the lumen. Ovaries have oocytes of various sizes lining the gonadal tubule wall and large ova start accumulating in the lumen.

These stages, along with measurements of the thicknesses of cell layers in males and oocyte and ova size frequencies in females, were used to follow the sequence of gametogenesis in *E. mathaei*. In each monthly sample, sections from 10 individual females haphazardly selected from all reefs were examined under a microscope. Fifty haphazardly selected oocytes (with a large nucleus and nucleolus) and ova (with nucleus) were measured from histological sections of each female using an ocular micrometer (Pearse, 1969a). The cells were grouped into 17 u size classes and the average frequency of oocytes and ova of different sizes were plotted for each monthly sample. Additionally, the nutritive phagocytic tissue layer of ten individuals per month was measured in 10 gonadal lobes of each individual male and female gonad from the edge of gonadal tubules to the middle of the lumen. The mean (± sem) monthly thickness of the nutritive phagocytic layer was calculated and plotted against the month for a year.

Male gonads were analyzed by measuring the thicknesses of the spermatogenic and spermatozoa layers in 10 testicular tubules (200 um in diameter) to the center of the lumen for 10 individual males each month. The mean (± sem) thickness of the spermatogenic and spermatozoa layers of 10 males per monthly sample was calculated and plotted against the month for one year.

Additional information on the proportion of ripe urchins in each monthly sample was collected after microscopic examination of histological samples. Since variable amounts of gametes in gonadal tubules indicate ripeness, a standardized method was used following Pearse and Phillips (1968). All individuals in each sample that contained mature gametes (sperm or ova) filling over half the gonadal tubules were considered ripe individuals.

The proportion of ripe individuals in each monthly sample was then calculated as a percentage of the total number of animals per monthly sample and plotted against the month for a full year.

Temperature, light and chlorophyll measurements

Measurements of temperature and light were made at each site on a monthly basis. Seawater temperatures were measured during low tide using a Baxter Scientific Products mercury bulb thermometer accurate to 0.1° C. Light measurements in sea water were taken with a LI-COR LI-189 photometer equipped with an underwater radiation sensor Type SA. Mean monthly light (MJ/m^{-2}/day) and mean monthly air temperature (°C) data were also accessed from the Kenyan meteorological department at the Mombasa met station. The data are presented as plots of the mean monthly temperature and light for 1992 to 1994.

The concentration of chlorophyll pigments in water is often used as an indicator of the biomass of phytoplankton. During this study, water samples were collected monthly at each reef during spring low tides in four, 5 Lt. plastic bottles and transported to the KMFRI laboratory. The samples were each filtered through 4.7 cm Whatman glass fibre filters. The filters were immediately put into graduated centrifuge tubes and macerated and the pigments were extracted with 90% acetone.

The pigments were allowed to extract for about 20 hr. in the dark. The extinctions of the pigment extracts were measured with a UV spectrophotometer following the methods of Strickland and Parsons, (1972).

The equations of Strickland and Parsons, (1972) were used for calculating chlorophyll a concentrations. The mean monthly concentration of these pigments were plotted against the month for all reefs pooled for one year. The influence of temperature, light, and chlorophyll a concentration on reproductive behavior was determined by performing a correlation between the mean monthly levels of these variables against the mean monthly gonad index of *E. mathaei*.

RESULTS

Annual Maturity cycle and spawning

The sex ratios of a total of 2,256 urchins collected from Diani, Kanamai and Vipingo were 0.99, 0.85 and 0.87 respectively (Table 2.1). A Chi-squared test presented in Table 2.1 shows that these sex ratios did not differ significantly from a ratio of 1:1.

Table 2.1. Summary table of Chi-squared tests comparing the sex ratios of male and female *Echinometra mathaei* at Diani, Kanamai and Vipingo.

Reef	*Females*	*Males*	*Total*	*Sex ratio*	X^2
Diani	212	214	426	0.99	0.01 ns
Kanamai	191	225	416	0.85	2.78 ns
Vipingo	229	262	491	0.87	2.22 ns

A comparison between the gonad indices of male and female urchins was performed using a two-factor ANOVA with sex and sampling date as the two factors. Urchins were grouped by sex and month and the mean monthly gonad indices of each sex in each month were calculated and used in the ANOVA. A significant difference was found in the gonad index between months within each reef, but no significant difference was found between the gonad index of females and males collected on the same dates at either Diani, Kanamai or Vipingo (Table 2.2). Therefore the gonad index data of males and females were pooled for each sampling date for all future comparisons.

Table 2.2. Summary table of a two-factor ANOVA comparing the gonad index of male and female *Echinometra mathaei* in different months at Diani, Kanamai and Vipingo. Twenty animals were haphazardly selected at each reef each month.

Reef	*Source*	*df*	*MS*	*F*	*P*
Diani	Month	6	13.07	58.86	0.000
	Sex	1	0.04	0.19	ns
Kanamai	Month	4	8.67	26.76	0.004
	sex	1	0.06	0.19	ns
Vipingo	Month	5	16.02	18.98	0.003
	sex	1	0.06	0.07	ns

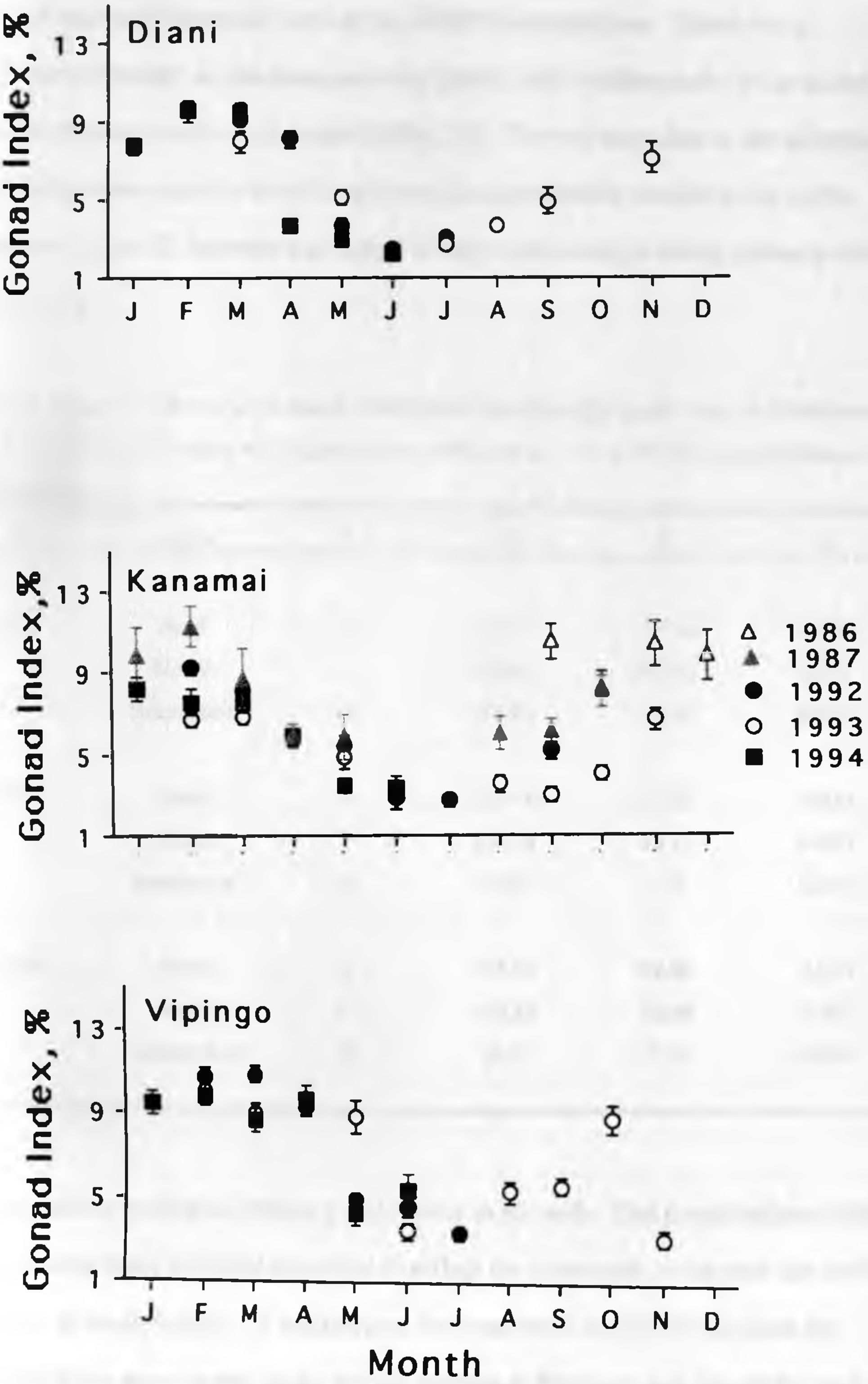
The overall mean gonad index for all urchins at Vipingo was 7.82 ± 0.14 (sem), n = 759 and this was significantly higher ($p < 0.0005$; Students t-test) than the gonad indices at either Kanamai (6.15 ± 0.12; n = 746) or Diani (6.46 ± 0.12; n = 751). There was no significant difference between the mean gonad index of urchins at Kanamai and Diani ($p > 0.05$).

Figure. 2.2 shows the annual pattern of reproduction of urchins at each reef from 1992 to 1994. The pattern shows a well defined annual cycle with a peak in February and March followed by a sharp decrease usually in April or May. The gonad index then gradually decreases to a low of about 3% in June and July. From August to October the gonad index starts to gradually increase reaching levels by November and December similar to the previous January.

This pattern is repeated at all the reefs in all the three years. Gonad index data collected previously in 1986 and 1987 at Kanamai also show an identical pattern (Fig. 2.2). Most of the reproductive activity appears to be restricted to the North-East monsoon season (i.e. between October and March.

The differences between reefs and between years at each reef were tested using a two-factor ANOVA with reef and sampling time (i.e. month) as the factors.

Figure. 2.2. The seasonal pattern of reproduction of *Echinometra mathaei* at Diani. Kanamai and Vipingo in the years 1992 to 1994 measured as the mean monthly gonad index (± sem. n = 20 - 60). Kanamai was also sampled in 1986 and 87 (Muthiga. unpublished data).


Diani
Kanamai
Vipingo
Gonad Index, %
Month
1
5
9
13
J
F
M
A
M
J
J
A
S
O
N
D
△ 1986
▲ 1987
● 1992
○ 1993
■ 1994

The mean monthly gonad index of 20 haphazardly selected urchins in each month at each reef was calculated and used in the ANOVA comparison. There was a significant difference in the mean monthly gonad index within each reef in all the years and between reefs in all years (Table 2.3). The variation due to the differences in the GI between months at each reef was stronger than the variation due to the differences in the GI between the reefs, further emphasizing a strong annual pattern of reproduction.

Table 2.3. Summary table of a two-factor ANOVA comparison of the gonad index of 20 *Echinometra mathaei* from Diani, Kanamai and Vipingo, each month within reefs in all the years and between reefs in all the years.

Year	*Source*	*df*	*MS*	*F*	*p*
1992	Reef	2	219.77	42.16	0.000
	Month	5	660.05	126.63	0.000
	Interaction	10	29.87	5.73	0.000
1993	Reef	2	210.18	32.78	0.000
	Month	7	276.78	43.17	0.000
	Interaction	14	47.62	7.43	0.000
1994	Reef	2	155.26	28.60	0.000
	Month	6	412.56	75.99	0.000
	Interaction	12	29.12	5.36	0.000

Gonad indices peaked in February and March at all reefs. The gonad indices during these months were assumed therefore to reflect the maximum investment the urchins allocated to reproduction. A comparison between reefs was therefore made by calculating the mean gonad index for the months of February and March for each reef from 1992 to 1995 Table 2.4. Urchins at Vipingo had the highest mean gonad index in 1992 but had similar gonad indices to Diani in 1993 and 1994. The gonad indices at Diani during the peak period did not vary much from year to year but urchins at

Kanamai showed the lowest gonad index of all reefs especially in 1993. The results show no significant differences in the gonad indices during the peak reproductive period at Diani from year to year (Table 2.5). Both Kanamai and Vipingo however show significant fluctuations in the gonad indices during the peak reproductive period from 1992 to 1995.

Table 2.4. The mean (± sem) of gonad indices of *Echinometra mathaei* at Diani, Kanamai and Vipingo at the peak of reproductive activity, February to March 1992 to 1995.

Reef	*1992*	*1993*	*1994*	*1995*	*All years*
Diani	9.18 ±0.23 n = 115	9.39 ± 0.29 n = 138	9.58 ± 0.36 n = 40	8.02 ± 0.49 n = 40	9.18 ± 0.16 n = 333
Kanamai	8.85 ± 0.23 n = 182	6.74 ± 0.25 n = 136	7.58 ± 0.38 n = 40	6.47 ± 0.50 n = 20	7.83 ± 0.16 n = 378
Vipingo	10.77 ± 0.27 n = 128	9.68 ± 0.31 n = 153	9.35 ± 0.40 n = 49	9.23 ± 0.57 n = 39	9.97 ± 0.18 n = 369

The results show no significant differences in the gonad indices during the peak reproductive period at Diani from year to year (Table 2.5). Both Kanamai and Vipingo however show significant fluctuations in the gonad indices during the peak reproductive period from 1992 to 1995.

Table 2.5. Summary table of single factor ANOVAs comparing gonad indices of individual *Echinometra mathaei* at each reef each year (1992 to 1994).

Reef	*Source*	*df*	*MS*	*F*	*p*
Diani	Between years	3	21.18	2.43	ns
	Within years	349	8.71		
Kanamai	Between years	3	129.73	14.93	0.000
	Within years	374	8.69		
Vipingo	Between years	3	45.01	3.79	0.011
	Within years	365	11.89		

Table 2.6 shows that Vipingo had significantly higher gonad indices than either Kanamai or Diani in 1992, although the later sites did not differ significantly from each other in 1992. In 1993 and 1994, however, Vipingo and Diani had gonad indices that did not differ significantly from each other although both reefs had gonad indices that were significantly higher than those recorded at Kanamai in both years.

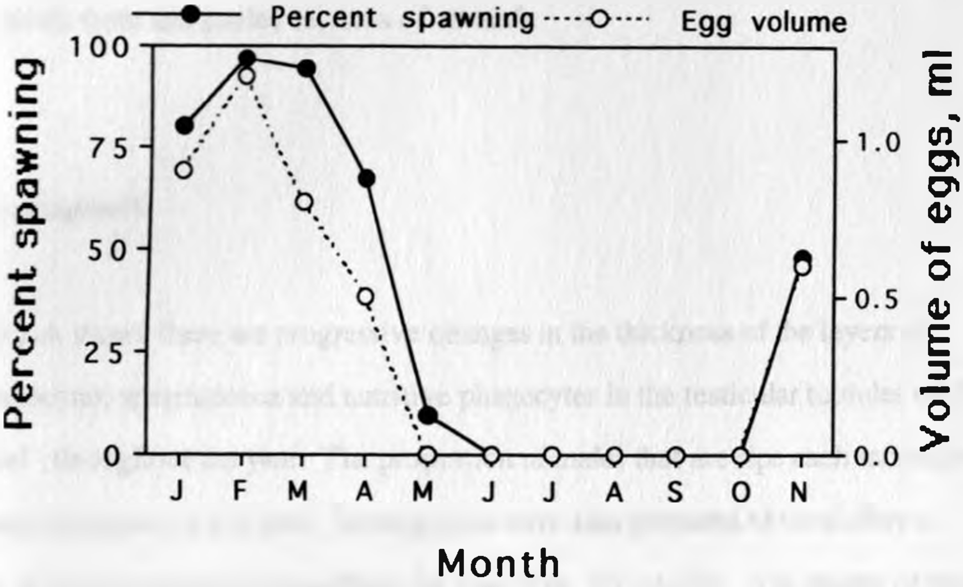
Table 2.6. Summary tables of single factor ANOVA comparisons between reefs of the gonad index of *Echinometra mathaei* during the peak months of reproduction in 1992 to 1995.

Year	*Comparison*	*Source*	*df*	*MS*	*F*	*p*
1992	Diani vs Kanamai	between reefs	1	8.00	0.94	ns
		within reefs	295	8.53		
	Diani vs Vipingo	between reefs	1	153.10	19.26	0.000
		within reefs	241	7.95		
	Kanamai vs Vipingo	between reefs	1	278.96	28.4	0.000
		within reefs	308	9.82		
1993	Diani vs Kanamai	between reefs	1	477.52	48.41	0.000
		within reefs	290	9.86		
	Diani vs Vipingo	between reefs	1	10.05	0.77	ns
		within reefs	309	13.00		
	Kanamai vs Vipingo	between reefs	1	623.50	52.95	0.000
		within reefs	287	11.78		
1994	Diani vs Kanamai	between reefs	1	79.71	14.42	0.000
		within reefs	78	5.53		
	Diani vs Vipingo	between reefs	1	1.12	0.16	ns
		within reefs	87	6.78		
	Kanamai vs Vipingo	between reefs	1	69.09	9.83	0.002
		within reefs	87	7.03		
1995	Diani vs Kanamai	between reefs	1	31.78	3.9	ns
		within reefs	58	8.15		
	Diani vs Vipingo	between reefs	1	29.26	2.63	ns
		within reefs	77	11.12		
	Kanamai vs Vipingo	between reefs	1	100.80	10.03	0.002
		within reefs	57	10.05		

Figure 2.3 shows the proportion of urchins at all reefs that spawned after KCl injection every month from February 1993 to February 1995. The data were pooled for all the reefs because a) the plot served to give a general picture of the spawning activity of *E. mathaei* without site specific influences and b) not all reefs were studied every month of every year. The mean monthly volume of eggs spawned, representing the seasonal availability of eggs, for all reefs was also calculated and plotted on the same graph.

The seasonal spawning pattern of induced urchins was very similar to that seen from gonad index data. There was a positive and highly significant correlation ($r = 0.98$, $p < 0.01$) between the percent of urchins spawning each month and the mean monthly volume of egg spawned after KCl injection. Both the number of females spawning and the volume of eggs released peaked in February corresponding to the high gonad indices during this time. In February females released a mean of 1.2 ml of eggs (all reefs). Forty-eight percent of females are ready to spawn by November although they spawn only 35% of the total volume of eggs potentially available during the peak month of reproduction. By January 80% of urchins that were injected with KCl spawned releasing 70% of the potential egg volume. Spawning had ceased by May since females induced to spawn during this month released no eggs.

Figure. 2.3. The seasonal production of *Echinometra mathaei* (all reefs pooled) measured as the percentage of urchins spawning copious gametes and the mean volume of eggs released after KCl injection every month for a year (n < 60.



Percent spawning
Egg volume
Percent spawning
100
75
50
25
0
Volume of eggs, ml
1.0
0.5
0.0
J
F
M
A
M
J
J
A
S
O
N
Month

Gametogenesis

The sequence of cellular events occurring during the annual cycle of *E. mathaei* was investigated by histological analysis of gonads from each reef. A general examination of all the sections collected for each month at each reef showed a similar sequence of cellular changes hence pooled data for all reefs are presented. A haphazard selection of gonadal sections of 10 males and 10 females was made for each month from the pooled sections of all reefs.

Spermatogenesis

Figure 2.4. shows there are progressive changes in the thickness of the layers of spermatocytes, spermatozoa and nutritive phagocytes in the testicular tublules of *E. mathaei* throughout the year. The proportion of males that are ripe each month is also superimposed on this plot. Micrographs were also prepared of the different stages of spermatogenesis throughout the year (Fig. 2.5, (A-D)). The lumen of most (70%) males were full of densely packed spermatozoa from October to May, indicating that males were ripe during this time (Fig. 2.5(D)). The amount of spermatozoa within the lumen of testicular tubules reached a peak in March (143 um thick) corresponding to the peak in gonad index, and decreased drastically between April and June. Only 30% of males had any sperm in July, a time when gonad indices were at their lowest.

During the same period a thin spermatogenic layer was present that did not change much in magnitude but followed the same sequence as the spermatozoa with a decrease in July. There was a very short recovering and growing stage (Fig. 2.5(A)) since by September the spermatogenic layer was back up to its maximum size (17 um thick) and sperm had already started accumulating in the lumen of the testicular lobes. By October up to 70% of males had lobes filled with sperm (Fig. 2.5(B))

Figure. 2.4. The seasonal reproductive changes of male *Echinometra mathaei* from Diani, Kanamai and Vipingo measured as the mean (± sem) monthly thickness of the layers of spermatogenic cells, nutritive phagocytes and spermatozoa from ten randomly selected males per month. The solid line represents the monthly percentage of males at all reefs containing mature gametes filling more than 50% of the testicular lobes.

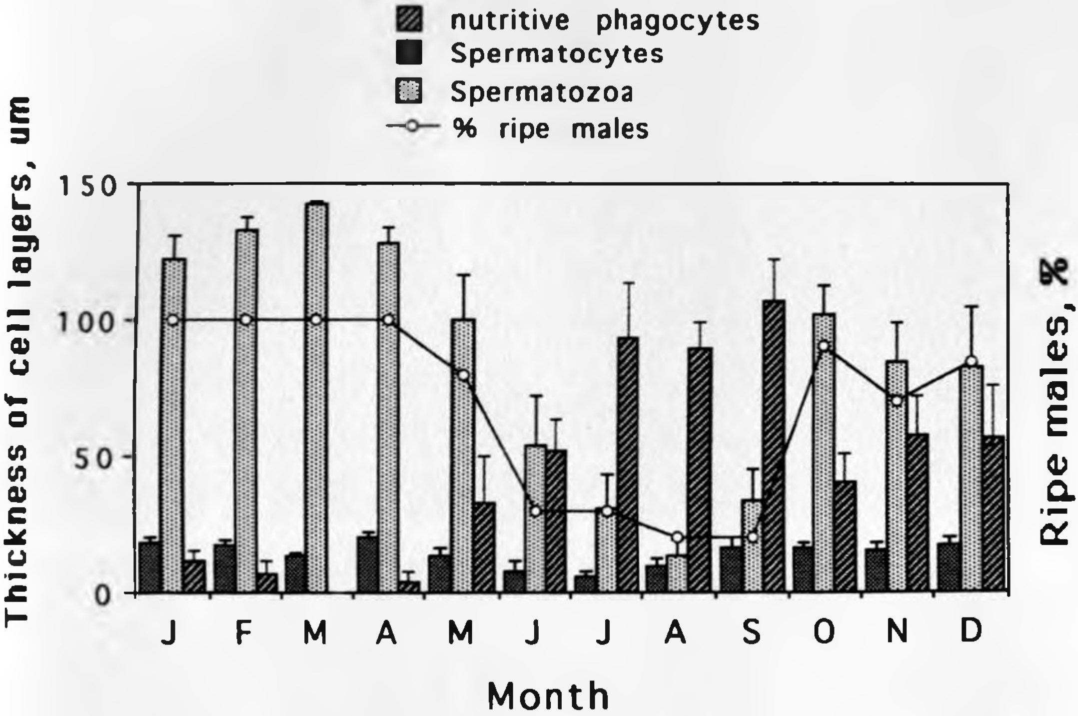
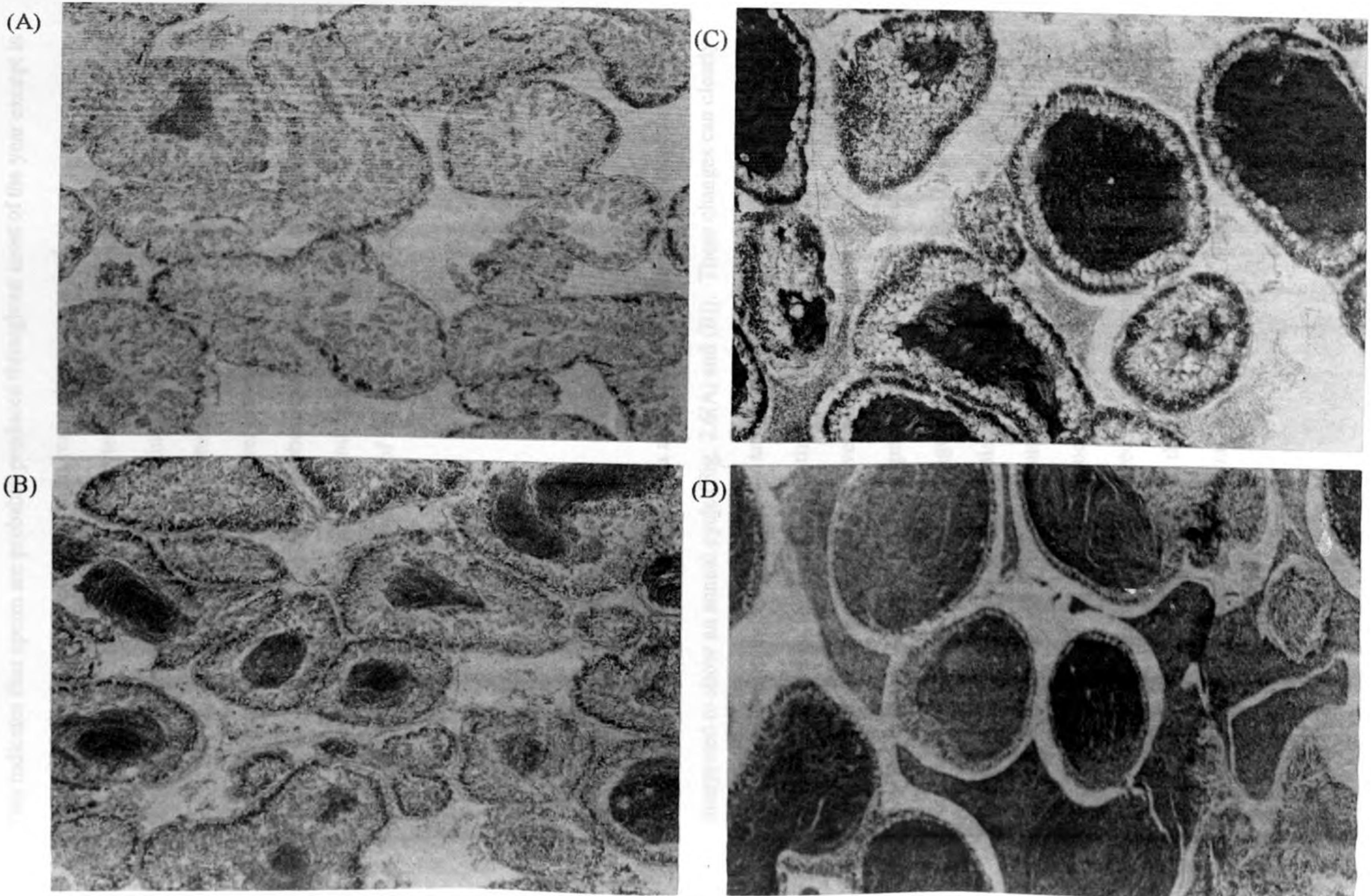

nutritive phagocytes
Spermatocytes
Spermatozoa
% ripe males
Thickness of cell layers, um
Ripe males, %
150
100
50
0
J
F
M
A
M
J
J
A
S
O
N
D
Month

Figure. 2.5. The developmental stages of *Echinometra mathaei* during spermatogenesis. Micrographs of histological sections of individual male *E. mathaei* collected in different months from Diani, Kanamai or Vipingo reef lagoons in Kenya. The micrographs show a recovery stage (A) with testicular tubules full of nutritive phagocytes, a growing stage (B) showing a thicker spermatogenic layer and some sperm accumilating in the lumen of the tubules, an early ripe stage (C) with tubules almost completely filled with sperm but with a thin spermatogenic layer and a late ripe stage (D) with the tubules and spaces between tubules full of sperm and a barely dicernible spermatogenic layer.


(A)
(C)
(B)
(D)

This indicates that sperm are probably produced throughout most of the year except in July to September when there is a short resting/growing period.

The amount of nutritive phagocytes showed a marked increase in May to June coinciding with the decrease in the amounts of spermatozoa. Nutritive phagocytes continued to increase and peaked in September a time when the amounts of spermatozoa and spermatogenic tissue were beginning to increase. The sharp decrease of nutritive phagocytes in October coincided with a sharp increase in spermatozoa at the same time possibly indicating the importance of nutritive phagocytes in the energy requirements of the urchin during spermatogenesis (Fig. 2.5(C)).

Oogenesis

The size frequencies of oocytes and ova also go through changes that can be interpreted to show an annual cycle (Fig. 2.6(A) and (B)). These changes can clearly be seen in the micrographs of the cellular changes occurring during oogenesis shown in Figure 2.7 (A-D)). From December through April, more then 55% of females contain numerous mature ova, filling over 50% of the ovarian tubules. Growth of oocytes begins in August when a new generation of oocytes between 8 - 16 um dominate the samples and nutritive phagocytes fill the tubules (Fig. 2.7(A)). However only 20% of the females in this month have oocytes of this size and one female still had relic ova from a previous generation, the rest of the females had in growing nutritive phagocytes and no oocytes or ova. By September all the females had small and medium (30-40 um) sized oocytes growing along the tubule wall and nutritive phagocytes filling up most of the ovarian tubules ((. 2.7(B)). Twenty percent of females in this sample still had relic ova showing signs of degeneration.

Figure. 2.6. (A). The seasonal reproductive changes of *Echinometra mathaei* females at Diani, Kanamai and Vipingo measured as mean monthly size frequencies of oocytes (bottom histograhs) and ova (top histograhs) for ten females randomly selected from histological sections at all the reefs. (B). The thickness (± sem) of the nutritive phagocytic layer of these individuals is also shown. The solid line represents the monthly percentage of females at all reefs containing mature gametes filling more than 50% of the ovarian lobes.

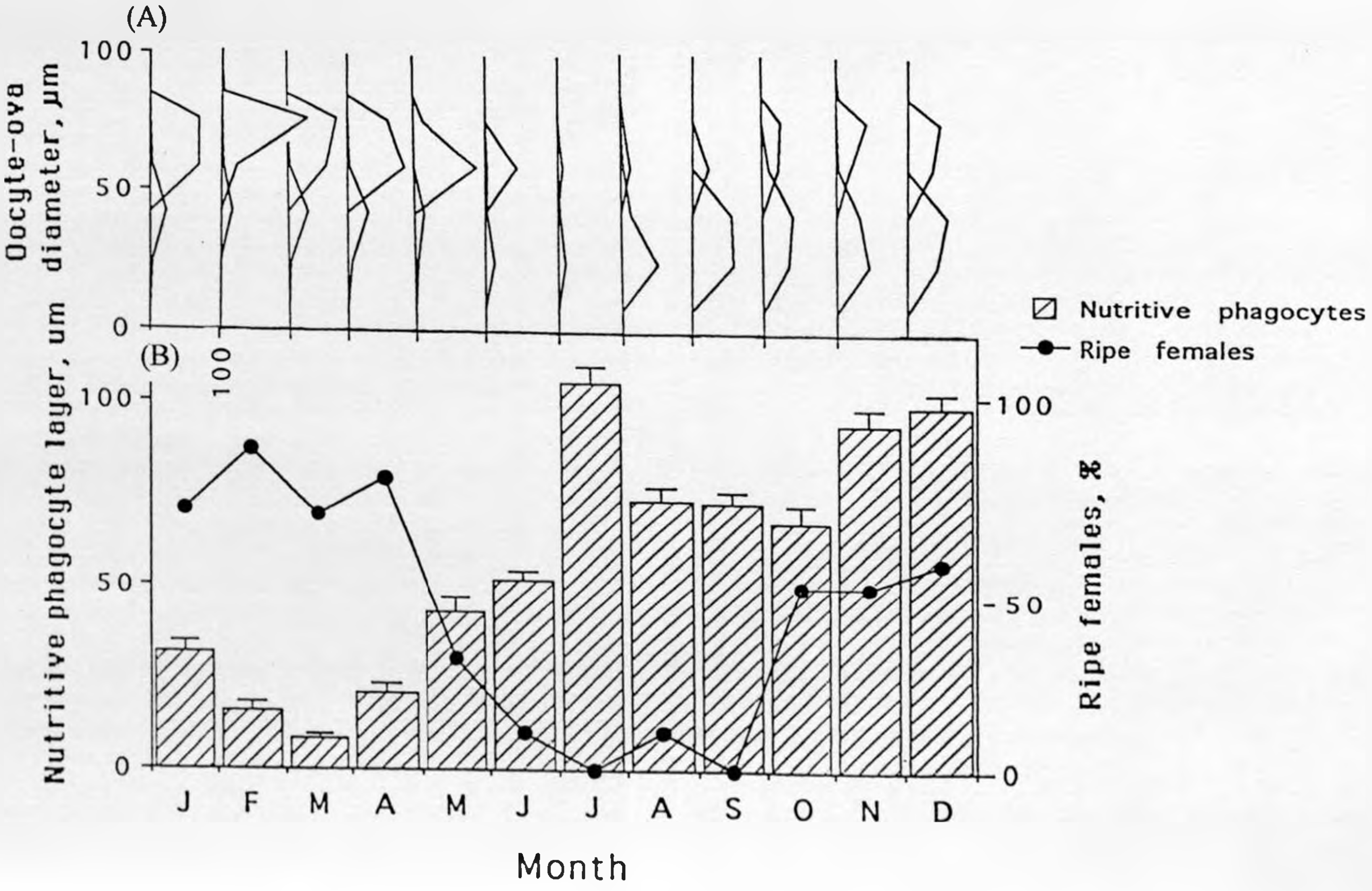
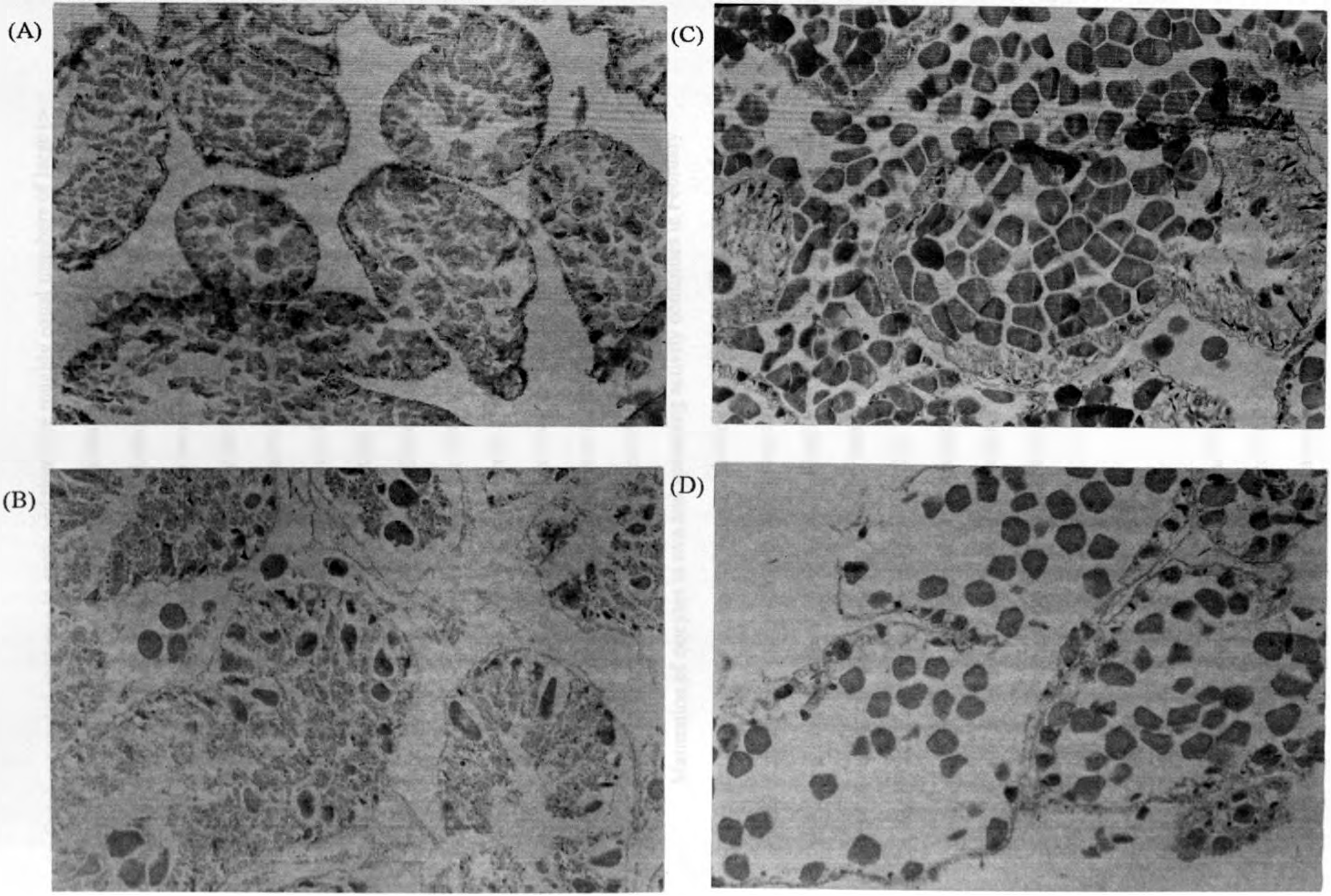

(A)
Oocyte-ova diameter, µm
100
50
0
100
(B)
Nutritive phagocyte layer, um
100
50
0
Ripe females, %
100
50
0
▨ Nutritive phagocytes
● Ripe females
J
F
M
A
M
J
J
A
S
O
N
D
Month

Figure. 2.7. The developmental stages of *Echinometra mathaei* during oogenesis. Micrographs of histological sections of individual female *E. mathaei* collected in different months from Diani, Kanamai or Vipingo reef lagoons in Kenya. The micrographs show; a recovery stage (A) with the ovarian tubules full of nutritive phagocytes, a growing stage (B) showing oocytes of different sizes, a ripe stage (C) with tubules full of mature ova and a spent stage (D) with a few ova in the mostly empty tubules.


(A)
(C)
(B)
(D)

In October oocytes continue to grow and there are roughly equal numbers of large (> 40 um) medium and small oocytes in the ovarian tubules. Eighty percent of females in this sample had some mature ova accumulating in the lumen of the tubules indicating that the time taken from oocyte to ova is approximately three months. The oocyte-ova frequency distributions look very similar in November and December with oocytes of many sizes growing along the tubule walls and mature ova filling up the lumen in all but two females. The amount of nutritive phagocytes has not declined appreciably during this time indicating a continued period of growth.

Some spawning apparently starts in December since 20% of females in this sample had empty spaces in the lumen. By January no oocytes less than 16 um in diameter are present in the sections and there is a rapid decline of nutritive phagocytes indicating the end of the growing phase. The ovarian tubules are packed full of mature ova in all but two females and medium sized oocytes line the tubule walls (Fig. 2.7(C)). A few females also show some evidence of spawning in January.

Maturation of oocytes to ova and spawning activity continues in February through April with the number of oocytes declining with time. The amount of nutritive phagocytes also continues decreasing and reaches the lowest values in March and then start slowly increasing in April. By May a few females have a few large oocytes and relic ova scattered in the lumen which have large empty spaces corresponding to the spent stage (Fig. 2.7(D)). However 40% of the sections have no oocytes or ova and in growing nutritive phagocytes. In June and July most tubules have in growing nutritive phagocytes with only a few disintegrating oocytes and ova indicating the end of the spent stage and the beginning of a new growth cycle.

Lunar pattern

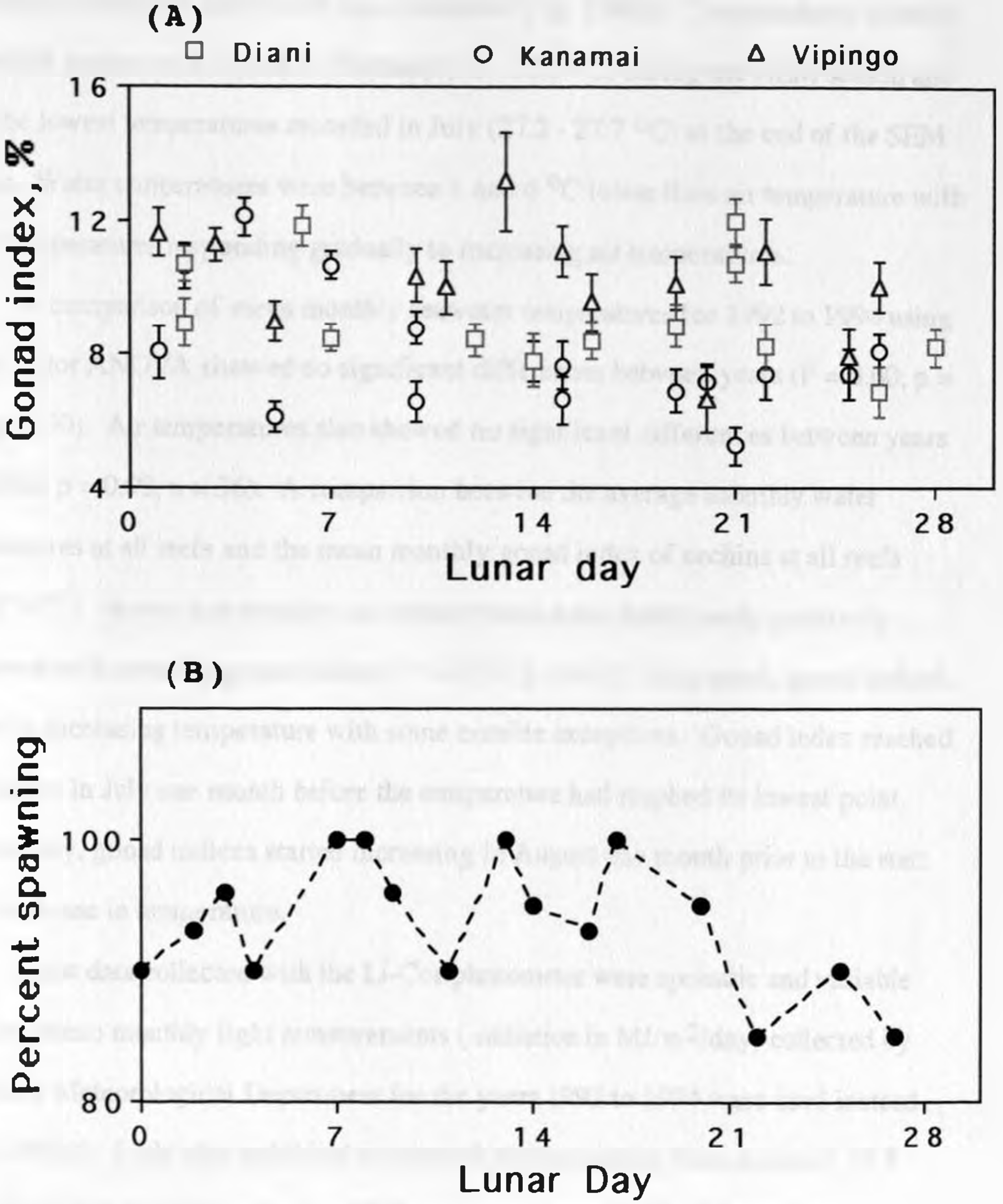
Figure 2.8(A) shows plots of the mean gonad index of urchins on a specific lunar day at the three reefs during February and March in 1992-93. The gonad indices fluctuate significantly between lunar days (single factor ANOVA, Table. 2.7) with a general trend of decreasing gonad indices towards the end of the lunar cycle (lunar day 28) at all the reefs. This trend is especially prominent at Kanamai in 1992 where the gonad indices were high (>12%) during the early part of the lunar cycle (new moon) to a few days after the last quarter and gradually decreased to low levels (8%) around the full moon. However, this pattern did not repeat itself in 1993 at Kanamai and in any of the years at Diani or Vipingo.

Table 2.7. Summary table of single factor ANOVA comparisons of the gonad index of *Echinometra mathaei* at Diani, Kanamai and Vipingo on different lunar days.

Site	*Source*	*df*	*MS*	*F*	*p*
Diani	Between lunar days	10	18.03	1.89	0.047
	Within lunar days	282	9.56		
Kanamai	Between lunar days	12	74.07	9.25	0.000
	Within lunar days	285	8.01		
Vipingo	Between lunar days	12	47.94	4.28	0.000
	Within lunar days	263	11.19		

The frequency of spawning on different lunar days shows that more than 80% of the urchins spawned copious amounts of gametes when induced with injections of KCl (Fig. 2.8(B)). This indicates that these urchins were all ripe and ready to spawn during these months. The slight decrease in gonad index towards the end of the lunar cycle, therefore represents the annual decrease in March due to spawning rather than to a lunar pattern. An examination of histological sections of gonads collected on different lunar days during this time shows females with large oocytes lining the ovarian tubule walls and large mature ova in the lumen and male urchins with testicular tubules with lumen full of sperm. Gonads of males and females from different lunar days were similar regardless of lunar day.

Figure. 2.8. The lunar pattern of reproduction of *Echinometra mathaei* for a complete lunar cycle in February and March, 1992 and 1993 at Diani, Kanamai and Vipingo. (A) Average gonad indices (± sem) of 20 individuals for each lunar day. (B) The percentage of urchins releasing gametes after KCl injections on different lunar days.


(A)
□ Diani
○ Kanamai
Δ Vipingo
Gonad index, %
16
12
8
4
0
7
14
21
28
Lunar day
(B)
Percent spawning
100
80
0
7
14
21
28
Lunar Day

Temperature, light and phytoplankton

The mean monthly water temperatures pooled from all reefs are shown on Figure. 2.9(A). Mean monthly air temperatures from collected by the Kenya meteorological department Mombasa Station are also presented (Fig. 2.9(B)). Temperatures showed a seasonal pattern with a peak in February (33 - 33.5 °C) during the NEM season and with the lowest temperatures recorded in July (27.2 - 27.7 °C) at the end of the SEM season. Water temperatures were between 1 and 6 °C lower than air temperature with water temperatures responding gradually to increasing air temperatures.

A comparison of mean monthly seawater temperatures for 1992 to 1994 using single factor ANOVA showed no significant differences between years ($F = 0.60$; $p = 0.89$, $n = 30$). Air temperatures also showed no significant differences between years ($F = 0.02$; $p = 0.98$, $n = 36$). A comparison between the average monthly water temperatures at all reefs and the mean monthly gonad index of urchins at all reefs (Fig. 2.9(C)), shows that monthly sea temperatures were significantly positively correlated with monthly gonad indices ($r = 0.79$, $p < 0.01$). In general, gonad indices rose with increasing temperature with some notable exceptions. Gonad index reached a minimum in July one month before the temperature had reached its lowest point. Additionally, gonad indices started increasing in August one month prior to the start of the increase in temperature.

Light data collected with the Li-Cor photometer were sporadic and variable therefore mean monthly light measurements (radiation in $MJ/m^2/day$) collected by the Kenya Meteorological Department for the years 1992 to 1994 were used instead (Fig. 2.10(A)). Light also exhibited a seasonal pattern ranging from a low of 15.5 - 17.8 $MJ/m^2/day$ in July (during the SEM season) to a peak of 23.2 $MJ/m^2/day$ between February and March (NEM season). A single factor ANOVA comparison showed that the variation in light between years was not significant ($F = 0.60$; $p = 0.55$, $n = 36$).

Figure. 2.9. (A) The seasonal pattern of water temperature measured as mean monthly temperatures (all reefs in all years pooled). (B) The mean monthly air temperature collected by the Kenya meteorological department at Mombasa station for 1992 to 1994. (C) A comparison of the mean monthly gonad indices of *Echinometra mathaei* and the mean monthly seawater temperatures for all reefs in 1992-1994.

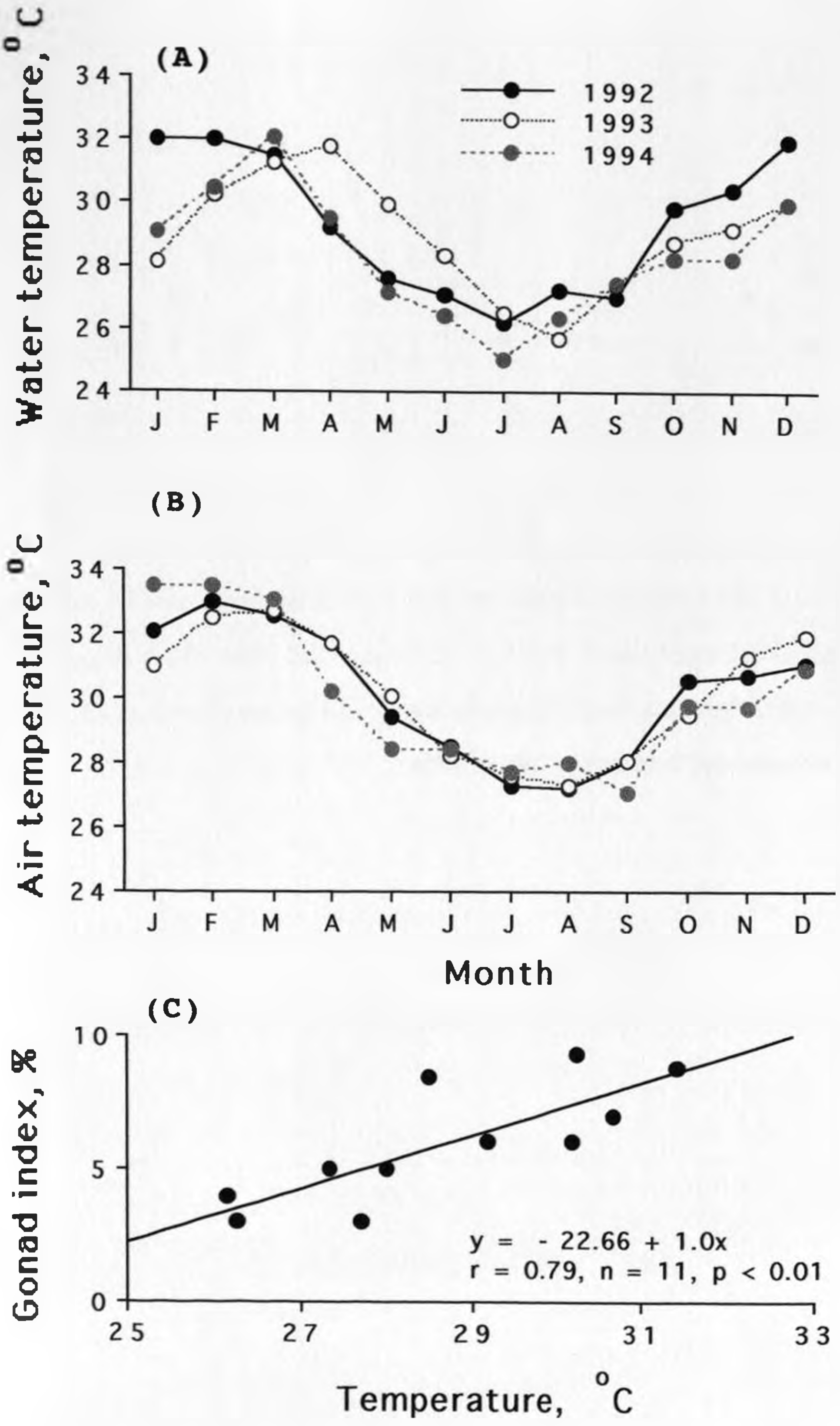
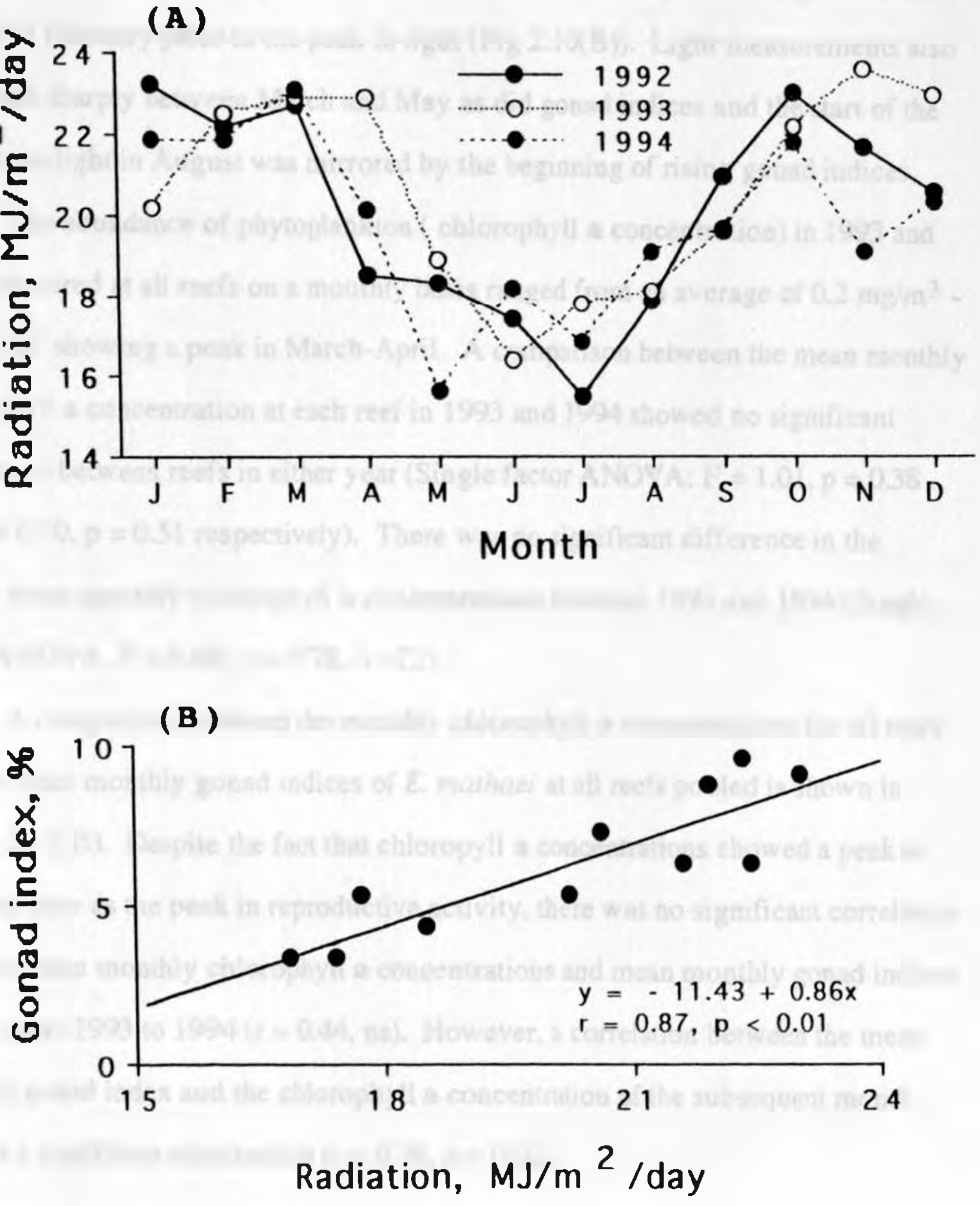

(A)
Water temperature, °C
34
32
30
28
26
24
J F M A M J J A S O N D
1992
1993
1994
(B)
Air temperature, °C
34
32
30
28
26
24
J F M A M J J A S O N D
Month
(C)
Gonad index, %
10
5
0
25
27
29
31
33
Temperature, °C
y = - 22.66 + 1.0x
r = 0.79, n = 11, p < 0.01

Figure. 2.10. (A) The mean monthly radiation (MJ/m^3/day) measured by the Kenya Meteorological Department at Mombasa station for 1992-1994. (B) A comparison of the mean monthly light measurements and the mean monthly gonad index of urchins from Diani, Kanamai and Vipingo for 1992 to 1994.

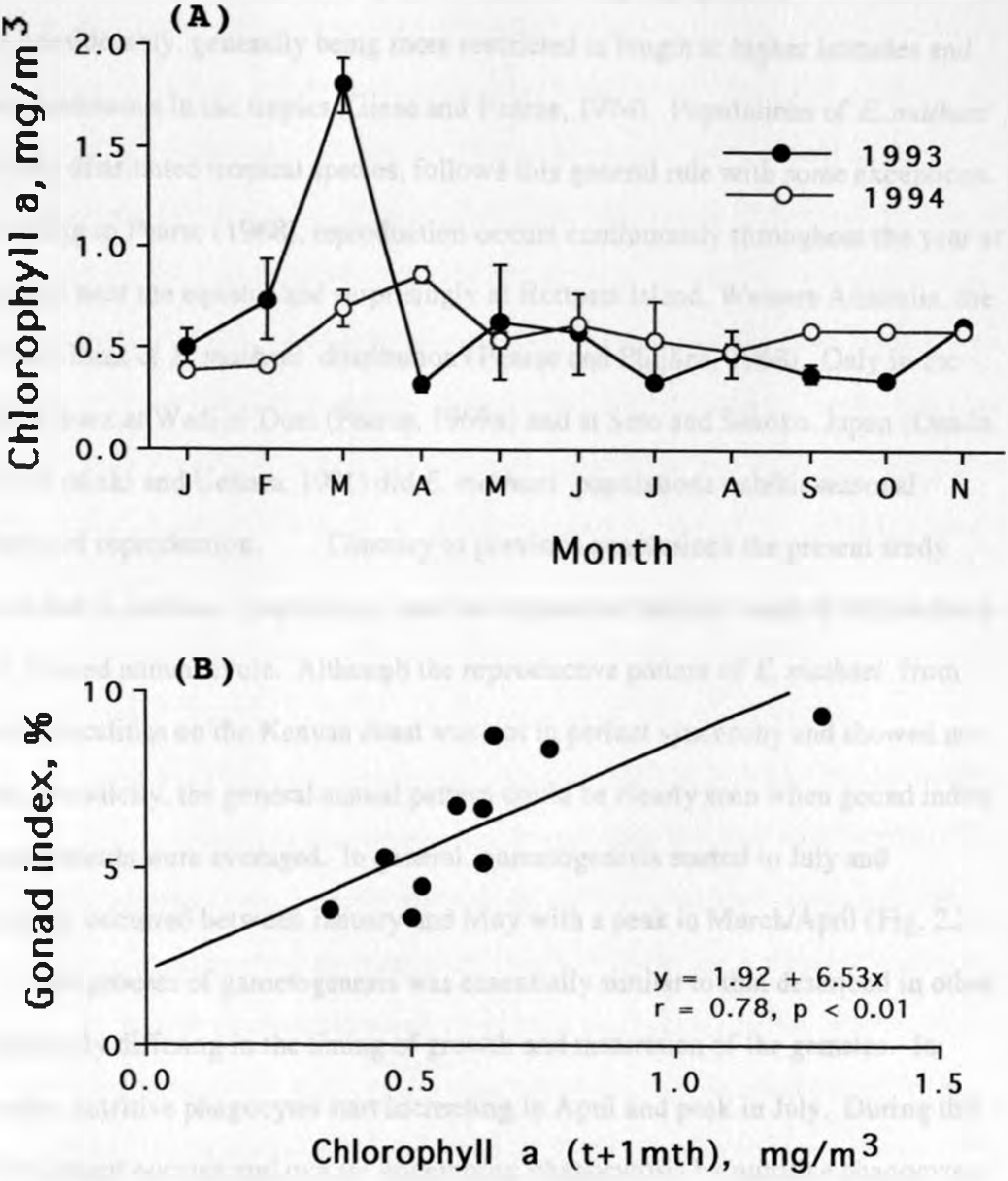

(A)
Radiation, MJ/m 2 /day
24
22
20
18
16
14
1992
1993
1994
J
F
M
A
M
J
J
A
S
O
N
D
Month
(B)
Gonad index, %
10
5
0
15
18
21
24
y = - 11.43 + 0.86x
r = 0.87, p < 0.01
Radiation, MJ/m 2 /day

A correlation between the mean monthly gonad indices of *E. mathaei* for 1992 - 1994 (monthly means were calculated for all reef lagoons pooled), and the mean monthly radiation measurements for these years, revealed that mean monthly radiation measurements were significantly correlated with mean monthly gonad indices ($r = 0.87$, $p < 0.01$). In general gonad indices closely followed light except gonad indices peaked in February prior to the peak in light (Fig 2.10(B)). Light measurements also decreased sharply between March and May as did gonad indices and the start of the increase in light in August was mirrored by the beginning of rising gonad indices.

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 mg/m^3 - 1.8 mg/m^3 showing a peak in March-April. A comparison between the mean monthly chlorophyll a concentration at each reef in 1993 and 1994 showed no significant differences between reefs in either year (Single factor ANOVA: $F = 1.01$, $p = 0.38$ and $F = 0.70$, $p = 0.51$ respectively). There was no significant difference in the overall mean monthly chlorophyll a concentrations between 1993 and 1994 (Single factor ANOVA, $F = 0.08$; $p = 0.78$, $n = 22$).

A comparison between the monthly chlorophyll a concentrations for all reefs and the mean monthly gonad indices of *E. mathaei* at all reefs pooled is shown in Figure. 2.11(B). Despite the fact that chloropyll a concentrations showed a peak at the same time as the peak in reproductive activity, there was no significant correlation between mean monthly chlorophyll a concentrations and mean monthly gonad indices for the years 1993 to 1994 ($r = 0.44$, ns). However, a correlation between the mean monthly gonad index and the chlorophyll a concentration of the subsequent month showed a significant relationship ($r = 0.78$, $p < 0.02$).

Figure. 2.11. (A) The overall mean monthly (± sem) chloropyll a measurements for 1993 and 1994 at Diani, Kanamai and Vipingo. (B) A comparison of the mean monthly gonad indices of *Echinometra mathaei* and the mean monthly chlorophyll a measurements pooled for all reefs for 1993 and 1994.


(A)
Chlorophyll a, mg/m3
2.0
1.5
1.0
0.5
0.0
J F M A M J J A S O N
Month
1993
1994
(B)
Gonad index, %
10
5
0
0.0
0.5
1.0
1.5
Chlorophyll a (t+1mth), mg/m3
y = 1.92 + 6.53x
r = 0.78, p < 0.01

DISCUSSION

Gametogenic cycle

The reproductive patterns within species with a wide geographical distribution can vary considerably, generally being more restricted in length at higher latitudes and more continuous in the tropics (Giese and Pearse, 1974). Populations of *E. mathaei* , a widely distributed tropical species, follows this general rule with some exceptions. According to Pearse (1968), reproduction occurs continuously throughout the year at locations near the equator and surprisingly at Rottnest Island, Western Australia, the southern limit of *E. mathaei* distribution (Pearse and Phillips, 1968). Only in the Gulf of Suez at Wadi el Dom (Pearse, 1969a) and at Seto and Sesoko, Japan (Onada, 1936; Arakaki and Uehara, 1991) did *E. mathaei* populations exhibit seasonal patterns of reproduction. Contrary to previous conclusions the present study shows that *E. mathaei* populations near the equator on the east coast of Africa had a well defined annual cycle. Although the reproductive pattern of *E. mathaei* from various localities on the Kenyan coast was not in perfect synchrony and showed no lunar periodicity, the general annual pattern could be clearly seen when gonad index measurements were averaged. In general, gametogenesis started in July and spawning occurred between January and May with a peak in March/April (Fig. 2.2 - 2.7). The process of gametogenesis was essentially similar to that described in other studies only differing in the timing of growth and maturation of the gametes. In females, nutritive phagocytes start increasing in April and peak in July. During this time remnant oocytes and ova are undergoing phagocytosis by nutritive phagocytes. Oogenesis begins in July just as the layer of nutritive phagocytes reaches its peak (Fig. 2.7(A)). There is an immediate sharp decrease (30%) in nutritive phagocytes after the onset of oogenesis indicating that nutritive phagocytes are an important energy source during the process of differentiation of oogonia to oocytes.

Oocytes continue growing and mature to ova by October a period of approximately 3 months similar to *E. mathaei* at Wadi el Dom, (Pearse, 1969a). The oocytes of urchins at Wadi el Dom, however, did not all mature to ova since at 20-30 um, a group continues to grow to ova while the rest disintegrate and are phagocytosed. Pearse (1969a) postulated that this may have been a means of getting rid of excess oocytes as has been shown in other echinoids (Pearse, 1969b) and the nutrients released in this process are transferred to the growing oocytes. There was no evidence of production of excess oocytes in urchins at Diani, Kanamai and Vipingo since there was a smooth and continuous progression from small oocytes to large oocytes. The mean gonad indices of urchins at Wadi el Dom during this time were approximately 4% while those of urchins at Diani, Kanamai and Vipingo were approximately 6 to 7%. This coupled with the fact that the nutritive phagocyte layer decreases only slightly in urchins at Diani, Kanamai and Vipingo during the period of oocyte growth indicates that these urchins have adequate resources within the gonad for oocyte growth.

In female *E. mathaei* on Kenyan reefs the nutritive phagocyte layer undergoes another period of growth increasing by approximately 30% in November and December prior to the onset of spawning. The fact that both the gonad index and the layer of nutritive phagocytes increases prior to spawning and decrease sharply (60%) in January indicates that a great expenditure of energy is required during the final stages of oocyte maturation and spawning. The nutritive phagocyte reserves therefore had to be replenished before spawning could take place (Fig. 2.6(B)). Mature ova are present in great number as early as November and 50% of females spawned when induced with KCl indicating that spawning could start as early as November but ova may be retained until January a period of approximately two months similar to what was found in *E. mathaei* at Wadi el Dom (Pearse, 1969a).

Spermatogenesis also starts in July as nutritive phagocytes peak (Fig. 2.4). The process of differentiation from spermatogonia to spermatocytes is not as energetically expensive as oogonia to oocytes as evidenced by the fact that the layer of nutritive phagocytes does not decrease markedly during this time. As the spermatocytes mature to spermatozoa however and start filling up the testicular lumen the nutritive phagocytic layer decreases (Fig. 2.5(C)). The thicknesses of the spermatocytes and spermatozoa layers remain stable between October and December and some spawning maybe going on at this time. The nutritive phagocytic layer decreases dramatically (40%) in January as it did in female *E. mathaei*. The layer of sperm, however, did not decrease dramatically as would be expected during the peak spawning period. This could be due to spermatocytes differentiating very rapidly to sperm not allowing for the layer of sperm to diminish. Spawning in males is prolonged until May as evidenced by 80% of males still having testicular lobes full of sperm during this month. A prolonged spawning period in males was also shown in *E. mathaei* at Wadi el Dom (Pearse, 1969a). The fact that males start spawning earlier and finish later than females has adaptive significance for fertilization success. Since it is energetically more expensive to produce eggs than sperm a longer spawning period for males ensues that sperm are available during the entire period when eggs are mature.

The gonad index of *E. mathaei* during the peak months of reproduction fluctuated significantly between the years at Kanamai and Vipingo (Table 2.5) probably as a response to fluctuations in the availability of food at these reefs. The relative differences in gonad index between reefs, however, remained the same with Vipingo having consistently higher values than Diani and Kanamai. McClanahan and Kurtis (1991) found no significant differences between gonad indices of *E. mathaei* at Vipingo and Diani. This is not surprising as measurements were taken in July when reproductive activity is at its lowest for *E. mathaei* on the Kenyan coast. Vipingo was also the reef with the lowest population density of sea urchins with *E. mathaei* consisting of only 30% of the sea urchin population (McClanahan and Shafir, 1990). This could mean that inter and intraspecific competition for resources is low at Vipingo allowing for maximum allocation of resources to reproduction. Yearly variation in fecundity has also been demonstrated in the sea urchin *S.*

purpuratus (Gonor, 1973) and it has been suggested that this variation is a reflection of variation in environmental factors especially food availability.

Interestingly, *E. mathaei* populations at Diani showed relatively high gonad indices (as high as Vipingo in 1993 and 1994) despite Diani having a high population of urchins (90% consisting of *E. mathaei* (McClanahan and Shafir, 1990)). The urchins at Diani were on average smaller than the urchins at either Vipingo and Kanamai, however, indicating a tradeoff between growth and reproduction. *E. mathaei* at Diani channeled relatively more resources to reproduction at the expense of growth an appropriate response to food limitation (Thompson, 1982).

Reproductive periodicity

Reproductive periodicity has two main functions (a) it allows individuals of a population to take advantage of the best time of the year for reproduction and (b) it ensures reproductive synchrony among conspecifics (Lessios, 1981). Contrary to expectations, *E. mathaei* on the east coast of Africa has a seasonal reproductive cycle. The factors responsible for restricting the length of the reproductive season of *E. mathaei* at the equator are difficult to identify as none of the factors normally thought to be involved in higher latitudes i.e. temperature, light and chlorophyll showed large variations in East Africa.

For example, although sea water temperatures have a seasonal pattern on the east African coast ranging from 24 °C to 33 °C, these temperatures are well above the suggested minimum (18 °C) required for gametogenesis to begin in *E. mathaei* (Pearse, 1968; Pearse and Phillips, 1969). One would expect *E. mathaei* to have continuous reproduction throughout the year under these temperature conditions as occurs in *E. mathaei* under similar conditions at Rottnest Island, Western Australia (Pearse and Phillips, 1968). Additionally, temperature conditions in Seseko Japan and the Gulf of Suez vary between 15 - 30°C (Pearse, 1969a) a much higher range of temperature than in east Africa and *E. mathaei* in these areas exhibit seasonal reproductive behaviour. Despite the significant correlation between monthly sea water temperatures and *E. mathaei* monthly gonad indices (Fig. 2.9(C)) temperature is not necessarily the critical cue that triggers the onset of gametogenesis in *E. mathaei* on Kenyan reefs. For conclusive evidence, experiments to stimulate or enhance gametogenesis in *E. mathaei* with temperature manipulations would have to be carried out.

The mean monthly radiation measurements are also highly correlated to *E. mathaei* gonad development as gonad indices started to increase as light increased and peaked with light (Fig. 2.10(B). The seasonal pattern of light on the east African coast is very regular and would make a reliable cue for the onset of gametogenesis with a critical light value acting as the triggering mechanism. Although correlative evidence indicates that light may have an influence on reproduction of *E. mathaei* on the east coast of Africa, the present study does not explore the mechanism by which light intensity influences reproductive behavior in *E. mathaei*. Further experimentation on the direct effects of different light intensities on gonad growth of *E. mathaei* would have to be carried out before a conclusion can be drawn.

Another aspect of light i.e. seasonally changing daylength (photoperiod) has been shown to strongly influence gametogenesis and growth in the temperate zone sea urchin *S. purpuratus* (Pearse *et al*., 1986) and the sea star *Pisaster ochraceus* (Pearse and Eernisse, 1982). Long daylength was the cue that triggered gametogenesis in *P. ochraceus* while short daylength was the cue in *S. purpuratus*. Photoperiod varies by a maximum of 30 minutes throughout the year on the east African coast and is therefore not expected to influence gametogenesis in *E. mathaei* in East Africa.

Light and temperature may also have an indirect effect on gonad growth by increasing benthic algae and therefore available food for gonad growth thus acting as an ultimate cause of seasonal reproductive behavior. Changes in food availability would act as an ultimate cause for the adaptive selection of seasonal reproductive behavior. If a "critical" level of nutrient reserves in the gonad (built up in the nutritive phagocytes) is required before gametogenesis can begin (Pearse, 1969a), then availability of food could also act as a proximate cause of seasonal reproductive behavior. The rate of build up of nutrient reserves will be influenced by environmental factors including light and temperature as these control benthic productivity.

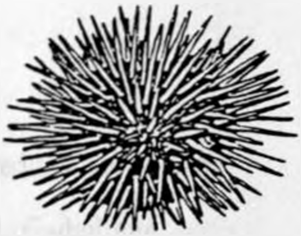
Spawning in sea urchins has been shown to coincide with the spring phytoplankton bloom in temperate environments (Himmelman, 1980) thereby ensuring adequate food as well as favorable environmental conditions for the larvae. Recent evidence has shown that extracellular metabolites released by various species of phytoplankton can induce spawning in sea urchins (Starr, *et al.*, 1992). Phytoplankton is therefore an ideal spawning cue especially if it coincides with other environmental factors indicating favorable conditions for larval growth and survival.

In the present study chlorophyll **a** concentrations also showed a seasonal pattern with a peak in March in 1993 and in April in 1994 at about the time light and temperature peaked (Fig. 2.11(A)). Phytoplankton concentrations were also shown to peak in March in Tudor creek Kenya in 1992 (Kasyi, 1994). Bryceson (1982) also showed that phytoplankton, nitrates and the nitrogen fixing bacteria *Oscillatoria erythraea* (Linnaeus) also peaked around this time in inshore waters off the coast of Tanzania.

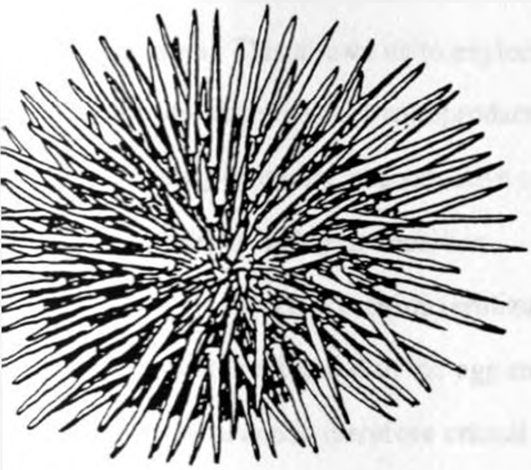
The correlation between the mean monthly gonad index and the mean monthly chlorophyll **a** concentrations of the studied reefs was not significant (Fig. 2.11(B)) however the correlation between mean monthly chlorophyll **a** concentrations off set by one month against mean monthly gonad indices showed a significant correlation. There is a delay between spawning which peaks in February- March and the peak of phytoplankton in March-April. *E. mathaei* larvae in the laboratory may start feeding within 2 days of fertilization (Hinegardener, 1969), this period however may be longer in nature. Spawning before rather than at the phytoplankton peak would ensure that there is enough food resources for the extended larval planktonic period which could be up to 30 days. A similar scenario was suggested by Lessios (1981) in *Echinometra vanbrunti* where spawning maybe initiated before the peak in phytoplankton to allow feeding larvae to reach maximum size when food resources are also at a maximum.

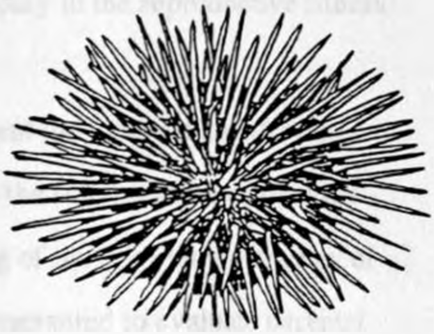
Whether chlorophyll a concentrations actually induced *E. mathaei* to start spawning was not established in the present study. Starr *et al*., (1990) showed that concentrations of chlorophyll a between 2 - 4 mg /m^3 could induce spawning in *S. purpuratus* . The highest measurements of chlorophyll a encountered in this study were between 1.8 and 1.9 mg/m^3. Bryceson (1982) reported chlorophyll a measurements of between 0.9 to 1.0 mg/m^3 in surface waters off the Tanzanian coastline and Kasyi (1994) reported mean monthly concentrations between 0.6 to 2.5 mg/m^3 in creek waters at the mouth of the Tudor creek, Kenya. It is not inconceivable therefore, that chlorophyll concentrations that are high enough to induce spawning could occur periodically on these reefs during the NEM period when light and temperatures are high and winds are low. A more intensive sampling program than was carried out in the present study could measure high concentration chlorophyll spikes capable of triggering spawning. Further experimentation however on the effects of chlorophyll concentrations would have to be carried out before conclusive statements about the influence of phytoplankton concentration on the spawning activity of *E. mathaei* can be made.

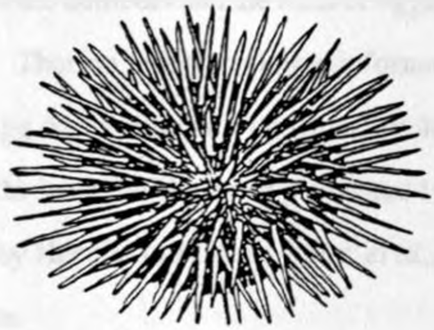
CHAPTER THREE

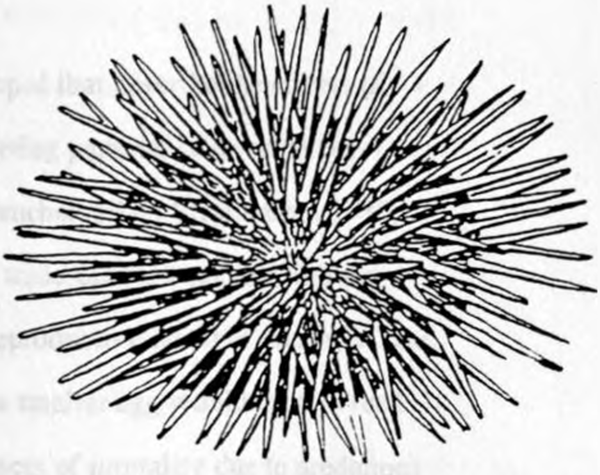


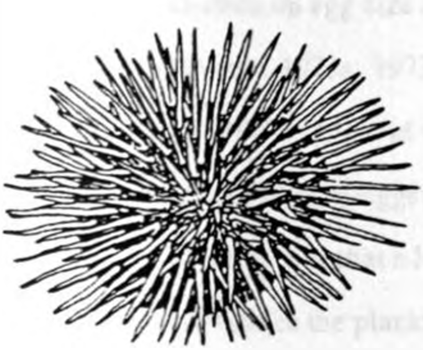
Reproductive Output, Fecundity and Egg size in three populations of the Indo-Pacific Sea urchin *Echinometra mathaei* (de Blainville) on Kenyan reefs











INTRODUCTION

Traditional population biology theory states that animals have limited resources and must partition them between growth, reproduction and maintenance (Gadgil and Bossert, 1970). In its simplest form the allocation model suggests that animals with adequate food resources will allocate more of these resources to the production of gametes thereby showing higher reproductive fitness then animals without adequate resources. The sea urchin *Echinometra mathaei* occurs at different densities on reefs in Kenya. This allows us to explore the effects that population density has on the allocation of resources to reproduction and to test the role that life history parameters including fecundity, reproductive output and egg size play in the reproductive fitness of urchins at different densities.

In most sea urchins fertilization and development are external and the amount of resources allocated to the egg and sperm represents the full measure of parental investment and is therefore critical to an understanding of the life history strategy of the animal. The main life history parameters that are measured to evaluate parental investment are the numbers and the sizes of eggs that a female produces relative to maternal size. Thorson (1950) reviewed information from marine invertebrates and showed that egg size correlated with fecundity, larval development (feeding or non-feeding) and the length of the larval period and larval habitat. More recent reviews on echinoderms by Hendler (1975) and Emlet *et al*., (1987) have further supported these generalizations.

Several qualitative models have been developed that describe the effects of natural selection on egg size and number given differing parental investment per offspring (Vance 1973a, 1973b; Christiansen and Fenchel, 1979; Strathmann, 1985; Emlet *et al*., 1987). Most of these models predict a trade-off between the numbers (fecundity) and sizes of eggs a female produces if reproductive effort is constant. The basic assumption was that a larva developing from a smaller egg would need to feed for a longer time in the plankton (increasing its chances of mortality due to predation) than a larva developing from a larger egg (Emlet *et al.*, 1987). Hence females would either produce large numbers of small eggs or small numbers of large yolky eggs.

The implicit assumption in all these models is that egg size is related to egg quality hence egg size reliably indicates the level of parental investment (i.e. larger eggs contain more organic material). Egg size, however, is a very variable parameter and can vary within a single individual, among individuals and may also vary within species at different locations and time (Emlet *et al.*, 1987; Lessios, 1987). It is also difficult to make reliable comparisons between studies because different measures of egg size are used including egg diameter and egg volume. Emlet *et al.*, (1987) summarized data from several sources (Turner and Rutherford, 1976; Strathmann and Vedder, 1977; Turner and Lawrence, 1979; Lawrence *et al.*, 1984; Emlet, 1986) and concluded that egg diameter is a generally reliable measure of parental investment in echinoderms since larger eggs generally had more organic matter per egg.

Emlet's *et al.*, (1987) conclusion was drawn from studies comparing egg sizes of different species and even different families of echinoderms. The variation in egg size within a species, however, may be much more useful for looking for relationships between egg size and other life history parameters because many confounding factors are thus eliminated (Lessios, 1987). McEdward and Carson (1987) also argue that natural selection would operate directly on intraspecific variation in egg size and not on interspecific variation in egg size and therefore the use of interspecific results to predict parental investment and adult fitness may not be appropriate.

Several studies have been carried out on the relationship between egg size and organic content within a species. McEdward and Coulter (1987) showed that egg size (measured as egg volume) and organic content varied considerably within a single spawn of the star fish *Pteraster tesselatus* and that larger eggs did not have higher organic content. McEdward and Carson, (1987) also showed that in the starfish *Solaster stimpsoni* Verrill, egg size varied considerably between locations and that there was no relationship between egg volume and organic content. George *et al.*, (1991) looked at the effects of maternal nutrition on the size of the eggs of the starfish

Luidia clathrata (Say) and showed that egg size was not a reliable measure of egg quality. Egg size is not always an unreliable measure of parental investment in a species, however, since in a recent study by George (1994b) large eggs had a higher protein content then small eggs in the brooding starfish *Leptasterias epichlore* (Brandt).

Population biologists have also used the generalization that within the species a larger individual will have greater reproductive success because they produce more gametes (Williams, 1975). Larger individuals have been shown to produce more gametes in starfish (Chia, 1966; Himmelman *et al*., 1982; George, 1994a, 1994b) and sea urchins (Ebert, 1968; Gonor, 1972). However, the size an animal attains is often a function of the availability of resources. The resources available to an animal are controlled by many factors including spatial and temporal availability (Levitan, 1989; George *et al*., 1991), the ability of the animal to acquire resources which may depend on, among other things, the size of the food gathering apparatus or competition with conspecifics (Ebert, 1982; McClanahan, 1988a; Levitan, 1989).

In a study by George (1994b) females of the brooding starfish *Leptasterias epichlora* from a favorable environment (more and larger prey items) were larger on average and produced more and larger eggs with higher protein content than females collected from an unfavorable environment. This study validated life history models that incorporate the nutritional state of the female with size of females and parental care. Levitan (1991) argued a simplified strategy to maximize reproductive fitness in a population influenced by spatial and temporal fluctuations in food availability would be a trade-off between (1) large individuals with high individual gamete production at low population density or (2) small individuals with low gamete production and higher population density. The disadvantage of low population density (i.e. lowered fertilization success) could be balanced by production of more gametes as a result of larger maternal size. Conversely, the lowered reproductive output of small-sized animals could be balanced by increased fertilization success due to the close proximity of conspecifics.

The sea urchin *E. mathaei* is widely distributed throughout the Indo-Pacific (Clark and Rowe, 1971). In Kenya it is a common inhabitant of reef lagoons where it occurs at different densities correlated to the level of human use (McClanahan and Kurtis, 1991). No studies on the influence of population density on the life history parameters of animal size, egg size and fecundity of *E. mathaei* have been reported. Comparison between different populations of *E. mathaei* on Kenyan reefs allows for the testing of life history models that incorporate population density, animal size and egg size and reproductive output. The specific objectives of this study were to determine 1) the influence of population density on maternal size, reproductive output and fecundity and 2) the influence of population density on egg size of *E. mathaei*.

MATERIALS AND METHODS

Study sites

A detailed description of the study sites is given in chapter one. The three reef lagoons differ in population density of *Echinometra mathaei* with Vipingo having a lowest density, Kanamai an intermediate density and Diani the highest density of *E. mathaei*. This enabled comparisons to be made between reefs in relation to population density.

Reproductive output

The reproductive output of *E. mathaei* was investigated by inducing urchins to spawn using 0.5 M KCl. Sampling was carried out twice during the peak months of reproduction (February and March) in 1993,1994 and 1995. Approximately 100 urchins were collected at each reef and transported to the KMFRI laboratories. Individual urchins were induced to shed eggs by a 0.5 ml to 1 ml injection of 0.5 M KCl solution through the peristomial membrane into the perivisceral cavity. KCl stimulates muscles in ovaries and testis to contract thus causing a release of gametes (Thompson, 1982). The volume of eggs released can therefore be assumed to be a relative measure of the reproductive output of an urchin. Urchins that started spawning in the bucket prior to injection were discarded to avoid errors introduced due to the loss of eggs. The test diameter and weight of females that started spawning were quickly measured and the urchins were then inverted over a petri dish and allowed to spawn until no more eggs were released.

Egg samples were washed with filtered sea water into graduated centrifuge tubes and spun at 2000 g for 1 minute. This procedure does not damage or distort the eggs (Hinegardner, 1975). The total volume of eggs released by each individual female was measured to 0.01 ml. Twenty 0.1 ml samples of eggs from individual urchins at each reef were preserved in 4% formalin for future counts.

The number of eggs per unit volume were calculated by counting eggs in the 0.1 ml preserved samples. The 0.1 ml preserved samples were individually poured into a 200 ml stoppered plastic container filled with water. The container was then inverted 10 times to disperse the eggs evenly in the water column. The eggs in five 0.1 ml subsamples (sampled with an automatic pipette) were counted under a dissecting microscope. The variability between subsamples was very low ($F = 0.43$, $p = 0.76$) and therefore only 2 subsamples were counted for each individual urchin. The relationship between the volume of eggs spawned and the number of eggs in the same volume of eggs was estimated using regression analyses. There was a positive and significant relationship between egg number and egg volume (for Vipingo: Egg number = $1.8 \times 10^5 + 7.75 \times 10^5$ egg volume; $r = 0.87$; $n = 17$; $p < 0.01$ and For Kanamai and Diani: Egg number = $1.2 \times 10^5 + 6.15 \times 10^5$ egg volume, $r = 0.79$; $n = 15$; $p < 0.01$). These formulae were used to convert the volume of eggs released by all urchins to the equivalent number of eggs.

Fecundity estimation

The fecundity of *E. mathaei* was measured in February and March of 1995. The months of February and March were selected because a) gonad indices peaked at all reefs during these months indicating a readiness to spawn (Fig. 2.3), b) the percentage of large ova (75 - 80 um) was highest in ovarian lobes in February indicating the gonads were ripe during this time (Fig. 2.7) and c) the frequency of urchins spawning after KCl injection also peaked in February and March indicating that most of the urchins were ready to spawn at this time (Fig. 2.4).

Several estimates of fecundity were used including a) absolute fecundity (AF) or the total number of eggs that can be produced per female during the reproductive period each year, b) relative fecundity (RF) which refers to the number of eggs per unit maternal weight c) population fecundity (TF) or the number of eggs a population produces per unit area.

Urchins were collected at each reef and transported in a bucket to the KMFRI laboratory. Urchins were weighed, their test diameter measured and the gonads dissected. The gonad of each individual urchin was weighed and macerated using a mortar and pestle in 4% formalin. The eggs were then passed through a 200 um sieve (to eliminate debris and excess ovarian tissue) onto a 50 um sieve. The eggs were washed several times with fresh water and the sieve with eggs was drained on absorbent paper.

The total weight of eggs was measured for each urchin and the eggs from a subsample of known weight were counted. The total number of eggs in the gonad (AF) was calculated using the formula: AF = the total weight of eggs/weight of subsample of egg x number of eggs in a subsample). Since the estimation of fecundity required extraction of all the eggs from the gonads and sub-sampling a portion of the eggs for counting, there was a potential of introducing error at various stages. A test was, therefore, performed a) to estimate the variability between egg counts from subsamples of eggs extracted from each individual gonad and b) to estimate variability in the number of eggs counted from different aliquots of eggs in each subsample c) to determine if all females had to be processed and counted separately or whether a general factor could be used to calculate the fecundity of any gonad of known weight.

The test was carried out on five females which were haphazardly selected and processed. The eggs were extracted from each gonad and the total weight of eggs from each female was measured (total weight of eggs or TEW). Five replicate subsamples from each female were weighed (weight of sub-sampled eggs or SEW) and processed for counting. Each subsample was mixed with 200 ml fresh water and five 0.1 ml aliquots were counted under a dissecting microscope. The number of eggs in each sample was calculated using the following formula: Egg count = number of eggs in an aliquot x the dilution factor x (TEW/SEW): where TEW = total weight of eggs extracted from an individual female, SEW = weight of eggs of a subsample and the dilution factor = volume of egg suspension/volume of the aliquot (200 ml/0.1 ml).

A two factor ANOVA was performed to test for differences between the subsamples of each female.

Table 3.1. Summary table of two factor ANOVA comparisons of a) differences between egg counts of subsamples from individual females of *Echinometra mathaei* and differences between egg counts of subsamples from different females and b) differences between egg counts in different aliquots from the same sample and differences between aliquots from different samples.

Source	*df*	*MS*	*F*	*p*
a) Subsamples within individuals	4	5.4×10^{10}	1.82	ns
Samples between individuals	4	1.1×10^{12}	36.33	0.0000
Error	16	3.0×10^{10}		
b) Aliquots within individuals	4	1.0×10^{10}	0.71	ns
Samples between individuals	4	7.1×10^{11}	49.54	0.0000
Error	16	1.4×10^{10}		

As there was no significant difference between the number of eggs in replicate subsamples from each gonad (Table 3.1), it was decided therefore to take only one subsample for counting to minimize time spent counting. However, there was a significant difference (p = 0.000) between the number of eggs calculated for samples from different individuals indicating that a general factor could not be used to extrapolate the number of eggs in each gonad from the TEW and that samples from each female had to be counted separately. The differences between the numbers of eggs counted in different aliquots from the same gonad were also tested using a two factor ANOVA (Table 3.1). Again a significant difference was found between individual samples ($p = 0.000$) but not between aliquots of the same sample. A decision was therefore made to take only two aliquots per sample to minimize counting time.

Several regressions were performed to test for relationships between a) AF and urchin body size (test diameter) and (b) AF and gonad weight. A single factor ANOVA was also performed to test for significant differences between the AF at all the reefs. To determine whether eggs at one reef were heavier than at another, a regression was also performed between the weight of eggs in relation to the number of eggs at each reefs. The relative fecundity of *E. mathaei* at each reef was also calculated for the same urchins using the formula: $RF = AF/(TW - TEW)$ where AF = absolute fecundity, TEW = total egg weight (gm) and TW = total body weight (gm). The mean (± sem) RF was calculated for each reef. A single factor ANOVA was also performed to test for significant differences of the RF between reefs.

Egg size

Two measures of the egg size of *E. mathaei* were investigated, namely the diameter and the weight of the eggs. The weight of the eggs was investigated by extrapolation from the relationship between the numbers of eggs and their weight, data collected during fecundity studies. The diameter of the eggs at each site were measured on fresh material. Samples for egg measurements were collected in February 1994 and 1995 to check for differences between years at each reef and in January 1995 for comparison between months within the same year at each reef. Samples from each reef were treated following the same general procedure. A sample of eggs from batches of eggs released after KCl injection was mounted onto a slide with a central depression to avoid distorting the eggs. Since *E. mathaei* eggs are round, the diameters of 100 to 200 haphazardly selected eggs were then measured using an ocular micrometer mounted in a Leitz compound microscope.

For comparison between reefs, eggs were collected from several individuals and pooled for each reef prior to measurement. Eggs from 10 to 20 individual urchins of known size (test diameter) were also measured to test for a relationship between urchin size and egg size at each reef.

The data were processed in several ways. For comparisons between reefs and between years at each reef, a mean egg diameter (± sem) was calculated for each reef each year, and the results were plotted for each reef against the year. An ANOVA analysis was performed on the individual egg sizes at each reef to test for differences between reefs and within reefs between years. The relationship between urchin size and egg size was analyzed by correlating mean egg diameter and urchin test diameter at each reef.

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 to 1994, *E. mathaei* density was estimated by haphazardly tossing a $1m^2$ quadrat onto the reef and counting all *E. mathaei* encountered in 30 quadrats and calculating the mean number of urchins per m^{-2}. The variability between reefs and between years at each reef was tested using a two-way ANOVA test.

Food quality and quantity

The availability and quality of food at each reef was assessed by comparing the size of the guts and the amount of organic matter within the guts of urchins as well as taking measurements of the size of the stomach of urchins at each reef. This was carried out by dissecting and weighing the guts from the esophagus to the anus and contents of at least 100 urchins from each reef and calculating a gut index (Gut index = wet weight of gut/wet weight of urchin x 100). The amount of organic matter in the guts was estimated by drying the guts, treating the dry guts with 0.5 M HCL (which removes $CaCO_3$), drying and weighing the contents of the guts again, to estimate the fraction of organic matter in the guts .

The ability to acquire and digest food was assessed by measuring the relative sizes of the stomachs and of the Aristotle's lanterns (jaws) of urchins at each reef. The stomachs of 20-30 urchins of known weight were removed and all the contents discarded before weighing to the nearest 0.001 gm and calculating a stomach index. The jaw of urchins was also removed and weighed and a jaw index calculated for urchins at all reefs (n = 200).

The availability of potential food sources was additionally assessed using substrate cover data collected in 1987, 1991 to 1994 at all three reefs (McClanahan unpublished data). The mean percent cover of algal turf, fleshy, calcareous and coralline algae and seagrass were calculated for twelve 10 m long line transects laid haphazardly at each reef each year. The average percent cover and standard error of the mean of each substrate category for each years at each reef are graphically represented.

RESULTS

Reproductive output

Table 3.2 shows the mean reproductive output (mean volume of eggs spawned after KCl injection) for a) each reef each year for pooling data for February and March of each year, and b) for each reef in all years by pooling data from 1993 to 1995.

Table 3.2. The reproductive output of *Echinometra mathaei* at Diani, Kanamai and Vipingo represented as the mean volume (ml ± sem) of eggs released after injection with KCl in February and March each year. The numbers in brackets represent the mean volume of eggs converted to the number of eggs (x10^6).

Reef	*1993*	*1994*	*1995*	*All years*
Diani	0.71 ± 0.03 n = 83 (0.55 ± 0.02)	1.06 ± 0.08 n = 89 (0.76 ±.0.05)	1.30 ± 0.1 n = 56 (0.90 ± 0.06)	0.99 ± 0.04 n = 228 (0.72 ± 0.03)
Kanamai	0.60 ± 0.02 n = 80 (0.48 ± 0.01)	1.00 ± 0.08 n = 113 (0.76 ± 0.05)	0.89 ± 0.09 n = 40 (0.66 ± 0.15)	0.85 ± 0.04 n = 233 (0.63 ± 0.03)
Vipingo	0.99 ± 0.06 n = 95 (0.95 ± 0.05)	1.36 ± 0.16 n = 95 (1.23 ± 0.08)	1.69 ± 0.18 n = 51 (1.48 ± 0.14)	1.28 ± 0.06 n = 241 (1.17 ± 0.05)

The number of eggs corresponding to the mean egg volume is also included. The reproductive output was variable and increased from 1993 to 1995 at Diani and Vipingo. At Kanamai there was an increase from 1993 to 1994, but there was no difference between 1994 and 1995. Urchins at Vipingo had a higher mean reproductive output (~ 20% or higher) each year than urchins at Diani or Kanamai, while urchins at Diani had a mean reproductive output that was higher than urchins at Kanamai in all years.

Table 3.3. Summary table of a two way ANOVA comparison of the volume of eggs (ml) released by *Echinometra mathaei* after KCl injection between reefs and differences in the egg volume released within each reef between years.

Source of Variation	*df*	*MS*	*F*	*p*
Reef	2	6.58	9.22	0.0001
Year	2	18.06	25.30	0.0000
Interaction	4	1.65	2.31	ns
Within	351	0.71		

A two-factor ANOVA analysis was performed to test whether the reproductive output differed significantly from year to year and also whether the observed differences in the volume of eggs released between reefs were significant. The test requires an equal sample size so some data from Diani and Vipingo were haphazardly excluded for a sample size of 40. Reproductive outputs of *Echinometra mathaei* differed significant at the three reefs ($p = 0.000$) attributable to the higher reproductive output of urchins at Vipingo (Table 3.3). The reproductive output also differed significantly ($p = 0.0001$) between years at all the reefs, the variation between years at each reef was higher than the variation between reefs (Table 3.3).

Test diameter was significantly correlated ($p < 0.01$ level) to reproductive output at all the reefs (Table 3.4, and Fig. 3.1 A). The weight of urchins was also significantly correlated ($p < 0.01$) to reproductive output (Table 3.4 and Fig. 3.1B).

Figure. 3.1. (A) The relationship between reproductive output measured as the volume of eggs released after KCl injection and test diameter of *Echinometra mathaei* at Diani, Kanamai and Vipingo. (B) The relationship between reproductive output and the weight of *E. mathaei* from Diani, Kanamai and Vipingo.

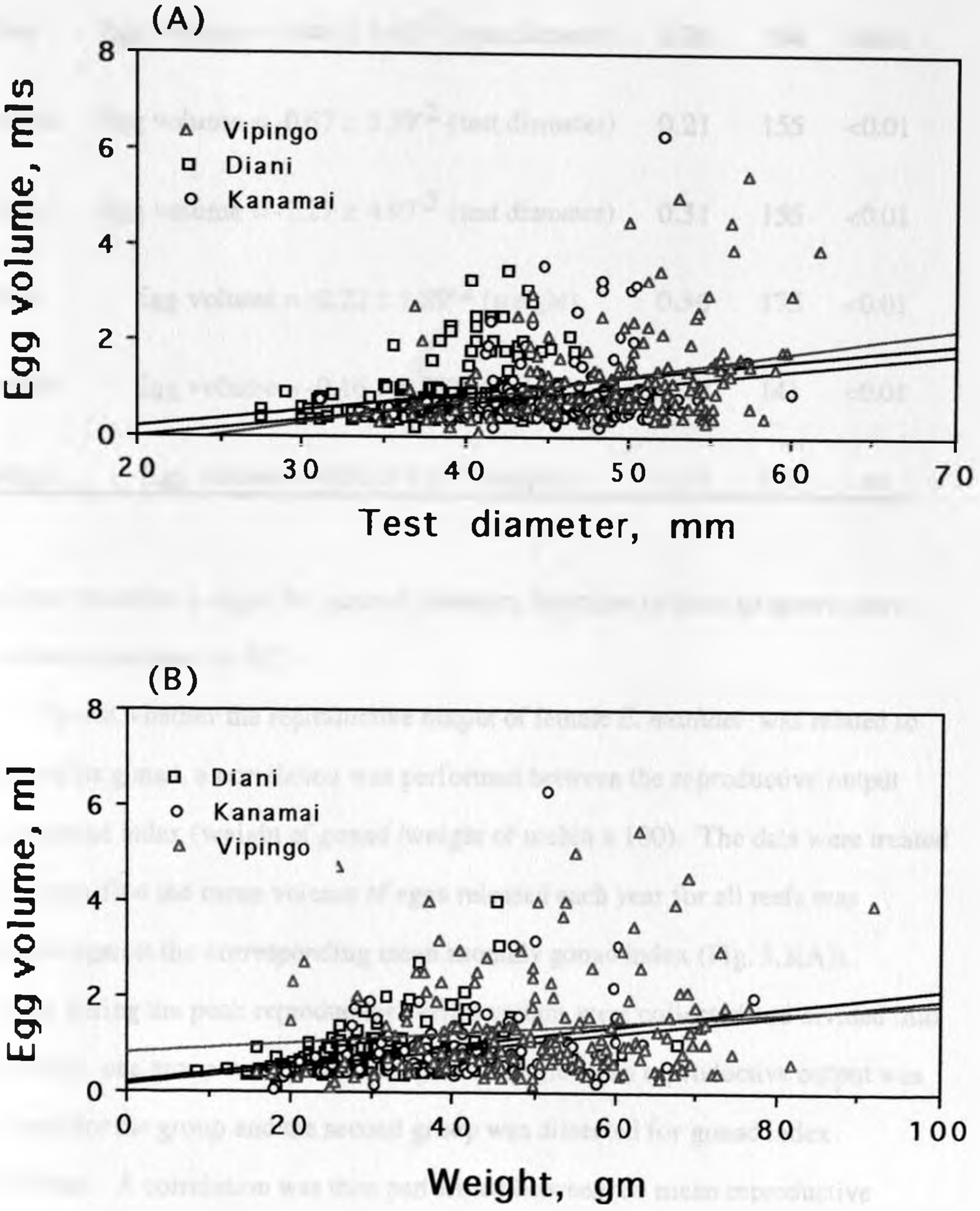

(A)
Vipingo
Diani
Kanamai
Egg volume, mls
0
2
4
6
8
20
30
40
50
60
70
Test diameter, mm
(B)
Diani
Kanamai
Vipingo
Egg volume, ml
0
2
4
6
8
0
20
40
60
80
100
Weight, gm

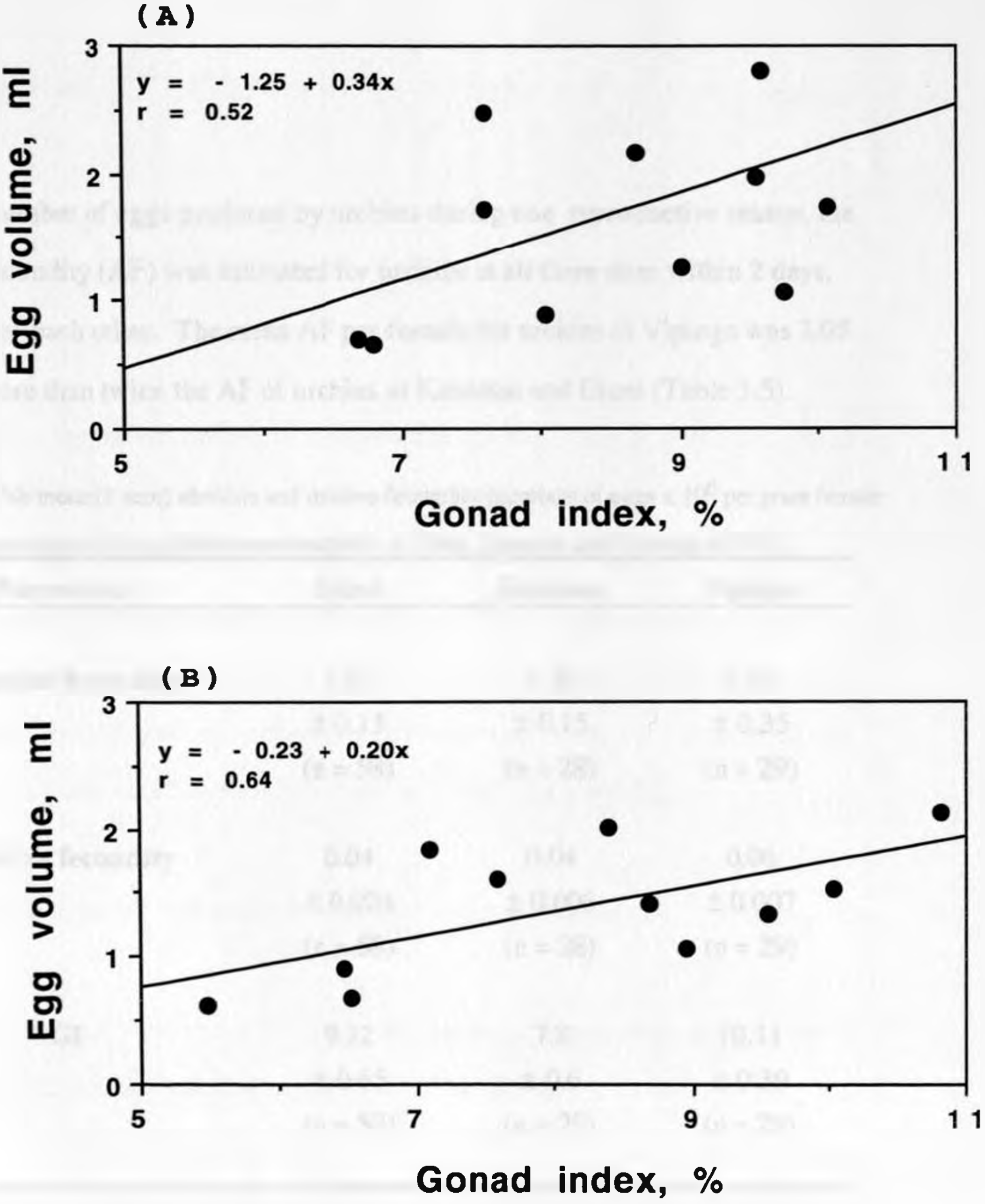
Table 3.4. The relationship between the volume of eggs (ml) released by individual *Echinometra mathaei* after KCl injection and their test diameter (mm) and weight (gm), collected from Diani, Kanamai and Vipingo.

Reef	*Correlation*	*r*	*n*	*p*
Diani	Egg volume = -0.48 ± 3.43^{-2} (test diameter)	0.26	184	<0.01
Kanamai	Egg volume = -0.67 ± 3.39^{-2} (test diameter)	0.21	155	<0.01
Vipingo	Egg volume = -1.27 ± 4.97^{-2} (test diameter)	0.31	155	<0.01
Diani	Egg volume = -0.22 ± 1.89^{-2} (weight)	0.36	175	<0.01
Kanamai	Egg volume = -0.16 ± 1.78^{-2} (weight)	0.28	141	<0.01
Vipingo	Egg volume = -0.81 ± 1.0^{-2} (weight)	0.14	175	ns

There was therefore a slight but general tendency for larger urchins to spawn more eggs when stimulated by KCl.

To test whether the reproductive output of female *E. mathaei* was related to the size of its gonad, a correlation was performed between the reproductive output and the gonad index (weight of gonad /weight of urchin x 100). The data were treated in two ways, first the mean volume of eggs released each year for all reefs was correlated against the corresponding mean monthly gonad index (Fig. 3.2(A)). Secondly during the peak reproductive period urchins were collected and divided into two groups, one group was induced to spawn and the mean reproductive output was calculated for the group and the second group was dissected for gonad index calculations. A correlation was then performed between the mean reproductive output and the mean gonad index of urchins collected on the same day (Fig. 3.2(B)). This was carried out at each reef three times in February and March 1995.

Figure. 3.2. (A) The relationship between the mean monthly reproductive output measured as the volume of eggs released after KCL injection and the mean monthly gonad index of *Echinometra mathaei* at all reefs, $n < 60$. (B) The relationship between the mean reproductive output and the gonad index of urchins collected on the same day during the peak reproductive months in 1994 and 1995 for all reefs, $n < 60$.


(A)
y = - 1.25 + 0.34x
r = 0.52
Egg volume, ml
0
1
2
3
5
7
9
11
Gonad index, %
(B)
y = - 0.23 + 0.20x
r = 0.64
Egg volume, ml
0
1
2
3
5
7
9
11
Gonad index, %

The relationship between the mean monthly reproductive output and the mean monthly gonad index was not significant ($r = 0.52$, $n = 11$). The relationship between the reproductive output and the gonad index of urchins sampled on the same day however was significant ($r = 0.64$, $p < 0.05$, $n = 11$). In general therefore urchins with larger gonads tended to release more eggs.

Fecundity

The total number of eggs produced by urchins during one reproductive season, the absolute fecundity (AF) was estimated for urchins at all three sites within 2 days, collection of each other. The mean AF per female for urchins at Vipingo was 3.05 million, more than twice the AF of urchins at Kanamai and Diani (Table 3.5).

Table 3.5. The mean (± sem) absolute and relative fecundity (numbers of eggs x 10^6 per gram female) and the gonad index (%) of *Echinometra mathaei* at Diani, Kanamai and Vipingo in 1995.

Parameters	*Diani*	*Kanamai*	*Vipingo*
Absolute fecundity	1.26 ± 0.13 (n = 58)	1.40 ± 0.15 (n = 28)	3.05 ± 0.35 (n = 29)
Relative fecundity	0.04 ± 0.004 (n = 58)	0.04 ± 0.006 (n = 28)	0.06 ± 0.007 (n = 29)
GI	9.12 ± 0.65 (n = 58)	7.8 ± 0.6 (n = 29)	10.11 ± 0.39 (n = 29)

A single factor ANOVA (Table 3.6) showed this difference to be significant ($F = 16.4$, $df = 2,89$ and $p = 0.000$).

Table 3.6. Summary table of single factor ANOVA comparisons of the differences between reefs of the absolute fecundity, the relative fecundity and the gonad index (%) of *Echinometra mathaei* at Diani, Kanamai and Vipingo reef lagoons.

Comparison	*Source*	*df*	*MS*	*F*	*P*
Absolute fecundity	Between reefs	2	2.7×10^{13}	16.4	0.0000
	Within reefs	89	1.6×10^{12}		
Relative fecundity	Between reefs	2	3.5×10^{9}	3.44	0.0361
	Within reefs	92	1.0×10^{9}		
GI	Between reefs	2	59.04	7.11	0.001
	Within reefs	101	8.3		

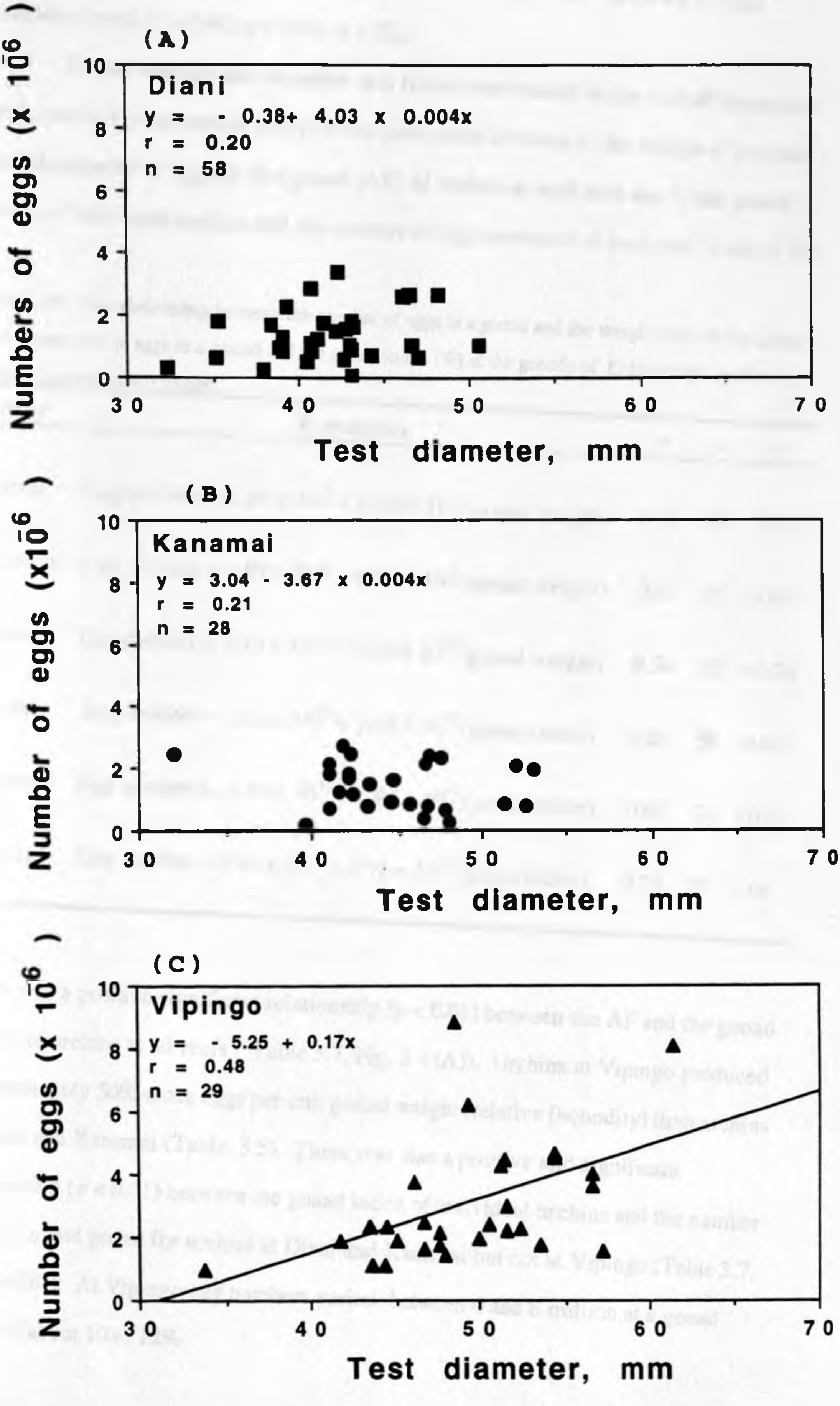
There was no significant difference between the number of eggs produced by females at Diani and Kanamai (F = 0.05, df = 1,61 and p = 0.83).

The mean number of eggs produced per gram of female (RF) was also higher at Vipingo than at either Diani or Kanamai (Table 3.5). This difference was significant (F = 3.44, df = 2,92 and p = 0.036) shown in Table 3.6) and again there was no significant difference between the mean number of eggs per gram produced by urchins at Diani and Kanamai (F = 0.31, df = 1,62 and p = 0.58).

Relationship between fecundity, urchin size and gonad size

To find out whether maternal size influenced fecundity, a regression analysis was performed between the test diameter of urchins and the AF at all the reefs (Fig. 3.3 A, B, C). There was no relationship between the number of eggs an urchin produced and its diameter for urchins at Diani and Kanamai . At Vipingo however there was a tendency for larger animals to produce more eggs (Fig. 3.3(C)).

Figure. 3.3. The relationship between fecundity (eggs/individual) and urchin size (test diameter) of *Echinometra mathaei* at Diani (A), Kanamai (B) and Vipingo (C).


(A)
Diani
y = - 0.38+ 4.03 x 0.004x
r = 0.20
n = 58
Numbers of eggs (x 10⁻⁶)
0
2
4
6
8
10
30
40
50
60
70
Test diameter, mm
(B)
Kanamai
y = 3.04 - 3.67 x 0.004x
r = 0.21
n = 28
Number of eggs (x10⁻⁶)
0
2
4
6
8
10
30
40
50
60
70
Test diameter, mm
(C)
Vipingo
y = - 5.25 + 0.17x
r = 0.48
n = 29
Number of eggs (x 10⁻⁶)
0
2
4
6
8
10
30
40
50
60
70
Test diameter, mm

The relationship was expressed by the formula: AF ($X10^{-6}$) = -5.25 + 0.17 (test diameter/ mm) ($r = 0.48$, $p < 0.01$, $n = 28$).

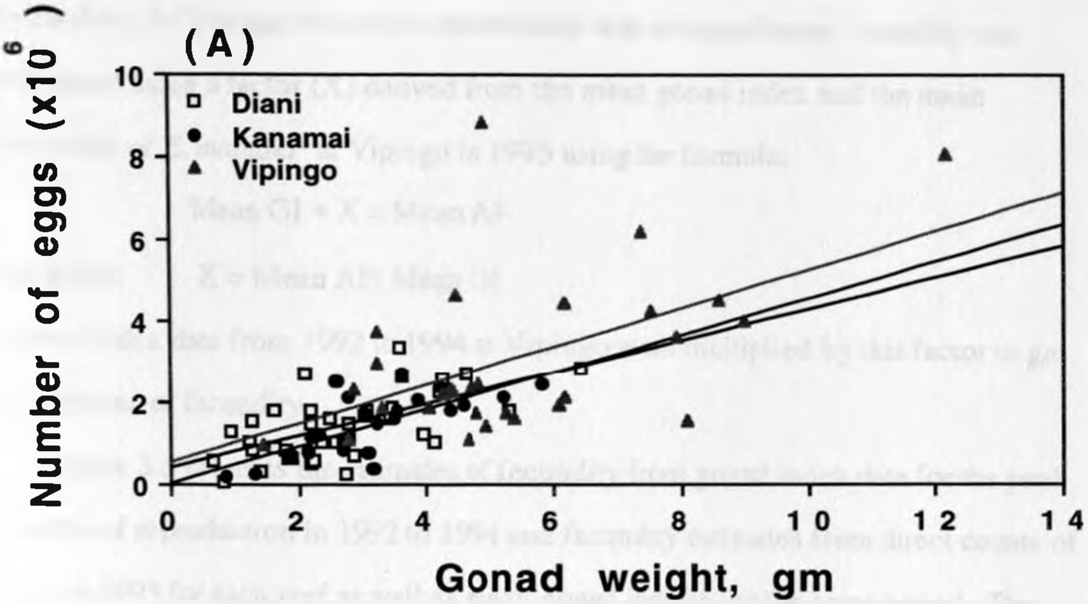
To test whether the fecundity of a female was related to the size of the gonad in *E. mathaei* a regression analysis was performed between a) the weight of a gonad and the number of eggs in that gonad (AF) of urchins at each reef and b) the gonad index of individual urchins and the number of eggs produced at each reef (Table 3.7).

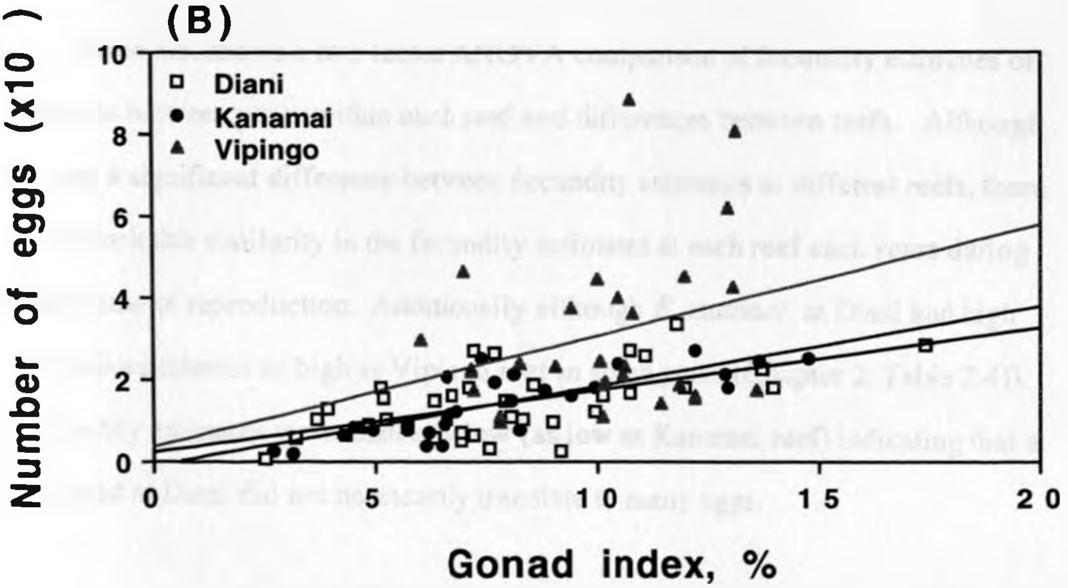
Table 3.7. The relationship between the number of eggs in a gonad and the weight (gm) of that gonad and the number of eggs in a gonad and the gonad index (%) of the gonads of *Echinometra mathaei* at Diani, Kanamai and Vipingo.

Reef	*Regression*	*r*	*n*	*p*
Diani	Egg number = $3.63 \times 10^5 + 3.89 \times 10^5$ (gonad weight)	0.61	37	<0.01
Kanamai	Egg number = $3.07 \times 10^4 + 4.50 \times 10^5$ (gonad weight)	0.64	28	<0.01
Vipingo	Egg number = $5.10 \times 10^5 + 4.69 \times 10^5$(gonad weight)	0.54	29	<0.01
Diani	Egg number = $1.05 \times 10^5 + 1.48 \times 10^5$ (gonad index)	0.63	58	<0.01
Kanamai	Egg number = $-1.34 \times 10^5 + 1.95 \times 10^5$ (gonad index)	0.80	28	<0.01
Vipingo	Egg number = $3.03 \times 10^5 + 2.71 \times 10^5$(gonad index)	0.29	29	ns

There was a positive significant relationship ($p < 0.01$) between the AF and the gonad weight of urchins at all reefs (Table 3.7, Fig. 3.4 (A)). Urchins at Vipingo produced approximately 50% more eggs per unit gonad weight (relative fecundity) than urchins at Diani and Kanamai (Table. 3.5). There was also a positive and significant relationship ($p < 0.01$) between the gonad index of individual urchins and the number of eggs in that gonad for urchins at Diani and Kanamai but not at Vipingo (Table 3.7, Fig. 3.4(B)). At Vipingo egg numbers varied between 4 and 8 million at a gonad index of about 10 to 12%.

Figure. 3.4. (A) The relationship between the fecundity (eggs/individual) and the gonad weight of *Echinometra mathaei* at Diani, Kanamai and Vipingo (n = 37, 28 and 29 respectively). (B) The relationship between fecundity and gonad index of *E. mathaei* at Diani, Kanamai and Vipingo (n = 38, 28 and 29 respectively).


(A)
Diani
Kanamai
Vipingo
Number of eggs (x10 6)
0
2
4
6
8
10
0
2
4
6
8
10
12
14
Gonad weight, gm


(B)
Diani
Kanamai
Vipingo
Number of eggs (x10 6)
0
2
4
6
8
10
0
5
10
15
20
Gonad index, %

Since gonad index data were available for urchins at all reefs in 1992 to 1994 (Chapter 2, Table 2.4), it was possible to estimate the fecundity of *E. mathaei* in those years using the relationship between gonad index and fecundity at Diani and Kanamai where a significant relationship was found between gonad index and fecundity. At Vipingo where this relationship was not significant, fecundity was estimated using a factor (X) derived from the mean gonad index and the mean fecundity of *E. mathaei* at Vipingo in 1995 using the formula:

Mean GI * X = Mean AF

therefore: X = Mean AF/ Mean GI

Gonad index data from 1992 to 1994 at Vipingo were multiplied by this factor to get an estimate of fecundity.

Figure 3.5 presents the estimates of fecundity from gonad index data for the peak months of reproduction in 1992 to 1994 and fecundity estimates from direct counts of eggs in 1995 for each reef as well as mean gonad indices for the same period. The fecundity estimates for *E. mathaei* at Vipingo are twice as high as those for Diani and Kanamai each year while the fecundity estimates for Diani and Kanamai are similar over these years.

Table 3.8. shows a two-factor ANOVA comparison of fecundity estimates of differences between years within each reef and differences between reefs. Although there was a significant difference between fecundity estimates at different reefs, there was a remarkable similarity in the fecundity estimates at each reef each years during the peak time of reproduction. Additionally although *E. mathaei* at Diani had high gonad indices (almost as high as Vipingo reef in some years (Chapter 2; Table 2.4)), the fecundity estimates were relatively low (as low as Kanamai reef) indicating that a large gonad at Diani did not necessarily translate to many eggs.

Figure. 3.5. Temporal variation in fecundity and gonad index of *Echinometra mathaei* at Diani, Kanamai and Vipingo in 1992 to 1995. Bars represent mean gonad indices and mean eggs/individual (± sem) during the peak reproductive period.

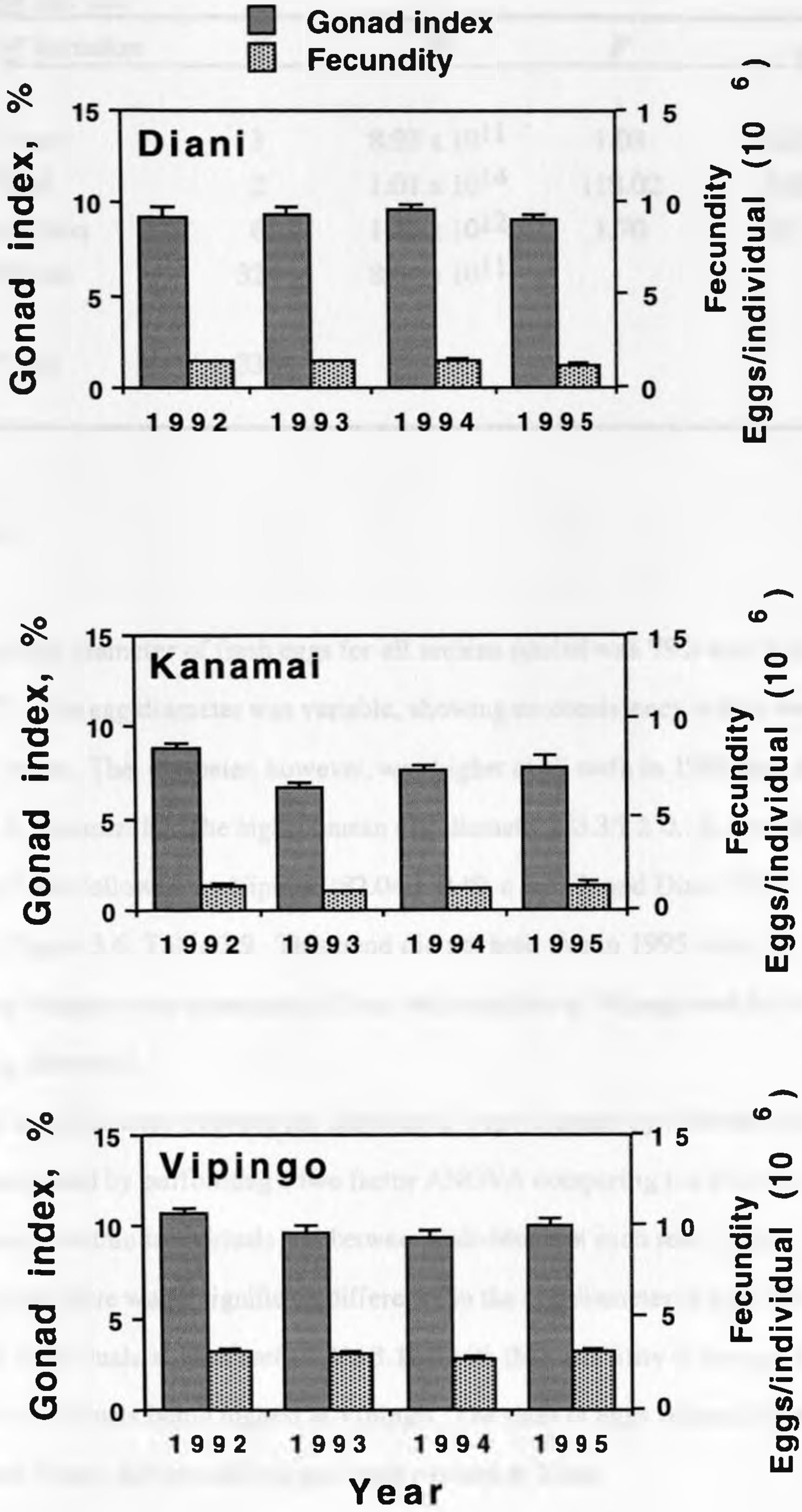

Gonad index
Fecundity
Diani
Kanamai
Vipingo
Gonad index, %
Fecundity Eggs/individual (10 6)
0
5
10
15
1992
1993
1994
1995
Year

Table 3.8. Two-factor ANOVA comparison of the fecundity of *Echinometra mathaei* within each reef between 1992 to 1995 and between reefs each year. A total of 28 fecundity estimates were used for each reefs each year.

Source of Variation	*df*	*MS*	*F*	*p*
Year	3	8.93×10^{11}	1.03	0.3781
Reef	2	1.01×10^{14}	118.02	0.0000
Interaction	6	1.47×10^{12}	1.70	0.1201
Within	324	8.64×10^{11}		
Total	335			

Egg Size

The mean egg diameter of fresh eggs for all urchins pooled was 79.3 um (± 0.11 sem, n = 1827). The egg diameter was variable, showing no consistency within reefs or between years. The diameter, however, was higher at all reefs in 1994 than in 1995. Urchins at Kanamai had the highest mean egg diameter (83.35 ± 0.18, n = 200) in February 1994 followed by Vipingo (82.04 ± 0.19, n = 557) and Diani (78.71 ± 0.17, n = 250) Figure 3.6, Table 3.9. This trend did not hold true in 1995 since the highest mean egg diameter was measured at Diani while urchins at Vipingo had the lowest mean egg diameters.

The differences between the diameter of eggs released by different individuals was investigated by performing a two factor ANOVA comparing the differences in egg diameter within individuals and between individuals at each reef. In all comparisons there was a significant difference in the egg diameter of eggs between different individuals at each reef (Table 3.10) with the variability of the egg diameter between individuals being highest at Vipingo. The sizes of eggs released by an individual female did not differ significantly except at Diani.

Figure. 3.6. The size of eggs (diameter) of *Echinometra mathaei* at Diani, Kanamai and Vipingo in 1994 and 1995. The numbers above the bars represent sample sizes.

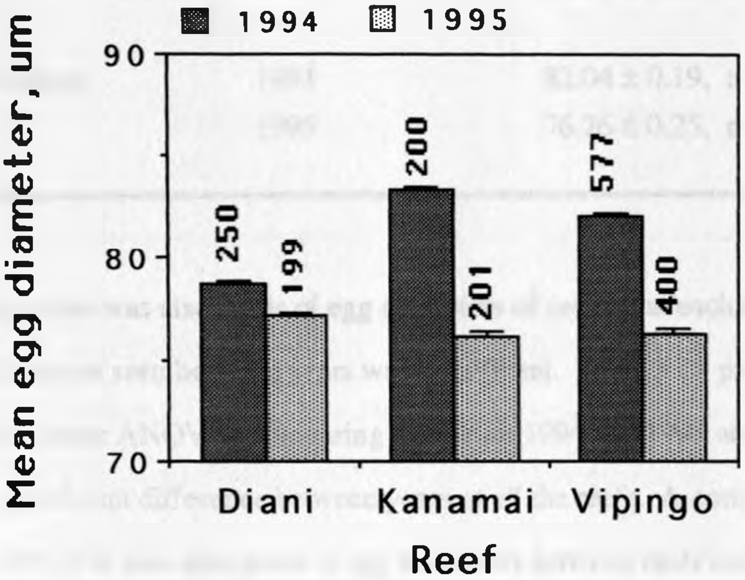

▩ 1994
▨ 1995
Mean egg diameter, um
90
80
70
250
199
200
201
577
400
Diani
Kanamai
Vipingo
Reef

Table. 3.9. The mean egg diameter (± sem) of *Echinometra mathaei* at Diani, Kanamai and Vipingo in 1994 and 1995.

Reef	***Year***	***Mean egg diameter (um)***
Diani	1994	78.71 ± 0.17, n = 250
	1995	77.10 ± 0.19, n = 199
Kanamai	1994	83.35 ± 0.18, n = 200
	1995	76.11 ± 0.22, n = 201
Vipingo	1994	82.04 ± 0.19, n = 557
	1995	76.26 ± 0.25, n = 400

A comparison was also made of egg diameters of urchins at each reef to test whether the differences seen between years was significant. Table 3.11 presents the summary of single factor ANOVAs comparing data from 1994 and 1995 at each reef. There was a significant difference between years at all the reefs. A comparison using single factor ANOVA was also made of egg diameters between reefs each year. In both years there was also a significant difference between the egg diameters of the three reefs (Table 3.12) further emphasizing the variability of egg diameter.

Table 3.10 Summary table of two-factor ANOVA comparisons of the egg diameter (um) of *Echinometra mathaei* within individuals and between individuals at Diani, Kanamai and Vipingo. Twenty five eggs per individual and ten individuals per reef were measured.

Reef	***Source of Variation***	***df***	***MS***	***F***	***p***
Diani	Within individuals	24	9.26	1.97	0.01
	Between individuals	9	60.37	12.81	0.00
Kanamai	Within individuals	24	4.44	0.86	ns
	Between individuals	9	41.69	8.04	0.00
Vipingo	Within individuals	24	9.59	1.00	ns
	Between individuals	9	571.72	59.45	0.00

Table 3.11. Summary table of single factor ANOVA comparisons of the egg diameter (um) of *Echinometra mathaei* in different years at Diani, Kanamai and Vipingo.

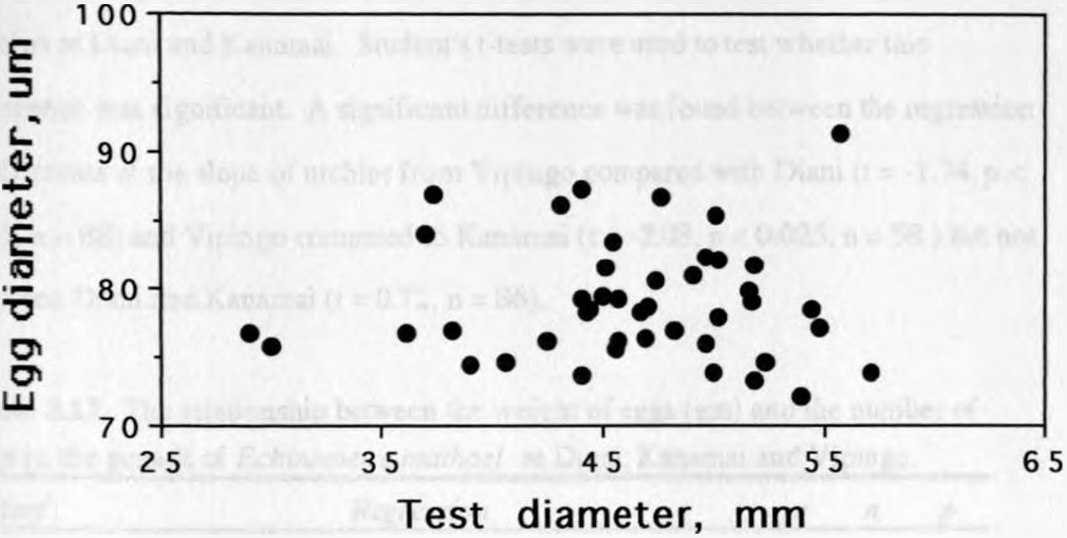
Reef	*Source of Variation*	*df*	*MS*	*F*	*p*
Diani	Between years	1	287.03	39.26	0.0000
	Within years	447	7.31		
Kanamai	Between years	1	5250.56	661.78	0.0000
	Within years	399	7.93		
Vipingo	Between years	1	7907.73	465.68	0.0000
	Within years	975	16.98		

Since individual *E. mathaei* differed in the diameter of their eggs at all the reefs, the question arose as to whether this difference was attributable to the size of the individual. A correlation analysis was therefore carried out between the test diameter of individual urchins and the average diameter of their eggs for data pooled from all reefs Fig. 3.7. There was no significant relationship between egg diameter and urchin test diameter ($r = 0.03$, $n = 44$). Therefore the differences between individual urchins were not due to the size of the urchin.

Table 3.12. Summary table of single factor ANOVA comparisons of *Echinometra mathaei* egg diameter (um) between reefs in 1994 and 1995.

Year	*Source of Variation*	*df*	*MS*	*F*	*p*
1994	Between reefs	2	60.67	6.30	0.0019
	Within reefs	797	9.64		
1995	Between reefs	2	74.98	7.22	0.0008
	Within reefs	418	10.39		

Figure. 3.7. The relationship between maternal size (test diameter) and egg size (diameter) of *Echinometra mathaei* individuals (n = 20 females) from Diani. Kanamai and Vipingo reef lagoons.


Egg diameter, um
100
90
80
70
25
35
45
55
65
Test diameter, mm

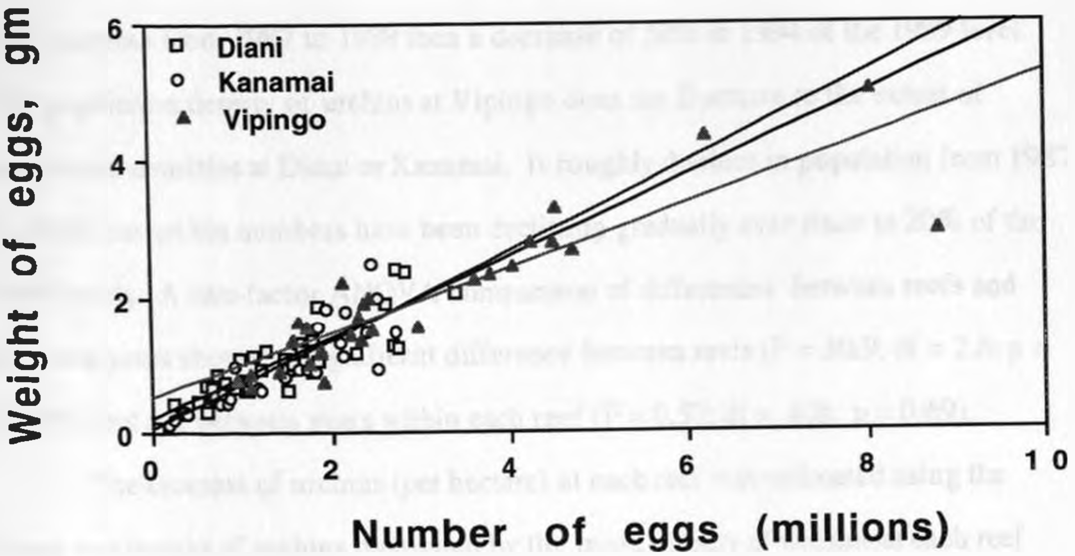
The second variable of egg size that was investigated was the weight. Since no direct measurements of individual eggs were made, data were derived from the weight of eggs in relation to the number of eggs for each reef. A regression analysis was therefore performed between the total weight of eggs (TEW) extracted from each gonad and the corresponding number of eggs (AF) at each reef. As expected there was a positive relationship between AF and TEW at all the reefs (Fig. 3.8, Table 3.13). The eggs of urchins at Vipingo were heavier on average than the eggs of urchins at Diani and Kanamai. Student's t-tests were used to test whether this difference was significant. A significant difference was found between the regression coefficients of the slope of urchins from Vipingo compared with Diani ($t = -1.74$, $p < 0.05$, $n = 88$) and Vipingo compared to Kanamai ($t = -2.03$, $p < 0.025$, $n = 58$) but not between Diani and Kanamai ($t = 0.72$, $n = 86$).

Table 3.13. The relationship between the weight of eggs (gm) and the number of eggs in the gonads of *Echinometra mathaei* at Diani, Kanamai and Vipingo.

Reef	***Regression***	***r***	***n***	***p***
Diani	Total egg weight = $0.18 + 5.97 \times 10^{-7}$ egg number	0.87	58	0.01
Kanamai	Total egg weight = $0.02 + 6.58 \times 10^{-7}$ egg number	0.86	28	0.01
Vipingo	Total egg weight = $0.51 + 4.71 \times 10^{-7}$ egg number	0.88	29	0.01

Comparisons of the regression coefficients of the intercept also showed significant differences between Vipingo and Diani ($t = 2.21$, $p < 0.025$, $n = 88$) and Vipingo and Kanamai ($t = 2.74$, $p < 0.005$, $n = 58$). Again no significance difference was found between the coefficients of the intercept between Diani and Kanamai ($t = 0.23$, $n = 86$).

Figure. 3.8. The relationship between the egg number and total egg weight of *Echinometra mathaei* at Diani, Kanamai and Vipingo, (n = 58, 28 and 30 respectively).


Diani
Kanamai
Vipingo
Weight of eggs, gm
Number of eggs (millions)
0
2
4
6
0
2
4
6
8
1 0

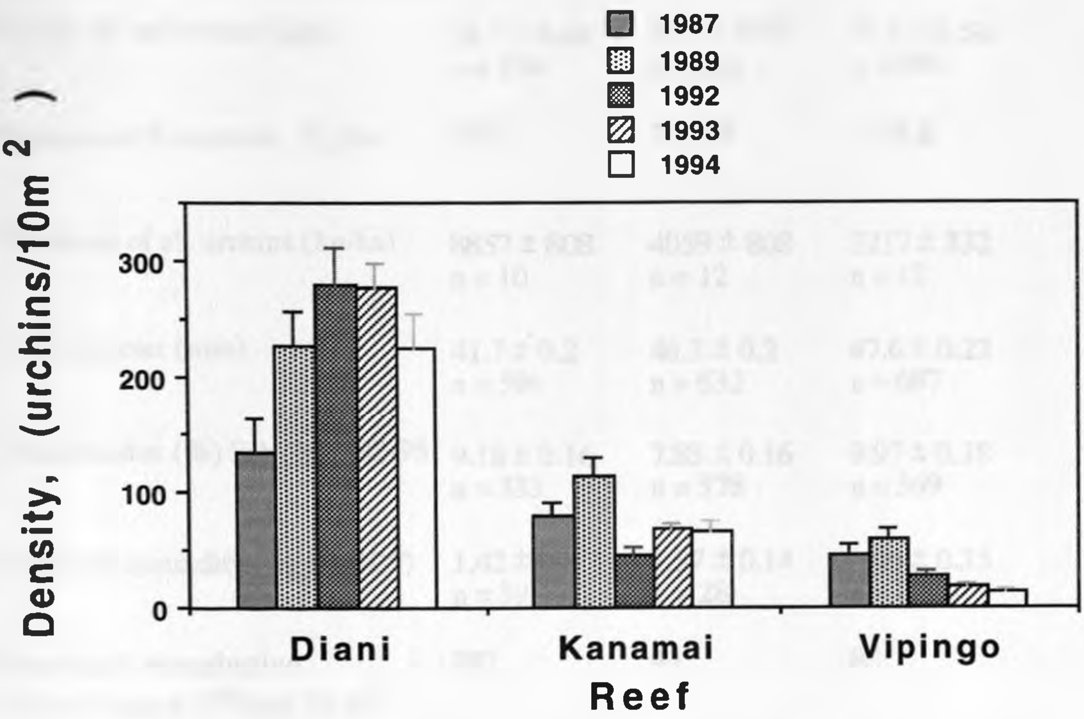
Population density

Figure. 3.9 shows the changes in *E. mathaei* density over a period of 9 years at all reefs. Diani consistently had the highest population of urchins ranging between 135 individuals/10 m^2 in 1987 to 280 individuals/10 m^2 in 1992. Vipingo consistently had the lowest population of urchins ranging from 59.6 individuals/10 m^2 in 1989 to 13 individuals/10 m^2 in 1994. Kanamai always had intermediate numbers of urchins.

The population of urchins shows varying degrees of fluctuation at all three reefs. Diani shows a doubling of the population from 1987 levels to 1992/93 then a decrease of 19% of the 1992 levels in 1994. The population at Kanamai showed a 30% increase from 1987 to 1989 then a decrease of 58% in 1994 of the 1989 level. The population density of urchins at Vipingo does not fluctuate to the extent of population densities at Diani or Kanamai. It roughly doubles in population from 1987 to 1989, but urchin numbers have been declining gradually ever since to 20% of the 1989 levels. A two-factor ANOVA comparison of differences 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 ($F = 0.57$; $df = 4,8$; $p = 0.69$).

The biomass of urchins (per hectare) at each reef was estimated using the mean wet weight of urchins multiplied by the mean density of urchins at each reef (McClanahan unpublished data). The biomass of urchins at Diani was more than 4 times the biomass of urchins at Kanamai and 8 times the biomass of urchins at Vipingo (Table 3.14). The relationship between population density and fecundity was investigated by performing a correlation analysis between the density of urchins each year at each reef and the corresponding fecundity for 1992 to 1994. The fecundity for 1992 to 1994 was estimated from the gonad indices in these years at each reef using the formula of the relationship between gonad index and fecundity (Fig. 3.4(B)). The variables were converted to log (natural) and plotted as this gave the best fit. The values for each reef tended to cluster together and there was a significant and negative relationship ($r = 0.85$, $p > 0.01$) between population density and fecundity

Figure. 3.9. The population density of *Echinometra mathaei* at Diani, Kanamai and Vipingo in 1987, 1989, 1992 to 1994. Data for 1987 and 1989 are derived from McClanahan and Muthiga, 1988 and McClanahan and Shafir, 1990. Each bar represents the mean (± sem) of *E. mathaei* in 20 to 30 quadrats.


1987
1989
1992
1993
1994
Density, (urchins/10m ^{2})
300
200
100
0
Diani
Kanamai
Vipingo
Reef

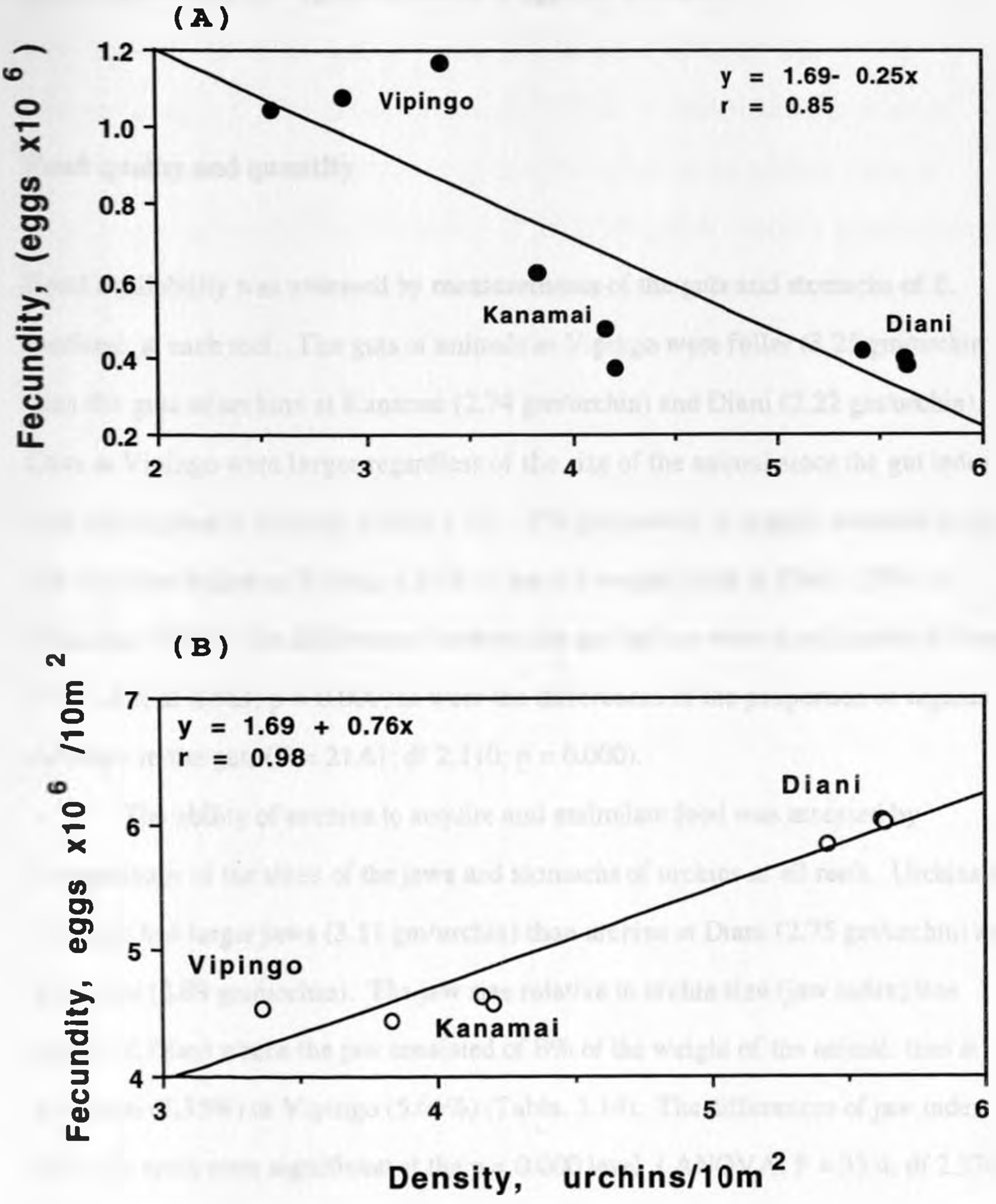
(Fig. fig 3.10(A)). Vipingo reef had high fecundity at low population densities followed by Kanamai and Diani. The variability between fecundity and population density seems to decrease rapidly above a population density of 60 urchin/10 m^2 as urchins at Kanamai

Table 3.14. Population Characteristics of *Echinometra mathaei* at Diani, Kanamai and Vipingo.

Characteristic	*Diani*	*Kanamai*	*Vipingo*
Weight of individuals (gm)	33.7 ± 0.40 n = 574	43.8 + 0.40 n = 632	47.1 ± 0.54 n = 686
Biomass of *E. mathaei* (kg/ha)	8762	2741.9	1318.8
*Biomass of all urchins (kg/ha)	8857 ± 808 n = 10	4059 ± 808 n = 12	3217 ± 332 n = 12
Test diameter (mm)	41.7 ± 0.2 n = 596	46.3 ± 0.2 n = 632	47.6 ± 0.22 n = 687
Gonad index (%) Feb- Mar 92-95	9.18 ± 0.16 n = 333	7.83 ± 0.16 n = 378	9.97 ± 0.18 n = 369
Absolute fecundity (eggs x10^6)	1.42 ± 0.8 n = 39	1.37 ± 0.14 n = 28	3.05 ± 0.35 n = 29
Population reproductive output (eggs x10^6) per 10 m^2	382	99	85
Egg size (um)	78.0 ± 0.13 n = 449	79.7 ± 0.23 n = 401	79.7 ± 0.16 n = 977
Gut index	5.98± 0.16 n = 187	6.41 ± 0.15 n = 188	7.3 ± 0.15 n = 191
Organic matter in gut (%)	19.56 ± 0.08 n = 28	28.14 ± 0.99 n = 40	29.91 ± 0.33 n = 28
Stomach index (%)	1.23 ± 0.06 n = 30	1.21 ± 0.06 n = 30	1.92 ± 0.05 n = 21
Jaw index (%)	8.17 ± 0.11 n = 234	7.35 ± 0.07 n = 176	5.66 ± 0.16 n = 391

* McClanahan unpublished data. Biomass estimates are calculated from the mean of 10 to 12 samples of 15 quadrats each

Figure. 3.10. (A) The relationship between fecundity and population density of *Echinometra mathaei*. (B) The relationship between the fecundity per unit area (eggs/$10m^2$) of *E. mathaei* and population density.


(A)
Fecundity, (eggs x10 6)
1.2
1.0
0.8
0.6
0.4
0.2
2
3
4
5
6
y = 1.69- 0.25x
r = 0.85
Vipingo
Kanamai
Diani
(B)
Fecundity, eggs x10 6 /10m 2
7
6
5
4
3
4
5
6
y = 1.69 + 0.76x
r = 0.98
Diani
Vipingo
Kanamai
Density, urchins/10m 2

and Diani have similar fecundities despite the great difference in population density. The relationship between fecundity per area (i.e. eggs/10m2) and population density shows the opposite trend (Fig. 3.10 (B)) with Diani with the highest population density producing the highest numbers of eggs per unit area

Food quality and quantity

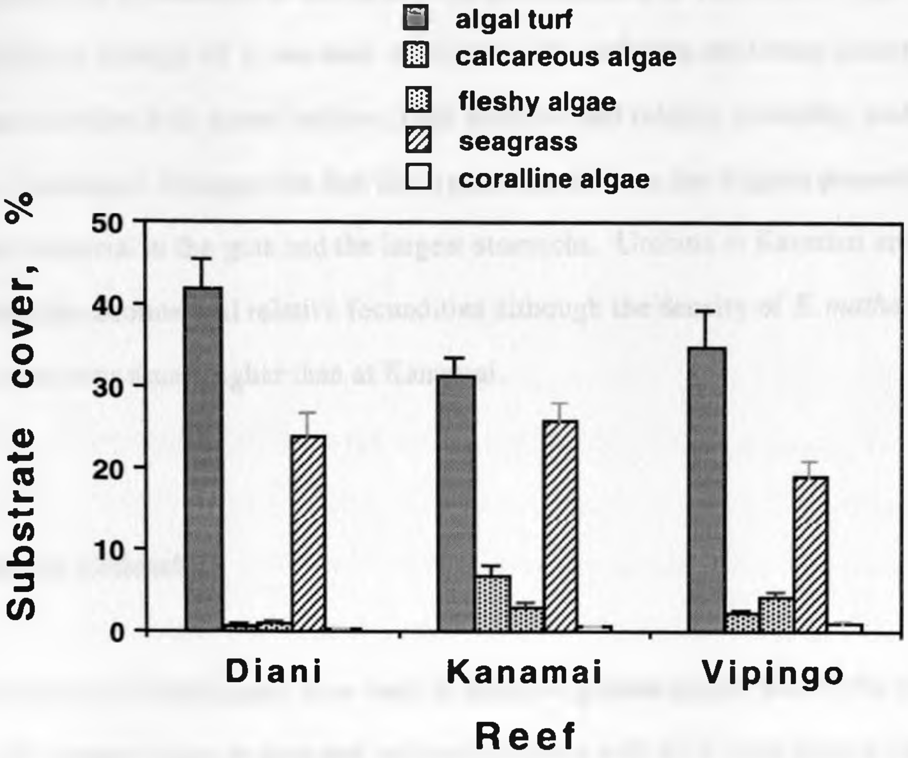
Food availability was assessed by measurements of the guts and stomachs of *E. mathaei* at each reef. The guts of animals at Vipingo were fuller (3.25 gm/urchin) than the guts of urchins at Kanamai (2.74 gm/urchin) and Diani (2.22 gm/urchin). Guts at Vipingo were larger regardless of the size of the animal since the gut index was still highest at Vipingo (Table 3.14). The proportion of organic material in the gut was also higher at Vipingo (30% of gut dry weight) than at Diani (20%) or Kanamai (28%). The differences between the gut indices were significantly different (F = 13.2; df 2,563; p = 0.000) as were the differences of the proportion of organic contents in the guts (F = 21.61; df 2,110; p = 0.000).

The ability of urchins to acquire and assimilate food was assessed by comparisons of the sizes of the jaws and stomachs of urchins at all reefs. Urchins at Vipingo had larger jaws (3.11 gm/urchin) than urchins at Diani (2.75 gm/urchin) and Kanamai (2.89 gm/urchin). The jaw size relative to urchin size (jaw index) was higher at Diani where the jaw consisted of 8% of the weight of the animal. than at Kanamai (7.35%) or Vipingo (5.66%) (Table. 3.14). The differences of jaw index between reefs were significant at the p = 0.000 level (ANOVA: F = 33.4; df 2,574).

The stomachs of urchins at Vipingo were heavier on average (0.8 gm/urchin) than the stomachs of urchins at Diani (0.37 gm/urchin) and Kanamai (0.61 gm/urchin). The stomach index was also higher at Vipingo (1.92%) than at Diani (1.23%) and Kanamai (1.21%), (Table 3.14). This difference in stomach index between reefs was significant at the p = 0.000 level (ANOVA: F = 29.3; df 2,78).

Figure 3.11 shows the percent cover of different types of substrate utilized as food by *E. mathaei* at the different reefs. More than 40% of the substrate cover at Diani consisted of algal turf which was significantly higher than algal turf cover at Kanamai and Vipingo. Kanamai and Vipingo had similar percent cover of 30 and 34% respectively. Diani had the lowest percent cover of fleshy algae (1%), calcareous algae (0.7%) and coralline algae (0.3%). Kanamai and Vipingo had similar percent cover of fleshy algae (3 and 4%) although the percent cover of calcareous algae was higher at Kanamai (7 vs. 2%) and the coralline algae was higher at Vipingo (0.9% vs. 0.5%). Diani and Kanamai had similar cover of seagrass (23 -26% respectively) while Vipingo had the lowest cover of seagrass (18%).

Figure. 3.11. The percent cover of potential sources of food for *Echinometra mathaei* at Diani, Kanamai and Vipingo reef lagoons, n = 12 transects per reef in 1992 - 1994.


algal turf
calcareous algae
fleshy algae
seagrass
coralline algae
Substrate cover, %
50
40
30
20
10
0
Diani
Kanamai
Vipingo
Reef

DISCUSSION

Results indicate significant differences in life history and other traits between the populations of *E. mathaei* at the three reefs (summarized in Table 3.14). The reproductive strategy of *E. mathaei* at Vipingo the reef with the lowest density of urchins included high gonad indices, high absolute and relative fecundity, and larger sizes. Urchins at Vipingo also had the highest gut indices, the highest proportion of organic material in the guts and the largest stomachs. Urchins at Kanamai and Diani had similar absolute and relative fecundities although the density of *E. mathaei* at Diani was four times higher than at Kanamai.

Fecundity Estimates

In this study two techniques were used to estimate gamete production 1) the volume of eggs released when urchins are induced to spawn with KCl, here termed the reproductive output (Thompson, 1982) and 2) a modification of the volumetric technique used in fisheries biology, here termed fecundity (Bagenal 1978). A comparison between the mean number of eggs measured by the two methods shows that the former method underestimates gamete production by between 48 and 63 %. This is not surprising as urchins that are induced to spawn will only release eggs that had migrated to the lumen of the ovarian tubules prior to spawning, while extraction using the above described technique would include all eggs in the gonad.

There is some uncertainty as to whether *E. mathaei* spawns once during its reproductive period or throughout the reproductive period as ova mature. This suggests that the estimate of fecundity based on eggs extracted from the gonad in February and March is quite likely to be an underestimation of the true fecundity.

Nonetheless the two methods gave consistent results over time (i.e. both estimates increasing consistently to a peak in February-March) and show a significant relationship with gonad index data. This allows for extrapolation of fecundity estimates for years when no direct measurements were made and only gonad index data are available. Fecundity measurements are quoted in the text instead of reproductive output measurements because they are closer to the true estimate of gamete production.

Factors affecting variability in fecundity

One of the major factors shown to influence the variation in the production of gametes between populations is the variation in the availability of food. The potential for an animal to acquire food resources is a result of the quantity and quality of food available. The ability to acquire food is also related to the efficiency and effectiveness of feeding and has an impact on how much food is ingested while feeding. Although the amount of food available to *E. mathaei* was not measured directly on these reefs the quantity and quality was estimated by measuring the relative size of the guts and the proportion of organic material in the guts of *E. mathaei* at each reef. As well a general idea of the quantity of food available at each reef was assessed by calculating the percent cover of various potential food source in the substrate. The ability to acquire food was assessed by measuring the relative size of the jaw and stomachs of *E. mathaei* at each reef.

E. mathaei are grazers, scraping or abrading hard substrate and ingesting substrate, plant material and encrusting organisms while feeding. According to McClanahan (1988a), *E. mathaei* gut contents consist of 40% coral sediment, 28% fleshy algae, 26% seagrass and 2% invertebrates. The coral sediment consists of a mixture of coral substrate and algal turf. Algal turf which is composed of filamentous algae was very abundant at all the reefs. The amount of organic material in this turf is very low and would probably not be able to sustain all the energy requirements of *E. mathaei*. There was however a higher percent of fleshy algae at Vipingo while the percent cover of seagrass, calcareous and coralline algae were higher or similar to the levels at Kanamai and Diani. This suggests that the quantity and the quality of food was higher at Vipingo than at the other reefs.

The fact that urchins at Vipingo had fuller guts, larger stomachs, and a higher proportion of organic matter in the guts is further evidence that there was a greater quantity and quality of food at Vipingo. *E. mathaei* at Vipingo were therefore able to consume larger quantities of high quality food leading to a larger size and the production of large numbers of eggs. Similar results have been shown in the sea urchin *Strongylocentrotus droebachiensis* (Keats *et al*., 1984) and *Arbacia lixula* (George *et al*., 1990) and the starfish *Leptasterias epichlora* (George, 1994a) where the females from populations where food was abundant were larger on average and produced more eggs.

The fecundity of *E. mathaei* at each reef fluctuated between the years 1992 to 1995 (Fig. 3.5). This yearly fluctuation in fecundity tended to follow the same direction at Diani and Kanamai and could be a response to fluctuations in the availability of food at these reefs. The relative differences between reefs however remained the same with Vipingo having consistently higher (2x) fecundity values than Diani and Kanamai and the latter reefs having fecundities that were similar over the years. This further emphasizes that *E. mathaei* at Vipingo have adequate resources to maintain high fecundity every year. Yearly variation in fecundity has also been demonstrated in the sea urchin *Strongylocentrotus purpuratus* (Gonor, 1973) and it has been suggested that this variation is a reflection of environmental factors especially food availability.

Several lines of evidence indicate that the quantity and quality of food for *E. mathaei* at Kanamai was higher than at Diani. Transect studies showed that fleshy algae and seagrass levels were equivalent to Vipingo levels and gut studies showed that *E. mathaei* at Kanamai had significantly fuller guts and higher organic material in the guts than urchins at Diani. There was also no significant difference in the relative size of the stomachs between the two reefs. Urchins at Diani however had relatively larger Aristotle's lanterns than urchins at any of the reefs and were similar to jaw indices recorded by McClanahan and Kurtis (1991). This coupled with the fact that *E. mathaei* at Diani had smaller guts with a higher proportion of calcium carbonate indicates that the quantity and quality of food at Diani was the lowest of all the reefs hence large jaws allowed for a more efficient acquisition of food. Large jaw size relative to animal size is suggested to be a response to food limitation, and has previously been recorded in *E. mathaei* at Rottnest Island Western Australia (Black *et al*., 1982) and in *S. purpuratus* in California (Edwards and Ebert, 1991). In both these studies urchins increased the size of the jaw as a response to decreased food.

When food is scarce gonad development is usually poor in sea urchins (Ebert, 1968). Interestingly, although *E. mathaei* at Diani showed signs of food limitation, the fecundity was as high as the fecundity of urchins at Kanamai. *E. mathaei* at Diani therefore allocated a high proportion of the available energy resources to the production of gametes. This allocation of available resources to reproduction was probably at the expense of growth since urchins were on average smaller at Diani than at any of the other reefs. The allocation of resources to reproduction at the expense of growth has been shown in many other organisms (Thompson, 1982) and is considered to be an appropriate response to food shortage. The fact that the fecundity of *E. mathaei* at Kanamai is as low as at Diani where food is limited could be an indication that *E. mathaei* at Kanamai are not allocating as high a proportion of available energy to reproduction. *E. mathaei* at Kanamai are larger in size than at Diani and there could be a trade off between growth and the production of gametes.

The ability to acquire food may also depend on differences in biotic interactions including competition which are density dependent (Ebert, 1982). Although the level of competition was not measured in this study, McClanahan, 1988a showed that competition for space was intense among *E. mathaei* the large differences in population density could be used as an indicator of the level of competition. The population density of *E. mathaei* fluctuated significantly between years at each reef but, it was consistently low at Vipingo compared to Kanamai and Diani. The biomass of sea urchins at Diani was 8857 gm/hectare of which more than 90% was *E. mathaei* . Intense intraspecific competition for food is therefore expected at Diani further reducing the amount of food available to each individual urchin. Urchin biomass at Kanamai was 4029 gm/hectare of which 50% was *E. mathaei* . Urchins at Kanamai are expected to experience varying levels of both intraspecific and interspecific competition. The density and biomass of urchins at Vipingo was the lowest of all the reefs at 3217 gm/hectare. *E. mathaei* consisted of only 30% of the urchin biomass at Vipingo. The fact that *E. mathaei* at Vipingo are large, have a high fecundity and full guts indicates that competition for food resources is probably very low and is not limiting growth and reproduction.

Maternal size, reproductive success and population density

maternal size is an important life history strategy in many organisms usually because larger females are associated with higher fecundity. Larger females have been shown to produce more eggs in many echinoderms including sea urchins and starfish (Chia, 1966; Ebert, 1968; George, 1994a and 1994b). In this study, *E. mathaei* at Vipingo were larger on average than *E. mathaei* at Kanamai and Diani and had higher fecundities. Individuals at Vipingo also showed a positive relationship between maternal size and fecundity (Fig. 3.3C). The size of females at Diani and Kanamai however did not show any relationship with the number of eggs present in their gonads (Fig. 3.3(A & B)). Maternal size was therefore not a reliable predictor of fecundity in these urchins.

A major generalization in population biology is that larger body size and hence a higher production of gametes translates to greater reproductive success. *E. mathaei* at Vipingo should therefore have a higher reproductive success than *E.*

mathaei at Diani or Kanamai. The population density of an animal however is an important factor when calculating reproductive success (Pennington, 1985). This is because reproductive success is not only determined by the number of gametes released by individuals but also the distance between the sources of gametes which affects the success of fertilization. High population densities may increase competition for food and space, but the trade off for animals that don't aggregate during spawning or synchronize their spawning, may be increased fertilization success. *E. mathaei* populations on the Kenyan coast probably spawn asynchronously during the extended spawning period (this study). Reproductive success will therefore depend more heavily on the success of fertilization which in turn depends on mean distance between individuals.

According to Levitan (1991) there is usually an important tradeoff between maternal size and population density with urchins either a) developing large maternal size with higher gamete production at low population density or b) small maternal size with lower gamete production at higher population densities. The results of this study fit this model as *E. mathaei* at Vipingo are larger, produce more gametes and have the lowest population density while urchins at Diani have small sizes, lower gamete production at high population densities. If we estimate the population reproductive potential as the number of eggs per unit area, Diani has 382 x 10^6 eggs/10m^{-2} compared to Vipingo and Kanamai at 85 and 99 x 10^6 eggs/10m^{-2} respectively. The population reproductive potential is more than three times higher at Diani than at Vipingo and Kanamai. Although Kanamai had a similar average individual fecundity to Diani, the population reproductive output is closer to Vipingo.

Figure 3.10 illustrates this point further where individual fecundity is very high at low population densities (Vipingo) but fecundity per unit area is very high at high population densities (Diani). This suggests that *E. mathaei* at Diani maybe more reproductively successful than urchins at Vipingo and Kanamai because the success of fertilization is likely to be higher. The reproductive strategy of *E. mathaei* at Kanamai does not fit either the Vance (1973) or Levitan (1991) models. Other factors including predation and environmental stress may be influencing reproduction at Kanamai. Stress due to high temperatures during low tides has been shown to adversely affect reproduction in urchins (George, 1994b) and is likely to affect urchins at Kanamai which is a shallower reef (McClanahan, 1988a).

Variability in egg size

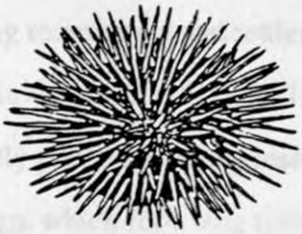
Classical reproductive strategy models predict a trade-off between egg size and egg number (Vance, 1973). Females with a given amount of resources available for reproduction will either produce large numbers of small (low quality) eggs or low numbers of large (high quality) eggs. Size usually measured as egg diameter is assumed to be a relative index of egg quality and by extension larval success. Although there was a significant and consistent difference in the number of eggs produced by females at each reef, no consistent differences were seen in egg diameters between the reefs. There was also no significant correlation between egg diameter and maternal size (Fig. 3.7).

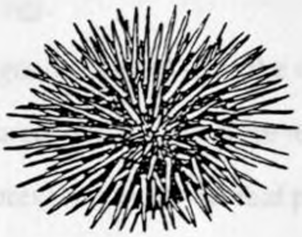
The diameters of eggs within individuals, between individuals of one population and another and at different time intervals showed significant variability (Fig. 3.6, Tables 3.10 - 3.12). This variability has been shown in many other species of echinoids (Lessios, 1987) indicating that egg size is not a reliable predictor of parental investment in many echinoids including *E. mathaei*. McEdwards and Carson (1987) postulated that for a species with small eggs like *E. mathaei*, egg size and content would be less variable in a population as a whole and therefore fecundity (egg number) would be a better predictor of parental investment.

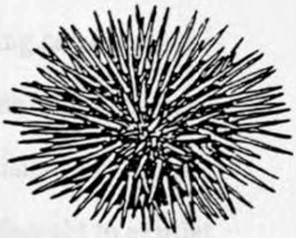
The weight of eggs however was higher at Vipingo than at Diani and Kanamai. Whether this difference in egg weight was an indication of higher organic content was not explored in this study. Thompson (1982) showed a reduction in the lipid content of the egg in response to food limitation while egg diameter remained the same in *S. droebachiensis* . It is therefore conceivable that eggs of *E. mathaei* at Vipingo are heavier due to higher quality (for example more protein) since both food quality and quantity is higher at Vipingo. Biochemical analysis of the eggs of *E. mathaei* from the different reefs need to be carried out however before any conclusions on egg quality can be made.

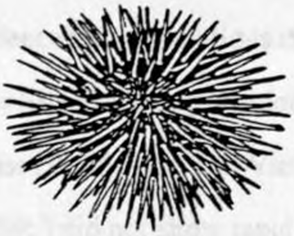
CHAPTER FOUR

Spatial and Temporal Patterns of Recruitment of *Echinometra mathaei* (de Blainville) on Kenyan reefs: The Effects of Seasonality and Population Density









INTRODUCTION

The processes that control the abundance and distribution of marine invertebrates have been a subject of interest to population biologists for a long time. Before Thorson's (1950) studies of the reproduction and larval development of marine invertebrates, the population ecology of marine invertebrates was thought to be largely controlled by physiological tolerances (Stevenson and Stevenson, 1949). Despite Thorson's historical data on larval ecology researchers paid little attention to the potential influence of larval ecology (including recruitment and settlement processes) on the population dynamics of marine invertebrates (Ehrlich, 1975; Doherty, 1991). This lack of interest was especially prevalent among researchers during the development of the equilibrium paradigm which for a long time was the classic view of population biology.

The equilibrium paradigm developed from the view that populations live in systems that have limited resources and are therefore regulated by competition for these limited resources. The prevalent view was that populations are held at average densities by biotic factors and that there is an environmental carrying capacity that is determined by biological processes including competition, predation and disturbance (Connell, 1961; Paine, 1966; Dayton, 1971). This view was especially widespread among coral reef ecologists because coral reef communities were thought to exhibit equilibrium properties of stability and self-regulation (Sale, 1980, 1991).

The equilibrium paradigm has been challenged in recent years by studies that have shown that the spatial and temporal variability of populations cannot always be explained by the equilibrium viewpoint. Evidence that populations that showed dramatic decreases due to natural disturbances like El Nino, predation by Crown of Thorns starfish or mass mortality due to disease (Wellington and Victor, 1985, 1988; Williams, 1986; Guzzman and Robertson, 1989;) did not show rapid increases with time led to the questioning of the capacity of some populations to track carrying capacity and the re-evaluation of recruitment as an important force structuring marine benthic invertebrates.

Several recent studies of coral reef fishes and sea urchins have provided further support for a second viewpoint that has emphasized the importance of variable factors (the non-equilibrium paradigm) such as seasonal availability of larvae (i.e. recruitment) rather than competition or predation in determining the structure of benthic communities (Doherty, 1982, 1983; Ebert, 1983; Connell and Keough, 1985; Roughgarden *et al*., 1988; Doherty and Williams, 1988).

Variable recruitment is common in organisms that disperse pelagic propagules especially larvae with lengthy development including marine plants (Hoffman and Ugarte, 1985), marine invertebrates (Loosanoff, 1964; Jamieson, 1986; Caffey, 1985; Dayton, 1984) and fishes (Doherty and Williams, 1988). In these populations the pre-settlement larvae carried to a local area are very likely spawned elsewhere. Consequently these populations are regarded as open non-equilibrium systems in which gains from external sources (i.e. recruitment) and losses to internal sinks (i.e. mortality) exert more control over abundance than the carrying capacity of the local environment (Williams, 1980).

Recruitment is the step linking larvae and adults and processes that have a strong effect on recruitment success can potentially determine adult population abundance and distribution. A number of factors are suggested that affect recruitment including 1) the distribution, abundance and fecundity of sexually mature individuals 2) the chemical, physical and biological oceanographic conditions during the planktonic larval stages and 3) larval settling preferences (Cameron and Rumrill, 1982; Keough and Downes, 1982; Ebert, 1983; Eckman, 1983). After settlement other factors like predation, competitive interactions, availability of food, shelter and other resources as well as other abiotic sources of mortality determine the survival of the recruits (Shulman, 1985; McClanahan and Kurtis, 1991).

How and whether recruitment affects the population dynamics of sea urchin populations is a question much debated among marine ecologists. Patterns of echinoid recruitment vary greatly with recruitment occurring either continuously throughout the year, seasonally and predictably from year to year, or episodic and unpredictably from year to year (Ebert, 1983; Pearse and Hines, 1987). Usually larvae of most sea urchins are very small at settlement or settle on cryptic substrates and are therefore difficult to census accurately. Thus recruitment estimates are usually separated in time from the settlement events and therefore reflect both early juvenile growth and mortality. Once sea urchins attain a size that can be observed in the field as recruits, they may have passed the major limitations of growing to adulthood (Highsmith, 1982). If this is the case recruitment rather than adult mortality may limit populations (Cameron and Rumrill, 1982; Ebert, 1983).

Several studies however have shown that predation can be a dominant control of sea urchin populations. For example, the sea otter *Enhydra lutris* Linnaeus can control adult sea urchin populations in kelp forests (Lowry and Pearse, 1973; Estes and Palmisano, 1974; Dayton, 1975). Kenner (1992), however showed that regular recruitment and adequate shelter from predation allowed the development of high densities of the sea urchin *S. purpuratus* despite predation by this sea otter. The sea star *Pycnopodia helianthoides* (Brandt) has also been implicated in the decline of the sea urchin *S. purpuratus* in a Californian kelp forest (Pearse and Hines, 1987). McClanahan and Kurtis (1991) also suggest that the adult populations of the sea urchin *Echinometra mathaei* were regulated by predation pressure especially by the triggerfish *Balistapus undulatus* in Kenyan reef lagoons.

The sea urchin *E. mathaei* is a common species in coral reef lagoons in E. Africa. Although McClanahan and Kurtis , (1991) implicated predation by triggerfish as the main force controlling abundance and distribution of *E. mathaei*, no studies have been carried out on the spatial and temporal patterns of recruitment of *E. mathaei*, the relationship between reproduction and recruitment or the role of recruitment in controlling the population density *E. mathaei* along the East African coast. The hypothesis that predation by the triggerfish balances recruitment and that when the numbers of triggerfish are reduced (due to fishing pressure) the population of *E. mathaei* increases and dominates other sea urchin species (McClanahan and Muthiga, 1988; McClanahan and Kurtis ,1991) cannot be validated without this detailed information on recruitment.

In this chapter, the spatial and temporal patterns of recruitment at three reef lagoons in Kenya, where long-term population data are available are studied. The reefs differ in the population density of *E. mathaei* allowing for a study of the relationship between reproduction and recruitment and the relationship between recruitment and population density.

MATERIALS AND METHODS

Larval supply

Recruitment of *E. mathaei* into the plankton was studied by first culturing the sea urchins in the laboratory and studying the various stages that might be encountered in the plankton. Individual sea urchins were induced to spawn by injection with 0.5 M KCl. The eggs were collected and rinsed several times in seawater filtered with 4.7 cm Whatman glass fibre filters. The eggs were then poured into a container with 4 liters of filtered seawater to which the antibiotic Gentamycin sulphate (40 mg/l) had been added. Sperm were collected directly from male urchins and diluted a few minutes before insemination of the eggs. One drop of dry sperm was diluted with 5 ml of filtered seawater and 2 ml of this solution was used to inseminate the eggs (Leahy, 1986). The larvae of *E. mathaei* were reared in several rearing experiments using algae of the genus *Chaetoceros* (which was cultured at the KMFRI laboratories) as food. Samples of the various growth stages were collected and fixed in 70% alcohol for microscopic observation to enable recognition of the different stages in the plankton.

Previous observations showed that newly metamorphosed *E. mathaei* appeared on the substrate in late May. Plankton tows were therefore carried out at each site during neap and spring high tides in April - May 1994 for measurements of the supply of the late larval stages. A 200 um mesh net, 60 cm in diameter was towed behind an inflatable dinghy for 10 minutes. The volume of water filtered was calculated using a General Oceanic Inc digital flowmeter which was tied across the mouth of the net. Plankton samples were fixed in 4% formalin solution. Samples were later washed through a coarse sieve to get rid of large bits of seagrass and algae before sorting and counting under a dissecting microscope.

Recruitment onto the substrate

Settlement and recruitment of the newly metamorphosed urchins onto the substrate were estimated in 20 1-m^2 PVC quadrats tossed haphazardly in the reef lagoon at each site and intensively surveyed for recruits. Swimming censuses were carried out every two months and every month during the peak recruitment period. Results are expressed as mean recruit numbers per m^2. The seasonal recruitment pattern is presented as the mean number of recruits each month from 1992 to 1994. Since recruitment was patchy only the means of recruits censused at the peak period of recruitment was used for comparisons between reefs. Additionally the test diameter of all recruits was measured with a caliper. Since recruits of *E. mathaei* are round only one axis was measured. Growth of recruits is presented as the average test diameter of recruits against the number of days since settlement.

During the course of this work, a sea urchin removal experiment was conducted at Diani and Vipingo within the vicinity of the study area as part of an ongoing reef monitoring program. In 1993 four 50/50m plots were established on these reefs. At each reef all urchins were removed within two experimental plots and at two adjacent control plots no urchins were removed (McClanahan *et al.*, 1995). I therefore took the opportunity to carry out recruit censuses in the urchin removal plots and control plots to study the effects of population density and adult density on settlement in these areas.

Predation of recruits

The rate of predation on recruits of *E. mathaei* was studied by tagging recruits onto transect lines at each reef. Recruits approximately 15 mm test diameter were collected and pierced with a 0.4 mm hypodermic needle. A monofilament line was threaded through the urchin and the urchin was tied onto a nylon transect line which was laid out onto the reef. The rate of mortality using this method was tested by tagging 30 recruits that were then kept in a sea water aquarium and provided with rocks encrusted with algae for food for 3 days. The rate of mortality was very low (0.07%). A total of 40 recruits on 4, 10 m lines were therefore laid out at each reef (10 recruits per line). Observations were made for one day and a predation index was calculated as the average number of days that it takes for the recruits to be preyed upon.

RESULTS

Rearing experiments

Five rearing experiments were carried out, however although fertilization was always successful the larvae died after about three weeks at the 8-12 arm stage. The cause of death was probably starvation since the larvae tended to die slowly showing gradual signs of emaciation (i.e. losing parts of the arms). I was therefore not successful in estimating the length of the larval period in the laboratory.

Larval supply in the plankton

Although I was not able to estimate the length of the larval period from rearing experiments, information from the literature (Emlet, quoted in Emlet *et al*., 1987) gave an estimate of approximately 23 and 18 days for *Echinometra lucunter* (Linnaeus) and *E. vanbrunti* respectively of larval life in the plankton.

Table 4.1 gives a summary of the sampling dates, the total volume sampled at each reef and the number of larvae counted. Only a total of 10 echinoid larvae were found i.e. an average of 0.003 larvae/m^3. The specimens included early plutei larvae at the four arm and six arm stages, late plutei with a few spines, tube feet and feeding arms as well as early metamorphosed larvae with a test. The number of larvae were too few to derive any relationships with reef or with tides, but it is evident that larvae are in the plankton a few weeks after spawning activity starts.

Table 4.1. Summary table of the samples of zooplankton collected at Diani, Kanamai and Vipingo in March-April 1994.

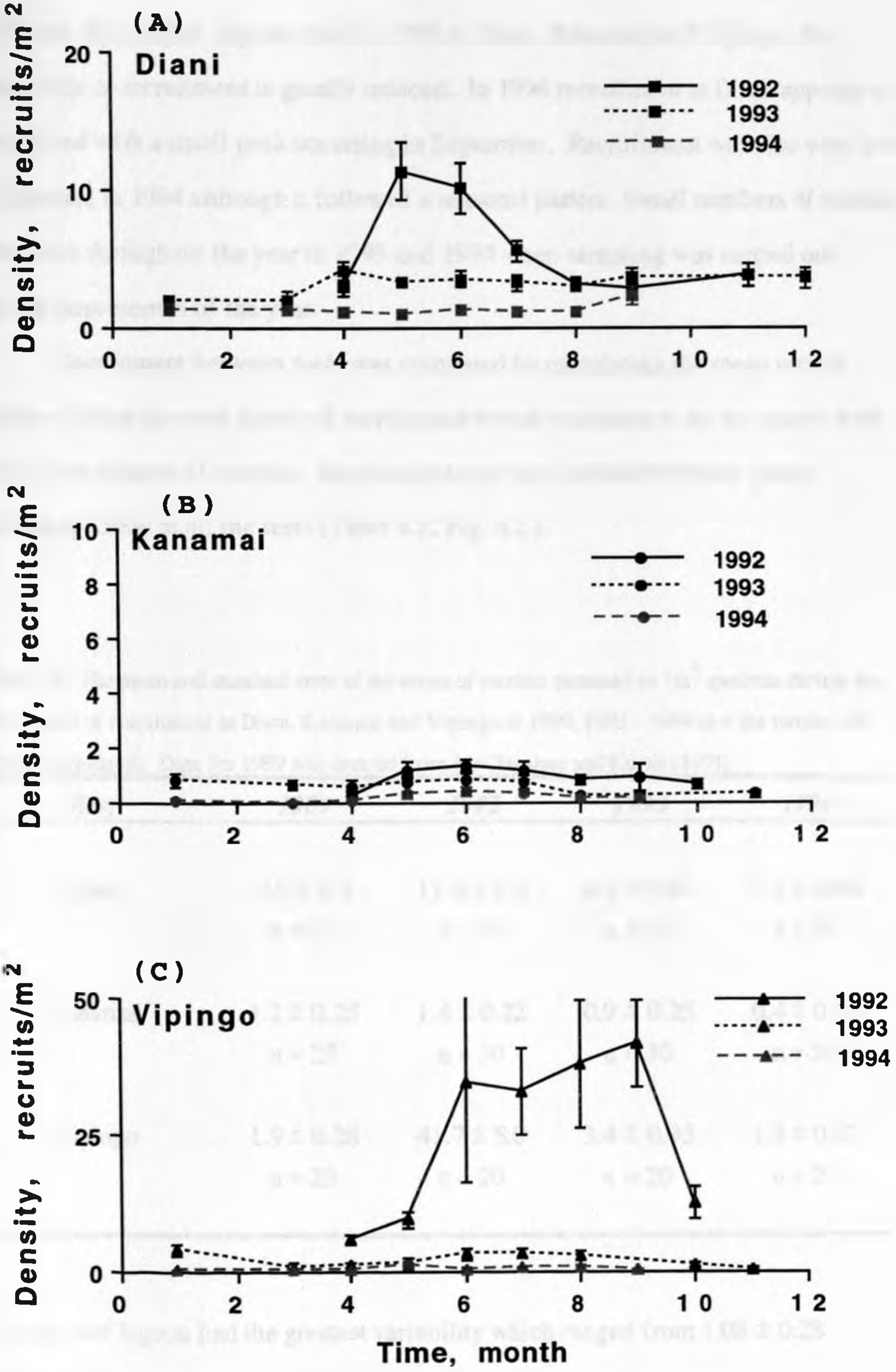
Reef	*Date*	*Tides*	*Vol filtered (Litres)*	*No. of larvae*	*larvae/m^3*
Vipingo	23/3/94	Neap	584	3	0.005
Vipingo	11/4/94	Spring	344	3	0.009
Kanamai	12/4/94	Spring	323	0	0.000
Diani	13/4/94	Spring	366	2	0.005
Kanamai	20/4/94	Neap	499	1	0.002
Diani	21/4/94	Neap	674	1	0.001
Vipingo	22/4/94	Neap	446	0	0.000

Recruitment onto the substrate

Recruitment of *E. mathaei* onto the substrate was studied by searching quadrats haphazardly placed on the reef and counting all urchins 15 mm and less in test diameter. Over 86% of recruits settled underneath coral rubble, 9% at the base and on blades of seagrass stems and 5% in the calcareous algae *Halimeda* and *Amphiroa* . In all 1,643 quadrats were searched and a total of 4,653 recruits were counted at all three reefs in 1992 to 1994. Data for recruit censuses carried out in 1989 (McClanahan and Kurtis, 1991) at Diani, Kanamai and Vipingo are also included for comparative purposes.

The seasonal pattern of recruitment is shown in Fig. 4.1A, B and C. At each reef the mean monthly number of recruits (± sem) are plotted against sampling month for 1992 to 1994. Twenty quadrats were searched in Diani and Vipingo and 30 at Kanamai each sampling month. The 1992 census shows a clear seasonal pattern, especially at Vipingo and Diani when recruits 2 - 4 mm in test diameter were first seen in April. The density of recruits increased as more urchins settled onto the substrate from the plankton and also because searching ability improved with an

Figure. 4.1. The seasonal pattern of recruitment of *Echinometra mathaei* at Diani (A), Kanamai (B) and Vipingo (C) reef lagoons measured as the mean (± sem) recruit number/m^2 censused in 20 to 30 quadrats on each sampling date.


(A)
Diani
Density, recruits/m2
20
10
0
1992
1993
1994
0
2
4
6
8
1 0
1 2
(B)
Kanamai
Density, recruits/m2
10
8
6
4
2
0
1992
1993
1994
0
2
4
6
8
1 0
1 2
(C)
Vipingo
Density, recruits/m2
50
25
0
1992
1993
1994
0
2
4
6
8
1 0
1 2
Time, month

increase in the size of the recruits until it peaked in June or July. The number of recruits then decreased due to mortality or as the average size of juveniles increased beyond the sampling size (15 mm) until few new recruits were seen in September. Although this pattern repeats itself in 1993 at Diani, Kanamai and Vipingo, the magnitude of recruitment is greatly reduced. In 1994 recruitment at Diani appears to be delayed with a small peak occurring in September. Recruitment was also very low at Kanamai in 1994 although it followed a seasonal pattern. Small numbers of recruits were seen throughout the year in 1993 and 1994 when sampling was carried out during most months of the year.

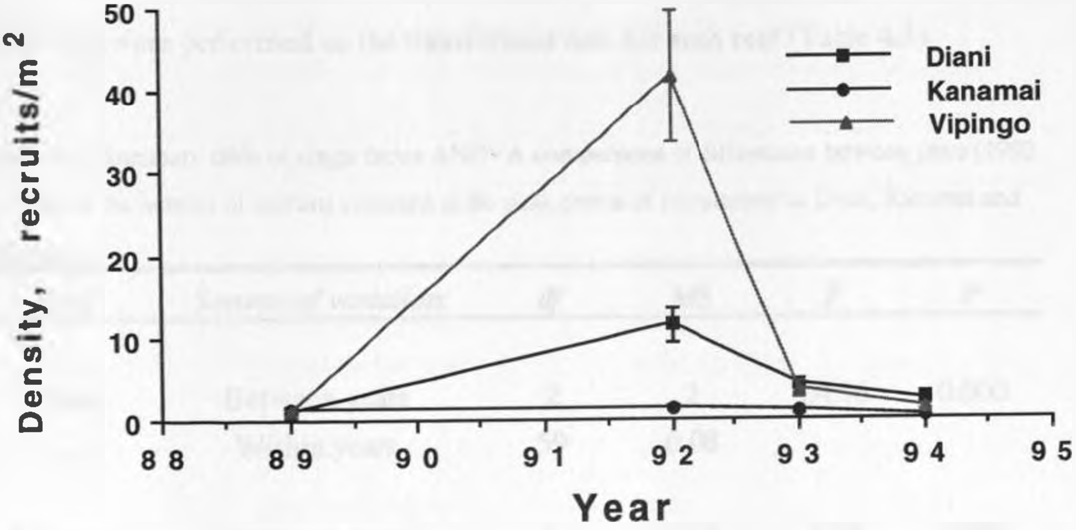
Recruitment between reefs was compared by calculating the mean recruit number during the peak month of recruitment which was taken to be the month with the highest number of recruits. Recruitment was very variable between years (including 1989) at all the reefs (Table 4.2, Fig. 4.2).

Table 4.2. The mean and standard error of the mean of recruits censused in $1m^2$ quadrats during the peak period of recruitment at Diani, Kanamai and Vipingo in 1989, 1992 - 1994 (n = the number of quadrats censused). Data for 1989 was derived from McClanahan and Kurtis (1991).

Reef	*1989*	*1992*	*1993*	*1994*
Diani	0.9 ± 0.2 n = 50	11.4 ± 2.2 n = 24	4.2 ± 0.67 n = 20	2.4 ± 0.66 n = 20
Kanamai	1.2 ± 0.25 n = 25	1.4 ± 0.22 n = 30	0.9 ± 0.25 n = 30	0.4 ± 0.14 n = 30
Vipingo	1.9 ± 0.28 n = 25	41.7 ± 8.0 n = 20	3.4 ± 0.95 n = 20	1.3 ± 0.42 n = 20

Vipingo reef lagoon had the greatest variability which ranged from 1.08 ± 0.28 recruits/m^2 in 1989 to 41.7 ± 8.0 recruits/m^2 in 1992.

Figure. 4.2. The annual variation in recruitment of *Echinometra mathaei* at Diani, Kanamai and Vipingo. Each value represents the mean (± sem) density of recruits during the peak month of recruitment (the month with the highest number of recruits) at Diani, Kanamai and Vipingo in 1989, 1992 to 1994. Data for 1989 was from McClanahan and Kurtis (1991).


50
40
30
20
10
0
Density, recruits/m 2
8 8
8 9
9 0
9 1
9 2
9 3
9 4
9 5
Year
Diani
Kanamai
Vipingo

Kanamai reef lagoon showed the lowest variability from 0.43 ± 0.1 recruits/m^2 in 1994 to 1.37 ± 0.22 recruits/m^2 in 1992.

Descriptive statistics of the numbers of recruits per quadrat at each reef showed a high degree of skewness and kurtosis indicating that the census data were patchy and not normally distributed. Therefore to test for the significance of any differences that may occur between reefs the data were transformed using a log transformation of the form Log (x + 1) since some of the data points were zero (log of zero is negative infinity).

To test for differences in recruitment between years at each reef single factor ANOVAs were performed on the transformed data for each reef (Table 4.3)

Table 4.3. Summary table of single factor ANOVA comparisons of differences between years (1992 to 1994) of the number of recruits censused at the peak period of recruitment at Diani, Kanamai and Vipingo.

Reef	*Source of variation*	*df*	*MS*	*F*	*P*
Diani	Between years	2	2	24.76	0.000
	Within years	59	0.08		
Kanamai	Between years	2	0.35	7.18	0.002
	Within years	59	0.05		
Vipingo	Between years	2	5.54	39.97	0.000
	Within years	59	0.14		

There was a significant difference in recruitment between years at all the reefs. Recruitment was highest in 1992 at all the reefs and shows a dramatic drop in Vipingo and Diani in 1993. At Kanamai there was no significant difference between mean recruit numbers in 1989 and 1992, however recruitment decreased significantly in 1993 and 1994. Recruitment at Vipingo increased in 1992 from 1989 levels but was back to 1989 levels by 1994.

The differences seen in the magnitude of recruitment between reefs each year were tested using Student's t-test, Table 4.4. In 1989 there was no significant difference in mean recruit numbers between reefs. Vipingo reef had significantly higher recruits/m^2 in 1992 than Diani and Kanamai, while Diani had significantly higher recruits/m^2 than Kanamai. In 1993 both Diani and Vipingo have significantly higher numbers of recruits than Kanamai but did not differ from each other. Diani and Vipingo reefs also had higher recruit numbers than Kanamai in 1994 although in this year Diani also showed significantly higher numbers of recruits than Vipingo.

Table 4.4. Summary table of Student's-t comparisons of the mean recruit numbers each year at the peak recruitment period between reefs. Data for 1989 was derived from McClanahan and Kurtis (1991).

Year	*Comparison*	*t-statistic*	*p*
1989	Diani vs Kanamai	0.90	ns
	Diani vs Vipingo	0.52	ns
	Vipingo vs Kanamai	0.32	ns
1992	Diani vs Kanamai	5.07	< 0.0005
	Diani vs Vipingo	3.95	< 0.0010
	Vipingo vs Kanamai	6.20	< 0.0005
1993	Diani vs Kanamai	5.31	< 0.0005
	Diani vs Vipingo	0.68	ns
	Vipingo vs Kanamai	3.05	< 0.0050
1994	Diani vs Kanamai	3.49	< 0.0005
	Diani vs Vipingo	1.47	< 0.1000
	Vipingo vs Kanamai	2.15	< 0.0250

Relationship with phytoplankton

The relationship between recruitment and phytoplankton concentrations was tested by performing a correlation between the mean density of recruits and the mean chlorophyll a concentration. The concentration of phytoplankton is not expected to show a direct relationship with recruitment since there is a time lag from the time it takes larvae to feed in the plankton and metamorphosis and settlement onto the substrate. A correlation analysis was therefore performed of the density of recruits at the time of the year when recruitment peaks (i.e. May and June) with the mean chlorophyll a concentration at the time when feeding larvae are expected to peak in the plankton (i.e. March and April) at all reefs each year. Unfortunately there are no data for 1992 however there was still a weak but significant relationship ($r = 0.88$; $p = 0.02$, $n = 6$) between the mean chlorophyll a concentration and the density of recruits (Fig. 4.3).

Relationship between adults and recruits

Figure 4.4 shows the change in urchin density (excluding recruits) over a period of 9 years. Urchin censuses were carried out by the author and other workers during this period including, the 1985 census (McClanahan and Muthiga, 1988), the 1987 census (McClanahan and Shafir, 1990) and the 1989 census (McClanahan and Kurtis, 1991). Diani consistently had the highest population of urchins ranging between 135 individuals/10m^2 in 1987 to 280 individuals/10m^2 in 1992. Vipingo consistently had the lowest population of urchins ranging from 13 to 59.6 individuals/10m^2 between 1994 and 1989. Kanamai always had intermediate numbers of urchins

The population of urchins shows varying degrees of fluctuation at all three reefs. Diani shows a 50% increase from 1985-87 levels to 1992 then a decrease of 19% of the 1992 levels in 1994.

Figure. 4.3. The relationship between the density of recruits of *Echinometra mathaei* and the chlorophyll a concentration. Each data point represents the mean recruit density at the peak of recruitment plotted against the concentration of chlorophyll a immediately after the peak spawning period (March- April) in 1993 and 1994.

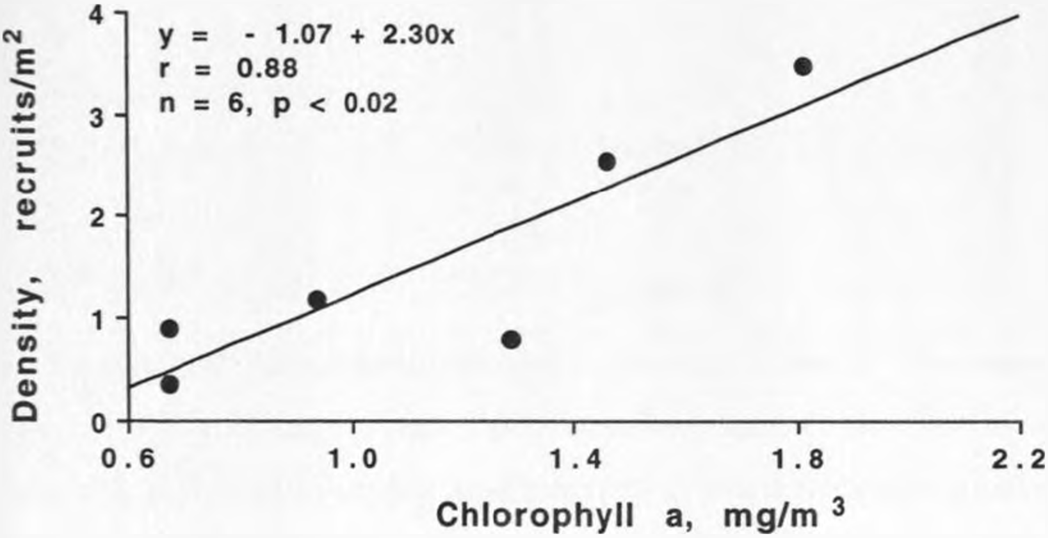
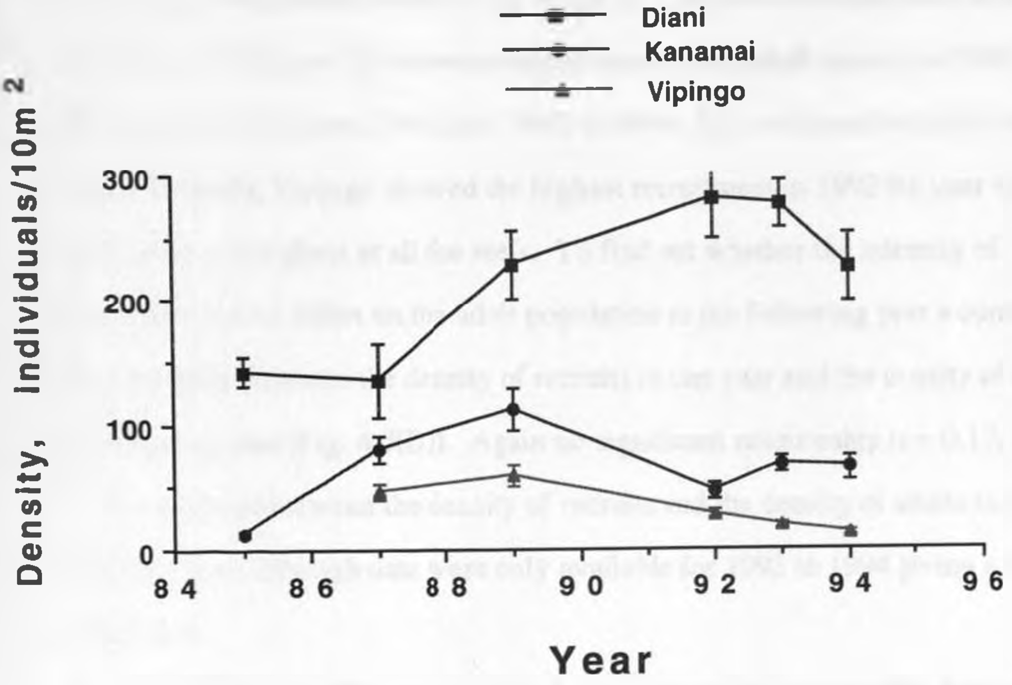

y = - 1.07 + 2.30x
r = 0.88
n = 6, p < 0.02
Density, recruits/m2
0
1
2
3
4
0.6
1.0
1.4
1.8
2.2
Chlorophyll a, mg/m 3

Figure. 4.4. The population density of *Echinometra mathaei* at Diani, Kanamai and Vipingo between 1985 and 1994 measured as the mean (± sem) of 20 - 50 quadrats censused at each reef lagoon in 1985 (McClanahan and Muthiga, 1987, 1988), 1987 (McClanahan and Shafir, 1990) and 1989 (McClanahan and Kurtis, 1991) and 1992 to 1994.


Diani
Kanamai
Vipingo
Density, Individuals/10m ^{2}
300
200
100
0
84
86
88
90
92
94
96
Year

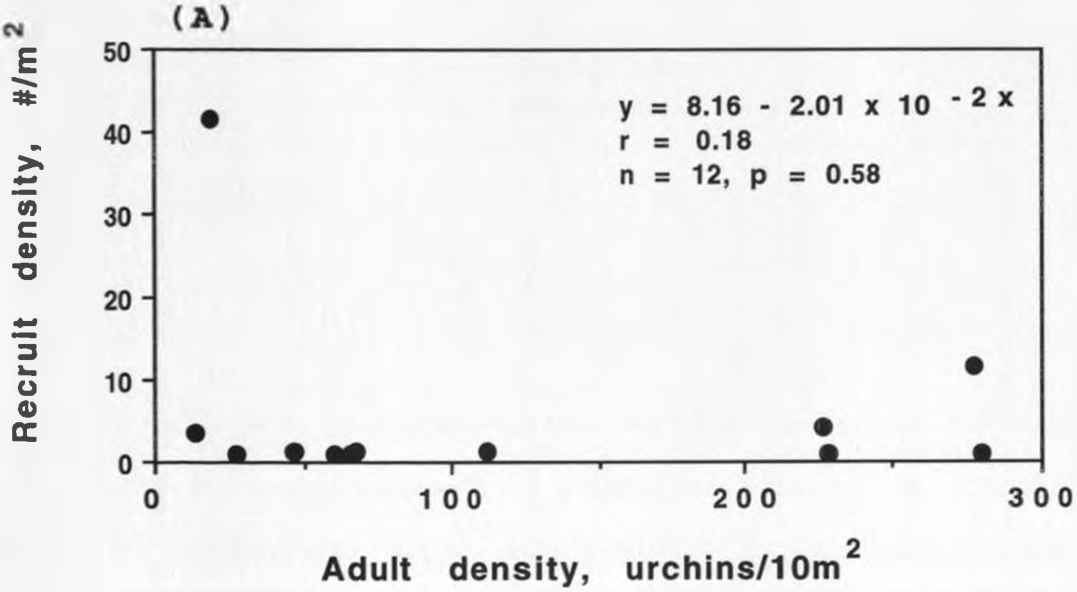
The population at Kanamai showed an 89% increase from 1985 to 1989 then a decrease of 60% in 1993 and is up to 42% of the 1987 level in 1994. The population of urchins at Vipingo does not fluctuate as much as that of either Diani or Kanamai showing an increase of 45% from 1987 to 1989, but the population has been declining since then to 16% of the 1989 levels.

To test for the relationship between recruits and adult density, a correlation analysis was performed between the mean number of adults censused at each reef and the corresponding recruit density (Fig. 4.5(A)). There was no significant relationship ($r = 0.18$; $p = 0.58$; $n = 12$) between recruit density and adult density in 1989 (McClanahan and Kurtis, 1991) and 1992 to 1994. In fact the reef with the lowest density of adults, Vipingo showed the highest recruitment in 1992 the year when recruitment was highest at all the reefs. To find out whether the intensity of recruitment had an effect on the adult population in the following year a correlation was performed between the density of recruits in one year and the density of adults in the following year (Fig. 4.5(B)). Again no significant relationship ($r = 0.17$; $p = 0.75$; $n = 6$) was found between the density of recruits and the density of adults in the following year, although data were only available for 1992 to 1994 giving a small sample size.

A further test of the relationship between recruitment and adult density was performed by comparing data collected during the sea urchin removal experiment carried out at Vipingo and Diani. The mean (± sem) density of recruits in experimental and control plots each month are shown in Figure 4.6 A and B. The mean density of recruits in experimental plots were lower each month than in control plots (except in May 1993 at Vipingo) at both reefs.

A two way ANOVA comparison (Table 4.5) of log transformed data of recruit counts per quadrat at each reef in the control and experimental plots showed that although the difference between months was significant, the difference between control and experimental plots was not significant .

Figure. 4.5. (A) The relationship between the density of adults and recruits of *Echinometra mathaei* at Diani, Kanamai and Vipingo reef lagoons in 1989 (McClanahan and Kurtis, 1991) and 1992 to 1994. (B) The relationship between the density of recruits of *Echinometra mathaei* at Diani, Kanamai and Vipingo reef lagoons in one year, and the density of adults in the following year from 1992 to 1994.


(A)
Recruit density, #/m 2
50
40
30
20
10
0
0
100
200
300
Adult density, urchins/10m 2
y = 8.16 - 2.01 x 10 -2 x
r = 0.18
n = 12, p = 0.58

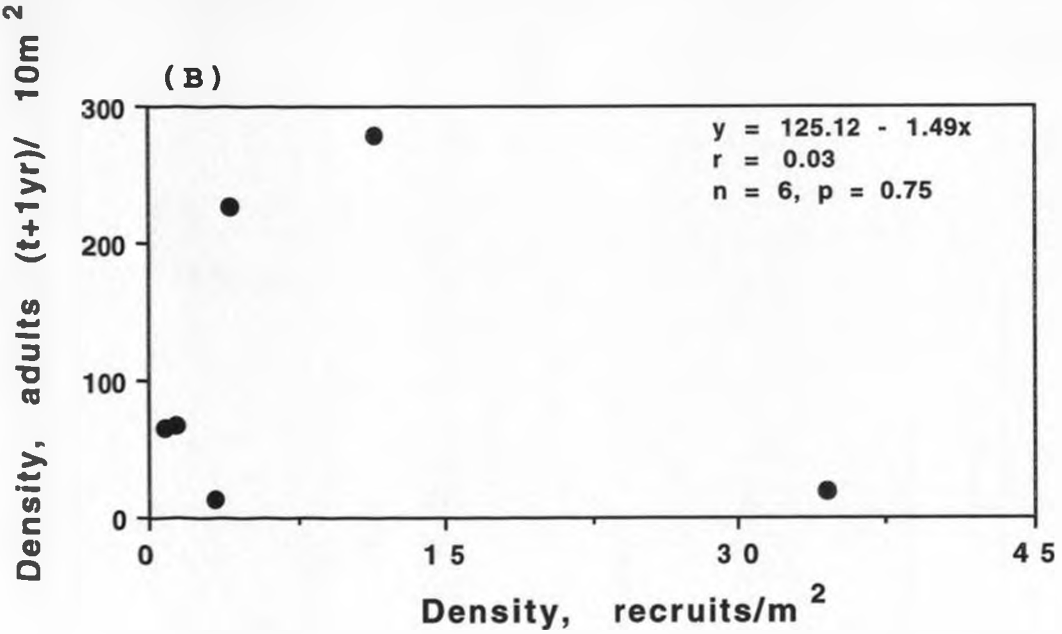

(B)
Density, adults (t+1yr)/ 10m 2
300
200
100
0
0
15
30
45
Density, recruits/m 2
y = 125.12 - 1.49x
r = 0.03
n = 6, p = 0.75

Figure. 4.6. The density of recruits of *Echinometra mathaei* in control and removal plots at Diani (A) and Vipingo (B) reef lagoons. All *E. mathaei* were removed from experimental plots while control plots were left with the natural population of *E. mathaei*. The values represent the mean (± sem) of *E. mathaei* recruits censused in 20 quadrats within each plot.

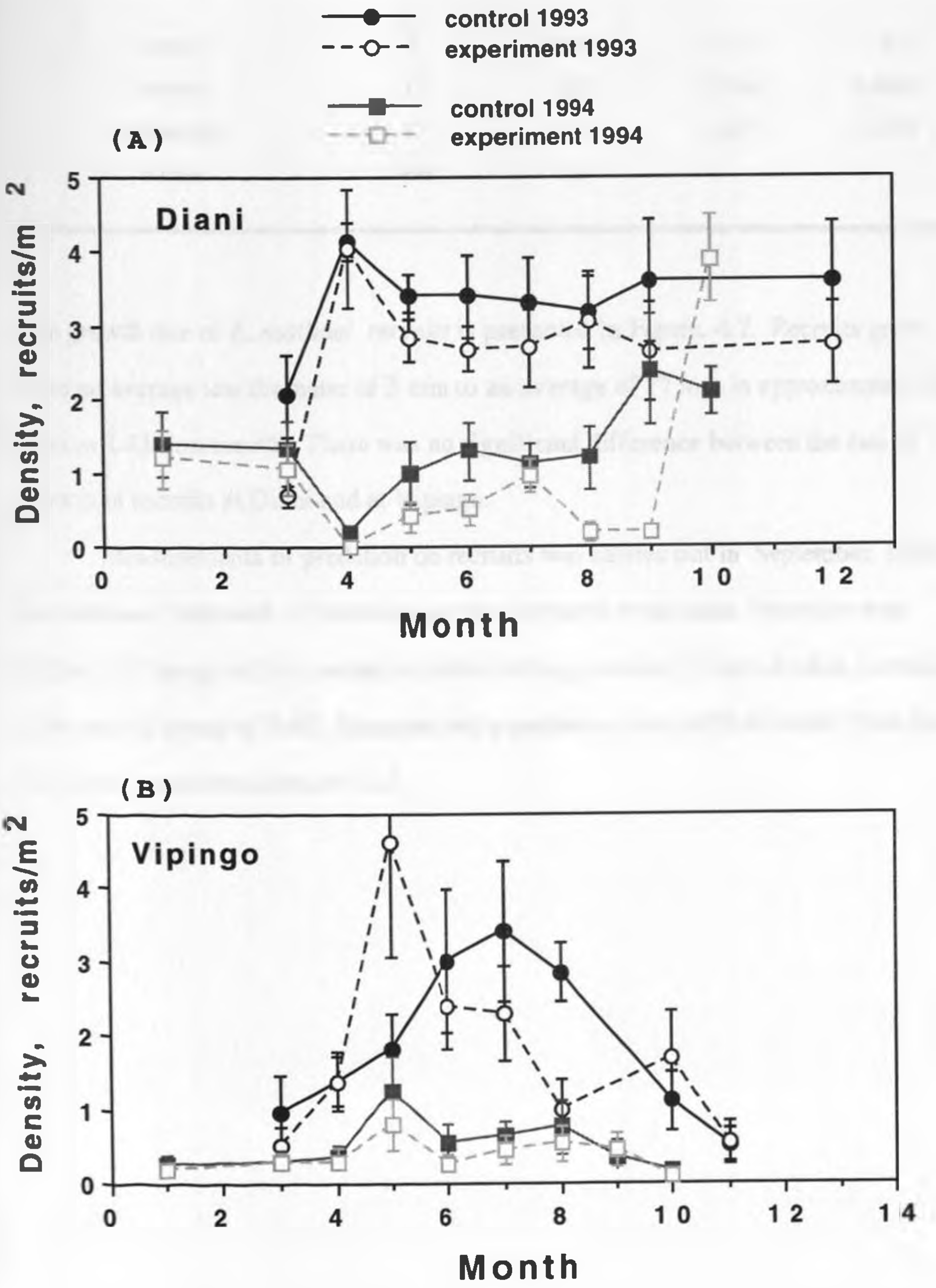

control 1993
experiment 1993
control 1994
experiment 1994
(A)
Diani
Density, recruits/m 2
0
1
2
3
4
5
0
2
4
6
8
1 0
1 2
Month
(B)
Vipingo
Density, recruits/m 2
0
1
2
3
4
5
0
2
4
6
8
1 0
1 2
1 4
Month

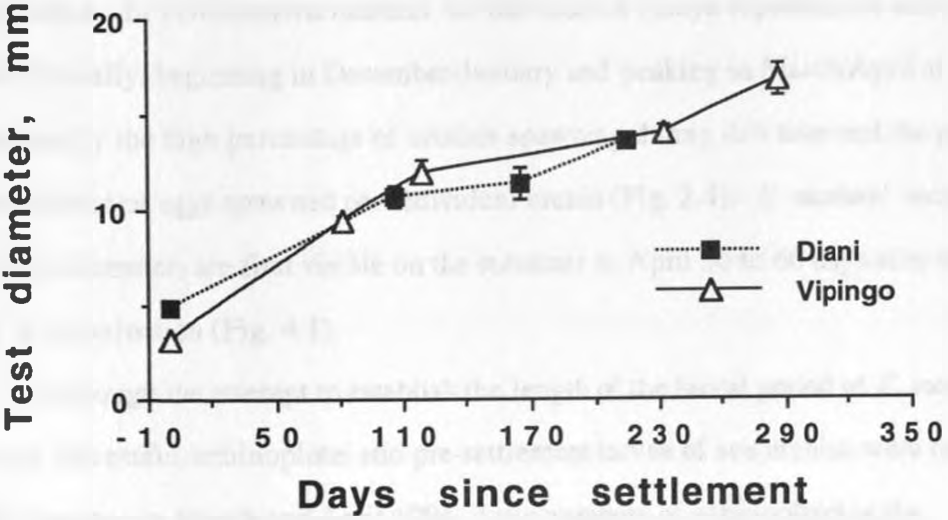
Table 4.5. Summary table of a two way ANOVA comparison of the density of recruits each month in 1993 -1994 in control and experimental plots of the sea urchin removal experiment at Vipingo and Diani. Twenty quadrats were censused each month in each plot at each reef and data are normalized by log transformation.

Source of Variation	*df*	*MS*	*F*	*p*
Sample	1	0.08	1.23	ns
Month	12	1.32	19.56	0.0000
Interaction	12	0.14	2.07	0.0172
Within	494	0.07		

The growth rate of *E. mathaei* recruits is presented in Figure. 4.7. Recruits grew from an average test diameter of 3 mm to an average of 17 mm in approximately 287 days or 1.43 mm/month. There was no significant difference between the rate of growth of recruits at Diani and at Vipingo.

Measurements of predation on recruits was carried out in September, 1994, on 4 transect lines with 10 juveniles per line tethered to the lines. Predation was highest at Vipingo with a predation index (average number of days it takes juveniles to be preyed upon) of 0.48. Kanamai had a predation index of 0.31 while Diani had the lowest predation index of 0.15.

Figure. 4.7. The growth of *Echinometra mathaei* recruits at Diani and Vipingo reef lagoons measured as the mean (± sem) test diameter of *E. mathaei* recruits collected on a monthly basis (approximately) from May 1992 to March 1993 (n = 20-80 recruits per sample).


Test diameter, mm
20
10
0
-10
50
110
170
230
290
350
Days since settlement
Diani
Vipingo

DISCUSSION

Seasonality of recruitment

For many marine species with seasonal reproductive patterns and planktonic larvae, recruitment onto the substrate follows with a longer or shorter time lag after reproduction. In *Echinometra mathaei* on the coast of Kenya reproductive activity occurs annually, beginning in December-January and peaking in March/April as evidenced by the high percentage of urchins spawning during this time and the peak in the volume of eggs spawned per individual urchin (Fig. 2.4). *E. mathaei* recruits (2 mm in diameter) are first visible on the substrate in April 30 to 60 days after the peak in reproduction (Fig. 4.1).

Although the attempt to establish the length of the larval period of *E. mathaei* was not successful, echinoplutei and pre-settlement larvae of sea urchins were found in the plankton in March and April 1994. Low numbers of echinoplutei in the plankton were also reported by Reay and Kimaro (1984) in Tudor creek in February and March 1983. Assuming that some of these were *E. mathaei* larvae, we can calculate a larval period of between 30 - 60 days. It is difficult to calculate the actual length of the larval period because sea urchin larvae only start growing 8 - 10 days after metamorphosis (Hinegardener, 1969) and are not visible to the naked eye for several weeks after settlement on the substrate. Hinegardener (1969) showed that it takes laboratory reared newly settled individuals of *Lytechinus pictus* two months (from fertilization to metamorphosis) to reach a size of 4 mm (test diameter).

The period from spawning to the time recruits are first visible in nature for *E. mathaei* in Kenyan waters can safely be estimated to be a minimum of two months. It follows therefore that recruits recorded in April were probably spawned in February at the peak of reproduction. This corresponds well with reports of the larval period of other species of *Echinometra* with development times from fertilization to metamorphosis of 18, 23 and 30 days for *E. vanbrunti* , *E. lucunter* and *E. viridis* A. Agassiz respectively (Cameron, 1986; Emlet as quoted in Emlet *et al*., 1987).

Small individuals of *E. mathaei* were recorded in April-May every year during this study. McClanahan and Kurtis (1991) also recorded *E. mathaei* recruits in July 1989. It follows therefore that recruitment of *E. mathaei* is seasonal on the Kenyan coast closely dependent on the seasonal reproductive peak. The seasonal nature of recruitment has been reported previously for several temperate species of sea urchins. *Tripneustes ventricosus* (Lamarck) recruits appear in July-August following spawning in May-June (Lewis, 1958; McPherson, 1969). *Strongylocentrotus purpuratus* and *Strongylocentrotus franciscanus* (A. Agassiz) both spawn in the spring and settle on the substrate in the fall after 2 to 3 months in the plankton (Strathman, 1978; Pearse, 1981). The Caribbean urchins *E. lucunter* and *E. viridis* also show seasonal recruitment, spawning in August-September and settling in September-October (Cameron, 1986).

The few other records available on the recruitment of tropical sea urchins also indicate seasonal recruitment following seasonal reproduction. For example, *T. gratilla* recruits annually in May-June in the Red sea (Dafni, 1992) after the spawning peak in December- January (Fouda and Hellal, 1990). Interestingly, at Rottnest Island, Western Australia *E. mathaei* reproduces year round (Pearse and Phillips, 1968) yet recruitment is seasonal occurring over several months including February (R. Black and J. Prince, quoted in Watts *et al*., 1990). This suggests that conditions for development of the larvae are present only for part of the year. During the present study, small recruits of at least three other species of urchins were recorded in May including *Diadema setosum*, *D. savignyi* Michelin and *T. gratilla*. Small individuals of star fish, sea cucumbers and brittle stars were also observed under coral rubble in the reef lagoons on the Kenyan coast in May.

Other marine invertebrates including the oyster *Crassostrea cucullata* (Born) (van Someren and Whitehead, 1961; Ruwa and Polk, 1994) and the barnacle *Balanus amphitrite* (Darwin) (Ruwa and Polk, 1994) also have a major peak of recruitment in

April-May in Kenyan waters. Ntiba and Jaccarini (1990) also reported seasonal spawning activity in the fish *Siganus sutor* (Cuvier &Valenciennes, 1835) in Kenyan waters including the period January-February with juveniles appearing in the samples in February-March. Unfortunately no other records of seasonal recruitment of sea urchins and other echinoderms are available from other parts of the East coast of Africa.

The fact that seasonal recruitment at around the same time of the year is widespread among different groups of marine animals in Kenyan waters indicates that April to May in the north east monsoon season is an ideal time for recruitment for marine animals with planktonic larvae in Kenyan waters. Similar species of sea urchins and other echinoderms occur along the whole East African coast from Mozambique to Somalia (Clark and Rowe, 1971). Recruitment is therefore also likely to be seasonal along the entire East African coast including off the coast of Tanzania since similar climatic and oceanographic conditions driven by the monsoonal system occur along this coast (McClanahan, 1988b). Further studies of the reproduction and recruitment of sea urchins in other areas of the East African coast need to be carried out before confirming these generalizations about the seasonality of recruitment on the East African coast .

Biogeography

Echinometra mathaei recruits were recorded every year at around the same time of the year following peak reproductive activity, thus indicating that these larvae are derived from a local source. Recruits (4 mm test diameter) however were also recorded in November-December in 1992, a time that does not coincide with local reproductive activity. The East African Coastal Current flows north along the East coast of Africa throughout most of the year and could bring pre-settlement larvae originally spawned in the south (off the coast of Tanzania for example). If populations of *E. mathaei* spawn later in the year in these areas, small individuals could settle off the Kenyan coast in November. However it is unlikely that *E. mathaei* populations off the coast of Tanzania are spawning at a different time because they are exposed to similar oceanographic and climatic conditions as the coast of Kenya.

Another source of late larvae which could be considered, would be *E. mathaei* populations in the Indian Ocean Island states for example the Seychelles where according to Pearse (1968) *E. mathaei* spawn throughout the year. These larvae could be dispersed by the Southern Equatorial Current (SEC) which travels across the Indian ocean and encounters the East African coast at Tanzania before heading north as the East African Coastal current (Johnson, *et al*, 1982; Hastenrath and Greischar, 1991). The SEC varies seasonally from 0 - 0.55 m/sec and averages 0.25 m/sec (Hastenrath and Greischar, 1991). Under the most ideal conditions larvae that mature in 30 to 60 days could be dispersed a maximum distance of 1426 to 2851 km not taking into account microspatial variations in current structure and speed, upwelling and downwelling and the formation of local gyres. Larvae from Seychelles would have to travel a distance of approximately 1600 km to reach the East African coast. Under ideal conditions of transport it therefore seems likely that *E. mathaei* larvae are recruiting from some Indian Ocean Island states.

The presence of small individuals later in the year might also be explained by late spawning (i.e. in April or May) coupled with very slow growth rates. There is some evidence that late recruits have lower fitness than early recruits because early recruits pre-empt resources or gain a competitive advantage in size (Raimondi, 1990). *E. mathaei* recruits grew at an average rate of 1.4 mm/month (Fig. 4.7). Larvae from a late spawning event (April-May) would be expected to reach an average size of 7 mm by November-December yet individuals as small as 4 mm were recorded in November-December 1992. This would require a growth rate of 0.6 mm/month which seems unlikely.

Although the presence of small individuals late in the recruitment season could not be adequately resolved in this study dispersal from a source outside of the general East African population is the most likely explanation. *E. mathaei* is a very widely distributed species ((Mortensen, 1943; Clark and Rowe, 1971) and it is conceivable that large scale dispersal of its larvae is one of the mechanisms for maintaining such broad geographical distribution. Studies of the genetic differences between populations of *E. mathaei* collected along the Western Australian coast showed that genetic variation of populations occurring close to each other was as great as the amount of variation of populations occurring several thousand km apart (Watts *et al*., 1990). Although the genetic character of a local population was dependent on recruitment, planktonic dispersal tended to decrease the variation of populations over large distances. Studies on the genetic variability of the East African *E. mathaei* population would have to be carried out, however, before a genetic input from outside sources could be validated.

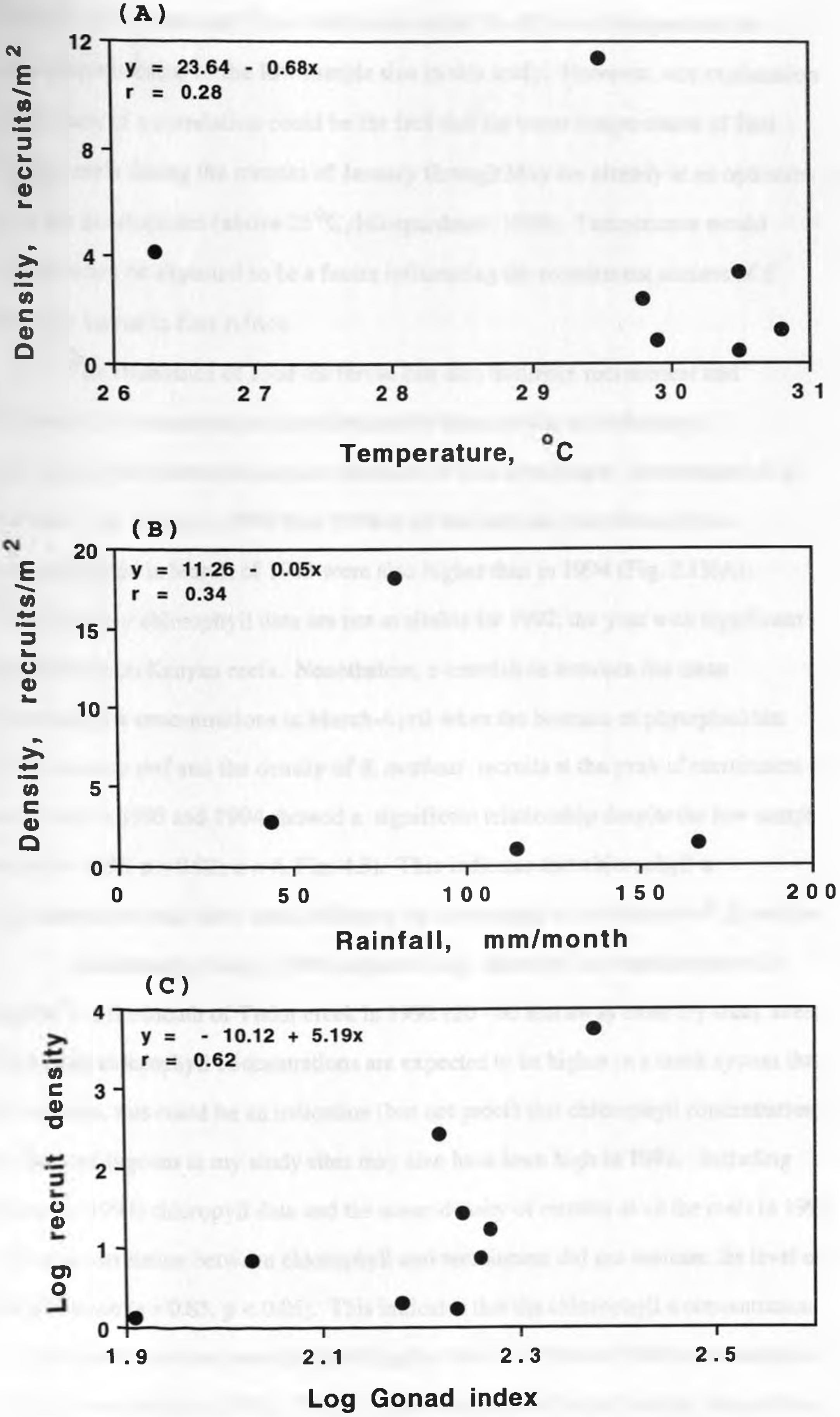
Temporal and spatial variation in recruitment

Many marine organisms show temporal and spatial variation in recruitment (Connell, 1961; Ebert, 1983; Pennings, 1991) and *E. mathaei* on the coast of Kenya was no exception. The pattern of year to year variation in recruitment included an exceptionally good year (1992) and years with low recruitment 1993 and 1994 (Fig. 4.1, Table 4.2). According to McClanahan (pers. comm), 1987 was also a noticeably good recruitment year. Recruitment was significantly higher at Vipingo and Diani reef lagoons than at Kanamai in 1992 to 1994 (Table. 4.4). McClanahan and Kurtis (1991) reported no significant difference between the reefs in 1989, however this data was recorded in July several months after settlement, when natural mortality would have reduced the numbers of recruits. The differences in recruitment at Vipingo and Diani are not consistent however, for example although Vipingo showed the highest recruitment in 1992, Diani had significantly higher recruitment than Vipingo in 1994 (Table 4.2, 4.4). Although recruitment was consistently higher at all the reefs in 1992 than in any other year, there was no reef where recruitment was consistently higher than other reefs every year indicating that the factors that may cause this variation are probably not related to conditions at one reef but are general conditions affecting all reefs.

Variability in recruitment has been shown in several other studies of sea urchins (reviewed by Ebert, 1983; Bak, 1985; Raymond and Scheibling, 1987;) and a number of factors have been suggested to cause this variability. Several of these factors were tested in this study including temperature, freshwater runoff and availability of food for the young, predation on juveniles and fecundity of the parent population. Water temperature is one of the main environmental factors that has been implicated in the control of recruitment (Thorson, 1950). Temperature increases the rate of larval development but may also indirectly affect recruitment success by increasing productivity in the water column and therefore the availability of food for planktonic larvae.

Although increased temperature is often invoked as a factor that increases larval development rates and thus potentially increases the success of recruitment (Kinne, 1970; Ebert, 1983), few studies have actually shown a direct correlation between temperature and recruitment (Ebert, 1983). For example, Matsui (1966) cited Kawana (1956) as having reported the enhancement of echinoid recruitment by the warm temperatures of the Tsushima current. Ebert (1983), on the other hand, reported the highest recruitment of *S. purpuratus* during the coldest winters between 1969 and 1977 off Southern California. Temperature appears to have no strong influence on larval success in *E. mathaei* as the correlation between the average temperatures recorded at each reef during the months when feeding larvae are expected in the water column (January - April) and the density of recruits at the peak recruitment period showed no significant relationship ($r = 0.28$; $p = 0.55$; $n = 7$) (Fig. 4.8(A)).

Figure. 4.8. (A) The relationship between the density of *Echinometra mathaei* recruits and water temperature measured as the mean water temperature between the hours of 10:00 and 12:00 at each reef in January through April plotted against the corresponding density of recruits. (B) The relationship between the mean monthly rainfall and the density of recruits of *Echinometra mathaei*. . Each data point represents the mean monthly rainfall at the Mombasa meteorological station in March - April at the peak of spawning plotted against the mean density of recruits in 1989, 1992 to 1994 pooled for all reefs. Data for 1989 are derived from McClanahan and Kurtis, 1991). (C) The relationship between the gonad index of *Echinometra mathaei* and the density of recruits. Each data point represents the log of the mean gonad index of *E. mathaei* at the peak of reproductive activity plotted against the log of the mean density of recruits at Diani, Kanamai and Vipingo in 1992 to 1994.


(A)
y = 23.64 - 0.68x
r = 0.28
Density, recruits/m^2
12
8
4
0
26
27
28
29
30
31
Temperature, °C
(B)
y = 11.26 - 0.05x
r = 0.34
Density, recruits/m^2
20
15
10
5
0
0
50
100
150
200
Rainfall, mm/month
(C)
y = - 10.12 + 5.19x
r = 0.62
Log recruit density
4
3
2
1
0
1.9
2.1
2.3
2.5
Log Gonad index

It is difficult to make any firm conclusions about the effects of temperature on recruitment because of the low sample size in this study. However, one explanation for the lack of a correlation could be the fact that the water temperatures of East African reefs during the months of January through May are already at an optimum level for development (above 25°C, Hinegardener, 1969). Temperature would therefore not be expected to be a factor influencing the recruitment success of *E. mathaei* larvae in East Africa.

The abundance of food for larvae can also influence recruitment and chlorophyll a concentrations have frequently been used as an indicator of phytoplankton concentrations and therefore of food abundance. Recruitment of *E. mathaei* was higher in 1993 than 1994 at all the reefs and the chlorophyll **a** concentrations in March of 1993 were also higher than in 1994 (Fig. 2.11(A)). Unfortunately chlorophyll data are not available for 1992, the year with significant recruitment on Kenyan reefs. Nonetheless, a correlation between the mean chlorophyll **a** concentrations in March-April when the biomass of phytoplankton peaks at each reef and the density of *E. mathaei* recruits at the peak of recruitment at each reef in 1993 and 1994 showed a significant relationship despite the low sample size ($r = 0.88$, $p = 0.02$; $n = 6$, Fig. 4.3). This indicates that chlorophyll **a** concentrations may have some influence on the strength of recruitment of *E. mathaei*.

Additionally, Kasyi (1994) reported high chloropyll **a** concentrations (2.5 mg/m^3) at the mouth of Tudor creek in 1992 (20 - 60 Km away from my study sites). Although chlorophyll concentrations are expected to be higher in a creek system than in lagoons, this could be an indication (but not proof) that chlorophyll concentrations in the reef lagoons at my study sites may also have been high in 1992. Including Kasyi's (1994) chloropyll data and the mean density of recruits at all the reefs in 1992 into the correlation between chlorophyll and recruitment did not increase the level of significance ($r = 0.83$, $p < 0.05$). This indicates that the chlorophyll **a** concentration in 1992 need not have been that much higher than in 1993 and 1994 for recruitment to have been higher in 1992. This is further emphasized by the fact that some of the factors that may cause higher pytoplankton biomass for example temperature and light were not significantly higher in 1992 than in 1993 and 1994 (Single factor ANOVA: F = 0.11, p = 0.89, n = 28, and F = 0.6, p = 0.55, n = 32 respectively).

The evidence for the influence of food availability on the larvae of planktonic marine invertebrates is of two types: 1) correlation studies showing recruitment or increased recruitment with increased pytoplankton biomass, and 2) experimental studies showing that increased food resulted in larger larvae and decreased time to metamorphosis (reviewed by Olson and Olson, 1989). Birkeland (1982) for example correlated the outbreak of the starfish *Acanthaster plancii* (Linnaeus) with terrestrial runoff two to three years earlier. He hypothesized that increased nutrients due to heavy runoff may cause phytoplankton blooms causing increased food supply for the larvae of the starfish which came to be known as the terrestrial runoff hypothesis. Lucas (1982) showed in rearing experiments that the levels of pytoplankton required for survival of *A. plancii* larvae were higher than field levels of pytoplankton which led to the hypothesis that *A. plancii* might be food limited in nature. Olson (1985) on the other hand failed to show food limitation in *A. plancii* larvae reared *in situ*. It is therefore very difficult to make generalizations about food limitation and the influence on larval success of echinoderms (Olson and Olson , 1989). Additionally very few studies have been carried out on tropical sea urchins making comparison with the present study difficult. The data from the present study are suggestive however of the potential importance of food availability to the larvae in the recruitment success of *E. mathaei*.

Increased nutrients in nearshore waters due to freshwater runoff could result in short term increases in phytoplankton when other conditions of temperature and light are favourable. Freshwater runoff has been correlated with recruitment in invertebrates like the Crowm-of-thorns starfish *A. plancii* (Birkeland, 1982) and the lobster *Homarus americanus* (Sutcliffe, 1973). No nutrient measurements were taken at these reefs, but rainfall data can be used as an indicator of the potential of freshwater runoff and therefore increased nutrients. A correlation performed between the mean rainfall data collected by the Kenya Meteorological department at Mombasa station in 1989, 1992 to 1994 against the mean density of *E. mathaei* recruits during the peak month of recruitment showed no significant relationship (Fig. 4.8(B)). However, the scanty data does not allow us to make any firm conclusions about the possible effects of rainfall on the recruitment of *E. mathaei*. Moreover, the period when rainfall peaks is also when illumination is low so chlorophyll would not be expected to be high during this time.

Assuming that the larvae that settle on the reefs are from a local source as discussed earlier, the variation in the fecundity of the adult population may also have an effect on recruitment variability. This was tested in *E. mathaei* by performing a correlation between the gonad index of *E. mathaei* (which is highly correlated to fecundity (Fig. 3.4(B))) at each reef against the density of recruits at the peak period of recruitment in 1992 to 1994. Although there was a general trend of increased recruitment with increased gonad index, the relationship was not significant ($r = 0.62$; $p=0.07$, $n= 9$, Fig. 4.8(C)) indicating that gonad index is not a good predictor of recruitment in *E. mathaei*. Additionally mortality of recruits could counteract effects of high fecundity. In this study, the highest juvenile mortality through predation was recorded in Vipingo where fecundity was high.

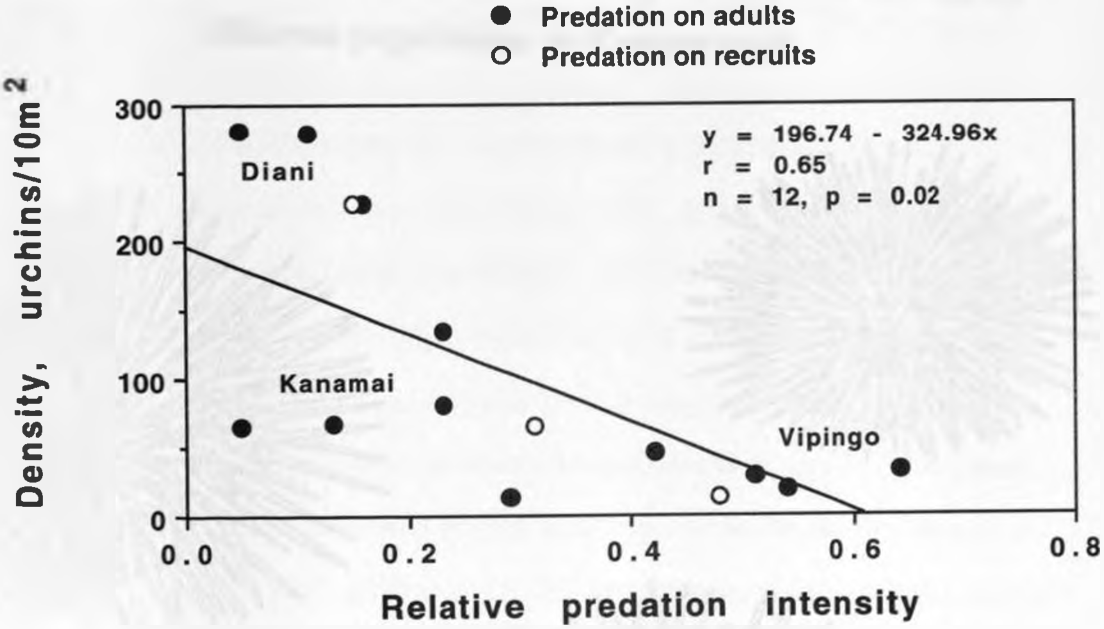
Relationship between recruitment and the adult population

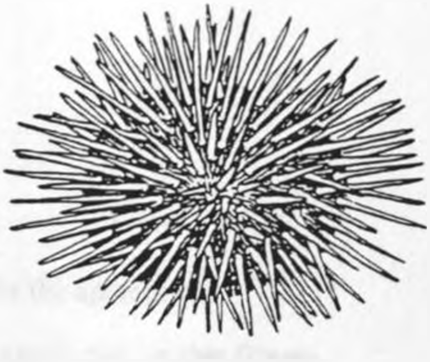
The population dynamics of marine invertebrates with planktonic larvae reflect fluctuations in both the larval as well as the adult phase. The influence of one phase upon the other was examined for *E. mathaei* by comparing the adult population and the intensity of recruitment at different reefs. The adult density at Diani, Kanamai and Vipingo reef lagoons showed considerable fluctuations with a general increase at all reefs between 1985 and 1989. The populations of *E. mathaei* have remained relatively stable over the last three years at these reefs. The pattern of year to year variation in recruitment included an exceptionally good year (1992) and years with low recruitment. A comparison of the trends in the adult population and in the rates of recruitment showed few clear associations. Several studies have reported heavy settlement of juveniles around or under adults (Moore *et al*., 1963; Ebert, 1968; Tegner and Dayton, 1977). The available evidence does not support this in the case of *E. mathaei*, since 1) heavy settlement of recruits of *E. mathaei* did not necessarily occur where high adult densities occurred (Fig. 4.5(A)) in fact Vipingo with the lowest density of adults had the highest density of recruits in 1992 and 2) recruitment was not necessarily lower in the sea urchin removal plots than in the control plots (Fig. 4.6(A and B))

Additionally, heavy settlement did not necessarily lead to a subsequent increase in the adult population (Fig. 4.5(B)). For example, the high recruitment at Diani and Vipingo in 1992 did not translate to an increase in the adult population in 1993, in fact a small but insignificant decrease in population was recorded at both these reefs in 1993. At Kanamai, recruitment in 1992 may have influenced the increase of adults in 1993. The mortality of recruits was very high in these reefs as evidenced by the sharp decrease in recruit numbers in July at Diani and October in Vipingo in 1992 (Fig. 4.1(A) and (B)). The lack of a correlation between recruitment and adult population changes has been reported for many other species of echinoids (Ebert, 1983) leading to the conclusion that other factors are more important in controlling population changes in sea urchins than recruitment.

Predation for example has been implicated in controlling echinoid populations including predation by the sea otter *Enhydra lutris* (which plays an important role in limiting sea urchin size and abundance, Estes and Palmisano, 1974), the starfish *Pycnopodia helianthoides* (Harrold and Pearse, 1987) and the triggerfish *Balistapus undulatus* (McClanahan and Muthiga, 1989; McClanahan and Kurtis, 1991). Several lines of argument can be made to illustrate that predation is a more important factor in controlling *E. mathaei* populations than recruitment. First, there was no relationship between recruitment strength and adult population density (Fig. 4.5(A)), nor was there a relationship when recruitment strength was plotted against adults density a year later (Fig. 4.5.(B)). Secondly, there was a significant relationship ($r = 0.65$; $p = 0.02$; $n = 12$) between the relative experimental predation intensity and the density of adults (Fig. 4.9). Additionally, predation intensity of recruits mirrored predation intensity of adults with the highest predation occurring at the reef with the highest population density (Vipingo) of *E. mathaei*. Predation measured experimentally on tethered animals was the best predictor of *E. mathaei* population density. This validates studies that have argued for the control of *E. mathaei* populations by predation pressure (McClanahan and Muthiga, 1989; McClanahan and Shafir, 1990; McClanahan and Kurtis, 1991). Although recruitment of *E. mathaei* was recorded at each reef every year, the strength of recruitment was very variable and was not a reliable predictor of adult population density.

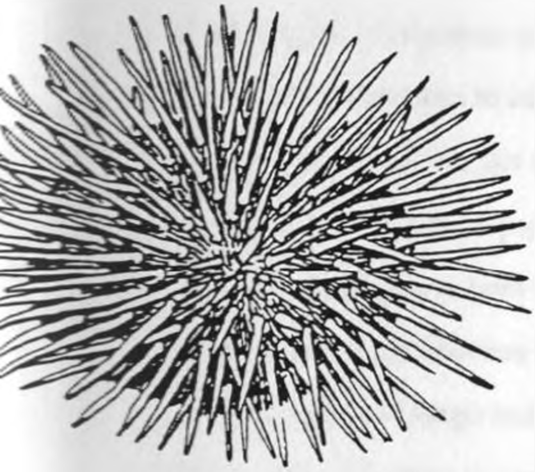
Figure. 4.9. The relationship between predation and the density of *Echinometra mathaei*. Each point represents the relative predation intensity on *E. mathaei* calculated from 4 experiments (10 urchins each) at Diani, Kanamai and Vipingo plotted against the mean density of *E. mathaei* in 18 to 24 quadrats at each reef in 1988 (data derived from McClanahan and Shafir, 1990), 1992 to 1994. The intensity of predation on recruits at each reef is also included, however the curve is fitted to the data on adults only.

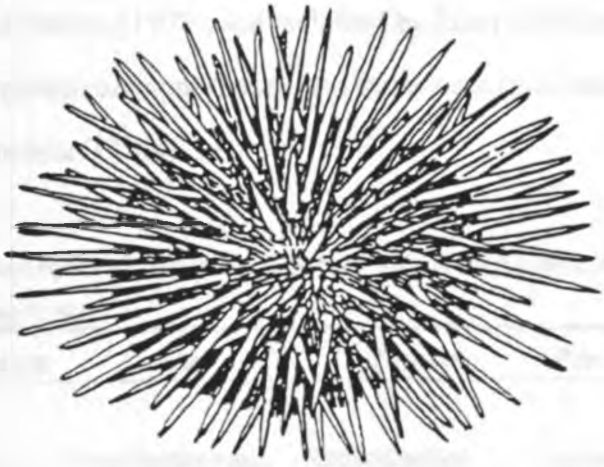

● Predation on adults
○ Predation on recruits
y = 196.74 - 324.96x
r = 0.65
n = 12, p = 0.02
Diani
Kanamai
Vipingo
Density, urchins/10m²
Relative predation intensity
0
100
200
300
0.0
0.2
0.4
0.6
0.8

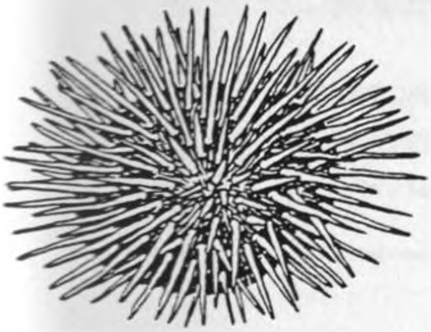


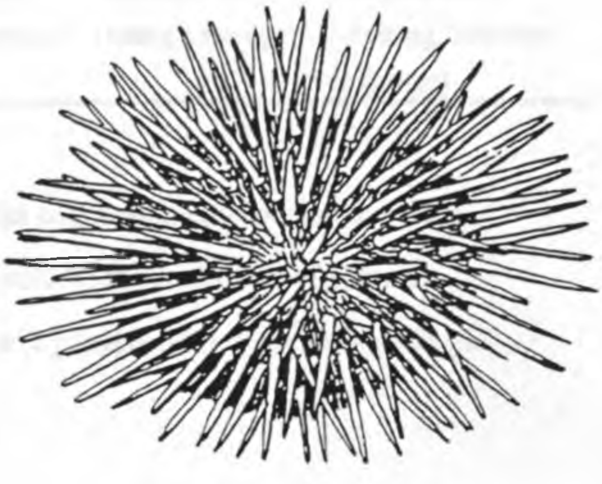
CHAPTER FIVE

Comparative Morphometrics of *Echinometra mathaei* (de Blainville): the Effects of Population Density on Size and Growth on different populations on Kenyan reefs









INTRODUCTION

One of the most important features of life history strategies is the appropriate allocation of resources between growth, maintenance and reproduction so that fitness is maximized (Gadgil and Bossert, 1970). The allocation model argues that resources are always limited because even though an organism lives in an environment where resources are in plenty, the assimilation of these resources is controlled by energetic, mechanical and physiological constraints. An organism can only assimilate a finite amount of food and this must therefore be appropriately allocated to growth, reproduction and maintenance processes (Ebert, 1982). Organisms have developed processes and mechanisms to adjust to different conditions that ultimately allow them to survive to reproduce. In this chapter the allocation of resources to these processes by *E. mathaei* in relation to population density is investigated. Many of the points raised in this chapter have been covered elsewhere in this thesis especially in chapter 3 and therefore the introduction will be brief touching only on the relevant points.

According to Gadgil and Bossert (1970), and reviewed by Ebert (1982) energy and materials acquired by an organism are apportioned into three basic functions: growth, reproduction and maintenance (Table 5.1).

Table 5.1 Body parts of sea urchins and their main functions. The body wall includes tube feet and all the related organs. Adapted from Ebert (1982).

Body wall	*Aristotle's lantern*	*Gut*	*Gonad*	*Perivisceral fluid*
Growth	Food gathering	Food processing	Reproduction	Space adjustment
Maintenance	Maintenance	Maintenance	Maintenance	Maintenance
Food gathering	(hole excavation)	(energy storage)	(energy storage)	(clotting, immune response)

Growth relates to the increase in body size and the consequent problems of how parts change in relation to each other. Reproduction includes the production of gametes and supporting tissues and reproductive behavior (e.g. aggregation prior to spawning).

Maintenance involves the physiological processes, morphological structures and behavioral characteristics that increase survival (including sharp or toxic spines, excavation of cavities). All these compartments are related either through physiological or through physical processes (Ebert, 1982)(Table 5.1).

Allocation of available resources to growth, reproduction or maintenance has metabolic and physiological constraints that are related to relationships between different body parts. Body size is the main morphological characteristic against which other morphological characteristics and physiological factors are measured. The relationships between body size and other morphological and physiological characteristics are described by allometric equations. The most basic and general allometric relationship occurs between body size and the amount of resources an individual requires. In general, large individuals have relatively lower metabolic rates and require less energy per gram than smaller individuals, however large individuals require more energy and nutrients per individual than small individuals. For sedentary marine invertebrates like sea urchins, food availability is therefore an important factor controlling body size.

Given that the availability of food is a limiting factor for the body size of sedentary organisms, there is usually a tradeoff between the number of individuals and the body size in a given space. In most cases there is a highly significant and negative relationship between population density and body size when different species are compared (Brown, 1995). The influence of population density on body size has also been reported at the intraspecific level in the sea urchins *Diadema antillarum* and *Strongylocentrotus purpuratus* (Levitan, 1988, 1989; Ebert, 1967; Edwards and Ebert, 1991). Experimental manipulation of density showed that these urchins are able to regulate body size in a density-dependent way, with food availability at different densities being the underlying cause of size regulation. McClanahan and Kurtis (1991) however failed to show a relationship between body size and population density for *E. mathaei* from several reefs in Kenya and hypothesize that predation was an important factor controlling population density and body size.

Body size has important implications on the way resources are allocated between reproduction and growth. The allocation of resources to reproduction for example is constrained not only by the availability of food but also by the size of the body. Body size is especially critical in sea urchins because gonads are the major structure within the inextensible test (taking up to 25% of coelomic space) and reproductive effort is therefore limited by space for the gonads when food is not limiting (Ebert, 1982). It follows therefore that if food is not limiting, larger individuals will have a higher reproductive effort because they can allocate a higher proportion of the available energy to reproduction. Reproductive effort has traditionally been used by population biologists as a measure of reproductive fitness (Thompson, 1982) with the fundamental assumption that larger individuals have a higher reproductive effort and therefore have a higher reproductive fitness than their smaller relatives.

In recent years the importance of population density on the success of fertilization has been shown to be a critical factor in the reproductive fitness of marine invertebrates (Pennington, 1985; Levitan, 1991). Population density is especially critical to the fertilization success of sedentary marine organisms that do not aggregate or synchronize spawning. Levitan (1991) develops a model of fitness that incorporates population density, body size and reproductive output. In this model, small individuals occurring at high densities could achieve equivalent reproductive fitness to large individuals at low density because fertilization success would be higher at the higher population density. In chapter 3, I show that the fecundity of individual E. mathaei is highest at Vipingo the reef with the largest animals and lowest population of *E. mathaei*. In this chapter I will explore further the allocation of resources to reproduction by *E. mathaei* and the concept of reproductive fitness under different conditions of population density.

The allocation of resources to growth is also constrained by food availability. Usually, under conditions of food limitation individuals are small and may even show negative growth (Levitan , 1988, 1989). The ability to reduce body size when food is limiting has been demonstrated in sea anemones (Sebens, 1981), sea stars (Feber, 1970) and sea urchins (Ebert, 1967; Levitan, 1988, 1989). With the exception of Ebert's (1975) study on the growth of three species of Echinometrids (based on a limited data-set) in Hawaii very little data is available on the growth rates of *E. mathaei*. Ebert (1975) postulates that fast growing urchins are also those that allocate more resources to growth and reproduction and less to maintenance resulting in a higher mortality for fast growing species. The fact that *E. mathaei* occurs at different population densities at Diani, Kanamai and Vipingo reef lagoons in Kenya gives us the opportunity to determine the way resources are allocated to growth, and to determine the relationship between growth and population density in this widespread sea urchin.

The objective of this study therefore was to determine what intraspecific differences occur in morphology and life history strategies of three populations of *Echinometra mathaei* with different population densities. Morphological features important in the processes of growth, reproduction and maintenance are compared and the way resources are allocated to these processes are determined for populations of *E. mathaei* at Diani, Kanamai and Vipingo reef lagoons in Kenya.

MATERIALS AND METHODS

Morphological differences

The differences in the morphology of *E. mathaei* at each reef was studied by compiling and analyzing morphological data collected during the studies on the reproduction of *E. mathaei* between February 1992 to March 1995. These data included urchin length (test diameter at the longest horizontal axis), width (test diameter at the shortest horizontal axis) and body weight, gut weight, stomach weight and jaw weight. Stomach weights were measured after removal of gut contents. Lengths and widths were measured to the nearest 0.1 mm with a vernier caliper and all weights were measured to the nearest 0.01 gm after blotting excess moisture with tissue paper. For all measurements, the mean and standard error of the mean was calculated for each reef. The relationship between size of body parts and that of the urchin was analyzed by calculating indices, including gonad, gut and jaw indices using the formula "wet weight of body part/wet weight of urchin x 100".

The Student's t-test was used to test for differences between the mean sizes of urchins (i.e. length and weights), the mean sizes of gonads, guts, stomachs and jaws at each reef. A regression analysis was performed of the relationship between the length and the weights of urchins at each reef. Regression analysis was also performed of the relationship between the size of an urchin (test diameter) and the size of its jaw (jaw weight) for each reef. The data for comparison between jaw weight and urchin weight were log transformed to give a better fit of the data. Student's t-test was used to test for differences between the slopes and intercepts of different reefs for all comparisons.

Growth

Growth rates of urchins at each reef were determined using two methods: 1) marking individuals with tetracycline and 2) following the progression of size-frequency modes through time. Sea urchins are able to absorb tetracycline which produces a fluorescent mark on the actively growing portions of the skeleton (Ebert, 1965; Pearse and Pearse, 1975). In May 1992, 200 urchins were haphazardly collected at each reef and injected with tetracycline solution made by dissolving tetracycline HCl capsules (250 mg) in sea water to make a solution of 5 mg/ml sea water. Each urchin was injected through the peristomial membrane with tetracycline solution to make up approximately 0.12 mg/gm urchin (Pearse and Pearse, 1975).

Urchins were returned to an area of the reef marked with a mangrove stake. One year later the three sites were searched in the vicinity of the mangrove poles and 250 urchins were retrieved and returned to the laboratory. The test diameter of each urchin was measured and the Aristotle's lanterns were removed and dried in an oven (60°C). The demipyramids of each Aristotle's lantern were examined for fluorescent markings under an ultraviolet lamp. Growth of jaws was measured using a dissecting microscope with a calibrated ocular micrometer.

From May 1992 through 1995, size-frequency data were collected at each reef by haphazardly placing a 1 m^2 quadrat on the substrate and collecting all urchins within the quadrats up to a total of 100 urchins. The test diameter of all individuals was measured to the nearest 0.01 mm. Sampling was carried out approximately three times in a year at each reef and reefs were sampled within two days of each other. The length data were used in a computer program FISAT developed by Gayanilo *et al.* (1994) which searches for the growth curve that best fits a set of length frequency data using a goodness of fit index Rn to assess the reliability of the estimates of K (the growth rate constant).

The growth curve is based on the von Bertalanffy growth function

$$L_t = L_{inf}(1 - e^{-K(t-t_o)})$$

where L_{inf} is the asymptotic length (the mean length an urchin would reach if it were to grow to a very old age), K is the growth constant and t_o is the 'length' an urchin would have at age zero and L_t is the length at age t.

RESULTS

A summary of the morphological characteristics of *Echinometra mathaei* at Diani, Kanamai and Vipingo is shown in Table 5.2. Comparisons between reefs were made of the mean measurements using Student's t-test and are also summarized in Table 5.2. In most cases the sample sizes are very large (> 150) yielding highly significant differences between reefs. *E. mathaei* is elliptical in shape and therefore the test size was estimated from measurements of the length and the width of the test. These measurements differed significantly between reefs with urchins at Vipingo being on average longer and wider then urchins at Kanamai and Diani (Table 5.2). Urchin test length ranged from 4.0 mm to 62.6 mm and 4.0 to 62.6 mm for Kanamai and Vipingo respectively. The largest urchin measured at Diani was 54.6 mm and Diani had consistently the smallest urchins of all the reefs.

Figure 5.1 shows the relationships between urchin test length and weight, and test width and weight of *E. mathaei* populations at all the reefs. Test length and test width were significantly correlated ($p < 0.01$) with weight at all the reefs with all comparisons showing r values larger than 0.70. Urchins at Vipingo start out smaller in size in relation to weight compared to Diani and Kanamai urchins but by 42 - 45 mm test diameter, they are larger than Diani urchins for a given weight.

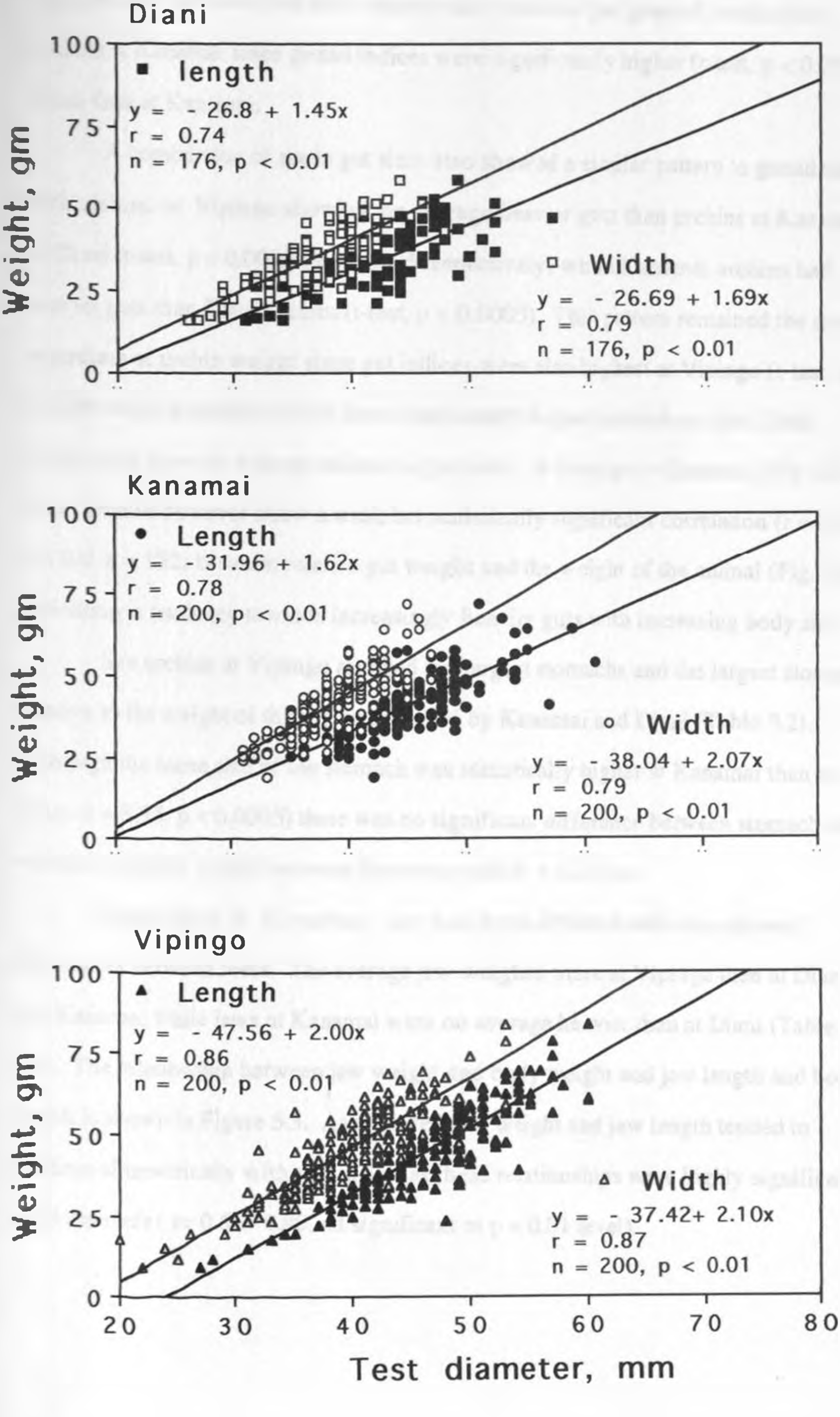
Differences were also recorded in the main internal organs of *E. mathaei* including the gut and the gonads. Mean gonad weights regardless of reproductive season, were higher at Vipingo than at Kanamai and Diani (t-test, $p < 0.0005$) while urchins at Kanamai had heavier gonads than at Diani (t -test, $P < 0.0005$). Mean gonad indices at each reef showed that Urchins had larger gonads for a given weight at Vipingo than at Diani (t-test, $P < 0.0005$) and Kanamai ($p < 0.05$).

Table 5.2. Morphological characteristics of *Echinometra mathaei* from Diani, Kanamai and Vipingo reef lagoons. Values include the mean (± sem) and the number of samples of each characteristic.

Characteristic	*Diani*	*Kanamai*	*Vipingo*	*Comparison*	*t*	*p-value*
Test length (mm)	41.7 ± 0.19	46.3 ± 0.19	47.6 ± 0.22	Diani vs Kanamai	-17.1	0.005
	n = 596	n = 632	n = 686	Diani vs Vipingo	-13.61	0.005
				Kanamai vs Vipingo	-4.59	0.0005
Test width (mm)	35.7 ± 0.20	39.6 ± 0.17	40.3 ± 0.20	Diani vs Kanamai	-14.9	0.0005
	n = 596	n = 631	n = 686	Diani vs Vipingo	-16.2	0.0005
				Kanamai vs Vipingo	-2.64	0.005
Body weight (g)	33.7 ± 0.40	43.8 ± 0.40	47.1 ± 0.54	Diani vs Kanamai	-17.8	0.0005
	n = 574	n = 632	n = 686	Diani vs Vipingo	-19.3	0.0005
				Kanamai vs Vipingo	-4.84	0.0005
Gonad weight (g)	2.20 ± 0.05	2.71 ± 0.06	3.88 ± 0.08	Diani vs Kanamai	-6.53	0.0005
	n = 791	n = 788	n = 820	Diani vs Vipingo	-17.7	0.0005
				Kanamai vs Vipingo	-11.6	0.0005
[a]Gonad index (%)	6.46 ± 0.13	6.17 ± 0.12	7.95 ± 0.14	Diani vs Kanamai	1.64	0.05
	n = 791	n = 785	n = 817	Diani vs Vipingo	-7.79	0.0005
				Kanamai vs Vipingo	-9.62	0.0005
Gut weight (g)	2.22 ± 0.08	2.74 ± 0.08	3.25 ± 0.09	Diani vs Kanamai	-4.59	0.0005
	n = 247	n = 235	n = 301	Diani vs Vipingo	-8.38	0.0005
				Kanamai vs Vipingo	-4.11	0.0005
Gut index (%)	6.33 ± 0.16	6.63 ± 0.15	7.29 ± 0.15	Diani vs Kanamai	-1.36	ns
	n = 247	n =228	n = 301	Diani vs Vipingo	-4.94	0.0005
				Kanamai vs Vipingo	-3.05	0.005
Jaw weight (g)	2.75 ± 0.05	2.89 ± 0.05	3.11 ± 0.05	Diani vs Kanamai	-1.94	0.025
	n = 234	n = 177	n = 311	Diani vs Vipingo	-4.94	0.0005
				Kanamai vs Vipingo	-2.88	0.005
Jaw index (g)	8.17 ± 0.11	7.35 ± 0.07	7.11 ± 0.10	Diani vs Kanamai	5.83	0.0005
	n = 234	n = 176	n = 311	Diani vs Vipingo	7.08	0.0005
				Kanamai vs Vipingo	1.68	0.05
Stomach weight (g)	0.37 ± 0.02	0.61 ± 0.05	0.80 ± 0.05	Diani vs Kanamai	4.46	0.0005
	n = 30	n = 30	n = 21	Diani vs Vipingo	-8.95	0.0005
				Kanamai vs Vipingo	-2.6	0.01
Stomach index (%)	1.24 ± 0.06	1.21 ± 0.06	1.92 ± 0.09	Diani vs Kanamai	0.35	ns
	n = 30	n = 30	n = 21	Diani vs Vipingo	-6.54	0.0005
				Kanamai vs Vipingo	-6.53	0.0005
Organic matter in the gut (%)	19.6 ± 0.08	28.1 ± 0.99	29.9 ± 0.33	Diani vs Kanamai	-12.7	0.0005
	n = 28	n = 40	n = 28	Diani vs Vipingo	-12.3	0.0005
				Kanamai vs Vipingo	-0.1	ns
[b]Density (#/10m^2)	260 ± 27	62 ± 6	28 ± 3	Diani vs Kanamai	7.16	0.0005
	n = 10	n = 12	n = 12	Diani vs Vipingo	8.54	0.0005
				Kanamai vs Vipingo	5.068	0.0005

[a] the mean gonad index for all urchins regardless of the month
[b] n = the number of quadrats sampled per reef in 1993

Figure. 5.1. The relationship between *Echinometra mathaei* test length and weight and test width and weight at Diani, Kanamai and Vipingo reef lagoons. Test length was measured at the longest axis and test width at the shortest axis of the test diameter.


Diani
Weight, gm
100
75
50
25
0
■ length
y = - 26.8 + 1.45x
r = 0.74
n = 176, p < 0.01
□ Width
y = - 26.69 + 1.69x
r = 0.79
n = 176, p < 0.01
Kanamai
● Length
y = - 31.96 + 1.62x
r = 0.78
n = 200, p < 0.01
○ Width
y = - 38.04 + 2.07x
r = 0.79
n = 200, p < 0.01
Vipingo
▲ Length
y = - 47.56 + 2.00x
r = 0.86
n = 200, p < 0.01
△ Width
y = - 37.42+ 2.10x
r = 0.87
n = 200, p < 0.01
20
30
40
50
60
70
80
Test diameter, mm

Diani urchins however had more reproductive material per gram of urchin than urchins at Kanamai since gonad indices were significantly higher (t-test, $p < 0.05$) at Diani than at Kanamai.

A comparison of mean gut sizes also showed a similar pattern to gonad size with urchins at Vipingo showing on average heavier guts than urchins at Kanamai or Diani (t-test, $p < 0.0005$; $p< 0.0005$ respectively) while Kanamai urchins had heavier guts than Diani urchins (t-test, $p < 0.0005$). This pattern remained the same regardless of urchin weight since gut indices were also highest at Vipingo (t-test, $p < 0.0005$) while Kanamai did not have significantly higher gut indices than Diani. Urchin size however was not related to gut index at Vipingo or Kanamai (Fig 5.2). Diani urchins however show a weak but statistically significant correlation ($r = 0.27$; $p < 0.0$, $n = 152$) between relative gut weight and the weight of the animal (Fig. 5.2) indicating a tendency towards increasingly heavier guts with increasing body size.

Sea urchins at Vipingo also had the largest stomachs and the largest stomachs relative to the weight of the urchin followed by Kanamai and Diani (Table 5.2). Although the mean size of the stomach was statistically higher at Kanamai than at Diani ($t = 8.95$, $p < 0.0005$) there was no significant difference between stomach sizes relative to urchin weight between these two reefs ($t = 0.35$, ns).

Comparisons of *E. mathaei* jaw size at the different reefs also showed differences between reefs. The average jaw weighed more at Vipingo then at Diani and Kanamai while jaws at Kanamai were on average heavier than at Diani (Table 5.2). The relationship between jaw weight and body weight and jaw length and body length is shown in Figure 5.3. As expected jaw weight and jaw length tended to increase allometrically with urchin size as these relationships were highly significant at all the reefs ($r= 0.63 - 0.89$, all significant at $p < 0.01$ level).

Figure. 5.2. The relationship between the gut index and the weight of *Echinometra mathaei* at Diani, Kanamai and Vipingo.

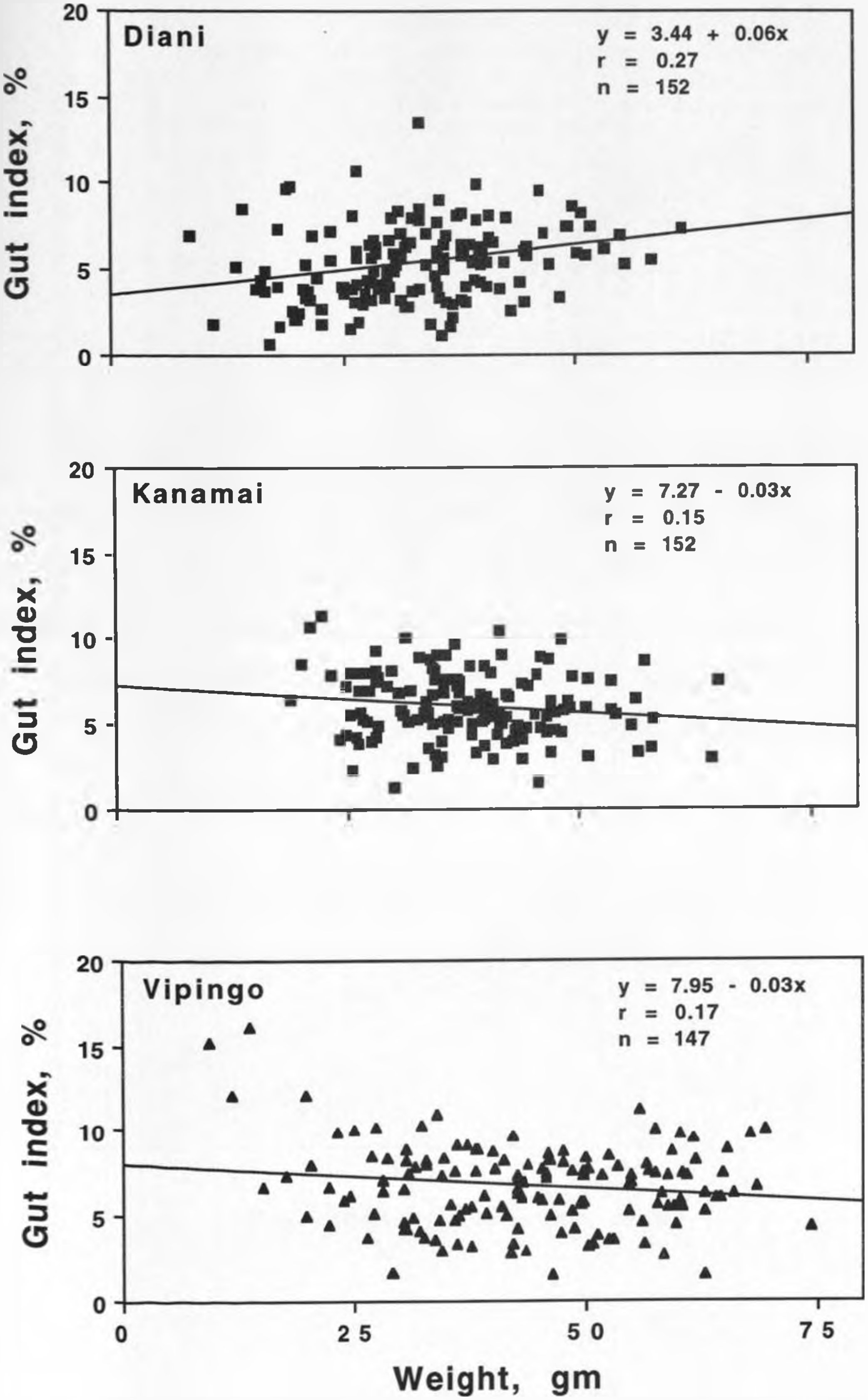
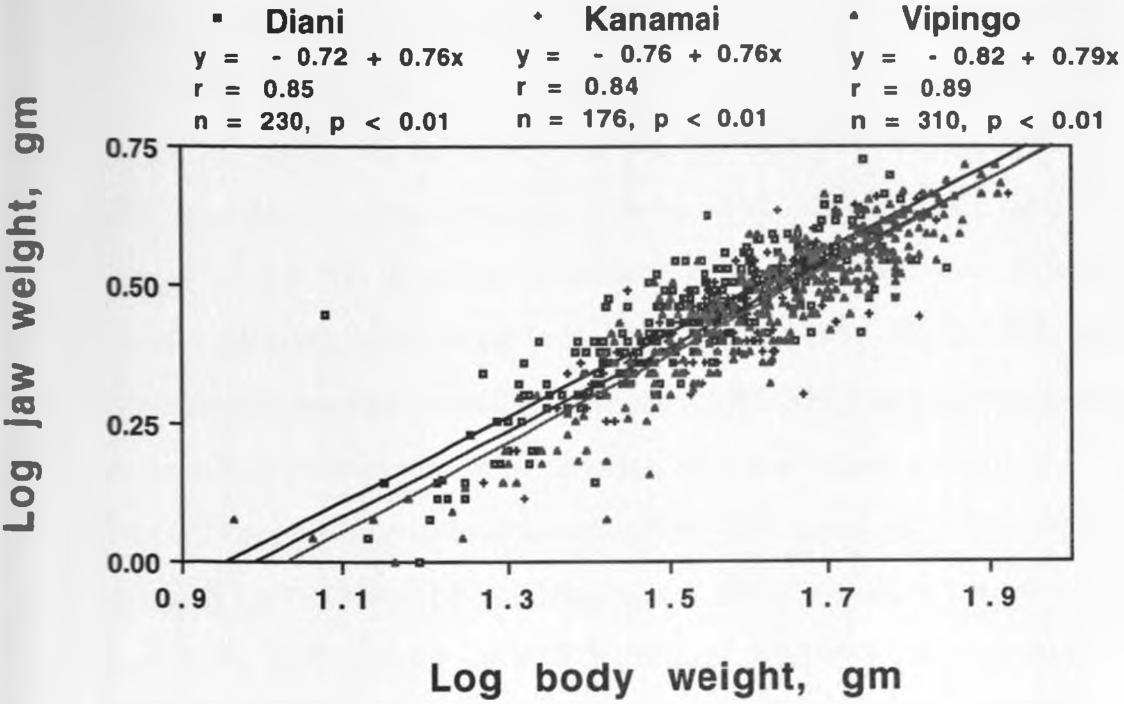
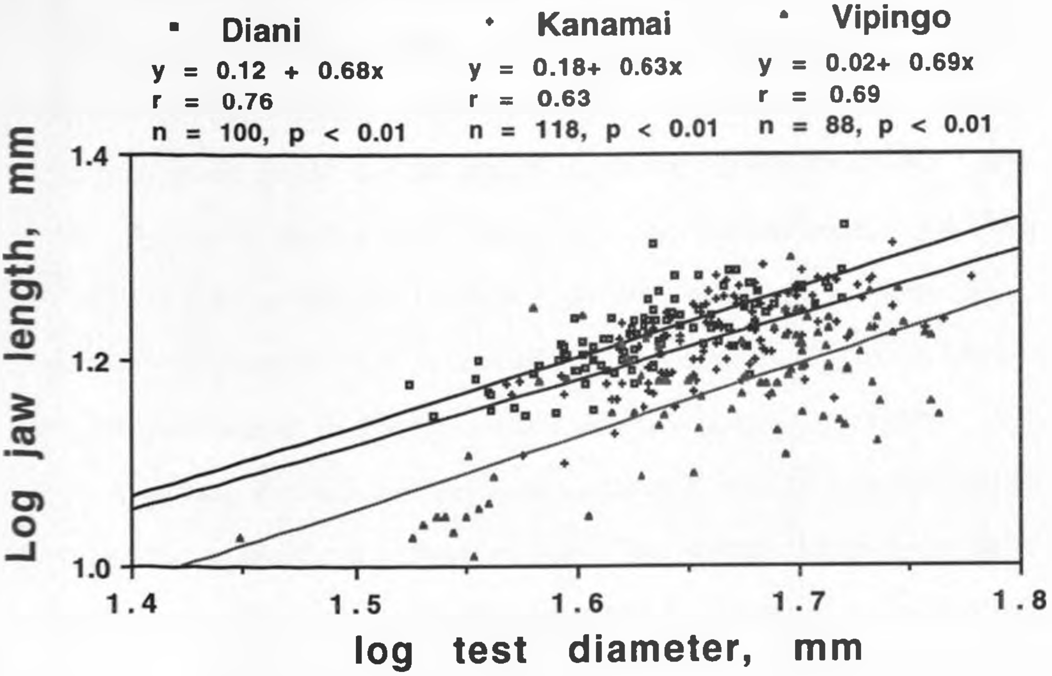

Diani
y = 3.44 + 0.06x
r = 0.27
n = 152
Kanamai
y = 7.27 - 0.03x
r = 0.15
n = 152
Vipingo
y = 7.95 - 0.03x
r = 0.17
n = 147
Gut index, %
0
5
10
15
20
0
25
50
75
Weight, gm

Figure. 5.3. (A) The relationship between log body weight and log jaw weight of *Echinometra mathaei* at Diani, Kanamai and Vipingo. All regressions are significant at $p < 0.01$ level. (B) The relationship between log urchin length and log jaw length of *Echinometra mathaei* at Diani, Kanamai and Vipingo. All regressions show a significant relationship at $p < 0.01$ level.

(A)


▪ Diani
y = - 0.72 + 0.76x
r = 0.85
n = 230, p < 0.01
• Kanamai
y = - 0.76 + 0.76x
r = 0.84
n = 176, p < 0.01
▴ Vipingo
y = - 0.82 + 0.79x
r = 0.89
n = 310, p < 0.01
Log jaw weight, gm
0.75
0.50
0.25
0.00
0.9
1.1
1.3
1.5
1.7
1.9
Log body weight, gm

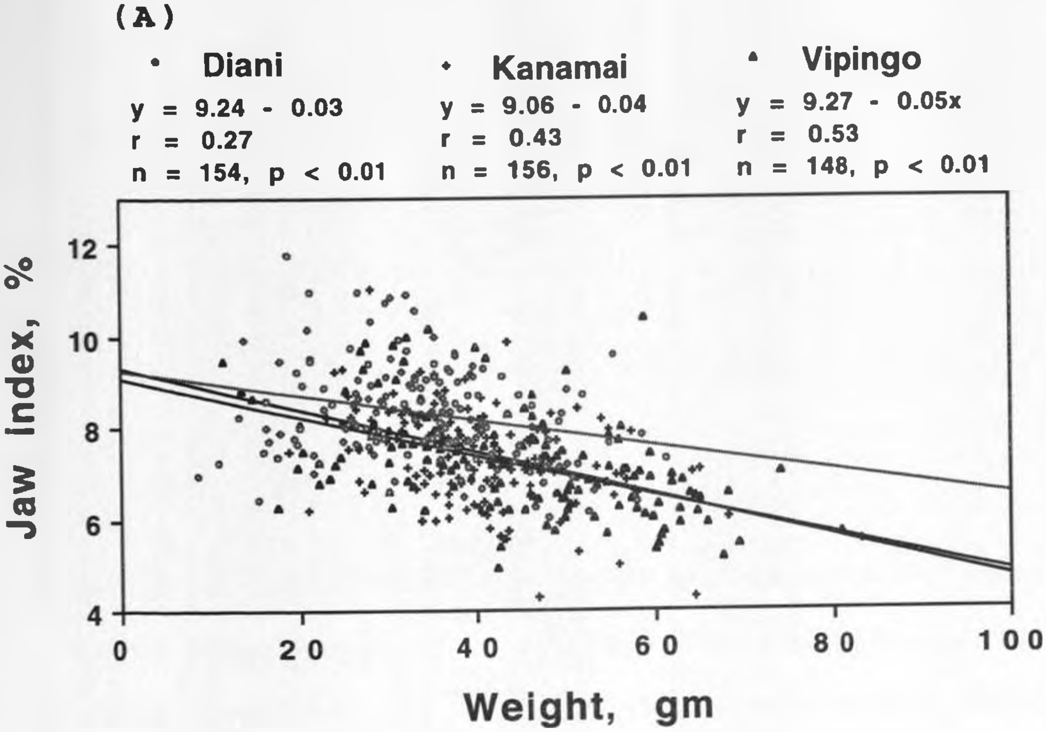
(B)


▪ Diani
y = 0.12 + 0.68x
r = 0.76
n = 100, p < 0.01
• Kanamai
y = 0.18+ 0.63x
r = 0.63
n = 118, p < 0.01
▴ Vipingo
y = 0.02+ 0.69x
r = 0.69
n = 88, p < 0.01
Log jaw length, mm
1.4
1.2
1.0
1.4
1.5
1.6
1.7
1.8
log test diameter, mm

A comparison of the best fit lines of the regressions of these relationships showed no statistical differences in the slope and intercept of these relationships between reefs. The size of the jaw relative to the size of the animal is often used as an indicator of food limitation. A comparison of the mean jaw index at these reefs showed statistically higher jaw indices at Diani then at Kanamai and Vipingo (Table. 5.2). Although relative jaw size decreased with increasing urchin size at all reefs, relative jaw sizes were always higher at Diani across all size ranges followed by Kanamai (Fig. 5.4(A and B)). The intercept and slope of the relationship between animal weight and jaw index (Fig. 5.4(A)) was not significantly different between reefs ($t = 1.41, p < 0.1$). A comparison of the intercepts of the relationship between test length and the relative jaw length (Fig. 5.4(B)) showed a statistical difference between Diani and Vipingo ($t = 2.3, p < 0.025$), but no significant difference between Kanamai and Vipingo ($t = 1.6, p < 0.1$) and no statistical difference between Diani and Kanamai ($t = 0.62$, NS).

Figure 5.5 shows the relationship of different body components to each other at each reef. A large proportion (> 50%) of the weight of *E. mathaei* is taken up by the body wall (test, tube feet and related water vascular system) and perivisceral fluid (~ 20%). The gonads, the gut and the jaw take up the next largest portion varying considerably in proportion depending on the reef. Diani urchins for example have jaws that take up an almost equal portion of the total weight of the animal as the gonad (8.2 vs. 9.2%) with the gut being reduced to ~ 5% of the total weight of the animal. Urchins at Vipingo have gonads that take up 10% of the total body weight while the jaws and guts take up an almost equal but much lower proportion (~ 5 - 7 %) of the body weight. Urchins at Kanamai on the other hand have gonads and jaws that take up an equal portion (~ 7-8%) and smaller guts (5%).

Figure. 5.4. (A) The relationship between the relative weight of the jaw measured as the Jaw index (= jaw weight/body weight * 100) and the weight of *Echinometra mathaei* at Diani, Kanamai and Vipingo reefs. (B). The relationship between the relative length of the jaw measured as the jaw index$_L$ (= jaw length/test diameter * 100) and test diameter of *E. mathaei* at Diani, Kanamai and Vipingo.


(A)
• Diani
y = 9.24 - 0.03
r = 0.27
n = 154, p < 0.01
+ Kanamai
y = 9.06 - 0.04
r = 0.43
n = 156, p < 0.01
▲ Vipingo
y = 9.27 - 0.05x
r = 0.53
n = 148, p < 0.01
Jaw index, %
12
10
8
6
4
0
20
40
60
80
100
Weight, gm

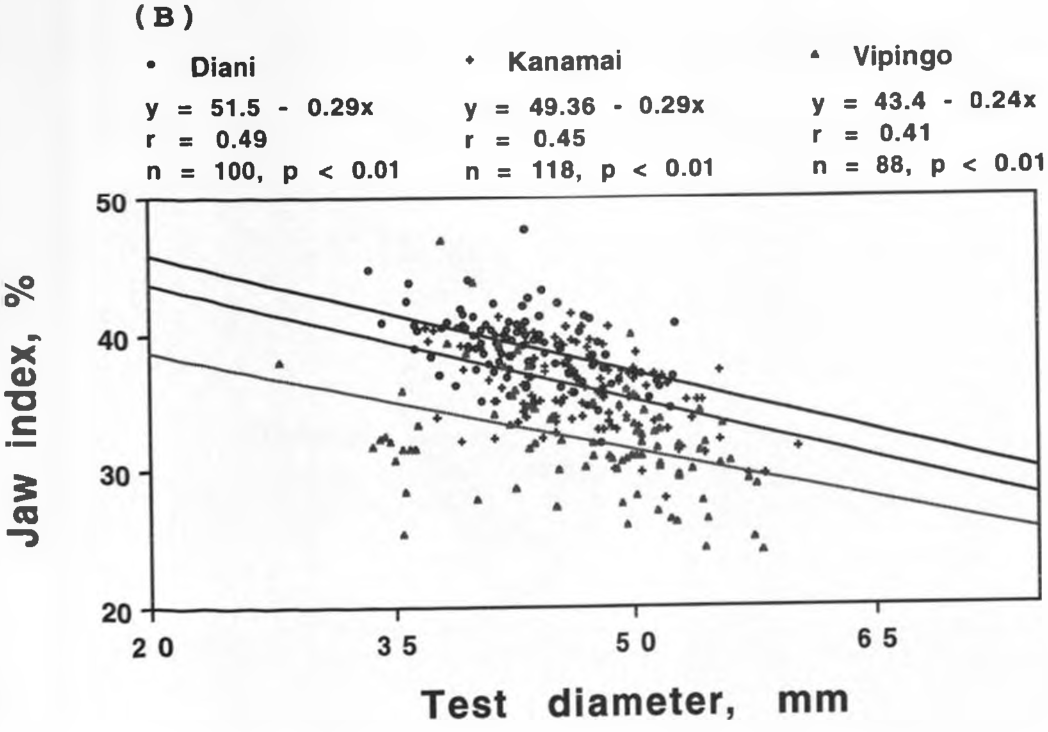
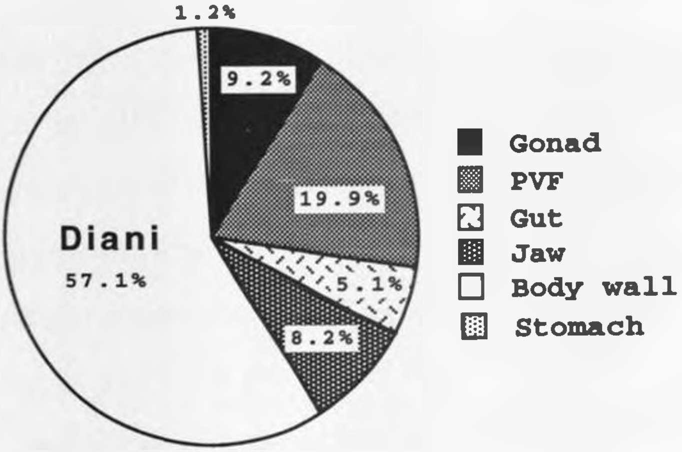
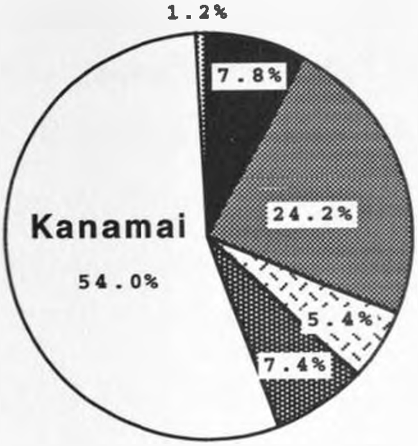
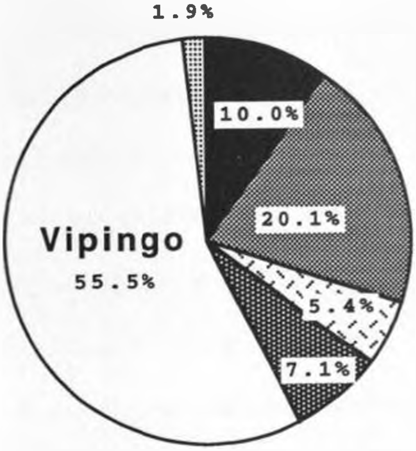

(B)
• Diani
y = 51.5 - 0.29x
r = 0.49
n = 100, p < 0.01
+ Kanamai
y = 49.36 - 0.29x
r = 0.45
n = 118, p < 0.01
▲ Vipingo
y = 43.4 - 0.24x
r = 0.41
n = 88, p < 0.01
Jaw index, %
50
40
30
20
20
35
50
65
Test diameter, mm

Figure. 5.5. The proportion of different body parts of *Echinometra mathaei* to the total weight of the animal at Diani, Kanamai and Vipingo reef lagoons. Stomach weight is measured after removal of gut contents. The gonad index was measured at the peak of reproductive activity (January - March). PVF = perivisceral fluid. Each data point represents the mean organ index calculated as wet weights of the body part relative to wet weights of the urchin. The number of samples at each reef is shown in Table 5.2.


1.2%
9.2%
19.9%
Diani
57.1%
5.1%
8.2%
Gonad
PVF
Gut
Jaw
Body wall
Stomach


1.2%
7.8%
24.2%
Kanamai
54.0%
5.4%
7.4%


1.9%
10.0%
20.1%
Vipingo
55.5%
5.4%
7.1%

The size of the gut and gonads of *E. mathaei* showed seasonal variation at all reefs (Fig. 5.6). These organs share a single space in the coelom and therefore the size of these organs oscillate in opposite direction to each other. The peak in gonad activity corresponds to the smallest guts and conversely the guts are largest when reproductive material is at its lowest (July - August). To find out whether feeding activity was also more efficient during the peak of feeding activity a comparison was made between the amount of organic material ingested in February versus June (the peak and trough of feeding activity). Urchins at Vipingo and Kanamai had on average a higher percentage of organic matter in the guts (28%) than urchins at Diani (26%) regardless of season. Kanamai and Vipingo also had a higher percent of organic material in the gut in June (30.5 and 28.3 % respectively) at the peak of feeding activity than in February (19.3 and 18.87 % respectively) the peak of reproductive activity. Diani urchins on the other hand showed the opposite pattern with higher organic content in the guts in February (21%) than in June (27.5%).

Growth

Figure 5.7 shows the size frequency histograms at each reef from 1992 to 1994. Annual recruitment took place in May- June and in September when recruits 2 - 4 mm test diameter appeared on the substrate. This recruitment peak shows clearly in the size frequencies of urchins at all the reefs in 1992 and 1994 but not so in 1993. Using this data FISAT yielded growth parameters K = 1.70, 4.9 and 2.6; and L_{inf} = 54.6, 62.5 and 62.5 for Diani, Kanamai and Vipingo respectively. K values obtained in this way proved unrealistic, predicting very high growth rates at all the reefs and showed poor goodness of fit for all these curves (R_n = 0.19, 0.12 and 0.17 for Diani, Kanamai and Vipingo respectively).

Figure. 5.6. The seasonal changes of *Echinometra mathaei* guts and gonads measured as the mean monthly gut and gonad indices of all reefs combined for each month. Each value has an n > 60.

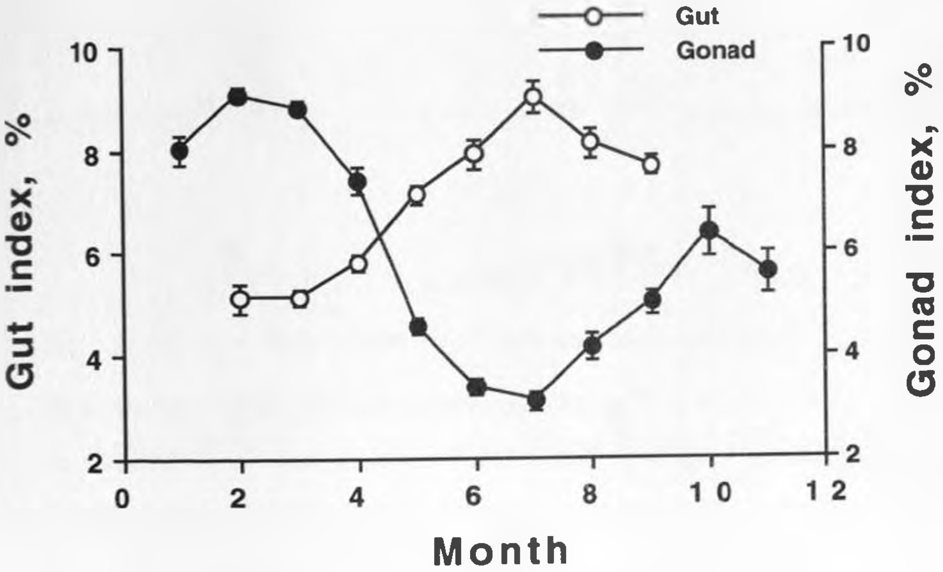
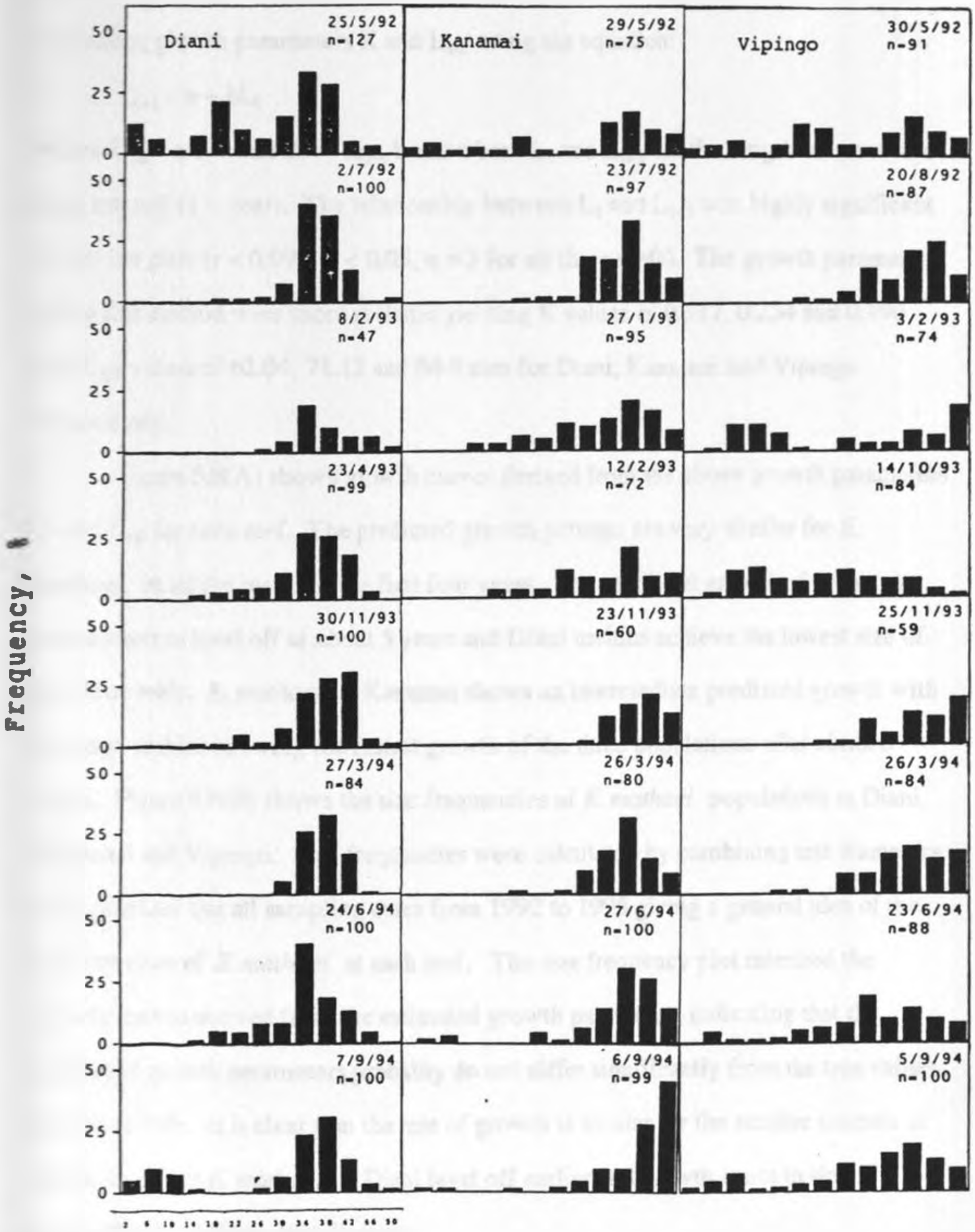

Gut
Gonad
10
8
6
4
2
Gut index, %
0
2
4
6
8
1 0
1 2
Month
10
8
6
4
2
Gonad index, %

Figure. 5.7. Size frequency histograms of *Echinometra mathaei* at Diani, Kanamai and Vipingo in 1992 to 1995. The test diameter size scale (mm) is shown on the bottom margin.


Frequency,
Diani
Kanamai
Vipingo
50
25
0
25/5/92
n-127
29/5/92
n-75
30/5/92
n-91
2/7/92
n-100
23/7/92
n-97
20/8/92
n-87
8/2/93
n-47
27/1/93
n-95
3/2/93
n-74
23/4/93
n-99
12/2/93
n-72
14/10/93
n-84
30/11/93
n-100
23/11/93
n-60
25/11/93
n-59
27/3/94
n-84
26/3/94
n-80
26/3/94
n-84
24/6/94
n-100
27/6/94
n-100
23/6/94
n-88
7/9/94
n-100
6/9/94
n-99
5/9/94
n-100
2 6 10 14 18 22 26 30 34 38 42 46 50

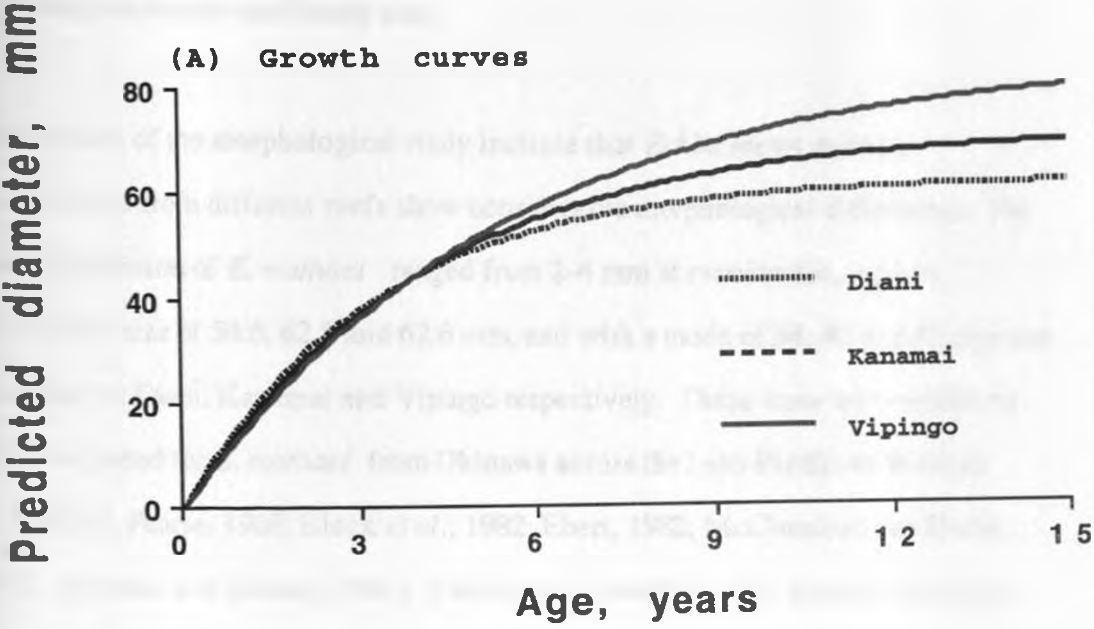
In an attempt to find more realistic parameters the May 1992 and June 1994 size frequencies were used for estimating the mean lengths of 1992, 1993 and 1994 cohorts. The Ford-Walford Plot based on the von Bertalanffy equation was used for estimating growth parameters K and L_{inf} using the equation:

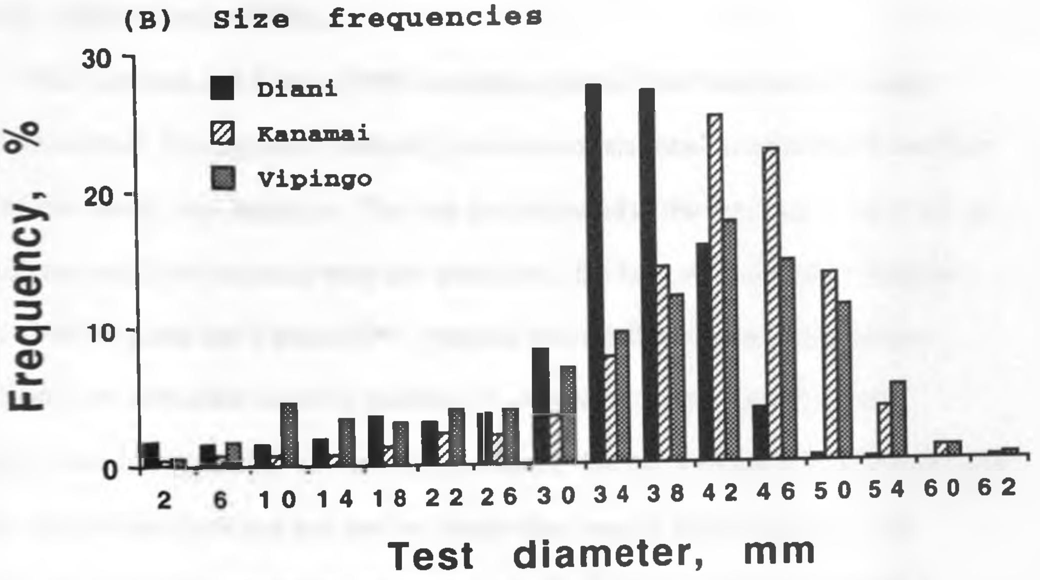
$$L_{t+1} = a + bL_t$$

where $L_{inf} = a/1-b$ and $K = -\log_e b$ and where L_t and L_{t+1} are the lengths at a constant time interval (1 = year). The relationship between L_t and L_{t+1} was highly significant for all the plots ($r < 0.998$, $p < 0.05$, $n = 3$ for all three reefs). The growth parameters using this method were more realistic yielding K values of 0.317, 0.254 and 0.190 and L_{inf} values of 62.04, 71.12 and 84.9 mm for Diani, Kanamai and Vipingo respectively.

Figure 5.8(A) shows growth curves derived from the above growth parameters K and L_{inf} for each reef. The predicted growth patterns are very similar for *E. mathaei* at all the reefs for the first four years. The predicted growth of urchins at Diani starts to level off at about 5 years and Diani urchins achieve the lowest size of the three reefs. *E. mathaei* at Kanamai shows an intermediate predicted growth with Vipingo urchins showing the fastest growth of the three populations after about 6 years. Figure 5.8(B) shows the size frequencies of *E. mathaei* populations at Diani, Kanamai and Vipingo. Size frequencies were calculated by combining test diameters of *E. mathaei* for all sampling dates from 1992 to 1995 giving a general idea of the size structure of *E. mathaei* at each reef. The size frequency plot mirrored the growth curves derived from the estimated growth parameters indicating that the estimated growth parameters probably do not differ significantly from the true values for these reefs. It is clear that the rate of growth is similar for the smaller animals at all the reefs but *E. mathaei* at Diani level off earlier and growth starts to slow markedly after 38 mm test diameter.

Figure. 5.8 (A). Growth curves of *Echinometra mathaei* from Diani, Kanamai and Vipingo derived from growth parameter estimates from size frequency data collected at each reef in May, 1992. Equations derived from Walford plots yielded growth rate values K of 0.317, 0.254 and 0.19 and asymptotic sizes L_{inf} of 62, 71 and 85 for Diani, Kanamai and Vipingo respectively. (B). The size structure of *Echinometra mathaei* populations at Diani, Kanamai and Vipingo reef lagoons in 1992 through 1995. The test diameter of all *E. mathaei* measured during the course of this study were pooled for each reef for the size frequency histograms increasing the sample size to n = 998, 982 and 860 at Diani, Kanamai and Vipingo respectively.


(A) Growth curves
Predicted diameter, mm
80
60
40
20
0
0
3
6
9
12
15
Age, years
Diani
Kanamai
Vipingo


(B) Size frequencies
Frequency, %
30
20
10
0
Diani
Kanamai
Vipingo
2
6
10
14
18
22
26
30
34
38
42
46
50
54
60
62
Test diameter, mm

DISCUSSION

Population density and body size

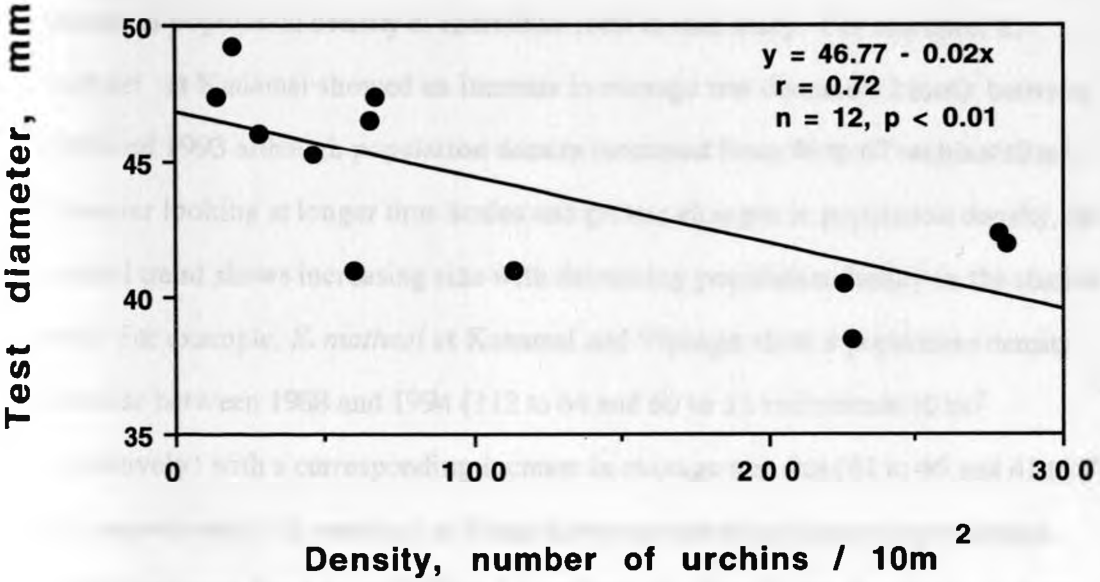
The results of the morphological study indicate that *Echinometra mathaei* populations from different reefs show considerable morphological differences. The size distribution of *E. mathaei* ranged from 2-4 mm at recruitment, up to a maximum size of 54.6, 62.5 and 62.6 mm, and with a mode of 34, 42 and 42 mm test diameter at Diani, Kanamai and Vipingo respectively. These sizes were similar to those reported for *E. mathaei* from Okinawa across the Indo-Pacific to Western Australia (Pearse, 1968; Black *et al.*, 1982; Ebert, 1982; McClanahan and Kurtis, 1991; Arakaki and Uehara, 1991). The largest *E. mathaei* (81 mm test diameter) was reported at Al Ghardaqa, Red sea (Pearse, 1968). However it is not possible to derive a general trend of *E. mathaei* body size in relation to geographical distribution from the information available.

McClanahan and Kurtis (1991) comparing data from four reefs in Kenya (Diani, Kanamai, Vipingo and Malindi), showed no relationship between *E. mathaei* population density and test size. This can be attributed to the fact that *E. mathaei* at Malindi are small yet occur at very low densities (the lowest recorded on Kenyan reefs). McClanahan and Kurtis (1991) explain this relationship by arguing that predation is an important factor controlling *E. mathaei* density and therefore indirectly controlling urchin size on Kenyan reefs. On reefs where predation pressure is high, population densities are low but body sizes maybe small or large. For example at Malindi where predation rates are high, *E. mathaei* are small bodied because predation pressure has increased the fitness of smaller animals as they avoid predators more effectively. Predation pressure on *E. mathaei* at Malindi was the highest recorded of any Kenyan reef (McClanahan and Muthiga, 1989). Alternatively at Vipingo where predation pressure is almost as high as at Malindi, mainly smaller animals are taken therefore urchins that survive predation at an early age can grow to be large bodied since food is not limited on this reef.

At the low predation pressure end of the spectrum lie reefs with high population densities and small bodied animals for example Diani. Competition for food is more intense on these reefs (as evidenced by larger jaws and low gut indices) which results in smaller animals. Diani the reef with the highest population density on Kenyan reefs had the lowest predation rates (McClanahan and Muthiga, 1989). Reefs with intermediate predation rates have *E. mathaei* with intermediate body sizes and intermediate population densities for example Kanamai (Muthiga and McClanahan, 1988; McClanahan and Shafir, 1990; McClanahan and Kurtis, 1991). Predation pressure has also been shown to be an important factor in the control of body size in other phyla (Vermeij, 1978).

In this study, the body size of *E. mathaei* was significantly inversely related to population density when the average test diameter in 1988 (from McClanahan and Shafir, 1991) and 1992 to 1994 were plotted against the corresponding population density at Diani, Kanamai and Vipingo (Fig. 5.9). This indicates that within the range of population densities studied, reefs with low population densities (i.e. Vipingo) had larger animals than reefs with high population density (i.e. Diani). An inverse relationship between urchin body size and population density has been previously reported in the sea urchins *Diadema antillarum* and *Strongylocentrotus purpuratus* (Carpenter, 1981; Hunte *et al*., 1986; Levitan, 1988, 1989; Ebert, 1967, 1968) and this type of relationship has been attributed to size regulation due to food availability.

Figure. 5.9. The relationship between test diameter and population density of *Echinometra mathaei* on Kenyan reefs. 1988 data are taken from McClanahan and Kurtis, 1991. The test diameter is based on the mean of $n > 85$ urchins per sample and the population density is based on the mean number of urchins in a minimum of 12 ($10 m^2$) quadrats at each reef.


y = 46.77 - 0.02x
r = 0.72
n = 12, p < 0.01
Test diameter, mm
50
45
40
35
0
100
200
300
Density, number of urchins / 10m 2

At high population densities the amount of food available per individual is reduced resulting in smaller animals. Laboratory and field manipulations with different population densities of *D. antillarum* (Levitan, 1988, 1989) showed that this urchin can adjust growth rates rapidly to correspond to food availability, increasing size when more food is available as a consequence of lowered density.

The annual change in body size of *E. mathaei* did not always correspond a change in population density at individual reefs in this study. For example, *E. mathaei* at Kanamai showed an increase in average test diameter (2 mm) between 1992 and 1993 although population density increased from 46 to 67 urchins/10 m^2. However looking at longer time scales and greater changes in population density, the general trend shows increasing size with decreasing population density in the studied reefs. For example, *E. mathaei* at Kanamai and Vipingo show a population density decrease between 1988 and 1994 (112 to 64 and 60 to 13 individuals/10 m^2 respectively) with a corresponding increase in average test size (41 to 46 and 41 to 47 mm respectively). *E. mathaei* at Diani shows no statistical change in population density between these years (228 to 226 individuals /10m^2) and the change in body size is very small (39 to 40.5 mm).

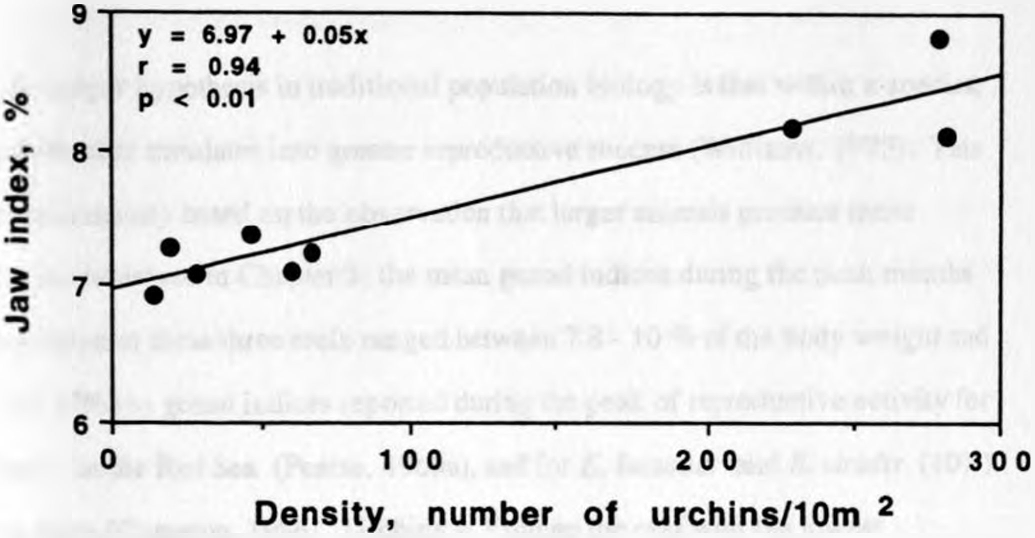
Several lines of evidence can be used to argue that food availability influences the relationship between population density and body size of *E. mathaei* at these reefs. Firstly *E. mathaei* from Vipingo (the reef with the lowest population density and largest urchins) had the largest guts (i.e. fullest guts), stomachs and gonads relative to urchin size and the highest percentage of organic matter in the guts of all three reefs every year. This indicates that *E. mathaei* at Vipingo are not food limited and therefore can grow larger and have a higher fecundity. McClanahan and Kurtis (1991) also reported higher gut and gonad indices at Vipingo compared to Diani in 1988 although their gonad index values were considerably lower (4.88% and 3.04% respectively) than the values reported in this study. This difference is attributed to the fact that gonad indices in that study were measured in July when reproductive activity of *E. mathaei* is at its lowest on the Kenyan coast (Fig. 2.3 and Fig. 5.6).

Secondly, *E. mathaei* at Kanamai had a population density, body size, jaw size, stomach size and gonad size (except at the peak reproductive period) that were intermediate but closer to Vipingo urchins. This indicates that resources are allocated according to availability with Kanamai having less resources (compared to Vipingo) therefore allocating less to growth and reproduction. Thirdly, *E. mathaei* at Diani (the reef with the highest population density and smallest urchins) had gut indices that were always lower than at the other reefs regardless of the time of year. Additionally average gonad indices are low except at the peak reproductive period and the relative size of the jaw of Diani urchins was the highest of all the reefs. This strongly suggest that food is more limited at Diani than at Kanamai and Vipingo.

Lastly, when the relative size of the jaw at each reef is compared against the corresponding density of *E. mathaei* a highly significant ($r = 94$, $P < 0.01$) positive relationship is derived (Fig. 5.10). This indicates that *E. mathaei* increases the size of the jaw as density increases because of a reduction in food availability with increasing density. A relative increase in jaw size is thought to be an appropriate response to food limitation (Ebert, 1980) and has been recorded in *E. mathaei* at Rottnest Island Western Australia (Black *et al*., 1982), *D. setosum* in Zanzibar (Ebert, 1980) and *S. purpuratus* in California (Edwards and Ebert, 1991). However the fact that reproductive activity continued at Diani and that the relative size of the gonad did not show a relationship to animal size (Fig. 2.1) indicates that starvation and stunting are not the cause of smaller body sizes at Diani.

Although both predation and food availability are probably the causes of the inverse relationship between size and density of *E. mathaei* at these three reefs, the exact mechanism that controls the change in size with decreasing or increasing population density was not tested in this study. Size regulation, the proportional adjustment of body parts to an optimal size depending on available resources is documented in many sea urchin species (Ebert, 1967; Regis, 1979; Levitan, 1988, 1989, 1991) including species in the Family Echinometridae (Dix, 1972; Constable 1990). It is therefore highly likely that *E. mathaei* can regulate its body size

Figure. 5.10. The relationship between the mean jaw index and the population density of *Echinometra mathaei* measured as the mean jaw index at Diani, Kanamai or Vipingo reef lagoons plotted against the mean population density between 1992 and 1994. The population density is based on the mean number of urchins in a minimum of 12 ($10m^2$) quadrats at each reef each year. The jaw index is based on the mean of 20 to 200 urchins depending on the year and reef.


y = 6.97 + 0.05x
r = 0.94
p < 0.01
Jaw index, %
9
8
7
6
0
100
200
300
Density, number of urchins/10m 2

depending on food availability. However experiments on the responses of the body size of individual *E. mathaei* to varying population densities would have to be carried out before size regulation in *E. mathaei* can be established.

Reproductive fitness and optimal body size

One of the major hypothesis in traditional population biology is that within a species, a larger body size translates into greater reproductive success (Williams, 1975). This hypothesis is mainly based on the observation that larger animals produce more gametes. As reviewed in Chapter 3, the mean gonad indices during the peak months of reproduction at these three reefs ranged between 7.8 - 10 % of the body weight and are similar (7%) to gonad indices reported during the peak of reproductive activity for *E. mathaei* in the Red Sea (Pearse, 1969a), and for *E. lucunter* and *E. viridis* (10%) in Puerto Rico (Cameron, 1986). Urchins at Vipingo the reef with the lowest population density and largest urchins allocated more resources to gonad growth every year than urchins at Diani and Kanamai as evidenced by the highest overall mean gonad index . This added to the fact that *E. mathaei* at Vipingo also had the fullest guts indicates that *E. mathaei* at Vipingo consistently had relatively more resources for intense reproductive activity. This fits in with the traditional allocation theory that states that animals will allocate relatively more resources to reproduction if food is not limited (Gadgil and Bossert, 1970).

Interestingly mean gonad indices during the peak months of reproduction are surprisingly high at Diani (Table 5.2) despite a small body size and in the face of limited food resources. This demonstrates that *E. mathaei* at Diani are very efficient at allocating limited resources to maximize their reproductive output. Whether this reproductive output translates into a high reproductive fitness ultimately depends on the number of offspring that survive to reproduce. Due to the logistical difficulty of estimating the number of offspring an organism produces that survive to reproduce.

estimates of the potential number of offspring that are produced by an individual are considered good indicators of reproductive success (Levitan, 1991).

Estimates of the number of offspring (zygotes) that an urchin produces can be calculated using Levitan's (1991) model which incorporates the average size of the urchin, the volume of eggs produced at spawning and the population density. The number of zygotes produced is a function of the number of eggs produced (which is related to the size of the animal) and the probability of fertilization which is a function of population density. Using Levitan's (1991) model and assuming that all the eggs that *E. mathaei* produces are spawned in February and March and not intermittently before this period, an average sized *E. mathaei* (41.7 mm test diameter) produces 1.42×10^6 eggs at Diani, an average sized individual at Kanamai (46.3 mm) produces 1.37×10^6 eggs and an average sized individual at Vipingo (47.6 mm) produces 3.05×10^6 eggs. The percent fertilization can be estimated from Levitan's (1991) equation 3:

$$\log \text{percent fertilization} = 0.72 \log \text{density m}^{-2} + 0.49$$

this yields 34%, 11.2% and 6.49% fertilization for Diani, Kanamai and Vipingo respectively. Percent fertilization of gametes is lowest at the reef with the lowest population density.

The estimated number of zygotes produced is a product of the number of eggs produced and the percent fertilization. This yields 4.83×10^5, 1.53×10^5 and 1.98×10^5 zygotes/individual at Diani, Kanamai and Vipingo respectively. The reef with the smallest animals and highest population density (Diani) had the highest estimated zygote production. Using this estimated number of zygotes produced per individual as a criterion for measuring reproductive fitness, *E. mathaei* at Diani have a higher reproductive fitness than *E. mathaei* at Kanamai and Vipingo both reefs with a lower population density and larger animals. The number of zygotes produced by *E. mathaei* at Kanamai are similar to Vipingo. This strategy fits Levitan's (1991) model since population density and sizes of urchins at Kanamai are closer to Vipingo and so the estimated number of zygotes that can be produced at Kanamai is similar to Vipingo.

Levitan (1991) made the following assumptions about the model (1) synchrony of spawning and the pattern of dispersion of gametes are independent of population density (2) different size urchins at different densities spawn in the same manner and frequency (3) there is no competition for sperm and eggs and (4) survivorship of adult urchins is size- independent. None of these assumptions were tested in this study. *E. mathaei* appears to release eggs during an extended period from December to March, however the sharp drop in April-May indicates that most of the spawning has occurred by then (Fig. 2.4). Additionally, no spawning activity was observed in the field and no change in the degree of aggregation was seen at any time during the course of the study. This makes it difficult to tell how close the estimates of zygote production reflect the true values. If we accept the assumptions of this model, even if the curve for percent fertilization against population density may be different for *E. mathaei* than for *D. antillarum* (making the absolute estimates of zygote production questionable), the relative difference in zygote production between reefs is probably valid. *E. mathaei* at Diani therefore have a higher reproductive fitness than at Kanamai or Vipingo. There is a cost of high reproductive output in the face of food limitation however, and at Diani the trade off is body size. Reduced growth in response to reduced food and increased reproductive effort has also been reported in the sea urchin *Strongylocentrotus droebachiensis* (Thompson, 1983) and in the fish *Oryzoas latipes* (Hirshfield, 1980).

Brown *et al*., (1993) developed another model of fitness based on the allometric energetic constraints of fitness among species. In this model, fitness is defined as the rate at which resources in excess of those required for growth and maintenance of the individual can be acquired from the environment and utilized for reproduction. Due to energetic constraints, although small individuals have a great capacity to convert resources into reproduction they are constrained by the rate of acquisition of the resources required for reproduction. In contrast large individuals have a great capacity to acquire resources for reproduction but are constrained by the rate at which these resources can be converted to reproduction. The trade-off between these two limiting processes results in an optimal size which is usually small (30g for birds, and 100g for mammals) (Brown, 1995).

The optimal size for sea urchin species is not known but an argument can be made that *E. mathaei* has the optimal body size for sea urchins. If you compare the guild of sea urchins in the reefs along the Kenyan coast, *E. mathaei* is by far the most dominant in terms of abundance and achieves the highest population densities of any urchin on Kenyan reefs (McClanahan, 1988a, McClanahan and Shafir, 1990). The guild of sea urchins that occurs on the reefs of Kenya include the small bodied *Echinostrephus molaris* (de Blainville) (20-30 mm test diameter), several members of the large bodied Diadematidae including *Diadema setosum* and *D. savignyi* (70 mm) and *Echinothrix calamaris* (70 mm) and the very large *Echinothrix diadema* (150 mm). Only *E. molaris* is smaller than *E. mathaei* and it is found permanently imbedded in hard substrate indicating a great vulnerability to predation. The Diademas are armed with long spines and exist in large groups and *Echinothrix* has poisonous spines in addition to being large bodied, all predator avoidance mechanisms (McClanahan, 1988a; McClanahan and Shafir, 1990). *E. mathaei* is the top competitor for space (McClanahan, 1988a) and may therefore force other species to occupy suboptimal niches and body sizes.

Growth

Estimates of growth in sea urchins have been reported using a variety of techniques including natural growth bands in test plates (Gage, 1992), tagging using tetracycline (Ebert, 1965, 1975, 1980, 1982; Ebert and Russell, 1992; Gage, 1992 ; Kenner, 1992), tagging using monofilament line (Ebert, 1965), observations of aquarium held animals (Lewis, 1966; Raymond and Scheibling, 1987; Dafni, 1992) and size distributions (Ebert, 1975, 1982; Dafni, 1992; Kenner, 1992). Few estimates of growth are available for tropical sea urchins (Ebert, 1975, 1982) and only two reports are available for *E. mathaei* both from Lani Overlook, Oahu Hawaii (Ebert, 1975, 1982).

Tetracycline tagging and size distribution techniques were used to estimate growth in this study. Problems were encountered with the tetracycline tagging technique because very few animals showing tetracycline marks were retrieved and the tetracycline marks on the jaws were also not clear making it difficult to measure growth. Ebert (1980, 1982) encountered both these problems in *E. mathaei* at Ras Iwatine (Mombasa, Kenya) and Eilat (Israel) and *Diadema setosum* which he attributed to low incorporation rates of tetracycline or reworking of the calcite (i.e. calcite was reabsorbed and redeposited) in the skeletal elements of the animals. Tetracycline is also reported to have a very short life once mixed in sea water reducing its ability to tag the skeleton after a period of a 1-2 days in tropical conditions (Barnes, 1971).

Growth rates were therefore estimated using size frequencies. The growth rate parameters estimated using the computer program FISAT (Gayanilo *et al*., 1994) were unrealistic yielding very high K values (1.7, 4.9 and 2.6 for Diani, Kanamai and Vipingo respectively). This situation is probably due to a variety of factors including the narrow scatter of the data between sampling periods making it difficult to distinguish between cohorts, the high mortality of some size classes and weak recruitment in 1993 and 1994. Fortunately, the 1992 data showed three clear cohorts at each reef and the modal sizes of these cohorts were used to derive growth parameters from Ford-Walford plots.

The growth rates estimated from Ford-Walford plots of size distributions in 1992 are similar (K = 0.32, 0.25, 0.19 for Diani, Kanamai and Vipingo respectively) to previous reports for *E. mathaei* (K = 0.29, 0.46) and *E. oblonga* (K = 0.4) in Hawaii (Ebert, 1975, 1982)(Table 5.3).

Assuming that peak settlement of *E. mathaei* occurs in May-June, the modal size of the smallest cohort recorded in May 1992 (19 - 20 mm test diameter) represents the annual growth of juveniles in their first year. This growth rate is within the range recorded for *E. mathaei* juveniles (Chapter 4) which increased in mean test diameter from 4.9 mm to 16.78 mm test diameter at Vipingo in approximately 8 months. Comparative data of recruit growth is not available from the region but *E. mathaei* appears to be growing at a similar rate to other sea urchins of its size for example *Strongylocentrotus droebachiensis* in Nova Scotia, which increased from 4.5 - 15 mm in one year (Raymond and Scheibling, 1987).

Table 5.3. Summary table of the growth rates of tropical sea urchins.

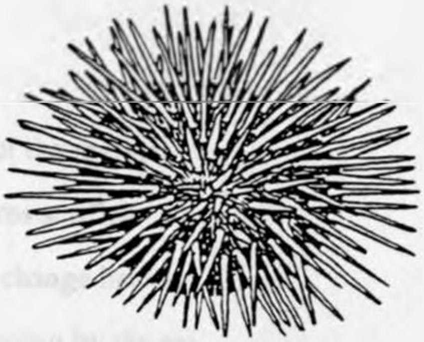
Species	*Location*	*N*	*K*	L_{inf}*(mm)*	*Reference*
Echinothrix diadema	Kapapa Island Hawaii	33	0.82*	90	Ebert, 1975
	Kapapa Island, Hawaii		0.05*	77.81	Ebert, 1982
Diadema setosum	Zanzibar, Tanzania	55	0.008	91.92	Ebert, 1982
	Elat, Israel	7	0.008	83.57	
Stomopneustes variolaris (Lamarck)	Negombe Sri Lanka	101	0.013	71.09	Ebert, 1982
Tripneustes gratilla	Elat, Israel	88	0.87	95	Dafni, 1992
Echinometra oblonga	Lani Overlook, Hawaii		0.4	32.2	Ebert, 1975
		35	0.358	30.87	Ebert, 1982
E. mathaei	Lani Overlook, Hawaii		0.46	38.1	Ebert, 1975
		77	0.292	40.95	Ebert, 1982
	Diani, Kenya	248	0.317	62.04	this study
	Kanamai, Kenya	175	0.254	71.12	this study
	Vipingo, Kenya	189	0.19	84.9	this study

* this discrepancy is found in the papers quoted.

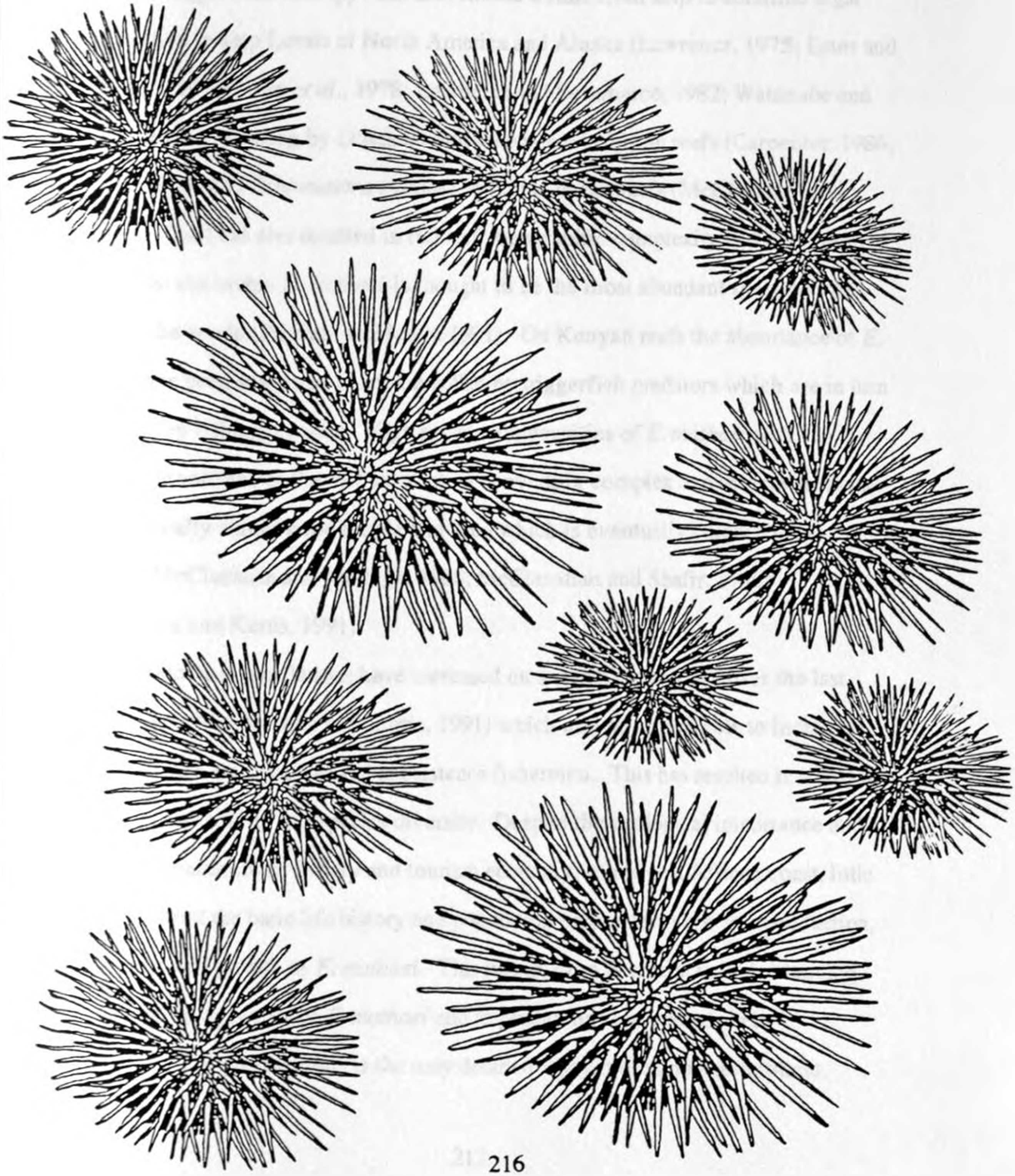
If the estimated growth equations are valid for these reefs, the size distributions and average sizes indicate a young age structure (Fig. 5.8(A and B)). 75% of the population at Diani is between 2 and 4 years old (34-38 mm test diameter) and only 6% are over 5 years old. The largest urchin recorded at Diani (54.6 mm test diameter) was approximately 7.4 years and 7.4 mm short of the predicted asymptotic size of 62.04 mm. The growth rate of urchins at Diani is very slow after this time and this is reflected in the sharp decrease in the frequency of larger animals (> 42 mm test diameter)(Fig. 5.8(B)). A comparison of the relative size of the jaw with the size of the animal (Fig. 5.4(A and B)) indicates that although the relative size of the jaw decreases with increasing animal size at all reefs, urchins at Diani still have larger jaws relative to urchin size even at the larger sizes than urchins at Kanamai and Vipingo. This indicates that larger animals at Diani are having increasing difficulty acquiring food and therefore allocate relatively more resources to the food gathering apparatus than urchins at Kanamai or Diani. Additionally the relative size of the gut also increases with increasing animal size (Fig. 5.2) at Diani, while it decreased with increasing urchin size at Kanamai or Vipingo, indicating an increased allocation of resources to food gathering at these larger sizes in Diani.

Kanamai and Vipingo had older populations with 50% of the population estimated as greater than 5 years old. The largest urchins recorded on these reefs (62.6 and 62.4 mm) were 8.4 and 10 years old for Vipingo and Kanamai respectively. Additionally, the estimated asymptotic sizes at Kanamai and Vipingo were much higher (71 - 84 mm) than the largest animals recorded on these reefs indicating that mortality of the larger animals was quite considerable at these reefs. No mortality measurements were estimated in this study but the highest predation on both adults (Muthiga and McClanahan, 1988) and juveniles was recorded at Vipingo the reef with the lowest population of urchins. Ebert (1975) found a positive correlation between the growth constant K and mortality M and found a general trend showing that the large urchins were also fast growing. Using this model urchins at Vipingo should have the fastest growth rates and highest mortality. Urchins at Vipingo however had the largest body sizes but had the lowest estimated K value (0.19). How close the growth estimates reflect the true growth rates at these reefs is difficult to say because the growth data are unfortunately based on a limited data-set. It is difficult therefore to apply Ebert's (1975) model to the growth estimates derived from this study.

CHAPTER SIX



General Discussion and Summary



Introduction

Some marine species have an inordinate influence on the structure of the marine communities they live in. These species include the Crown-of-Thorns starfish (*Acanthaster plancii*) in the central Pacific whose grazing activities change healthy coral reefs to algal turf communities (Moran, 1986). Destructive grazing by the sea urchins *Strongylocentrotus spp*. has also caused a shift from kelp to coralline algal communities in kelp forests of North America and Alaska (Lawrence, 1975; Estes and Palmisano, 1974; Estes *et al*., 1978; Lawrence and Sammarco, 1982; Watanabe and Harrold, 1991). Grazing by *Diadema antillarum* in Caribbean reefs (Carpenter, 1986; Lessios, 1988) and *Echinometra mathaei* in Indian ocean reefs (McClanahan and Muthiga, 1988) has also resulted in reduced topographic complexity and diversity.

The sea urchin *E. mathaei* is thought to be the most abundant species of sea urchin in the world (Palumbi and Metz, 1991). On Kenyan reefs the abundance of *E. mathaei* has been suggested to be controlled by triggerfish predators which are in turn controlled by fishing pressure. High population densities of *E. mathaei* result in increased bioerosion of the reef substratum converting complex and diverse reefs into topographically simple coral rubble and sand which is eventually colonized by seagrass (McClanahan and Muthiga, 1988; McClanahan and Shafir, 1990; McClanahan and Kurtis, 1991).

E. mathaei populations have increased on some Kenyan reefs over the last twenty years (McClanahan and Kurtis, 1991) which maybe attributable to increased removal of fish by aquarium and subsistence fishermen. This has resulted in a loss of reef area, productivity and species diversity. Despite the ecological importance and potential impacts on the fishery and tourism economy, of the east African coast, little is known about the basic life history and population parameters such as reproduction, recruitment and growth of *E. mathaei*. This information is crucial to understanding the population dynamics of *E. mathaei* and to predicting future trends in its population. The present study is the only detailed study monitoring recruitment, reproductive patterns and growth in several populations of *E. mathaei* on the Kenyan coast. The major findings of this study are summarized below and discussed in light of current knowledge about marine benthic invertebrates in general and sea urchins in particular.

Seasonality of Reproduction

There has been considerable speculation on how environmental factors influence the onset of gametogenesis and spawning in marine invertebrates (Giese and Pearse 1974). Many of the studies have been carried out in temperate environments where strongly marked seasons occur. Factors such as temperature, chloropyll concentrations in the water column and photoperiod have been shown to cue and entrain gametogenesis and spawning in many marine invertebrates in the temperate zone.

A study of *E. mathaei* on the east coast of Africa allows for the testing of the influence of seasonally changing environmental factors caused by monsoon seasons on the reproduction of a common tropical marine invertebrate. A comprehensive study of the reproductive pattern of *E. mathaei* at three reef lagoons in Kenya and the influence of environmental factors and population density on reproductive activity is detailed in Chapter 2. Table 6.1 summarizes reproductive patterns of *E. mathaei* through-out its range of distribution. Only studies that included the entire annual cycle are presented.

E. mathaei exhibits seasonal reproduction in the higher latitudes towards the limits of its distribution except at Rottnest Island Western Australia where annual ranges of temperature are as narrow as in the tropics (Pearse and Phillips, 1968; Pearse, 1969a). This suggests that temperature is probably the limiting factor in the reproduction of *E. mathaei* in Seto and Seseko in Japan and the Gulf of Suez where conditions in the winter are similar to temperate conditions (Pearse, 1969a).

Table 6.1. The breeding seasons of *Echinometra mathaei* throughout its geographical distribution.

Latitude	*Location / temperature range*	*Breeding season*	*Reference*
34°40'N	Seto, Japan 15 - 30°C	spawn July to August	Onada, 1936
29°26'N	Wadi el Dom Gulf of Suez 15 - 31°C	spawn August to September	Pearse, 1969a
27°15'N	Al-Ghardaqa Red Sea 15 - 30°C	peak spawning in July to August, ripe individuals maybe found year round	Pearse, 1969a
26°38'N	Sesoko Island Okinawa, Japan 20 - 30°C	spawn September to October	Arakaki and Uehara, 1991
04°00'S	Diani, Kanamai, Vipingo Kenya 24 - 31°C	spawn January to March	this study
32°00'S	Rottnest Island Western Australia 18 - 22°C	continuous throughout the year	Pearse and Phillips, 1968

Temperature range is much narrower (18 - 22°C) at Rottnest Island and reproduction is continuous year round suggesting that temperature is not a limiting factor of reproduction at Rottnest Island.

The present study partly fills the gap in the information about *E. mathaei* reproduction at the center of its range of distribution. *E. mathaei* has a seasonal reproductive pattern in East Africa (Fig 2.3, 2.3), gametogenesis begins in July - August and spawning peaks in February - March (Fig 2.4, 2.5 and 2.6). Although there was significant between-site and between-year variation in the reproductive output (as measured by gonad index: Table 2.5 and 2.6) the seasonal pattern repeated itself every year from 1987 - 1995. This study adds to the increasing body of evidence of seasonal reproduction in marine organisms on the east coast of Africa (Bwathondi, 1973; Nzioka, 1979; Ntiba and Jaccarini, 1990).

The fact that the seasonal pattern of reproduction was similar from year to year suggests that a strong reliable cue is responsible for entraining reproductive behavior in *E. mathaei* on the east coast of Africa. The reproductive pattern of *E. mathaei* on the Kenyan coast showed a significant and positive correlation with sea water temperature (Fig. 2.9c) and light (Fig. 2.10b) parameters which both follow a similar seasonal pattern (Fig. 2.9a and Fig. 2.10a respectively). Despite the correlation between sea water temperature and the reproductive activity of *E. mathaei* in east Africa, temperature is not considered to be the important cue for the onset of gametogenesis. This is because the minimum temperatures on East African reefs are above the critical temperature for the onset of gametogenesis in *E. mathaei* in other parts of the world (Pearse, 1969a). Moreover , at Rottnest Island which has a similar annual range of temperature, *E. mathaei* has continuous reproduction. Light on the other hand has a seasonal pattern that could act as a reliable cue for the onset of gametogenesis. However, it was not possible to tell from this study the mechanism by which gametogenesis was controlled by light in *E. mathaei*. Experimentation to test the effects of different light levels on the reproductive activity of *E. mathaei* would have to be carried in order to validate light as the proximate cause of gametogenesis.

The timing and distance of spawning individuals also has an important effect on the reproductive success of external spawners. Although a substantial amount of time was spent observing *E. mathaei* in the field including several times at night during the full and new moons, no spawning events were recorded. Additionally no aggregative behavior was observed perhaps because *E. mathaei* at Kanamai and Diani are usually in relatively close proximity to each other due to high population densities. Moreover gametogenesis began in different individuals at different times suggesting that individuals achieve a ripe state at different times. By January - February however, most individuals have gonads full of gametes (Fig. 2.5, 2.6, 2.7) suggesting that although the onset of gametogenesis is not synchronized among individuals, most individuals are ripe and possibly spawn at roughly the same time.

This lack of total synchrony in reproduction has been reported in many other sea urchins (Pearse, 1969a). The release of gametes over an extended period of time (i.e. from as early as December) and the relatively close proximity of conspecifics probably enhances reproductive success in *E. mathaei* on many Kenyan reefs.

Interestingly gonad indices correlated with chlorophyll **a**, although offset by one month (Fig. 2.11b) which means that peak reproductive activity precedes the peak in chlorophyll **a** concentrations. This suggests the possibility that spawning is induced by increasing phytoplankton concentrations, which would ensure maximum availability of food for the larvae at a time when food demand is high. This is the first correlative evidence of the influence of chloropyll **a** concentrations on the reproductive activity of *E. mathaei* in the Indo-Pacific region. This phenomenon is widespread among temperate species that produce gametes in the fall and winter and are ready to spawn in the spring when phytoplankton concentrations peak (Himmelman, 1980; Starr *et al.*, 1990; Starr *et al.*, 1991).

In conclusion, the east coast of Africa experiences monsoon seasons and although environmental parameters may not vary with as great a range as in temperate environments, temperatures, light and chlorophyll all peak at the same time of the year. The present study suggests that the combined effects of these environmental factors is a powerful ultimate cause controlling the timing of reproduction in marine invertebrates on the east coast of Africa.

Maternal size, fecundity, egg size and population density

The number (fecundity) and size of eggs of individual organisms are probably the most frequently reported reproductive life-history strategies in benthic marine invertebrates (Emlet, *et al.*, 1987). Both these life-history parameters are related to the mode of development and the allocation of resources to growth, maintenance or reproduction (Gadgil and Bossert, 1970; Vance, 1973; Strathmann, 1985; Emlet, 1986; Emlet *et al*., 1987; Lessios, 1987). In order to find the adaptive significance of these life-history parameters most studies have compared information from different species (reviewed by Emlet *et al*., 1987). Within species comparisons however may be more useful as confounding factors are kept to a minimum (Lessios, 1987). Chapter 3 gives details of the first comprehensive study of the estimates of fecundity and egg size for three populations of *E. mathaei*. Issues relevant to the population biology of *E. mathaei* including the influence of maternal size and population density on egg size and number are also explored.

The results of this study indicate that although there was significant year to year variation in fecundity at all reefs, *E. mathaei* always produced significantly more eggs at Vipingo, the reef where food was more abundant (Table 3.5). This is consistent with the classic allocation model (Gadgil and Bossert, 1970) which states that more resources will be allocated to reproduction when adequate food is available.

A major generalization in population biology however is that within a species, larger females have a higher fecundity (Williams, 1975). The relationship between maternal size and fecundity in *E. mathaei* populations on the Kenyan reefs however was variable with two reefs showing no relationship (Diani and Kanamai) while at Vipingo larger females tended to produce more eggs (Fig 3.3). Vipingo was also the reef with the larger females on average and the lowest population density. Larger urchins at Kanamai and Diani may be constrained in fecundity by food availability.

The size of the eggs of *E. mathaei* did not show any consistent relationship with fecundity or with maternal size (Fig. 3.7) which is contrary to life history models that predict the production of large numbers of small eggs or small numbers of large eggs (Vance, 1973a, 1973b; Roff, 1992). Lessios (1987) also reported a high degree of variability in egg size and no relationship between egg size and maternal size in several species of regular and irregular echinoids. The present findings add to the evidence suggesting that maternal size is generally not a good predictor of egg size in many echinoids.

Egg quality rather than egg size maybe a better predictor of parental investment in marine invertebrates like *E. mathaei* that show a high degree of variability in egg size. Several measures of egg quality have been used to predict parental investment including organic content measured as proteins or energy content measured as fats (Thompson, 1982; Emlet *et al*., 1987). The fact that the average weight of eggs was higher at Vipingo than at the other reefs (Fig. 3.8 Table 3.13) suggests a difference in the contents of the eggs. Whether this difference confers higher quality (i.e. more proteins) was not explored in this study. A study of the quality of the eggs of different populations of *E. mathaei* would yield some useful information about parental investment and the influence of population density.

The study further reinforces the importance of population density in the reproductive success of free spawning invertebrates (Pennington, 1985; Levitan, 1989; 1991; Levitan and Petersen, 1995). Contrary to expectations *E. mathaei* at Diani, the reef with the highest density of urchins, the smallest animals and lowest amounts of food resources, had the highest fecundity per unit area (Fig 3.10). Even more importantly, using Levitan's (1991) model which takes into consideration population density, *E. mathaei* were estimated to produce 4.82 x 10^5 zygotes per individual at Diani, almost 3 times more zygotes per individual than at Kanamai and Vipingo. This suggests that *E. mathaei* individuals have a higher reproductive fitness at Diani than at Kanamai and Vipingo. The results reinforce the idea that the concept of reproductive fitness must take into consideration not only the number of eggs an individual produces, but also the potential for fertilization (Levitan, 1991, Levitan and Petersen, 1995) which is a function of population density.

Finally with the recent interest in the concept of reproductive fitness, the need for realistic estimates of fecundity has been re-emphasized (Thompson, 1982). In this study, a modification of the volumetric technique in fisheries biology for fecundity estimation in sea urchins is described (Chapter 3). This technique gives realistic estimates of fecundity while being relatively simple and inexpensive. The technique relies on the extraction of all eggs from the gonad and counting a subsample of the eggs allowing for large numbers of samples to be processed in a relatively short period. This technique will be useful in estimating the reproductive state and output of sea urchins on reefs and could prove a useful tool for managers in the assessment of the health of benthic invertebrates and by extension the health of a reef.

Recruitment and population regulation

Many marine benthic invertebrates have two life stages, a larval planktonic stage and a sessile benthic stage. Understanding the processes that control the abundance and distribution of these organisms must therefore include a study of their larval ecology. Although there is a large body of literature on sea urchin recruitment, little information is available on the recruitment patterns of *Echinometra mathaei* (McClanahan, 1988a, McClanahan and Kurtis, 1991). In Chapter 4 the recruitment patterns of *E. mathaei* on three Kenyan reefs are described and the effects of recruitment on population density are explored.

Results show that *E. mathaei* recruits on an annual basis at the end of the north east monsoon period on the Kenyan coast. Recruitment is closely linked to the reproductive activities of the local *E. mathaei* population, with the early recruits appearing on the substrate in April-May, 1 to 2 months after the peak spawning period (February, March) (Fig. 4.1). As similar climatic conditions prevail along most of the east coast of Africa this pattern is expected to prevail all along the eastern coast of Africa except off Somalia where upwelling occurs. Additionally, the fact that other species of marine organisms recruit at this time including oysters and barnacles (Ruwa and Polk, 1994), fish (Ntiba and Jaccarini, 1990) and sea stars and sea cucumbers (pers. observation) suggests that conditions during this time of the year are ideal for the recruitment of animals with planktonic larvae.

Although recruitment was recorded every year for 3 years, the strength of recruitment was variable between years, between reefs and within reef among years

(Fig. 4.2, Table 4.3 and 4.4). This spatial and temporal pattern of recruitment has been reported for many marine organisms that disperse propagules including plants (Hoffmann and Ugarte, 1985), invertebrates (Loosanoff, 1964; Ebert, 1983; Raymond and Scheibling, 1987) and tropical fishes (Doherty and Williams, 1988). There is some indication that larvae from other non-local sources settled later in the year. This is not surprising as *E. mathaei* is a widely distributed sea urchin and dispersal of larvae from non-local sources over long distances maybe one of the mechanisms allowing for this wide distribution (Watts *et al.*, 1990; Palumbi and Metz, 1991).

Recruitment also showed no relationship with temperature, rainfall, or fecundity of the parent population (Fig. 4.8) factors that have been shown to correlate with recruitment in other echinoderms (Ebert, 1983). This suggests that these factors play a minor role in the recruitment of *E. mathaei* on the east coast of Africa. The density of recruits at the peak recruitment period however showed a significant relationship with chlorophyll **a** concentrations immediately after peak spawning (Fig. 4.3). Despite the small sample size, this positive and significant relationship suggests that increased food for the larvae was an important factor controlling the strength of recruitment of *E. mathaei*. According to a review by Olson and Olson (1989) larval starvation is rarely important in echinoderm larvae. There is an indication that this is true for *E. mathaei* since recruitment occurs almost every year indicating an adequate supply of food for the larvae regardless of chloropyll concentration. The number of larvae that survive long enough to settle may increase under conditions of increased food however and therefore larval success in *E. mathaei* maybe influenced by food availability with more larvae settling when food availability is higher.

There has been considerable debate among population biologists about the influence of recruitment on adult populations. One point of view, the equilibrium model states that populations are held at near average densities by biotic factors such as competition and predation (Connell, 1961; Ebert, 1983). The second point of view states that populations are usually increasing, with occasional mass mortality or usually decreasing, with occasional highly successful recruitment (non-equilibrium model) (Ebert, 1983). The results of this study validate the equilibrium model since recruitment of *E. mathaei* did not affect population density even after a highly successful recruitment year (1992) (Fig. 4.5a). This indicates that recruitment had very little effect on the control of population density. The relationship remained poor even when recruitment was plotted against the population density in subsequent years (Fig 4.5b). This lack of a relationship between recruitment and population density has been reported for other sea urchins including *Strongylocentrotus purpuratus* (Ebert, 1983).

Predation had a much stronger influence on *E. mathaei* population density (Fig. 4.9) with populations being higher at lower predation pressures. This pattern has persisted over the years (McClanahan and Muthiga, 1989; McClanahan and Shafir, 1990; McClanahan and Kurtis, 1991) indicating the strong influence of predation on the population density of *E. mathaei*. The dominant predator of *E. mathaei* is the triggerfish *Balistapus undulatus* which accounts for 85% of the mortality of adult *E. mathaei* in protected reefs (McClanahan, 1995b). Predation has also been shown to influence populations of the sea urchins *Strongylocentrotus* spp. by the sea otter *Enhydra lutris* (Lowry and Pearse, 1973; Estes and Palmisano, 1974; Dayton, 1975) and the star fish *Pycnopodia helianthoides* (Pearse and Hines, 1987).

Morphometrics and growth

Chapter 5 represents a compilation of all the morphometric data collected during this study and uses this information in a synthesis of the life history strategies of *E. mathaei* on different reefs and their effects on the population dynamics of this common sea urchin. This is the first comprehensive study of morphology and growth of *Echinometra mathaei* in the Western Indian ocean region. This data set (Table 5.1) will be valuable for comparative studies of *E. mathaei* elsewhere in the region as well as a tool to assess the health of Kenyan reefs.

E. mathaei appears to be well adapted to living under different conditions of food availability. When food is abundant, urchins are large and have a high individual fecundity e.g., at Vipingo. When food is scarce more resources are allocated to the food gathering apparatus (by growing relatively larger jaws) e.g., at Diani. Stomachs were relatively larger at Vipingo and gut contents had a higher percentage of organic matter indicating that food availability was not limiting at Vipingo. Additionally urchins under food limitation are efficient at allocating relatively more resources to reproduction at the expense of body size e.g., at Diani. The allocation of resources to reproduction and the food gathering apparatus in the face of food limitation is thought to be an adaptive response to food limitation (Black *et al*., 1982, Thompson, 1982). Although predation was an important factor in controlling the body size of *E. mathaei* populations, individual *E. mathaei* may have the ability to regulate size under varying conditions of food availability.

The dominance and abundance of *E. mathaei* in the western Indian Ocean region compared to other sea urchin species leads to the conclusion that *E. mathaei* is the optimal size for sea urchins. Brown *et al.* (1993) develop a model of fitness based on allometric energetic constraints. Small animals may have a greater capacity to convert food to reproduction than larger animals, but smaller individuals acquire food at a slower rate. In the guild of sea urchins in the region, the large sized urchins including *Diadema* and *Echinothrix* have venomous spines and occur in large groups indicating predator avoidance adaptations. The smallest urchins, *Echinostrephus* also have venomous spines and occur permanently imbedded in coral rock another predator avoidance mechanism. *E. mathaei* as the top competitor (McClanahan, 1988a) may force other species to occupy suboptimal niches and body sizes.

Estimates of the growth rate of *E. mathaei* reported in this study are similar to rates of growth reported in Hawaii (Ebert, 1975; 1982) and does not differ significantly from those of other tropical Echinometrids (Ebert, 1975; 1982). Urchins exhibited similar growth rates in the early stages of development but urchins at Diani, the reef with the lowest food availability showed slower growth in larger animals

(Fig. 5.8a). This indicates that food is probably not limiting for smaller urchins at all of these reefs and mortality is due to other factors. Additionally the fact that larger animals did not necessarily have larger gonads at Diani and Kanamai (a common phenomenon among urchins) indicates that larger urchins have difficulty getting enough resources for all their requirements at these reefs. Mortality of juveniles and adults due to predation was highest at Vipingo probably because there are more fish predators in Vipingo (McClanahan and Muthiga, 1988; McClanahan and Shafir, 1990). Ebert (1975) argues that sea urchins exhibit a positive relationship between mortality (M) and growth rate (K) with the fastest growing urchins experiencing the highest rates of mortality. It was not possible to test this model in this study because of lack of sufficient data.

Summary

The study was designed to answer both theoretical as well as practical questions. The main theoretical issues explored in this study include:

1) the role of seasonality in the reproduction of tropical marine invertebrates

2) the allocation of resources to maintenance, growth and reproduction in marine invertebrates

3) the importance of recruitment in controlling the population of benthic marine invertebrates.

The above issues are still relevant in population biology (Pearse, 1969a; Ebert, 1983; Moran, 1986; Doherty and Williams, 1988). *E. mathaei* is an ideal organism to use to test these basic questions because it is widespread and abundant in many hard substrate habitats worldwide allowing for comparisons with other studies on sea urchins and the formulation of general principles for recruitment in sea urchins.

The practical aspects of this study involve the use of *E. mathaei* as an indicator species to assess the health of East African reefs. The study summarizes morphological parameters, (i.e. body size), and body indices (i.e. gonad, gut, and jaw indices), from different reefs that will enable scientists and fisheries managers to gauge the health of a reef. Symptoms of overcrowding including low fecundity, small body size should enable fisheries managers to assess the state of a reef in terms of productivity. Finally this study increases our knowledge of the biology and ecology of the most widespread echinoid worldwide as well as increasing our knowledge of the effects of seasonality on reproduction and recruitment of marine benthic invertebrates in the tropics.

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