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Reproduction and recruitment of scleractinian corals on equatorial reefs in Mombasa, Kenya

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REPRODUCTION AND RECRUITMENT OF SCLERACTINIAN CORALS ON EQUATORIAL REEFS IN MOMBASA, KENYA

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DECLARATION

I certify that the work presented in this thesis is, to the best of my knowledge and belief, original, except as acknowledged in the text, and that the material has not been submitted, either in whole or in part, for a degree at this or any other university.

I acknowledge that I have read and understood the University's rules, requirements, procedures and policy relating to my higher degree research award and to my thesis. **I certify that I have complied** with the rules, requirements, procedures and policy of the University (as they may be from time to time).

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ABSTRACT

This study examined patterns of coral reproduction and recruitment on lagoonal reefs adjacent to Mombasa in Kenya, at latitude 4ºS. Very little detailed research has been done on the reproductive patterns of scleractinian corals on equatorial reefs, where it has been suggested that seasonality and spawning synchrony may break down due to the weak environmental cues that are thought to govern the onset and timing of reproduction.

Gametogenic data were collected for three faviid (*Echinopora gemmacea, Platygyra daedalea* and *Leptoria phrygia*) and three *Acropora* species *(A. tenuis, A. valida* and *Acropora* sp.1) in the Mombasa Marine National Park and Reserve between April 2003 – May 2005. A further 20 species of *Acropora* were identified (9 species represented range extensions) and marked to examine intra- and inter-specific spawning synchrony within this genus.

In comparison to other regions, the overall pattern of coral reproduction in Kenya was found to be asynchronous, with spawning occurring over 9 months of the year from August – April, with some level of 'temporal reproductive isolation' occurring between species in relation to the main lunar month and lunar quarter when spawning occurred. Proximate cues governing the timing of reproduction could not be clearly discerned in Kenya with spawning occurring during both rising and maximum temperatures, during both neap and spring tides and across all lunar phases.

Acropora species spawned over a 7-month period between October – April and faviid species over a 5-month period from December - April. The timing of reproduction in *Acropora* varied both within and among species, with the main release of gametes occurring from January – March when sea surface temperatures were at their summer maximum. Individual species released gametes over 2-5 months. The greatest overlap in spawning *Acropora* species occurred in February, which coincided with the spawning months of *P. daedalea* and *E. gemmacea* and suggests that some degree of multispecific spawning is a characteristic of Kenyan reefs. Within the main spawning period individual *Acropora* species had their main spawning in different lunar

months. *Acropora* species released gametes in all lunar quarters, with the highest number of colonies and species spawning in the 3rd lunar quarter (i.e. in the 7 nights after full moon). Spawning in the faviids was more synchronised than *Acropora* species with the majority of faviid corals spawning in the 3rd lunar quarter.

Single annual cycles of gametogenesis were recorded in *E. gemmacea, A. tenuis, L. phrygia*, most colonies of *A. valida* and *Acropora* sp.1, and in 84% of *P. daedalea* colonies. Biannual cycles of gametogenesis were recorded in 16% of *P. daedalea* colonies, which included two morphotypes identified in the Mombasa lagoon through morphometric and genetic studies. The presence of different oocyte sizes in *L. phrygia* during gametogenesis suggested that in some colonies there were two slightly overlapping oogenic cycles, which terminated in spawning within 1-2 months of each other. Overlapping oogenic cycles have not previously been recorded in hermaphroditic broadcast spawning corals in the tropics.

The findings from Kenya support the hypothesis of protracted breeding seasons and a breakdown of spawning synchrony nearer the equator. It is hypothesised that the high fecundities recorded in faviid and *Acropora* species in Kenya compared to other regions, may allow reef corals to stagger their reproduction over 2-5 months, without incurring a significant reduction in fertilisation rates.

Spat from the Family Pocilloporidae dominated settlement tiles in the Marine National Park and Reserve comprising 93.7% of spat, which contrasts with other tropical reefs where Acroporidae spat dominate. Patterns of settlement of Acroporidae spat generally coincided with the timing and extended spawning season in *Acropora* species in Kenya. The density and relative composition of coral recruits and juvenile corals on natural substrata recorded during this study were similar to those recorded before the 1997-98 bleaching event. There is no evidence to suggest that Kenya's reefs have undergone a phase-shift in community structure, and reef recovery is occurring post-bleaching with mean percent hard coral cover currently at 25%. The slow rate of recovery of Kenya's reefs is likely to reflect the scale of the mortality, source and availability of coral larvae as well as post-settlement processes operating at individual sites. In the medium-term, the recovery of Kenya's reefs appears to be more strongly dependent on larvae from local reefs.

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John W. Wells (1957)

CHAPTER 1: GENERAL INTRODUCTION

1.1 Introduction

Coral reefs have been in existence for hundreds of millions of years persisting through changes in climate, fluctuations in sea-level and extinction events (Chappell 1983; Achituv and Dubinsky 1990). Concentrated in the tropics within the 18 ºC surface isotherm (Veron 2000), coral reefs cover approximately 284 300 square kilometres (<1.2%) of the earth's continental shelf area (Spalding et al. 2001). Over the last two decades research on coral reefs has increased exponentially, reflecting a growing understanding of their intrinsic biological and biodiversity values, the 'goods and services' they provide humanity, and concern for their long-term health and survival in the wake of increasing exploitation and rapid climate change (Hoegh-Guldberg 1999; Pandolfi et al. 2003). Current estimates are that 20% of the world's coral reefs have been effectively destroyed and are unlikely to recover, 24% are at risk of collapse through anthropogenic pressures, and 26% are under long-term threat of collapse (Wilkinson 2004).

Coral bleaching events are becoming more intense and frequent, and are causing significant changes to some coral reef communities over relatively short time-scales (Hoegh-Guldberg 1999; Wilkinson 2000). The unprecedented mass bleaching event of 1998 following the 1997-98 El Niño Southern Oscillation, is considered the most severe on record, impacting many reefs worldwide with coral mortality as high as 100% recorded at some locations (Wilkinson 2000). Coral bleaching was particularly severe in the Western Indian Ocean (WIO) with broad-scale bleaching and subsequent mortality in the order of 50-100%, and local extinctions reported for some coral species (Obura 1999; Wilkinson et al. 1999; Wilkinson 2000).

Kenya, located in the tropics between the latitudes 1º41'S and 5º40'S, was one of the more severely affected countries in the WIO with reports that 50-90% of its corals bleached along its entire coast (Obura 1999; Wilkinson et al. 1999) with subsequent losses in live hard coral cover in the order of 66-88% (Obura et al. 2000b; McClanahan et al. 2001). Much of the coral reef research in Kenya post-1998, has

focused on the differential responses and mortality of corals during and immediately after the bleaching event, as well as broad-scale changes in community structure (Obura 1999, 2001b; Obura et al. 2000b; McClanahan et al. 2001, 2004; McClanahan 2004). There has been comparatively little research done on reef recovery processes (Tamelander 2002; McClanahan et al. 2005), and much of the current understanding of reef recovery in Kenya and the wider WIO has been hampered by the lack of data on the timing, seasonality and patterns of coral reproduction and recruitment. The state of knowledge of coral reproduction and recruitment in the WIO contrasts markedly with reefs in the Pacific, Atlantic and the Red Sea, some of which have been fairly well studied and documented (see reviews by Harrison and Wallace 1990; Richmond and Hunter 1990). In addition, there have been very few studies that have examined reproduction and recruitment in equatorial regions (10ºN to 10ºS) where it has been suggested that spawning synchrony may break down due to the weak environmental cues that are thought to govern the onset and timing of reproduction (Oliver et al. 1988).

1.2 State of knowledge in the Western Indian Ocean

The ability of corals to persist and recover from disturbances is dependent on a number of factors including the intensity, severity and frequency of the disturbance (Connell 1978, 1997; Pearson 1981; Sousa 1984), successful reproduction (Harrison and Wallace 1990; Richmond and Hunter 1990; Babcock 1995), availability of viable larvae (Harriott and Fisk 1988; Sammarco 1991; Hughes et al. 2000; Harrison 2006), oceanic current dynamics influencing larval dispersal (Bull 1986; Oliver and Willis 1987; Black and Moran 1991; Black 1993), and settlement and recruitment processes (Keough and Downes 1982; Sammarco 1991; Babcock and Mundy 1996; Richmond 1997). Knowledge of the patterns of coral reproduction and recruitment are therefore essential for understanding ecological and evolutionary processes on coral reefs and how well they respond to changes in their environment.

Prior to this study, there were only four papers published on the reproductive ecology of two species of scleractinian corals in the WIO (Fig. 1.1; Rosen and Taylor 1969; Sier and Olive 1994; Schleyer et al. 1997; Kruger and Schleyer 1998). *Pocillopora*

verrucosa was found to be a simultaneous hermaphrodite that spawned gametes annually on North Malé in the Maldives (4ºN, Sier and Olive 1994) and on the KwaZulu Natal reef complex in South Africa (27ºS, Schleyer et al. 1997; Kruger and Schleyer 1998). In the Maldives, spawning was inferred from the disappearance of gametes between sequential samples collected in March and April (Sier and Olive 1994), while in South Africa mature gametes were released over one or more nights at, or after, the new moon in January (summer) (Kruger and Schleyer 1998). Spawning was also recorded in six soft coral species in South Africa (five of which were gonochoric broadcast spawners and one species was a gonochoric brooder), with five of these species reproducing in late March (Schleyer et al. 1997; Kruger et al. 1998). The fourth paper described an unusual form of asexual reproduction observed in *Gonipora stokesi* at Aldabra Atoll in the Seychelles (9ºS), where 'polyp-balls' 3-20 mm in diameter bearing 1-30 polyps formed on the exterior of the parent colony, covering up to 25% of its surface area before they detached (Rosen and Taylor 1969).

Some additional unpublished data and *in situ* observations of coral spawning are known from the region (Fig. 1.1). Spawning slicks were observed in March 1997 on Ari Atoll in the Maldives (Loch and Loch 1997 cited in Loch et al. 2002) and *Acropora* species were observed spawning in October 1994 on Chumbe Island reef (6ºS), off Zanzibar (Franklin et al. 1998). Spawning was observed in a shallow water coral community dominated by *A. nobilis*, *A. robusta* and *A. cytherea* on 3 November 1998 between 21:00 and 22:00 hours, during full moon at spring tide in the lagoon of Albion in Mauritius (20ºS, Munbodh et al. 1999), and a short study at Misali Island reef in Tanzania (5ºS) undertaken from December 2002 - March 2003, found mature gametes present in 16 of the 19 colonies of *A. tenuis* (84%), and 4 of the 54 colonies of *A. valida* (7%) sampled in February, 1-2 days prior to full moon (A. Pharoah, unpubl. data). More recently, daytime spawning was observed in more than 100 individuals of *Fungia danai* between 9:00 and 10:00 hours on the 18 February 2006 (5 days after full moon) at Salomon Atoll in the Chagos Archipelago (5ºS, Mangubhai et al. 2007). Individuals appeared to be males, releasing a cloud of sperm in short repeated bursts lasting for a few seconds, creating a distinct cloud along the reef.

Given the paucity of available information on coral reproduction, this study was designed to fill three essential knowledge gaps in Kenya and the WIO. Firstly, to

provide data on the timing and patterns of scleractinian coral reproduction, focusing on two widespread and ecologically important families in the region, Acroporidae and Faviidae. Secondly, the equator passes through Kenya, and this provided a unique opportunity to examine spawning patterns in an equatorial region. To date, only one other medium-term multi-species study has been undertaken to describe reproduction in scleractinian corals at the equator (Guest 2004). Thirdly, spatial and temporal patterns of recruitment and their relationship to coral reproduction have not been studied in Kenya, and these processes are important for the long-term recovery of its coral reefs.

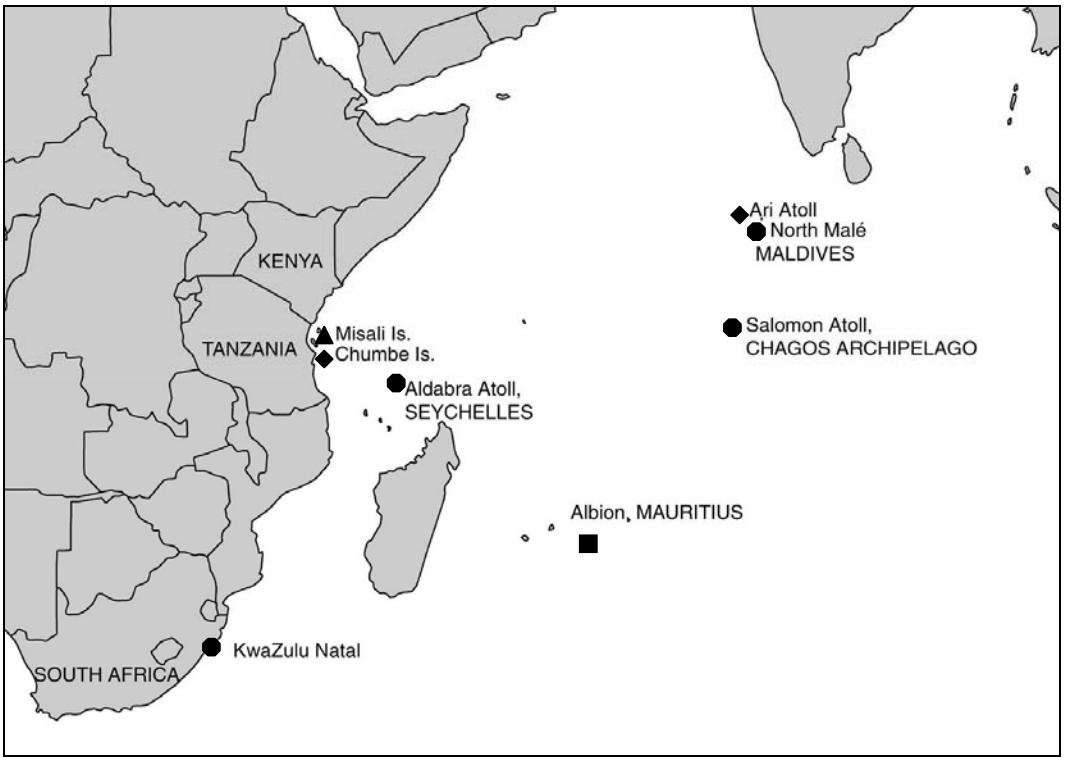

Figure 1.1: Map showing locations where information on coral reproduction is available. ●: peer-reviewed papers; ■: short report; ▲: unpublished data; ♦: *in situ* observations.

1.3 Research aims

The main aim of this study was to examine patterns of sexual reproduction in a broad range of reef coral species in Kenya. Specific objectives were to:

1) describe the pattern and timing of gametogenesis in six reef corals and document coral spawning events in the Mombasa Marine National Park and Reserve;
2) determine the level of spawning synchrony within and among species belonging to the families Faviidae and Acroporidae;
3) to test the hypothesis that spawning synchrony breaks down at the equator due to weak environmental cues governing the onset and timing of reproduction;
4) identify key environmental cues that may influence the timing of reproduction; and
5) quantify spatial and temporal patterns of settlement and recruitment in the Mombasa Marine National Park and Reserve, to examine relationships between larval settlement, and early recruit and juvenile coral populations.

Detailed skeletal taxonomic work was also required to confirm the identity of some *Acropora* species, and to separate morphological types ('morphotypes') of *Platygyra daedalea*. The results of this work are also presented in this thesis because they provide taxonomic clarity for other researchers working in Kenya, and contribute to our understanding of coral biogeography, particularly in the WIO.

1.4 Overview of thesis

The remaining sections of Chapter 1 provide a general introduction to coral reproduction, focusing on the topics that are most relevant to this thesis. Chapter 2 describes Kenya's coral reefs and the study sites, focusing on coastal geomorphology, physical oceanographic processes, seasons and climate, and the marine environment. Chapter 3 resolves the taxonomy of *Acropora* species found at the study sites. Chapter 4 examines phenotypic variation observed in *Platygyra daedalea* and uses morphometric and genetic approaches to clarify boundaries between two morphotypes. Chapter 5 examines gametogenic cycles and the frequency and timing of spawning of three faviid species, and relates these to environmental variables. Fecundity is quantified in the three species and compared to other geographic regions. Chapter 6 examines gametogenic cycles, the frequency and timing of spawning in *Acropora* species, and relates these to environmental variables. This chapter also focuses on the level of reproduction synchrony within and among the different species of *Acropora*. Chapter 7 examines natural and tile larval settlement and recruitment patterns between two sites, and relates this to coral spawning patterns documented in the previous two chapters. Prospects for reef recovery in Kenya are discussed. Chapter 8 synthesises the major findings and conclusions from the study, and highlights directions for future research.

1.5 Sexual reproduction in scleractinian corals

Despite the anatomical simplicity of cnidarians, scleractinian corals show remarkable diversity and complexity in sexual reproduction patterns making generalisations difficult. Research on coral reproduction and recruitment has been substantial in the last two decades (see section 1.5.3) and reviews are available by Fadlallah (1983), Harrison and Wallace (1990) and Richmond and Hunter (1990). A comprehensive review of the state of knowledge of sexual reproduction in scleractinian corals is beyond the scope of this thesis. Instead, section 1.5 provides the relevant context and background to this study, focusing on the information available on hermaphroditic broadcast spawners, and particularly on the families Faviidae and Acroporidae, which contain the largest number of extant species, and which are widespread in the WIO (Sheppard 1987; Wallace 1999; Veron 2000).

1.5.1 Sexual reproduction patterns

Four main sexual reproductive patterns have been described in corals, which vary in relation to their sexuality ('hermaphroditic' or 'gonochoric') and mode of development ('broadcast spawning' or 'brooding'). Hermaphroditic corals produce female and male gametes within the same polyp and colony, while gonochoric ('dioecious') species produce female and male gametes in separate colonies. Broadcast spawners are corals that release gametes into the sea for external fertilisation and larval development, while brooders undergo internal fertilisation and planula larvae develop within polyps prior to release ('planulation'). The dominant view prior to the early 1980s was that corals brood their larvae and release planulae periodically throughout the year (see Fig. 7.1 in Harrison and Wallace 1990). However, research from 1981 to the present has shown broadcast spawning of gametes for external fertilisation and larval development to be the dominant mode of reproduction in scleractinian corals (Harrison and Wallace 1990; Richmond and Hunter 1990; Dai et al. 1992; Hayashibara et al. 1993; Van Veghel 1993; Schleyer et al. 1997; Baird et al. 2002; Penland et al. 2004; Carroll et al. 2006; Mangubhai and Harrison 2006 among others).

At the family level, there appears to be some consistency in sexuality, with hermaphroditism predominant in Acroporidae, Faviidae, Merulinidae, Mussidae, Pectiniidae and Pocilloporidae, while gonochorism occurs in Agariciidae, Caryophyllidae, Dendrophylliidae, Flabellidae, Fungiidae and Siderastreidae (Harrison 1985; see Table 7.2 in Harrison and Wallace 1990). More unusual patterns of sexuality have been reported in some species at particular locations. For example, *Galaxea fascicularis* exhibits 'pseudo-gynodioecy' on the Great Barrier Reef (GBR) and in Okinawa, Japan where some colonies produce pigmented mature oocytes while other colonies produce sperm and white pseudo-oocytes which act as a buoyancy device and cannot be fertilised or undergo embryogenesis (Heyward et al. 1987; Harrison 1988). Gynodioecy has been recorded in *Porites astreoides* from Jamaica where 52% of colonies with gonads were female and 48% were hermaphroditic (Chornesky and Peters 1987).

Systematic trends are less clear with the mode of development, with both broadcast spawning and brooding observed within individual families, within genera and sometimes between species from different regions, suggesting a higher level of plasticity (Harrison 1985). For example, *Pocillopora verrucosa* is a broadcast spawner in the Red Sea, Maldives and South Africa (Fadlallah 1985; Sier and Olive 1994; Kruger and Schleyer 1998) but is reported to be a brooder at Enewetak Atoll, Marshall Islands (Stimson 1978). *Pocillopora damicornis* from Western Australia and *Goniastrea aspera* from Okinawa exhibit both modes of reproduction at their respective locations (Ward 1992; Sakai 1997). A histological study suggested that brooded planulae in *G. aspera* from Japan were produced sexually (Sakai 1997), while an electrophoretic study indicated that the brooded planulae of *P. damicornis* from Western Australia were produced asexually (Stoddart 1983, 1984).

Other genera, such as *Acropora* (excluding those belonging to the subgenus *Isopora),* are less variable in their mode of development and mostly spawn gametes (reviewed by Fadlallah 1983; Harrison and Wallace 1990; Richmond and Hunter 1990; see also Wallace 1985a; Harrison et al. 1984; Willis et al. 1985; Babcock et al. 1986; Guest et al. 2005a; Carroll et al. 2006; Mangubhai and Harrison 2006 among others).

1.5.2 Gametogenesis

A single annual cycle of gametogenesis is the most common reproductive pattern found in broadcast spawning scleractinian corals (Harrison and Wallace 1990). Oogenesis can from 3-10 months and precedes spermatogenesis which can take as little as 1-2 months (Kojis and Quinn 1981a, 1981b, 1982; Wallace 1985a; Szmant 1986; Shlesinger et al. 1998). The onset of gametogenesis may vary among individual colonies by up to a few weeks, but as cycles progress, populations of corals become more synchronised with rapid maturation of gametes occurring in the 1-2 months prior to spawning (Kojis and Quinn 1981a, 1981b; Harriott 1983a; Szmant 1986; Shlesinger et al. 1998). Three to six weeks prior to spawning, oocytes may become brightly pigmented (Harrison et al. 1984; Babcock et al. 1986) and in *Acropora* and faviid species which produce large oocytes (>300 μm, Harrison and Wallace 1990), these changes are often visible with the naked eye in fractured samples in the field (Fig. 1.2). However, not all mature oocytes are pigmented and white or pale mature eggs have been recorded in some species and in some colonies within species at different locations (Babcock et al. 1986; Shlesinger et al. 1998; Mangubhai and Harrison 2006). In the week prior to spawning, sperm motility increases and spermatozoa heads become condensed, and these changes can be seen in sperm squashes under a compound microscope (Harrison et al. 1984; Harrison 1990).

Gametogenic cycles in broadcast spawning corals usually terminate in short annual spawning periods in spring or summer that are consistent and mostly predictable at any particular location, with individual corals displaying a high level of spawning synchrony within populations (Harrison and Wallace 1990; Richmond and Hunter 1990). Following spawning there is a quiescent non-breeding period before the next reproductive cycle begins (Harrison and Wallace 1990). Extended gametogenic cycles of greater than 12 months length have been recorded in a small number of annually spawning species, which they achieve through overlapping oogenic cycles. For example, *Turbinaria mesenterina*, *Astrangia lajollaensis, Paracyathus stearnsii*, *Balanophyllia elegans, B. europaea* and *Leptopsammia pruvoti* have extended gametogenic cycles (14-24 months), but achieve annual spawning through overlapping oogenic cycles (Fadlallah 1982; Fadlallah and Pearse 1982a, 1982b; Willis 1987 cited in Harrison and Wallace 1990; Goffredo et al. 2002, 2006).

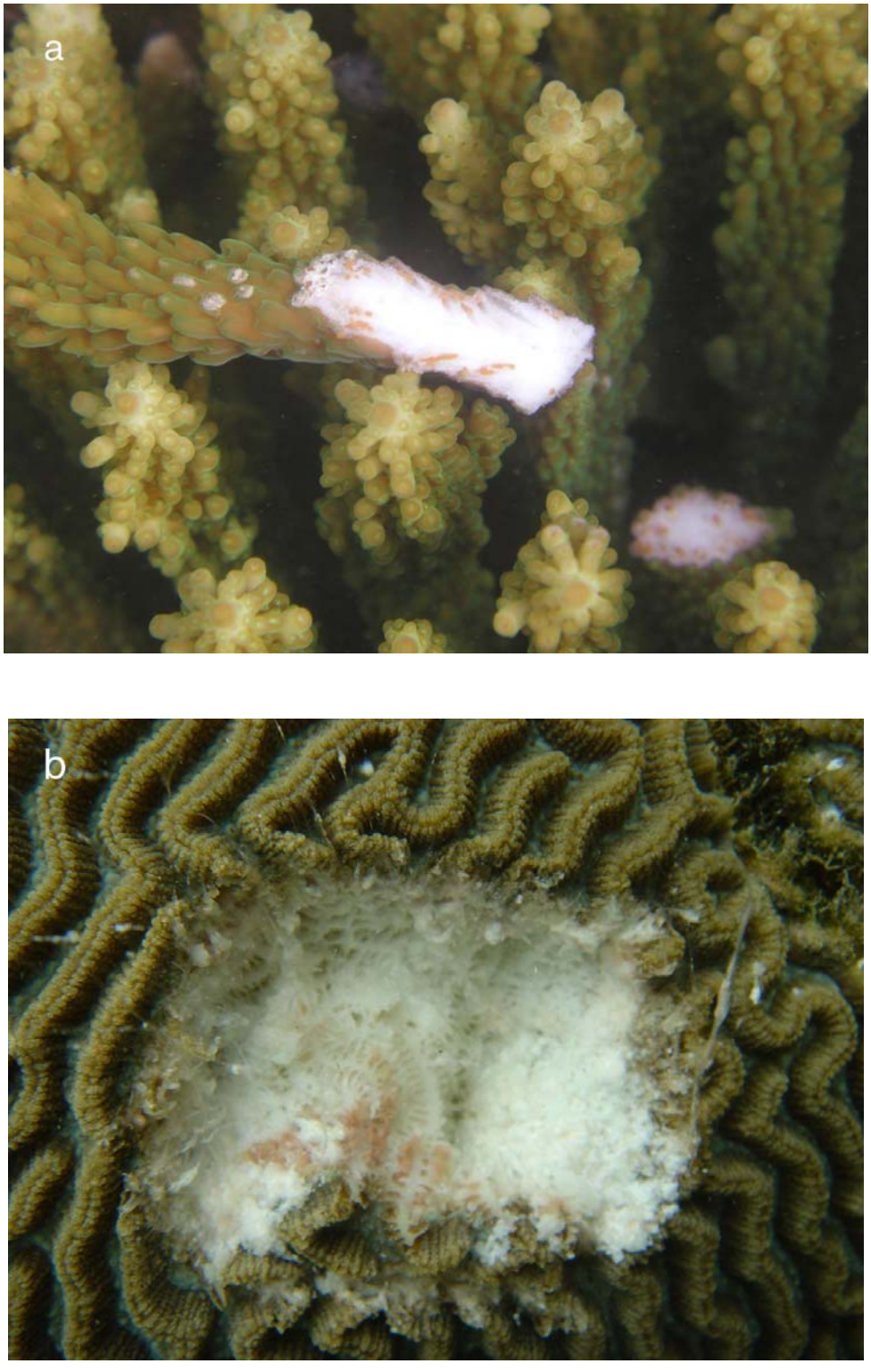

Figure 1.2: Photographs showing mature pigmented ('pink') gametes visible in coral polyps in the field in (a) *Acropora valida* and (b) *Platygyra daedalea* in Kenya.

In contrast to broadcast spawners, many brooding corals have multiple gametogenic cycles including those that exhibit lunar periodicity (reviewed by Fadlallah 1983; Harrison and Wallace 1990; Richmond and Hunter 1990; see also Harriott 1983b; Shlesinger and Loya 1985; Szmant-Froelich et al. 1985; Dai et al. 1992; Tanner 1996; Zakai et al. 2006 among others). Multiple gametogenic cycles are not common in broadcast spawning corals, but have been recorded in *Montipora digitata* (and possibly two congeners) at Magnetic Island on the central GBR, which spawned in both autumn and spring (Stobart et al. 1992). Biannual gametogenic cycles were recorded in *Acropora hyacinthus, A. gemmifera* and one morphotype of *A. humilis* on reefs in Western Samoa (Mildner 1991), and in *A. formosa*, *A. hyacinthus, Platygyra daedalea, Turbinaria reniformis* and *Lobophyllia hemprichii* on reefs in northern Papua New Guinea (PNG) (Oliver et al. 1988).

It is important to note that biannual spawning does not necessarily imply biannual cycles of gametogenesis and can only be confirmed through repeated sampling of tagged colonies. The importance of this distinction was demonstrated by Rosser (2005) who showed that populations of *A. samoensis* and *A. cytherea* in the Dampier Archipelago off Western Australia spawned biannually in March and October each year, but that each individual colony underwent a single cycle of gametogenesis and released mature gametes in only one of these months.

1.5.3 Overview of spawning patterns

Comparisons of the reproductive patterns of scleractinian corals between different locations and regions have been hampered by the use and misuse of confusing terminology to describe coral spawning events. There are currently no clear definitions to separate ‘mass spawning’ from ‘multispecific spawning’ and ‘synchronous spawning’ from ‘asynchronous spawning’.

The term ‘mass spawning’ was first used to describe synchrony and multi-species coral spawning on the GBR, where more than 40 species of scleractinian corals have been observed to spawn together on one reef during one night, and more than 130 species have been recorded participating in mass spawning events during a few nights after full moon periods in the austral late spring to early summer over a wide

geographic area (Harrison et al. 1984; Willis et al. 1985; Babcock et al. 1986). Mass spawning was subsequently defined as "*the synchronous release of gametes by many species of corals, in one evening between dusk and midnight*" (Willis et al. 1985). While this definition did not state explicitly how many species need to be releasing gametes to fall under this definition, the scale of the spawning on the GBR was such that it left no doubt that it was a 'mass' event.

However, as coral spawning patterns were documented in other locations, it became clear that the GBR was not the 'norm' but an unusual phenomenon at one end of the spectrum, that together with mass spawning on Western Australian reefs (Simpson 1985, 1991; Babcock et al. 1994), was not replicated anywhere else in the world on the same magnitude and scale. Mass spawning on the GBR contrasts markedly with corals in the northern Red Sea, where synchrony between different species is much less pronounced and spawning occurs in different seasons, months or at different lunar phases despite a high degree of synchrony within individual species (Shlesinger and Loya 1985; Shlesinger et al. 1998). Similarly, spawning patterns in coral species in Puerto Rico show strong seasonality and within-species synchrony, but reproduction occurs at different times over 3 months for different species, rather than participating in a concentrated multispecific spawning event (Szmant 1986).

This led to the use of the term 'synchronous multispecific spawning' which has not been formally defined, but has been used to describe populations of more than two species of coral releasing gametes over the same night(s). Locations exhibiting multispecific spawning may have coral populations spawning over 2-5 consecutive lunar months: examples include Curaçao, Panama, Japan, Singapore, Taiwan, Palau, French Polynesia, and Venezuela (Soong 1991; Dai et al. 1992; Van Veghel 1993; Hayashibara et al. 1993; Penland et al. 2004; Guest et al. 2005a, 2005b; Bastidas et al. 2005; Carroll et al. 2006). Multi-species spawning has also been recorded in soft corals (Alino and Coll 1989), other reef invertebrates (Lessios 1981; Babcock et al. 1992; Van Veghel 1993) and in marine algae (Clifton 1997). However, many authors use the terms multispecific and mass spawning interchangeably, and as a result, some of the locations listed above have had both terms applied to describing coral spawning patterns.

To add to the confusion, the terms ‘synchrony’ and ‘asynchrony’ have been used loosely throughout the literature to refer to the timing of gametogenesis, differences in spawning periods within and between species, and the timing of spawning in relation to lunar quarters and/or lunar nights. There is no definition that specifies how focused or concentrated one or multiple spawning events need to be, to be considered synchronous. There appears to be a continuum with spawning on the GBR and Western Australian reefs sitting at the ‘synchronous extreme’ of the continuum (Harrison et al. 1984; Willis et al. 1985; Babcock et al. 1986, 1994; Simpson 1985, 1991), and the Red Sea reefs at the ‘asynchronous extreme’ (Shlesinger and Loya 1985; Shlesinger et al. 1998). ‘Split-spawning’ (*sensu* Willis et al. 1985) of coral populations over consecutive lunar months is relatively common and has been recorded in species of *Acropora* (Babcock et al. 1986; Shimoike et al. 1992; Hayashibara et al. 1993; Wolstenholme 2004; Guest et al. 2005a; Mangubhai and Harrison 2006), faviids (Szmant 1991; Van Veghel 1994; Fan and Dai 1995; Sakai 1997; Mangubhai and Harrison 2006), as well as in other coral groups (Heyward et al. 1987; Dai et al. 1992; Pires et al. 1999). On the GBR the extent to which split-spawning occurs within and between populations (and therefore the number of mass spawning events occurring in any given year), is thought to be determined by the timing of the full moon (earlier or later in the month) and the rise in sea surface temperatures (Willis et al. 1985). In other locations (e.g. Japan, Taiwan), split-spawning of species populations has been recorded in a number of consecutive years and its causal factors are not understood (Dai et al. 1992; Hayashibara et al. 1993). ‘Partial’ spawning also occurs at the colony level, where individual colonies can spawn over consecutive nights or consecutive lunar months, though these patterns are considered more unusual and their causative factors are not understood (Willis et al. 1985; Shimoike et al. 1992; Acosta and Zea 1997).

There are clear advantages and potential disadvantages to spawning in synchrony. Potential advantages to synchronous spawning include the swamping of predators, optimal fertilisation and maximising outbreeding, and successful hybridisation and introgression (Harrison et al. 1984; Babcock et al. 1986; Olive 1992; Babcock 1995; Willis et al. 1997). Asynchronous spawning may be advantageous for reducing gamete wastage through the development of non-viable hybrids in some species, increasing the probability of successful fertilisation in the absence of congeneric

gametes, and may reduce interspecific competition among new recruits (Hodgson 1988; Shlesinger and Loya 1985).

1.5.4 Spawning patterns in equatorial regions

Very little detailed research has been done on the spawning patterns of corals in equatorial regions (Table 1.1) compared to tropical reefs (reviewed by Harrison and Wallace 1990; Richmond and Hunter 1990). It has been hypothesised that seasonality and synchrony of reproduction may break down towards the equator due to narrower variation in environmental parameters such as temperature and tidal amplitudes, influencing the onset and timing of spawning events (Oliver et al. 1988). It has also been predicted that under these more 'favourable' constant conditions, marine organisms on equatorial reefs may (a) have a more protracted reproductive season, and (b) be capable of breeding year-round (Orton 1920; Pearse 1974).

These two hypotheses were initially supported by a number of earlier detailed studies of coral reproduction over large latitudinal scales. Oliver et al. (1988) compared reproductive data from five sites extending from Heron Island reef on the southern GBR (23.5ºS) to Madang on the north coast of PNG (5ºS), and found a progressive breakdown in spawning synchrony north of the latitude 14ºS. At Madang Lagoon, the study found two *Acropora* species with two gametogenic cycles per year, an extended reproductive season and spawning asynchrony both within and between species (Oliver et al. 1988). The same two *Acropora* species participated in a single synchronised mass spawning event on the central and southern GBR. Similarly, a latitudinal comparison found *A. palifera* released planulae throughout the year at Salamua (7ºS), south of Lae in PNG, which it achieved through overlapping cycles of gametogenesis, while at Heron Island reef reproduction occurred once annually in spring (Kojis 1986b).

Recently it has been suggested that there are studies from the Pacific that challenge these equatorial hypotheses (Baird et al. 2001, 2002; Guest et al. 2002, 2005a, 2005b). A brief two week study in the Solomon Islands (8ºS) found some level of spawning synchrony among 28 *Acropora* species, with 12 species spawning 3-5 days following full moon, despite the reefs being subject to small variations in temperature (2ºC) and

tide (0.8 m) (Baird et al. 2001, 2002). Corals from Singapore (1ºN) showed a high degree of synchrony with more than 18 species from 10 genera spawning over three nights in March 2002 (Guest et al. 2002, 2005b), and multispecific spawning and a protracted breeding season has been recorded in Palau (7ºN, Kenyon 1995; Penland et al. 2004). This led to the suggestion that no coastal environment was truly aseasonal and therefore, reproductive seasonality, multispecific spawning synchrony and mass spawning were also features of equatorial reefs (Guest et al. 2005b).

However, the majority of studies that have been undertaken at the equator have been either too short (e.g. Kenyon 1995; Edinger et al. 1996; Baird et al. 2001, 2002) and/or involve too few species (e.g. Kojis 1986b; Sier and Olive 1994; Colley et al. 2002; Mangubhai et al. 2007) to provide sufficient information to determine whether spawning patterns are synchronous or asynchronous and the extent to which breeding seasons are extended in equatorial regions. Therefore, the conclusions made by Baird et al. (2001, 2002) and Guest et al. (2002, 2005a, 2005b) that synchronous spawning are features of equatorial reefs are premature, and further studies are required across different geographic regions and over longer time scales to determine if synchronous multispecific or asynchronous spawning is the dominant pattern on equatorial reefs. In addition, none of the studies listed in Table 1.1 support the suggestion by Baird et al. (2002) and Guest et al. (2005b) that mass spawning events are features of equatorial reefs.

1.5.5 Ultimate factors and proximate cues

The timing of gametogenesis and spawning is thought to be controlled by a number of factors, which can be divided into the underlying evolutionary causes (‘ultimate factors’) and the mechanisms (‘proximate cues’) responsible for controlling reproductive patterns (reviewed by Harrison and Wallace 1990). Ultimate factors are evolutionary selective pressures that govern the timing of spawning within each species, such as physiology, enhanced fertilisation and predator avoidance, and which result in increase fitness or survival (Oliver et al. 1988; Pearse 1990; Olive 1992, 1995). Proximate cues are environmental regulatory mechanisms such as sea surface temperature, daylength, moonlight, tidal cycles, diel (light and dark) cycles, rainfall and food abundance that ‘fine-tune’ or ‘constrain’ the timing of reproduction in

marine invertebrates (Orton 1920; Korringa 1947; Fingerman 1957; Pearse 1974; Himmelman 1980; Babcock et al. 1986; Yoshioka 1989; Harrison and Wallace 1990; Richmond and Hunter 1990; Starr et al. 1990; Olive 1995).

Table 1.1: Summary of published studies on coral reproduction done in equatorial regions (± 10º), ordered from north to south. '-': not known.

Country	Location	Lat.	Spp.	Families	Reference
FSM*	Yap	9ºN	10	2	Kenyon (1995)
Costa Rica	Caño Is.	7ºN	3	8	Glynn et al. (1991, 1994, 1996, 2000)
Panama	Gulf of Panama, Gulf of Chiriqui	7ºN	3	8	Glynn et al. (1991, 1994, 1996, 2000)
Palau	Nikko Bay	7ºN	33	7	Penland et al. (2004)
	-	7ºN	27	5	Kenyon (1995)
Maldives	North Malé	4ºN	1	1	Sier and Olive (1994)
Singapore	Pulau Satumu	1ºN	24	6	Guest (2004); Guest et al. (2002, 2005a, 2005b)
Ecuador	Galapagos Is.	1ºS	4	9	Glynn et al. (1991, 1994, 1996, 2000); Colley et al. (2002)
Kenya	Mombasa	4ºS	26	2	Mangubhai and Harrison (2006), this study
Chagos Arch.	Salomon Atoll	5ºS	1	1	Mangubhai et al. (2007)
PNG	Madang	5ºS	3	2	Oliver et al. (1988)
	Lae	7ºS	1	1	Kojis (1986b)
Indonesia	Java Sea	7ºS	25	8	Edinger et al. (1996)
Solomon Is.	Gizo	8ºS	28	1	Baird et al. (2001, 2002)
PNG	Port Moresby	9ºS	3	2	Oliver et al. (1988)

*Federated State of Micronesia

It has been proposed that on the GBR temperature, monthly lunar (and associated tidal) cycles and the onset of darkness are the three main environmental cues that act progressively in that order, to fine tune and ultimately determine the month, day and hour of spawning (Babcock et al. 1986). However, it is important to note that much of the evidence presented to date for factors controlling seasonal cycles is based on correlation rather than experimental manipulation of single environmental parameters and therefore does not imply a causative relationship. The confounding effects of different non-independent environmental variables make it difficult to understand the

role(s) individual variables play in the reproductive processes in marine organisms. In addition, the interaction between proximate cues and endogenous rhythms are not well understood (Olive and Garwood 1983). The proximate cues most relevant to global coral reproductive patterns are summarised below.

1.5.5.1 Temperature

Temperature has been cited as the primary factor regulating breeding cycles in marine invertebrates, including scleractinian corals, through controlling gamete development and maturation (Orton 1920; Yonge 1940 cited in Fadlallah 1983; Pearse 1974; Babcock et al. 1986). In broadcast spawners, spawning commonly occurs when temperatures are rising or are at or close to their summer maximum, and a number of studies provide indirect correlative evidence of the importance of temperature on the maturation of gametes and timing of spawning (reviewed in Harrison and Wallace 1990). For example, at localities where there is a delay in the rise in temperature, there is a corresponding delay in the onset of gametogenesis and spawning time. This occurs on the GBR where inshore coral communities spawn one month earlier than offshore communities, most likely in response to a corresponding delay in the rise in water temperature at offshore reefs by one month (Willis et al. 1985; Babcock et al. 1986). In Taiwan, coral species in the south (21ºN) which experience warmer and lower annual variation in temperature, spawn 1-2 months earlier than corals in the north (25ºN) (Dai et al. 1992). Similar patterns have been recorded in the Caribbean where spawning in Curaçao and Bonaire takes place one month later than other localities, most likely in response to a corresponding delay in reaching maximum sea surface temperature (Van Veghel 1994).

Direct evidence for the role of temperature in the reproductive behaviour of coral species has been shown through a small number of manipulative experiments. Hunter (1988) found that exposure to winter seawater temperatures arrested or eliminated spawning in *Montipora verrucosa* and *M. dilatata* from Hawaii, but synchrony could be restored a month later if colonies were returned to ambient temperatures. *Astrangia danae* from temperate Rhode Island was capable of spawning year-round when kept under constant temperature and a feeding regime in a laboratory (Szmant-Froelich et al. 1980).

The annual temperature range (rather than the absolute temperature) has also been suggested as being important in determining the length of the reproductive period and degree of spawning synchrony (Shlesinger and Loya 1985; Babcock et al. 1986; Richmond and Hunter 1990). There were marked differences in the timing and length of reproduction in *Stylophora pistillata* between reefs of similar latitude in the Red Sea and Arabian Gulf (Fadlallah and Lindo 1988). In the central Red Sea where sea surface temperatures range from 25-31 ºC, *S. pistillata* underwent two cycles of oogenesis and had two peaks in planulation, while in the western Arabian Gulf where temperature variation is more extreme ranging from 15-35 ºC, the same species had a short cycle of gametogenesis and a brief period of planulation, which suggests that differences in temperature regimes between the regions are strong proximate factors driving reproductive patterns (Fadlallah and Lindo 1988). This study contrasts with the results of reefs of similar latitude on the east and west coast of Australia, where coral species participate in mass spawning events and experience similar temperature regimes, but exhibit a 6-month difference in the timing of spawning (Simpson 1991). In addition, Western Australian coral communities in the tropics (Ningaloo Reef) and subtropics (Houtman Abrolhos Islands) spawn in the same month despite a 3-month difference in the timing of winter minima and the spring rise in temperature (Babcock et al. 1994).

Orton (1920) proposed that in equatorial regions where there was little temperature variation and optimal temperatures for reproduction extend over a longer period, species would have protracted breeding periods with those closest to the equator capable of year-round reproduction. These concepts were also summarised by Pearse (1974) examining the relationship between temperature control and latitudinal variation as they pertained to echinoids.

1.5.5.2 Solar insolation

Recently it has been hypothesised that the "*electromagnetic energy incident to the earth surface*", termed 'solar insolation', is the primary factor driving coral reproduction and is a better predictor than temperature of the timing of spawning in different regions (Penland et al. 2004). Two papers have been published to investigate

this hypothesis. A study in Palau recorded multispecific spawning in February, April/May and August/September which coincided with the rise and fall from insolation maxima rather than the rise or fall of sea surface temperatures (Penland et al. 2004). The authors noted that spawning on the GBR and on reefs in Japan also occurred at a time when solar insolation was near maximum, and predicted two spawning periods for the geographic region between Singapore and Indonesia. Guest et al. (2005a) recorded two spawning events in *Acropora* species in Singapore as predicted by Penland et al. (2004), though <5% of corals had pigmented oocytes during the minor spawning in October and November. More recently, a meta-analysis of spawning events in the Caribbean showed that the rate of change and cumulative response of solar insolation cycles was a better predictor of coral reproduction in this region than temperature or solar intensity at the time of spawning (van Woesik et al. 2006).

1.5.5.3 Lunar and tidal cycles

A wide range of marine invertebrates including both brooding and broadcast spawning corals exhibit lunar periodicity in their reproductive behaviour (Babcock et al. 1986, 1992; Harrison and Wallace 1990; Richmond and Hunter 1990). Multispecific synchronous broadcast spawning occurs between full moon and the start of the last lunar quarter on the central GBR and at Akajima Island, Japan and the lunar period of spawning is often consistent between years for individual species (Harrison et al. 1984; Willis et al. 1985; Babcock et al. 1986; Hayashibara et al. 1993). Spawning around the new moon is more rare in broadcast spawners, but has been documented in a few species on the GBR, Hawaii, South Africa and Red Sea (Shlesinger and Loya 1985; Willis et al. 1985; Babcock et al. 1986; Hunter 1988; Kenyon 1992; Kruger and Schleyer 1998). The role of moonlight in determining spawning behaviour has been demonstrated by two manipulative experiments. Jokiel et al. (1985) and Hunter (1988) showed that the timing of planulae release in *Pocillopora damicornis* and gamete release in *Montipora verrucosa* in Hawaii could be altered by artificial light regimes, suggesting that moonlight is an entraining factor.

In contrast, the relationship between timing of spawning and tidal cycles is not clear. Corals on the GBR and Ningaloo Reef (Western Australia) tend to spawn on neap low

tides (Willis et al. 1985; Babcock et al. 1986; Simpson 1985, 1991), corals in the Houtman Abrolhos Islands (Western Australia) spawn mostly on spring high tides (Babcock et al. 1994), and in southern Taiwan and Japan spawning occurs on high tides from springs through to neaps (Dai et al. 1992; Hayashibara et al. 1993). Tidal cycles are likely to be important for reproductive success because of their effect on gamete dilution, fertilisation, dispersal and larval settlement rates (Babcock et al. 1986). However, the effects of tides may be less pronounced in locations where there is little tidal variation, such as PNG, the Solomon Islands and Houtman Abrolhos Islands (Oliver et al. 1988; Babcock et al. 1994; Baird et al. 2002). Therefore, moonlight is probably a stronger proximate cue for coral spawning than tides, although the two may be linked to differing degrees at different locations depending on the effect of these parameters on fertilisation rates and larval dispersal.

1.5.5.4 Photoperiod

Spawning in mature coral colonies occurs predominantly between dusk and midnight, with the sequence of events leading to spawning being triggered by the onset of darkness (Babcock et al. 1986). Avoidance of predators that are visual feeders (such as planktivorous fish) and the effects of damaging ultraviolet light on gametes and developing embryos, have been cited as the main selective advantages to spawning in darkness (Harrison et al. 1984; Babcock et al. 1986; Wellington and Fitt 2003). Daytime spawning is rare, but has been recorded in *Goniastrea favulus, Fungia concinna* and *Pavona cactus* on the GBR (Kojis and Quinn 1981a; Harrison and Wallace 1990), *Fungia granulosa* in the northern Red Sea (Kramarsky-Winter and Loya 1998), *Pavona* sp. in the Gulf of Thailand (Plathong et al. 2006) and *Fungia danai* in the Chagos Archipelago (Mangubhai et al. 2007), and has been observed in *Herpolitha limax* in the Phoenix Islands, Kiribati (D. Obura, pers. comm.; pers. obs.).

The role of photoperiod in controlling the final synchronisation and timing of spawning has been demonstrated in some scleractinian corals by the experimental manipulation of light and dark cycles. Babcock (1984) showed that the timing of spawning could be offset in *Goniastrea aspera* by modifying photoperiods, and Harrison et al. (1984) noted that artificially extending light periods delayed spawning in a number of species. While photoperiod cycles are more consistent because of their

independence from seasonal and inter-annual variation in climate, their role in synchronising annual gametogenic cycles has not been well demonstrated in corals, though it has been shown in other marine invertebrates (e.g. Garwood 1980; Pearse and Eernisse 1982; Pearse and Walker 1986) and in plants in equatorial regions (Borchert et al. 2005). It is possible that photoperiod may play a more significant role in the reproductive cycles of scleractinian corals than simply triggering spawning after sunset, and may act in synergy with temperature and tidal cycles.

1.5.5.5 Other cues

Other proximate cues suggested to influence reproduction in marine invertebrates are rainfall, salinity and food abundance. Mendes and Woodley (2002) analysed spawning data from twenty locations and concluded that spawning occurred most frequently during periods of high seasonal temperatures and low rainfall. Food availability can increase with rainfall and may be beneficial to coral larvae or young recruits, and may explain why in locations of low temperature variation (e.g. Solomon Islands, Palau, Guam), spawning periods coincided with the period just prior to peak annual rainfall (Starr et al. 1990; Mendes and Woodley 2002). However, rainfall is too variable from year to year, and therefore is unlikely to be a reliable proximate cue for spawning, though it may interact with more reliable cues such as sea surface temperatures. In addition, spawning has been recorded in Guam, Okinawa and Hong Kong during the rainy season, despite the deleterious effect reduced salinity can have on fertilisation success (Richmond 1993; Harrison 1995; Lam 2000).

1.5.6 Fecundity

The allocation and partitioning of resources towards growth, maintenance and reproduction are still poorly understood in scleractinian corals. Fecundity is used as a measure of the reproductive effort of corals, and is expressed as the number of oocytes or planulae produced per polyp, or the number of oocytes per cm^2. Brooding species tend to produce small numbers of large, well developed planulae, while broadcast spawners typically produce larger numbers of smaller sized gametes (Harrison and Wallace 1990). The number of oocytes per cm^2 is a more useful estimate of fecundity, because it allows comparisons across species with different

polyp morphologies, and is not biased by variation in polyp size or density (Harrison and Wallace 1990). However, to make comparisons of the annual reproductive effort of corals, data must also be available on (a) the number of reproductive cycles a coral undergoes each year, (b) inter-annual temporal variability, (c) the proportion of the colony that is involved in reproduction, (d) age or size-related differences in fecundity, and (e) any stresses occurring at the time of reproduction (reviewed by Harrison and Wallace 1990). Examples are provided below to illustrate these factors.

The importance of the number of reproductive cycles on fecundity was shown by Kojis (1986b), who found *Acropora palifera* near Lae was 4.5 times more fecund than the population at Heron Island because it had more frequent reproductive cycles, and its fecundity was variable between the different spawning months. High temporal variability between reproductive seasons has been recorded in the Red Sea and GBR (Wallace 1985a; Rinkevich and Loya 1987), and can therefore affect estimates of fecundity and comparisons with other regions.

A number of studies have shown that polyps located at the margin of colonies or rapid growing branch tips may be sterile or have a lower fecundity than the rest of the colony, and should be considered when estimating total colony fecundity (Wallace 1985a; Szmant 1986, 1991; Chornesky and Peters 1987; Soong and Lang 1992; Sakai 1998). Kojis and Quinn (1985) showed through manipulative experiments that fecundity in *Goniastrea favulus* was determined by the interaction of colony size and polyp age, where older colonies were found to be more fecund than younger colonies of the same size, and the minimum size at reproduction was larger in unfragmented colonies. Szmant-Froelich (1985) found colony size affected reproduction in *Montastrea annularis* with fragmentation and partial mortality reducing fecundity.

Studies have also shown that stresses such as sedimentation (Kojis and Quinn 1984), fragmentation (Wallace 1985a), inter-colony competition (Rinkevich and Loya 1985; Tanner 1995), anthropogenic pollution stresses (Rinkevich and Loya 1977, 1979b; Tomascik and Sander 1987; Guzmán and Holtz 1993; Harrison 1995) and coral bleaching (Ward et al. 2002; Baird and Marshall 2002), may reduce overall coral fecundity.

1.5.7 Coral recruitment

Following successful spawning and subsequent fertilisation and embryo development, larvae of most broadcast spawning corals remain in the water column for a minimum of 2-6 days before they are competent to settle on substratum, during which time they have limited movement ability and are therefore planktonic (reviewed by Harrison and Wallace 1990; Harrison and Booth 2007; see also Nozawa and Harrison 2002, 2005; Miller and Mundy 2003; Nishikawa et al. 2003; Harrison 2006). This planktonic development period is followed by 'attachment' (Harrison 2006), then 'settlement', which occurs after metamorphosis of larvae and permanent attachment to the substratum (Harrison and Wallace 1990; Harrison and Booth 2007). During this period, mortality may be high depending on the 'active choices' by larvae, local physical conditions and interactions with other organisms (Keough and Downes 1982; Connell 1985; Hurlbut 1991; Babcock and Mundy 1996). Coral recruitment refers to the stage when newly formed individuals become large enough to be censused, and is therefore a measure of the reproductive success of an individual coral or community of corals (Harrison and Wallace 1990). Recruitment is dependent on the interaction of recruits with biotic (e.g. predation, competition) and abiotic (e.g. environmental variation, disturbance) factors (Richmond and Hunter 1990), and plays an important role in determining community structure and dynamics (Gaines and Roughgarden 1985; Connell et al. 1997; Hughes et al. 2002).

Artificial settlement substrata have been widely used to detect coral settlement and recruitment patterns on reefs and to infer larval availability (reviewed by Harrison and Wallace 1990). Initial stages of settlement onto artificial substrata and subsequent survival and growth has been termed 'invisible' recruitment (Wallace 1983) because coral 'spat' are small in size, usually <1 cm, and can only be identified under a microscope. Settlement and recruitment can vary over spatial scales of site, depth, habitat and reef zone, and over temporal scales of months, seasons and years (Wallace and Bull 1981; Birkeland et al. 1981; Wallace 1985b; Harriott and Fisk 1988; Fisk and Harriott 1990; Sammarco 1991; Baird and Hughes 1997; Hughes et al. 1999; Glassom et al. 2006), with complex space-time interactions occurring (Dunstan and Johnson 1998; Hughes et al. 2000; Glassom et al. 2004).

Studies focusing on 'visible' recruitment (Wallace 1983), where coral recruits are >1 cm in size and can be measured directly on natural substrata, have increased in the last decade, partly in response to more frequent coral bleaching events and a greater focus on post-bleaching reef recovery (e.g. Edwards et al. 2001; Tamelander 2002; McClanahan et al. 2005; Loch et al. 2002; Bianchi et al. 2006; Schuhmacher et al. 2006). Small-sized corals on natural substrata have been under the influence of post-settlement processes for at least 8-10 months (Harrison and Wallace 1990), and therefore provide a measure of recruitment and potential recovery on a reef (Bak and Engel 1979; Rylaarsdam 1983; Harriott 1985; Smith 1992).

The rate of recovery of a reef following disturbances will depend, in part, on whether reefs are largely 'self-seeding' or reliant on larvae transported from other source reefs (Pearson 1981; Done 1982; Sammarco and Andrews 1988; Willis and Oliver 1988). In some taxa, recruit populations are similar to adult populations, which has led some authors to conclude that reefs may be self-seeding, while for other taxa recruits are disproportionately higher or lower than adult populations suggesting that dispersal and/or post-settlement processes play important roles in determining community structure and dynamics (Bak and Engel 1979; Rylaarsdam 1983; Rogers et al. 1984; Smith 1992). The extent to which coral communities and reefs are self-seeding or interconnected by larval dispersal is still a strongly debated topic, with larval dispersal influenced by mode of development (i.e. internal versus external), competency periods, mortality rates, oceanography, and the location and topography of reefs (reviewed by Harrison and Wallace 1990; Harrison and Booth 2007).

CHAPTER 2: A DESCRIPTION OF KENYAN CORAL REEFS AND STUDY SITES

2.1 Coastal geomorphology

The East African continental shelf is mostly narrow (200 km), and slopes steeply to the ocean floor to about 4000 m (Richmond 2002). The coastline is composed of fossil limestone reefs formed during the Pleistocene epoch (1.6 million to 10 000 years ago) when glacial cycles caused numerous fluctuations in sea levels (Crame 1981). Sea level has remained relatively constant in the Western Indian Ocean (WIO) over the last 6000 years, following a net drop of 15 m at the end of the Pleistocene (Richmond 2002).

The Kenyan coast, located in the tropics between the latitudes 1º41'S and 5º40'S has a narrow 500 km long continental shelf with an estimated area of 19 120 km^2 (UNEP 1998) that stretches from its border with Tanzania north to Somalia (Fig. 2.1). For the most part, the shelf width is narrow, less than 5 km, though it extends almost 60 km out to sea near the mouth of the Tana River. Geologically, the Kenyan coast is divided into two regions. The southern region extends from Kenya's southern border with Tanzania to Malindi (Fig. 2.1), and comprises layers of Pleistocene reefs that have formed an almost continuous intertidal fringing reef and a marine lagoon on the seaward side, and rocky shorelines and steep coastal cliffs on the landward side (Obura 2001a). Freshwater and sediment inputs to the southern coastal region are blocked by coastal hills that extend 20 km wide and 500 m high above sea level. The northern region extends north of Malindi to the Somali border (Fig. 2.1), and is composed of sedimentary plains that were formed during the Quaternary and Tertiary period. This region is drained by the Tana and Athi-Sabaki Rivers, Kenya's two largest rivers, whose discharges have helped form expanses of soft-substrata environments (Obura 2001a).

2.2 Physical oceanographic processes

There are four oceanic currents that influence the biophysical environment along the Kenyan coast: the South Equatorial, East African Coastal (EACC), Equatorial Counter and Somali Currents (Fig. 2.2). The South Equatorial Current transverses east to west across the Indian Ocean (10˚ below the equator) until it reaches the African coast near the border of Tanzania and Mozambique, where it splits into the northerly EACC and the southerly Mozambique Current, running parallel to the coast (Richmond 2002). The EACC always moves in a northward direction during all seasons, at least as far as Malindi in Kenya. However, during the northeast (NE) monsoon season the EACC (flowing at <0.5 m s^{-1}) converges with the southward flowing colder up-welled waters of the Somali Current (flowing at 0.8-1.0 m s^{-1}) between Malindi and Lamu, and moves offshore forming the Equatorial Counter Current (UNEP 1998; Obura et al. 2000a; Obura 2001a). During the southeast (SE) monsoon, the EACC (flowing at 0.5-0.75 m s^{-1}) moves further north, accelerated by trade winds, and southerly winds and the Somali current reverses its direction of flow and increases its velocity to 1.0-1.3 m s^{-1}, reducing the strength of the Equatorial Counter Current (UNEP 1998; Obura et al. 2000a; Obura 2001a). The direction and strength of these oceanic currents are likely to play an important role in the large-scale dispersal and recruitment of marine organisms, including corals, along the Kenya coast.

2.3 Seasonality, climate and the marine environment

2.3.1 Seasonality and climate

Weather conditions in Kenya and wider East Africa are influenced by the Inter-Tropical Convergence Zone, a zone of low pressure that migrates north and south of the equator according to the movement of the sun and creates two distinct seasons, the SE (*kusi* in Swahili) and NE (*kaskazi*) monsoon. The SE monsoon, from May to October, is characterised by cool sea surface temperatures (mean 26.4 ºC), high cloud cover, long and heavy rains, rougher seas and strong winds (8.2-9.8 m s^{-1}), whereas the NE monsoon, from December to March, is characterised by warm sea surface

temperatures (mean 28.4 ºC), low cloud cover, short rains, calm seas and steady light winds (5.5-7.9 m s^{-1}) (McClanahan 1988; UNEP 1998; Obura et al. 2000a). The strongest winds occur from mid-June to mid-July and in mid-February in the SE and NE monsoon seasons, respectively (Johnson et al. 1982). There is a transitional period of 1-2 months between seasons that is characterised by variable and lower winds. Relative humidity is highest during the wet months from April to July.

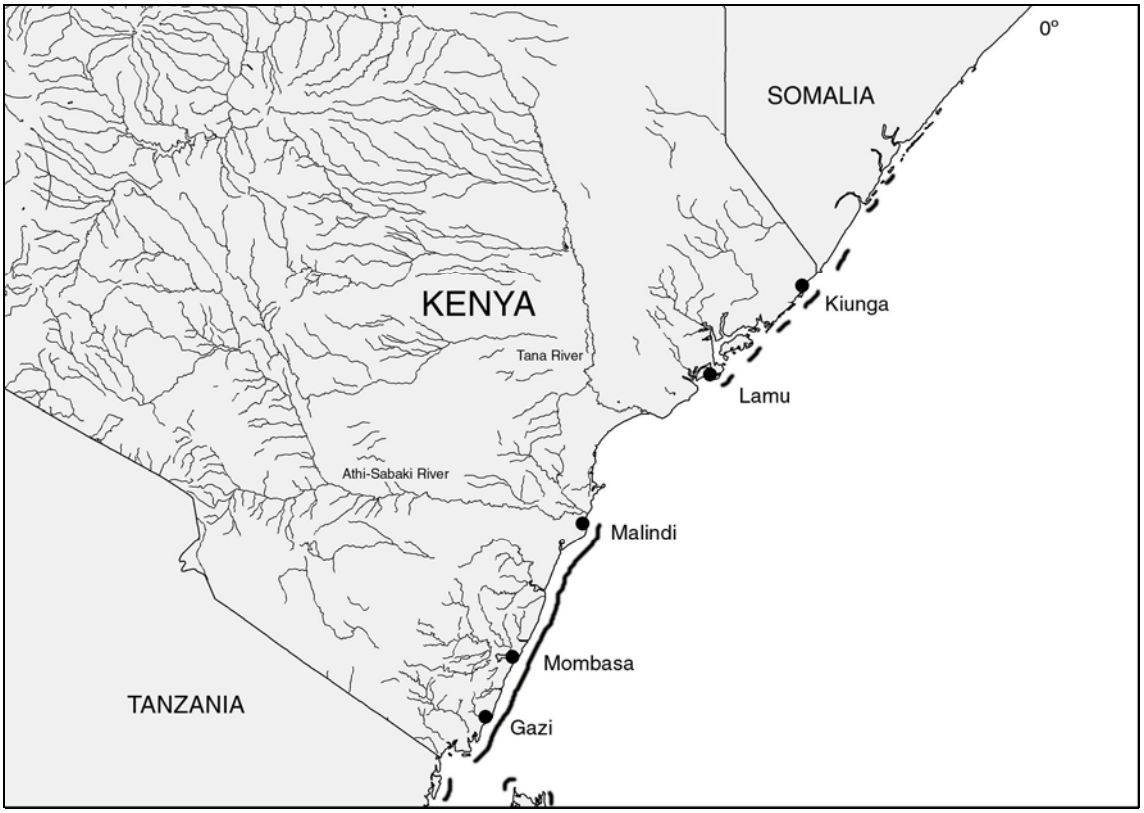

Figure 2.1: Map of the Kenyan coast showing the major reef systems, rivers, catchments and towns. The top border of the map marks the position of the equator. Source: Southern Cross University G.I.S. Laboratory. Modified with permission.

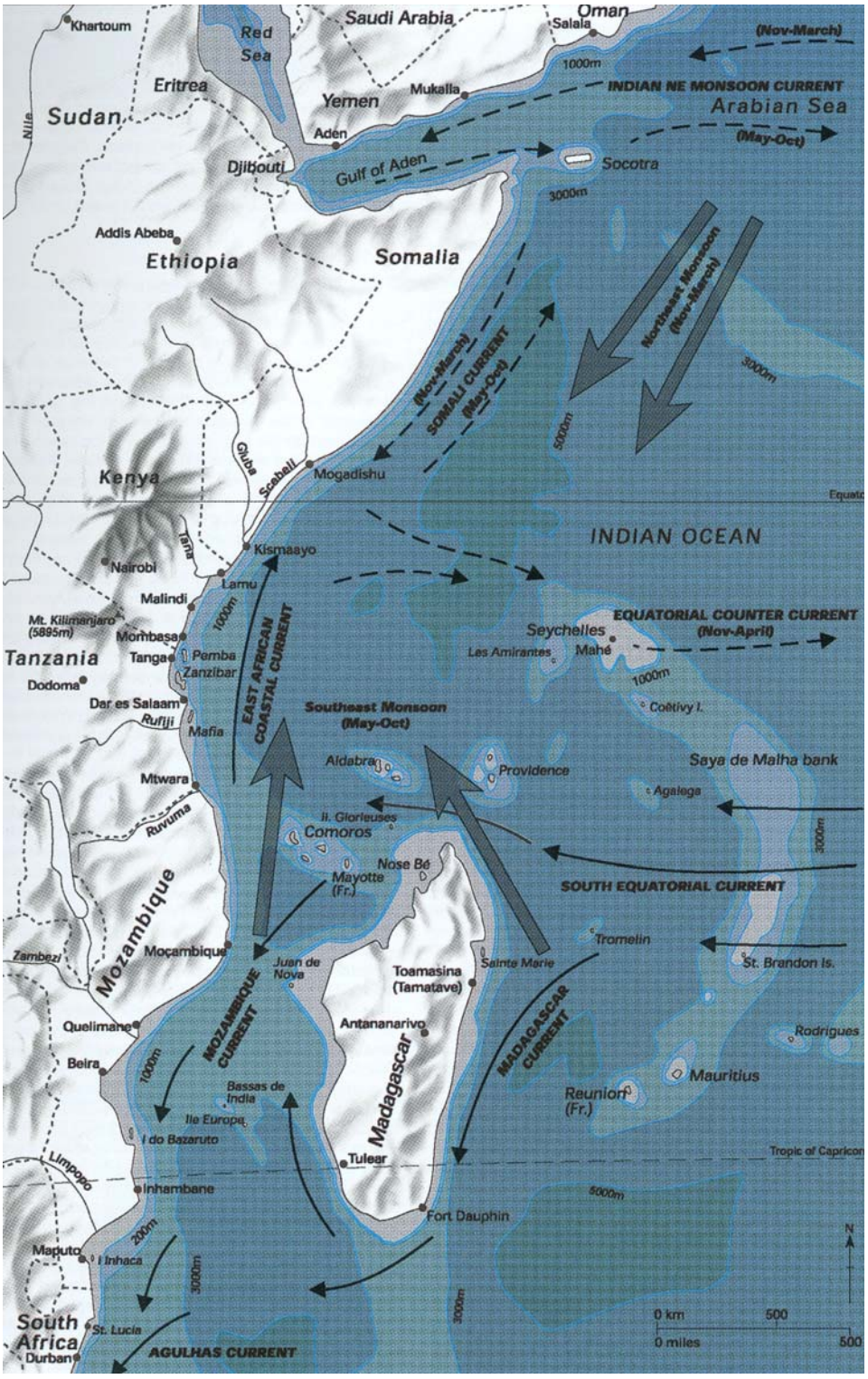

Figure 2.2: Map of the oceanic currents (small arrows) and monsoon winds (large arrows) along the East Africa coast. Source: A Field Guide to the Seashores of Eastern Africa (Richmond 2002). Used with permission from author.

2.3.2 Tidal regimes and lagoon circulation patterns

The Kenyan coast, including its lagoons and creek waters are predominantly under the influence of semi-diurnal tides. This means there are two tidal cycles, two high and two low tides every lunar day (24 hours and 50 minutes). During flood tide, water penetrates through channels in backreef areas, filling the lagoon until oceanic water passes directly over backreef areas, and water enters the creeks (Kirugara et al. 1998). The cycle is reversed on the ebb tide. The extent of these changes is dependent on the lunar cycle and changes in spring and neap tidal cycles. The lowest tides occur during the NE monsoon when combined with prevailing winds, water is driven offshore. The highest tides occur in April and October of each year coinciding with the equinoxes (i.e. where the sun and moon are positioned in the same plane). Currents are generally weak in the lagoon, and the difference between high and low tide can be in the order of 2.5-4 m, which is relatively high for a tropical coast and has been termed macro-tidal (Brakel 1982). This macro-tidal system plays an important role in increasing current strength and mixing inshore waters and results in the alternate emersion and submersion of fringing reefs.

In addition, oceanic swell continuously breaks on the reef crest and results in 'wave-induced volume flux' where oceanic water flows into the lagoon and returns to the ocean through tidal channels (Kirugara et al. 1998). The fringing reef, particularly during low water spring tides acts as a barrier and provides 4-6 hours of calm conditions in the lagoon and backreef areas per tidal cycle. During neap low tides, the fringing reef is permanently submerged and oceanic water constantly enters the lagoon for the complete tidal cycle, which maintains a slightly higher water level in the lagoon (Kirugara et al. 1998). Tidal flushing and prevailing winds have a strong influence on the flow and movement of inshore, lagoonal and forereef waters, more so than the EACC (Obura et al. 2000a).

2.3.3 Sea surface temperatures (SST)

Sea surface temperatures during the SE monsoon are cooler, averaging 26.4 ºC (minimum 24 ºC), while temperatures during the NE monsoon average 28.4 ºC (maximum 32 ºC) with reef waters generally 1 ºC warmer than offshore waters (UNEP 1998; Obura et al. 2000a). There are two temperature maxima that occur in Kenya when solar radiation is high. The first maximum occurs in October/November and sea surface temperatures can rise to 30 ºC (Fig. 2.3). The second maximum occurs in February/March when the sea is calmest and solar radiation is highest, and temperatures can reach 31-32 ºC. Air temperature shows a similar cyclical pattern to sea surface temperatures, with the largest temperature difference between the two occurring in July, and smallest difference occurring in December to February (Fig. 2.3).

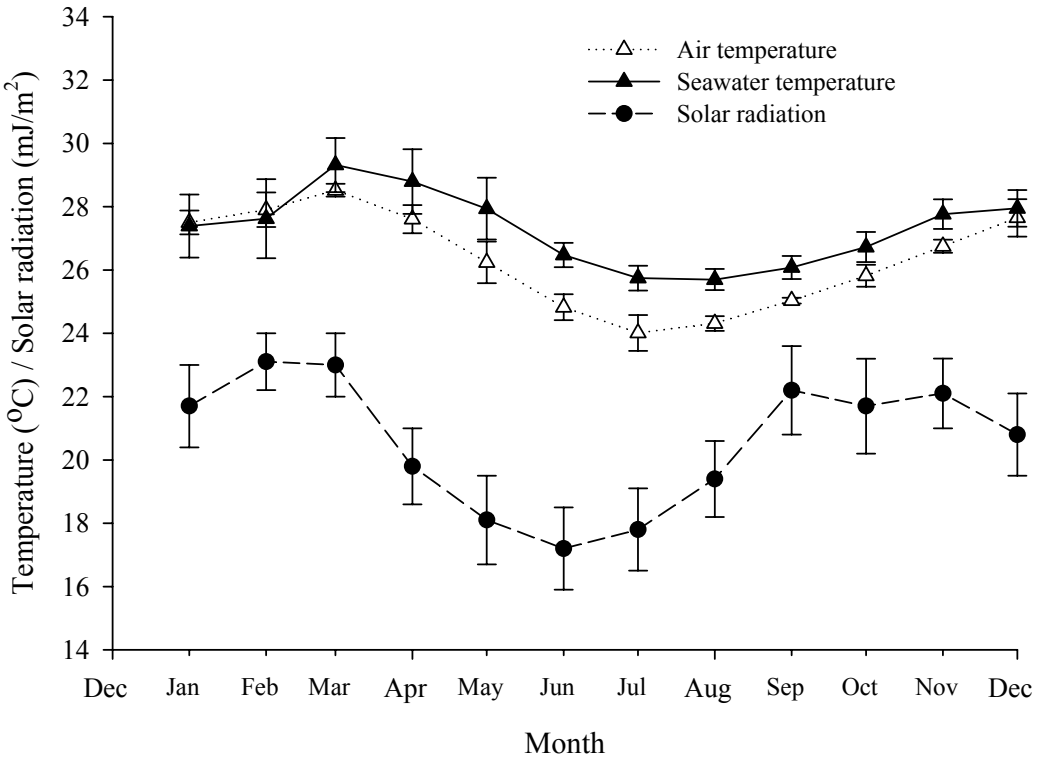

Figure 2.3: Annual changes in mean sea surface and air temperatures, and the pattern of solar radiation in Mombasa, Kenya. Mean monthly sea temperatures were recorded at Coral Gardens from 1996 - 2002 (CORDIO East Africa). Mean air temperature and solar radiation were recorded from 1997 - 2003 (Kenya Meteorological Department). Error bars are standard deviations.

2.3.4 Salinity and rainfall

Salinity variation is low, especially along the southern region where there are no large river systems, and coastal hills prevent inland rivers from accessing the sea. Salinity averages 34.5 ‰, with values of 32-33 ‰ recorded in inshore areas following heavy rainfall or discharge from the Tana or Athi-Sabaki Rivers (Obura et al. 2000a). During the 1997-98 El Niño, heavy rainfall for 5 months resulted in salinity being reduced on shallow reefs to 12 ‰ (Mdodo 1999 cited in Obura 2001a). However, the 'normal' pattern on the Kenya coast is for two dry and two wet seasons, with long periods of rain occurring in May, and short periods of rain occurring in November (Fig. 2.4).

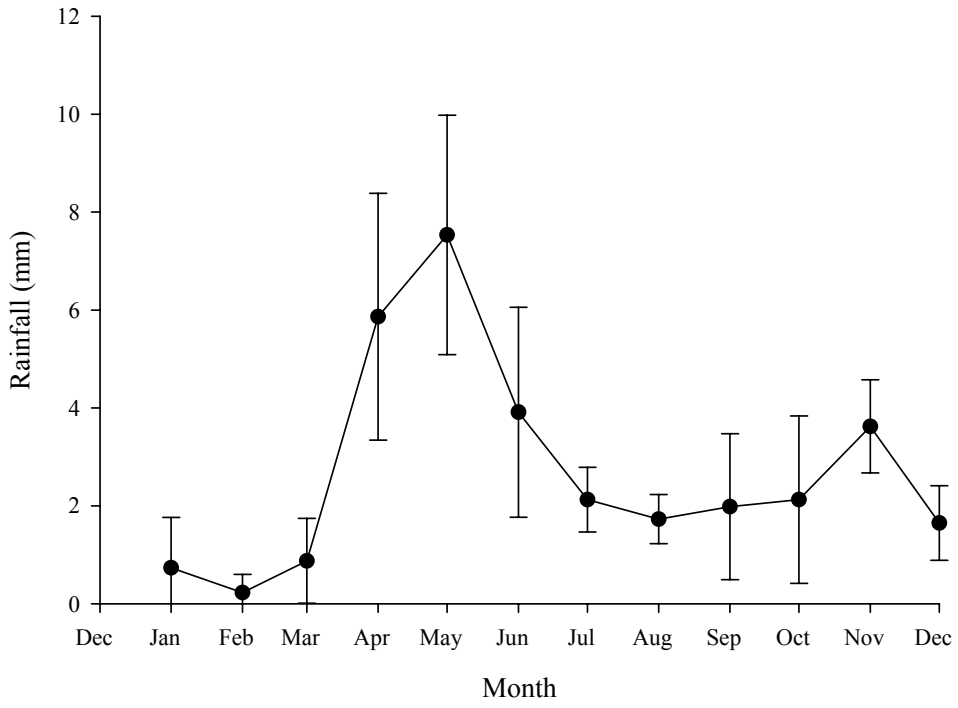

Figure 2.4: The pattern of annual rainfall in Mombasa, Kenya from data collected from 1997 – 2003 (Kenya Meteorological Department). Error bars are standard deviations.

2.4 Kenyan coral reefs

Fringing reefs are the most dominant reef type in the WIO and occur in Kenya, Tanzania, Mozambique and around many of the Indian Ocean islands. The total area of Kenya's reefs has been estimated at 630 km^2, which equates to 0.22% of the world's coral reefs (Spalding et al. 2001). The reefs are divided into two main areas: a fairly continuous 200 km fringing reef in the south extending from Shimoni (near the border with Tanzania) to Malindi, and patch reefs (both protected and exposed) and fore-reef slopes in the north from Lamu to the Somali border (Fig. 2.1). Both areas are interspersed with sand, seagrass and algae beds with hard substrata dominated by coral and algal communities. The southern reef is the focus of this study and is characterised by a fringing reef crest dissected by channels formed at the mouth of creeks, and a shallow lagoon with patch reefs along its length. The depth of the lagoon varies between 0-8 m, with some areas becoming inaccessible by artisanal fishing canoes (*dau*) and boats during low tide. The lagoon and backreef areas can be accessed in most weather conditions during both monsoon seasons, and hence are heavily utilised by fishers. Beyond the reef crest, the fringing reef forms platforms at 8-15 m and 25-30 m depth, and corals can be found, on average, down to 20-25 m. At 30 m the continental shelf slopes into sand and rubble substrata.

Terrigenous inputs from the Tana and Athi-Sabaki rivers persisting throughout the Pleistocene coupled with the colder waters of the Somali Current, have resulted in patchy development of corals reefs immediately north and south of Ungwana Bay (UNEP 1998; Obura 2001a). The northern reefs have less accreted carbonate structure, are less diverse and have lower coral cover compared to the south, which has been attributed to the Somali Current system that creates marginal conditions for coral growth (McClanahan 1988; Obura 2002).

Prior to the 1990s, a total of 59 genera and 183 species of scleractinian corals were recorded from Kenya and Tanzania from studies undertaken by Hamilton (1975 cited in Obura 2001a), Hamilton and Brakel (1984) and Lemmens and Smeets (1987 cited in Obura 2001a). The most abundant genera recorded were *Porites, Pocillopora, Acropora, Platygyra, Galaxea, Echinopora, Montipora* and *Astreopora* (Obura et al. 2000a).

Kenya's reefs changed dramatically following the convergence of the El Niño Southern Oscillation and the Indian Ocean Dipole in 1997-98 (Saji et al. 1999), resulting in widespread bleaching of 50-90% of the corals along the entire coast (Wilkinson 1998; Obura 1999). Mortality was particularly high along Kenya's southern reef with losses of live coral in the order of 66-80%, particularly of branching corals such as *Acropora, Pocillopora, Stylophora* and *Seriatopora* (Obura et al. 2000b). Mean coral cover on southern fore-reef slopes and lagoon patch reefs was about 30% prior to the 1998 bleaching, and decreased to 5-11% post-bleaching (Obura et al. 2000b). Following bleaching, fleshy, turf, calcareous and coralline algae on dead coral surfaces increased on unfished and fished reefs, in the order of 88-115% and 220% respectively, and there was a shift in coral community structure with *Porites, Galaxea, Pavona* and a number of faviids becoming more dominant due to the loss of *Acropora* and other branching corals (McClanahan et al. 2001). Corals in northern Kenya were less impacted due to the influence of the cold-water Somali upwelling system further north, though coral mortality rates on shallow reefs were similar to those in the south, and only those corals below 10 m bleached less (<50%) and suffered lower mortality (Obura et al. 2000b). Many of the reefs in Kenya showed signs of some recovery in the first three years post-bleaching, though this varied between different locations (Obura 2001b).

2.5 Study sites

The study was completed at four patch reef sites within the southern Kenya reef complex, from April 2003 – May 2005 (Fig. 2.5). Coral Gardens (3º59.429'S, 39º45.016'E) is within the Mombasa Marine National Park (approximate area 10 km^2), which has been closed to all forms of extraction since 1986 and has been set aside for tourism and research (Fig. 2.5-2.7). Twenty glass boat operators frequent the area, though 5-6 operate at any given time (pers. obs.). Sampling for coral reproduction was focused on the reef adjacent to and south of a small and narrow channel, where regular mixing of oceanic and lagoonal waters was likely to reduce heat stress on corals (Fig. 2.6). Coral Gardens is shallow (0.5-1.5 m depth at mean low water) with low coral diversity compared to the other three sites (D. Obura,

unpubl. data). The reef topography is dominated by massive *Porites, Galaxea* and different faviid species and there are extensive areas of substrata covered by filamentous turf algae (Fig. 2.7). The nearest waterway is Mtwapa Creek, situated about 3 km north of Coral Gardens.

Nyali (4º3.738'S, 39º42.736'E), Kijembe (4º3.62'S, 39º42.735'E) and Mamba (4º3.74'S, 39º42.78'E) Reefs are 10 km south of Coral Gardens, in the Mombasa Marine National Reserve (approximate area 200 km^2, Fig. 2.5-2.6, 2.8) which was established as a buffer area around the Park. The extraction of reef resources in the Reserve is limited to traditional fishers who access the reefs by artisanal fishing canoes or by swimming or wading out on the low tide. The Reserve is heavily fished, and fish wet-weight is about a tenth of that in the Marine Park, and fish species richness is about half (McClanahan and Kaunda-Arara 1996). Reserve sites are at a similar depth to Coral Gardens, and are influenced by oceanic waters flowing through small channels in the reef crest and a medium-sized channel that runs parallel to the sites, closer inshore (Fig. 2.6). Nyali and Mamba Reefs are separated by a small channel of seagrass, sand and rubble. Kijembe Reef is 250 m north and is separated from the other two sites by an area of seagrass, soft coral, sand and rubble. The scarcity of reefs with sufficient numbers of species of *Acropora* and meandroid faviids limited the choice and distance between the three sites in the Reserve. The reef topography is dominated by massive *Porites, Galaxea, Pocillopora, Acropora* and different species of faviids intermingled with patches of seagrass and fleshy algae (Fig. 2.8).The nearest waterway is Mombasa Creek, situated about 1.8 km south of Nyali Reef. Unlike Coral Gardens, none of the study sites in the Reserve are frequented by tourists. Spearfishing and traditional trap fishing (*malema*) were the predominant activities observed at the Reserve sites during the study period.

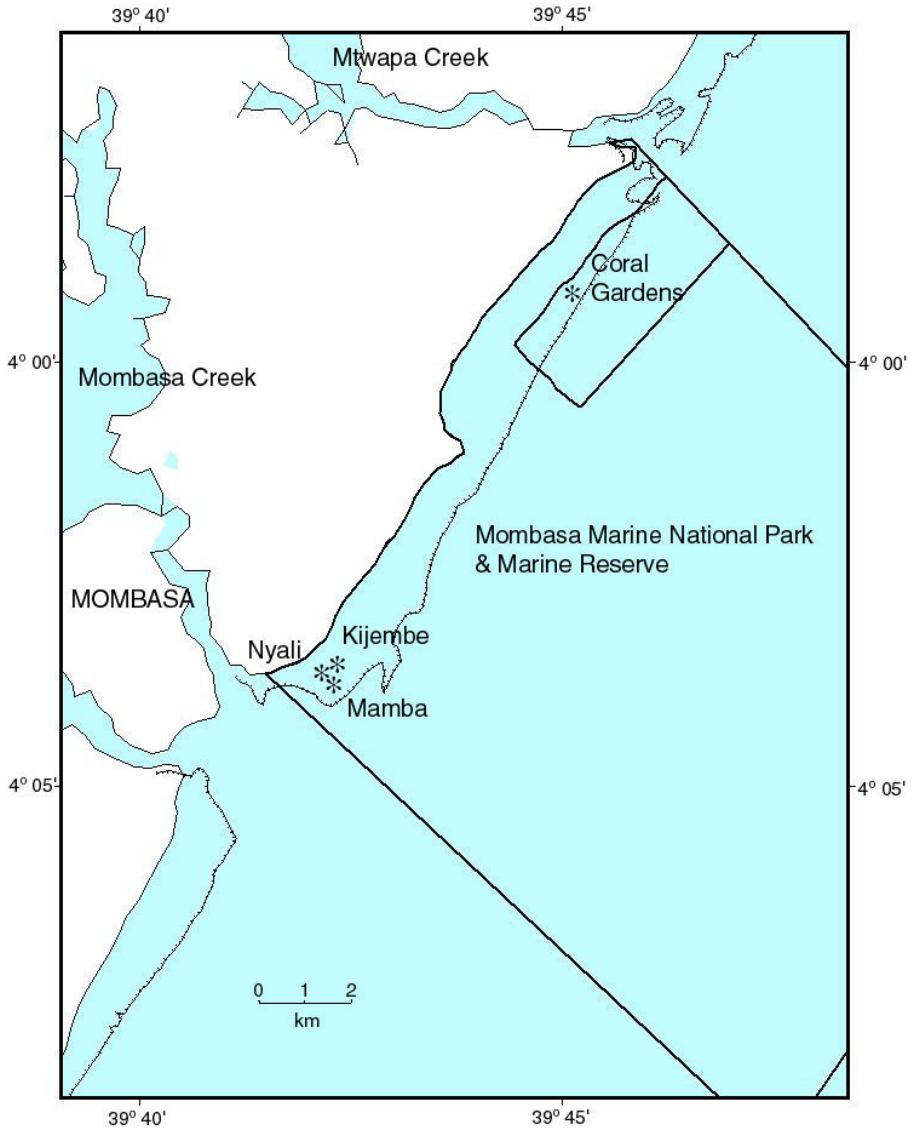

Figure 2.5: Map showing the four study sites in Mombasa Marine National Park and National Reserve, Kenya. The outline of the reef and the boundary of the Marine Park (small box) and the Marine Reserve (large box) are shown. Source: H. Ong'anda, Kenya Marine Fisheries Research Institute data centre. Used with permission.

Figure 2.6: Aerial photographs showing the study sites and fringing reef structure in the Mombasa Marine National Park (above) and Reserve (bottom). Photos taken at low tide. Source: CORDIO East Africa. Used with permission.

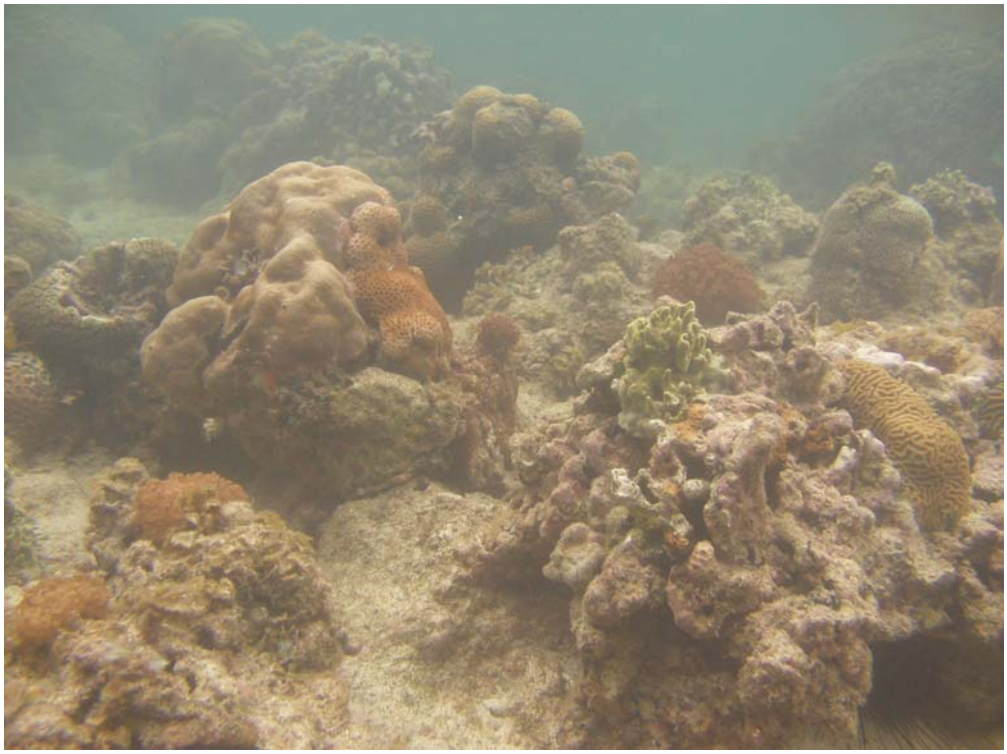

Figure 2.7: Photographs of Coral Gardens in Mombasa Marine National Park at low tide. The reef crest can be seen in the distance, in the top photo.

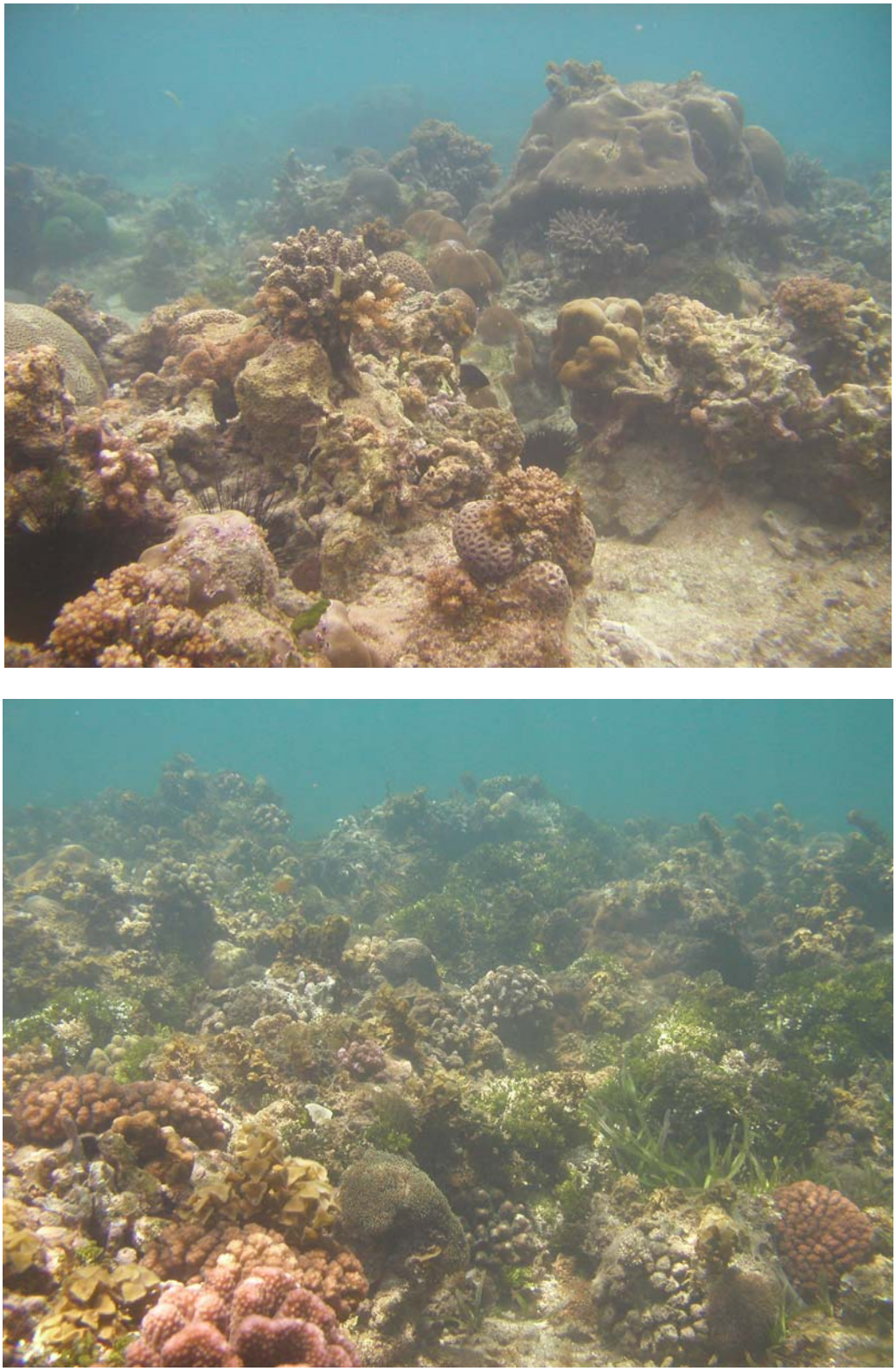

Figure 2.8: Photographs of Nyali (top) and Mamba (bottom) Reefs in Mombasa Marine National Reserve at low tide.

CHAPTER 3: TAXONOMY OF *ACROPORA* SPECIES IN THE MOMBASA MARINE NATIONAL PARK AND RESERVE

3.1 Introduction

The genus *Acropora* Oken 1815 (Scleractinia: Astrocoeniina: Acroporidae) contains the largest number of extant species of all scleractinian corals and is found in all tropical oceans including the Western Indian Ocean (WIO) (Sheppard 1987; Wallace 1999; Veron 2000). *Acropora* species are taxonomically complex because they are highly polymorphic and morphological species may or may not align with reproductive or genetic boundaries (Wallace and Willis 1994; Willis et al. 1997). The taxonomy of this genus has been reviewed by Wallace (1978), Veron and Wallace (1984) and more recently by Wallace (1999), who described 113 species of *Acropora* and summarised their biogeographic patterns and proposed phylogenetic relationships among *Acropora* species groups.

Species records for *Acropora* were compiled for Kenya and Tanzania by Hamilton (1975), Hamilton and Brakel (1984), Lemmens and Smeets (1987) and Lemmens (1993) during field surveys and from the specimen collections they made. A complete reference collection from the study by Hamilton (1975) is housed at the University of Dar es Salaam in Tanzania and collections by Lemmens and Smeets (1987) and Lemmens (1993) were deposited at the Nationaal Natuurhistorisch Museum in the Netherlands and at the University of Nairobi in Kenya. However, due to the confused status of the genus prior to the mid-1980s, the list provided by Hamilton and Brakel (1984) contains many synonyms, and the actual number of *Acropora* species recorded should be 22 not 31 (Wallace 1999), which is quite low given the geographic scope of the study. Sixteen species of *Acropora* were recorded by Lemmens (1993) in the Watamu Marine National Reserve during an expedition from November 1982 - April 1983.

The coral landscape in Kenya has changed since the 1997-98 El Niño Southern Oscillation bleaching event, which had the greatest impact on species of *Acropora,* with mortality levels approaching or at 100% (Obura et al. 2000b). There is no

published information on the number of species of corals currently present in Kenya. The purpose of this chapter is to record the species of *Acropora* found in lagoonal reefs in the Mombasa Marine National Marine Park and Reserve and to clarify the more taxonomically complex species, by providing descriptions of their skeletal morphology and field characteristics.

3.2 Methods

Four hundred colonies of *Acropora* were tagged and 1-2 branches of each colony were collected from Coral Gardens, Nyali, Kijembe and Mamba Reefs between 2003 - 2005 for taxonomic purposes. Photographs were taken *in situ* of the whole colony, and of individual branches and associated corallites, using an underwater digital camera (Olympus 4040). Skeletal samples were soaked in dilute household bleach for 1-2 days until all the tissue and pigmentation had gone, then rinsed in tap water and dried in the sun.

Outer and inner axial corallite diameter and branch diameter were measured using digital vernier calipers, and branch length was measured with a flexible tape for selected species. The number of specimens measured per species varied from 5-25 depending on the number of colonies tagged. No measurements were taken for *A. lutkeni* because only three colonies were tagged and skeletons were available for only two colonies. Corals were initially identified in Kenya using descriptions in Wallace (1999), and representative specimens of each species were taken to Australia for comparison with the coral collection in the Museum of Tropical Queensland (MTQ) in Australia. Where possible, Kenyan specimens were compared to those in the MTQ collected from the WIO region. A complete reference collection was deposited at CORDIO East Africa in 2005, and representative specimens of each species were deposited in the MTQ in 2004 and 2006 (Table 3.1).

3.3 Results and Discussion

Acropora species in the lagoon are fairly robust compared to those on the outer fringing reef (pers. obs.), with corymbose forms dominating. Twenty-three *Acropora* species were identified in the Mombasa Marine National Park and Reserve (Table 3.1). Among these, seven were found in low abundance with less than five individuals observed during the study, and nine species represented range extensions (Table 3.1). A further five species, *A. florida, A. aculeus, A. austera, A. latistella* and *A. cerealis*, previously recorded from Kenya with specimens available in the MTQ, were not found at the study sites.

Of the seven species described in the *Acropora nasuta* group, five have been identified in the WIO and Indo-Pacific (*A. valida, A. secale, A. nasuta, A. lutkeni* and *A. cerealis*), and the remaining two have more restricted ranges in Papua New Guinea (*A. kimbeensis*) and the Arabian Gulf (*A. arabensis*) (Wallace 1999). *Acropora valida*, *A. secale* and *A. lutkeni* were (at times) remarkably similar in the field and taxonomic descriptions have been provided to clarify morphological boundaries between these species. *Acropora valida* and *A. secale* were generally more sturdy (i.e. thicker and longer branches), while *A. lutkeni* was less sturdy and radial corallites were more 'organised' into rows compared to specimens from other regions. *Acropora* sp.1 has been included in the *Acropora nasuta* group because it shares skeletal characteristics with three species, but taxonomic resolution is not possible at this point in time (C. Wallace, pers. comm., see section 3.3.1.4). The potential for *Acropora* sp.1 to be a more 'extreme' form of *A. secale* or *A. valida* or a more 'conservative' form of *A. lutkeni* cannot be overlooked, and there is also the possibility that hybridisation may be occurring between the different species. Breeding trial experiments have suggested that hybridisation occurs more readily between morphologically similar species with hybrids competent to settle, undergo metamorphosis and survive for up to 3.5 years (Willis et al. 1997). Detailed morphometric and genetic studies, and the further narrowing of spawning times presented in this thesis (see Chapter 6), may resolve the taxonomic status of this putative 'species' at a later date.

Acropora mossambica, A. sordiensis and *A. branchi* were described from specimens collected in South Africa and Mozambique by Riegl (1995) but were listed as

'unresolved' species in Wallace (1999). Veron (2000) synonymised *A. mossambica* with *A. retusa*, and synonymised *A. sordiensis* with *A. appressa*, based on field identifications. Kenyan specimens were compared with photographs of holotype and paratype specimens of *A. mossambica* (Fig. 3.1; Fig. 8 and 9 in Riegl 1995) and *A. sordiensis* (Fig. 3.2; Fig. 6 and 7 in Riegl 1995) housed at the South African Museum and the Oceanographic Research Institute in South Africa, and were found to be anatomically similar to the holotypes and paratypes, and mostly consistent with descriptions in Riegl (1995). The '*Acropora retusa* Biogeographic Collection' in the MTQ had four *A. mossambica* specimens collected from Mauritius, Seychelles and the Gulf of Aden and no specimens from other regions, suggesting that this species may be endemic to the WIO (Table 3.1). Kenyan specimens were remarkably similar to the two specimens from Mauritius, and there now appears to be sufficient morphological evidence to support the separation of *A. mossambica* and *A. retusa* into two species (C. Wallace, pers. comm.).

Three *A. sordiensis* specimens in the MTQ were collected from juveniles and therefore, were too small to provide taxonomic clarity. A photograph of the holotype specimen of *A. appressa* and the original description by Ehrenberg written in 1834 lacked the detail required to determine whether the synonymy of *A. sordiensis* with *A. appressa* proposed by Veron (2000) was valid. Therefore, Kenyan specimens are referred to as *A. sordiensis* in this thesis.

Acropora branchi is currently recognised as a species by Veron (2000) who recorded it in Southern Africa and Sri Lanka. No skeletons were available in the MTQ for comparison with Kenyan specimens. Specimen G58127 (A97) donated to the MTQ has initially been classified as *A. lutkeni* by C. Wallace until the validity of *A. branchi* as a species can be resolved at a later date. This species has been recorded in Kenya and Tanzania but has not been recorded in the Seychelles, Comoros or the Chagos Archipelago (D. Obura, unpubl. data). Kenyan specimens are referred to as *A. branchi* in this thesis.

Of the five species described in the *Acropora divaricata* group, three (*A. divaricata*, *A. solitaryensis* and *A. clathrata*) have been identified in Kenya, while the remaining two (*A. kosurini* and *A. hoeksemai*) have limited distributions in southeast Asia

(Wallace 1999). *Acropora divaricata* and *A. solitaryensis* are morphologically very similar and are distinguished by growth form, with branches in the latter anastomosing to form (in many instances) a solid plate (Wallace 1999). In Kenya, these two species could not be consistently separated in the field, or by examination of skeletal material, despite their abundance at the study sites. Following a review of specimens in the MTQ and discussions with C. Wallace, these two species have been grouped together and are referred to as *A. divaricata* in this thesis. *Acropora kosurini* is currently known from Thailand and Indonesia. Three colonies in Kenya had skeletal characters that more closely resembled *A. kosurini* than *A. divaricata,* and have been deposited and identified in the MTQ collection as *A. kosurini* (Table 3.1).

Field and skeletal taxonomic descriptions are provided below for the more abundant and complex species, using the taxonomic arrangement and terminology in Wallace (1999). Skeletal descriptions are restricted to corallite structures and arrangement, and unless stated otherwise, the other characters are consistent with Riegl (1995) and Wallace (1999).

Table 3.1: Species of *Acropora* in lagoonal reefs in the Mombasa Marine National Park and Reserve, Kenya. Group names are in accordance with Wallace (1999). MTQ corals: specimens examined in the Museum of Tropical Queensland (MTQ). Additions to MTQ: registration numbers for corals donated to the MTQ, with original serial numbers indicated in parentheses. C: Coral Gardens, K: Kijembe Reef, N: Nyali Reef, M: Mamba Reef. *: an extension of the range described by Wallace (1999). #: <5 colonies observed.

Species	Described by	Sites	MTQ corals	Additions to MTQ
Acropora nasuta group				
A. valida	Dana (1846)	C, K, M, N	G54920-23, G35575, G35577-78 Kenya; G52100, G52014, G52016, G53045 Maldives; G49211 Seychelles.	G59610 (A80), G59611 (A41), G59612 (AX27), G59613 (AX8), G59614 (AX12), G59615 (AX29)G59616 (A22) G59617 (A5), G59618 (AX39), G59619 (AX9), G59620 (A40), G59621 (A39)
*A. lutkeni**#	Crossland (1952)	K, N	G51425, G51428, G51458, G51460 Chagos Arch.	G58942 (AX5), G59629 (AX10), G59630 (AX24), G59631 (A12), G59632 (AX7), G59633 (A28), G59634 (AX1), G59635 (AX2)
A. nasuta	Dana (1846)	K, M, N	G35573-74, G35576, G54926-27, G58935 Kenya.	G58935 (A14), G58940 (A52).
A. secale	Studer (1878)	K, M, N	G35562, 35570-72, G54938, 59128-33 Kenya; G36938-40 Seychelles.	G59128 (AX13), G59133 (A57), G59132 (AX37), G59133 (A57), G59129 (AX11), G59130 (A13), G59131 (A15), G59607 (AX19), G59608 (AX16), G59609 (AX20)
Acropora sp.1	'unresolved'	C, K, M, N	(samples listed above)	
A. humilis group				
A. digitifera	Dana (1846)	K, M, N	G54932-34 Kenya; G57780 Red Sea.	G58939 (A25)
*A. gemmifera**	Brook (1892)	K, M, N	G52086 Maldives; G52590 Solomon Islands.	G58944 (A67)
*A. samoensis**	Brook (1891)	M, R	G51457 Chagos Arch.; G52095 Maldives; G51884 Seychelles.	G58933 (A69), G58934 (A34), G58941 (A32)
A. humilis	Dana (1846)	K, M, N	G51363 Chagos Arch.; G35561 Kenya; G52090 Maldives; G51825 Mauritius.	G58926 (A8), G58927 (A4), G58928 (A9), G58929 (A17), G58930 (A33), G58931 (A84), G58932 (A86)

Species (cont.)	Described by	Sites	MTQ corals	Additions to MTQ
A. divaricata group				
A. divaricata	Dana (1846)	C, K, M, N	G35567 Kenya; G41044 South Africa; G54940 Sudan.	G59605 (A59), G59606 (A76)
A. solitaryensis	Veron & Wallace (1984)	K, M, N	G55092 Comoros; G57415 Gulf of Aden; G54917 Kenya; G53031 Maldives.	G59595 (A46), G59596 (A88), G59597 (A64)
*A. kosurini**[#]	Wallace (1994)	N	G59154 Malaysia; G37296, G59319 Thailand.	G59592 (A2), G59593 (A102), G59594 (A94)
A. latistella group				
A. subulata	Dana (1846)	C, K, M, N	G54928, G54937, G35563 Kenya.	
*A. nana**[#]	Studer (1878)	K, M, N	G35996 Australia (Lord Howe Is.); G53590 PNG.	
A. hyacinthus group				
A. hyacinthus[#]	Dana (1846)	K	G54924-25 Kenya; G54904 Mauritius.	
A. cytherea	Dana (1846)	K, M, N	G51392, G51390 Chagos Arch.; G35568 Kenya.	G58938
A. lovelli group				
*A. glauca**[#]	Brook (1893)	N	Identified by C. Wallace	G58943 (A54)
A. horrida group				
A. microphthalma[#]	Verrill (1869)	N	G35556 Kenya; G33203 Mauritius.	G58937 (A77)
A. robusta group				
A. abrotanoides[#]	Lamarck (1816)	K	G35555, G35579-81 Kenya.	
A.selago group				
A. tenuis	Dana (1846)	C, K, M, N	G53032 Maldives; G51859 Seychelles.	G58936 (AT14)
Undecided				
*A. mossambica**	Riegl (1995)	K, M, N	[a]G56963 Gulf of Aden; G51846, G51880 Mauritius; G51888 Seychelles.	G59599 (A110), G59600 (A31), G59601 (A56), G9602 (A56), G59603 (A21), G59604 (A38)
*A. sordiensis**	Riegl (1995)	K, M, N	G54935-36 Kenya; G41037 South Africa.	G59622 (A37), G59623 (A7), G59624 (A29), G59625 (A72), G59616 (A18), G59627 (A35), G59628 (A20)
*A. branchi**	Riegl (1995)	N		[b]G58127 (A97)

[a] all specimens identified as *A. retusa* in the MTQ. [b] specimen identified as *A. lutkeni* in the MTQ.

3.3.1 The *Acropora nasuta* group

3.3.1.1 Acropora valida (Dana 1846)

Field (Fig. 3.3a): Colonies are mostly brown with cream or purple axial corallites, though green colonies have occasionally been observed. Branches do not always taper and are fairly heavily calcified giving them a 'thick' appearance compared to specimens from the Maldives, Seychelles and the Great Barrier Reef. Colonies with secondary branching can be difficult to distinguish from *Acropora* sp.1.

Skeleton (Fig. 3.3b): Colonies are corymbose or caespito-corymbose with a central or side attachment, with branches of 13-21 mm diameter and up to 110 mm in length. Axial corallites outer diameter ranges from 1.9-2.9 mm and inner diameter from 0.6-0.9 mm. Radial corallites are tubular appressed or tubo-nariform with rounded openings, touching each other on branches, and are of similar size or a mixture of sizes. Mixed-sized radials are unevenly distributed, becoming strongly appressed against each other giving branches a spiny appearance towards the branch tip.

3.3.1.2 Acropora secale (Studer 1878)

Field (Fig. 3.3c): Colonies are brown with cream or purple axial corallites. Radial corallites in Kenyan specimens are generally less 'organised' into alternating rows and more densely packed compared to those from the Seychelles or the Chagos Archipelago, making them sometimes difficult to distinguish from *A. lutkeni* or *Acropora* sp.1 in the field.

Skeleton (Fig. 3.3d): Colonies are corymbose or caespito-corymbose with a central attachment, with branches of 9-16 mm diameter and up to 100 mm in length. Axial corallites outer diameter ranges from 2.6-3.2 mm and inner diameter from 0.8-1.3 mm. Radial corallites are touching or just touching, and are of two sizes consisting of long tubular corallites with round to nariform openings, alternating with shorter nariform corallites (sometimes sub-immersed), giving branches a 'spiny' appearance. Some radial corallites become quite long and can project straight out from the branch, or are angled towards the branch tip.

3.3.1.3 Acropora lutkeni (Crossland 1952)

Field (Fig. 3.3e): Colonies are brown with cream axial corallites, with branches of varying thickness giving the species a 'sturdy' appearance.

Skeleton (Fig. 3.3f): Colonies are corymbose with a central attachment and with branches up to 112 mm in length. This species can be confused with *A. secale*, but is distinguished by more heavily calcified radial corallites of mixed sizes with a more irregular arrangement (i.e. not as neatly arranged into rows). Radial corallites are not touching or just touching, tubular with rounded openings, and can have the appearance of being laterally squeezed. Kenyan specimens are 'less sturdy' in appearance than those from the Chagos Archipelago and the Great Barrier Reef. Branches are all of similar length, though this may reflect the small colony sizes at the study sites.

3.3.1.4 Acropora sp.1

Field (Fig. 3.4a-b): Colonies are mostly brown with brown or cream axial corallites. Towards the base of branches radial corallites become white giving them a scale-like appearance. Branches are rarely tapering, with branch thickness mostly made up by the radial corallites. However, these skeletal characters also occur in a small number of *A. valida*, *A. secale* and in *A. lutkeni*, making field identification of *Acropora* sp.1 difficult.

Skeleton (Fig. 3.4c-h): Colonies are corymbose or caespito-corymbose with a central or side attachment, with branches of 12-22 mm diameter and up to 140 mm in length. Axial corallites outer diameter ranges from 2.3-3.0 mm and inner diameter from 0.6-1.0 mm. Radial corallites are touching and are a mixture of sizes with fairly thick walls. The branch tip (10-20 mm) has tubular radial corallites with round to nariform openings, sometimes alternating with smaller sub-immersed corallites so that it bears a strong resemblance to *A. secale*. However, below about 20 mm, radial corallites can become strongly appressed so that the remaining portion of the branch more closely resembles *A. valida*. The presence of secondary sub-branches and long tubular radial

corallites of different lengths gives the branches a sturdy robust appearance that resembles *A. lutkeni*.

3.3.2 *Acropora mossambica*, *A. sordiensis* and *A. branchi*

3.3.2.1 Acropora mossambica (Riegl 1995)

Field (Fig. 3.5a-b): Colonies are brown with brown or cream axial corallites. Colonies are consistent in colour, shape and form, with little intraspecific variation making them easy to distinguish from other species. Kenyan specimens have longer branches with some secondary branching and are much less fused towards the base of the colony compared to the holotype specimen from Mozambique.

Skeleton (Fig. 3.5c-f): Colonies are corymbose with a central attachment, with terete branches of 11-17 mm in diameter and up to 90 mm in length. Axial corallites are large, conspicuous, only slightly exert, with an outer diameter ranging from 3.1-3.9 mm and inner diameter from 1.1-1.5 mm. Radial corallites are tubo-nariform with rounded flaring lips with some corallites becoming more cochleariform towards the branch tip. Radial corallites are of similar size, not touching or just touching, with a regular arrangement.

Remarks: *Acropora mossambica* can look similar to *A. retusa* which is also found in the WIO, but is distinguished by the distinct large flattened axial corallite and more rounded radial corallites, giving the former a more rosette appearance, similar to *A. tenuis*. The outer diameter of the axial corallites are 0.5-1.3 mm larger than those of *A. retusa*. In contrast, radial corallites in *A. retusa* are dimidiate or tubular dimidiate, giving the branches a more ‘spiny’ appearance.

3.3.2.2 Acropora sordiensis (Riegl 1995)

Field (Fig. 3.6a-b): Colonies are brown or beige with cream or purple axial corallites. Towards the branch tip radial corallites can become smaller and less densely packed, giving them a 'bead-like' appearance.

Skeleton (Fig. 3.6c-d): Colonies are corymbose with a central attachment or side attachment, with branches up to 90 mm in length. Axial corallites are conspicuous, conical and exert, with an outer diameter ranging from 2.3-3.5 mm and inner diameter from 0.7-1.2 mm. Radial corallites are tubular with round to nariform or dimidiate openings, with the outer wall (in some corallites) becoming pointed or hook-like. Radial corallites are mostly of similar size with a semi-regular arrangement, mostly touching.

3.3.2.3 Acropora branchi (Riegl 1995)

Field (Fig. 3.6e): Colonies are brown or purple with the axial corallites around the growing edge appearing lighter in colour.

Skeleton (Fig. 3.6f): Colonies form a solid plate up to 10 mm thick, with small branchlets visible along the growing edge. Axial corallites are conical and exert, often fusing with each other along the growing edge with small openings. Radial corallites are tubular appressed becoming sub-immersed to immersed on the basal plate, and are of mostly similar size that are not touching.

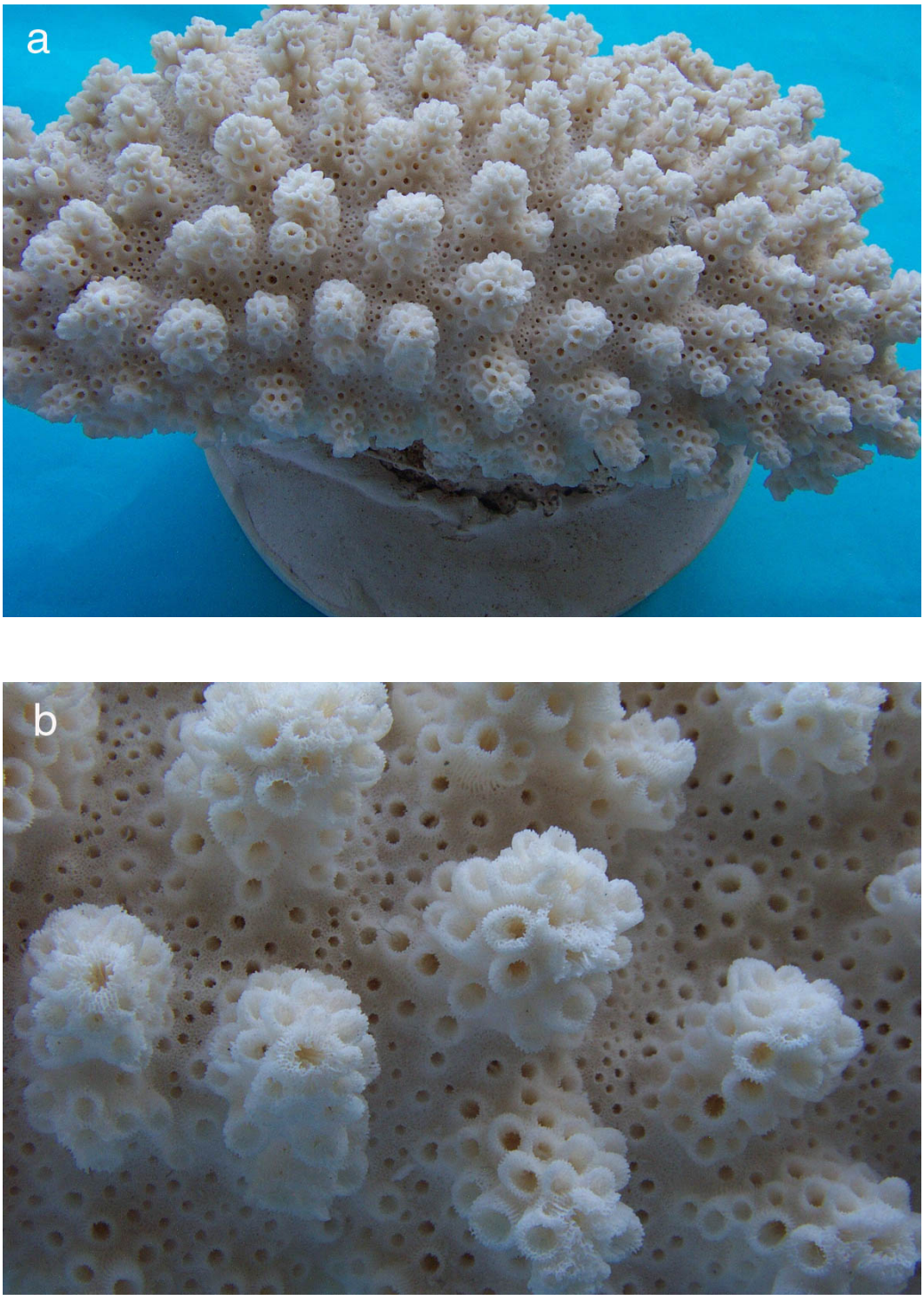

Figure 3.1: Paratype specimen of *Acropora mossambica* (Accession number ORI/A1C1-3) collected from Umdloti, Natal, South Africa. Used with permission from the Oceanographic Research Institute, Durban.

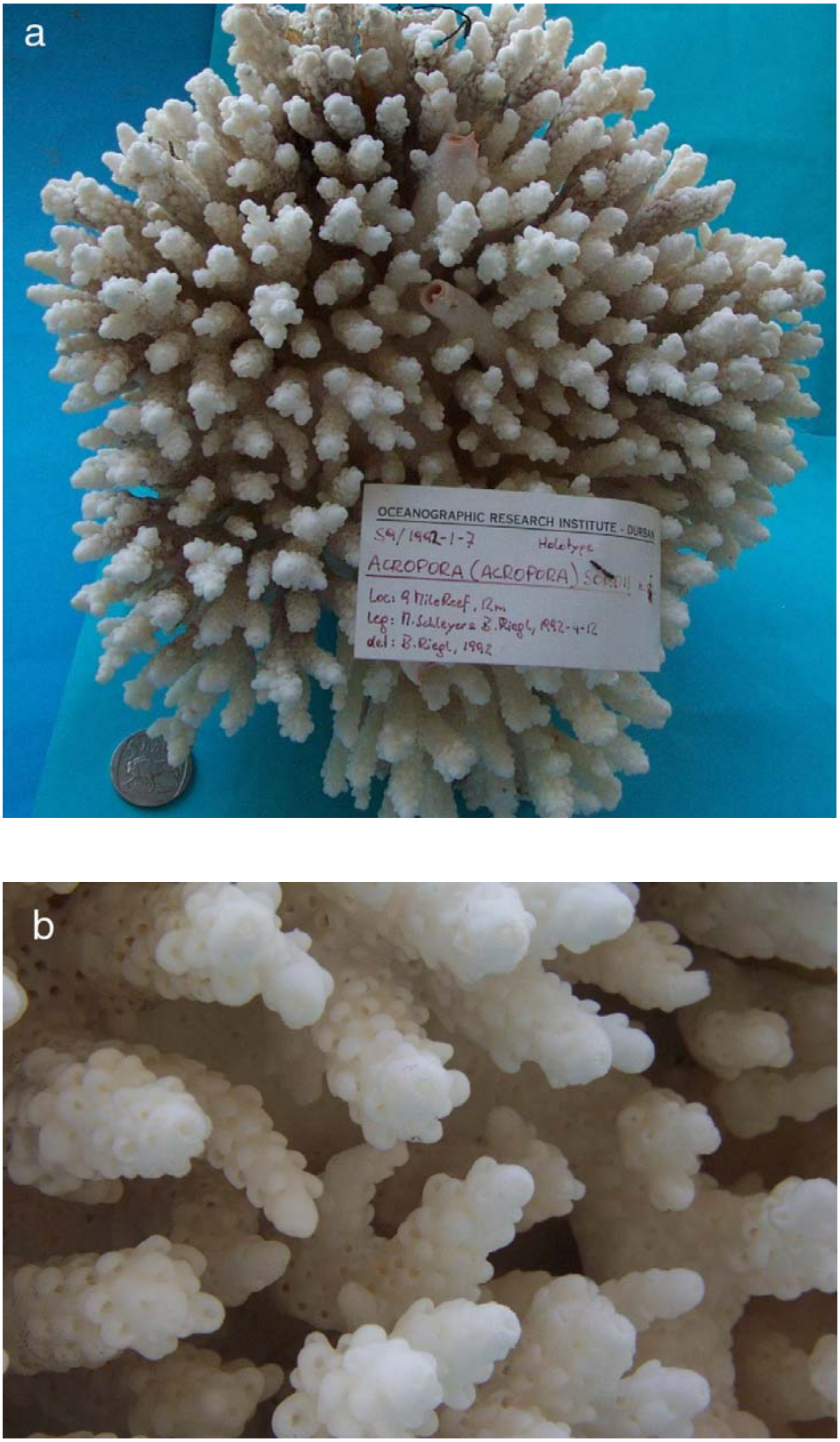

Figure 3.2: Paratype specimen of *Acropora sordiensis* (Accession number ORI/S9/1992-1-7) collected from Nine Mile Reef, Natal, South Africa. Used with permission from the Oceanographic Research Institute, Durban.

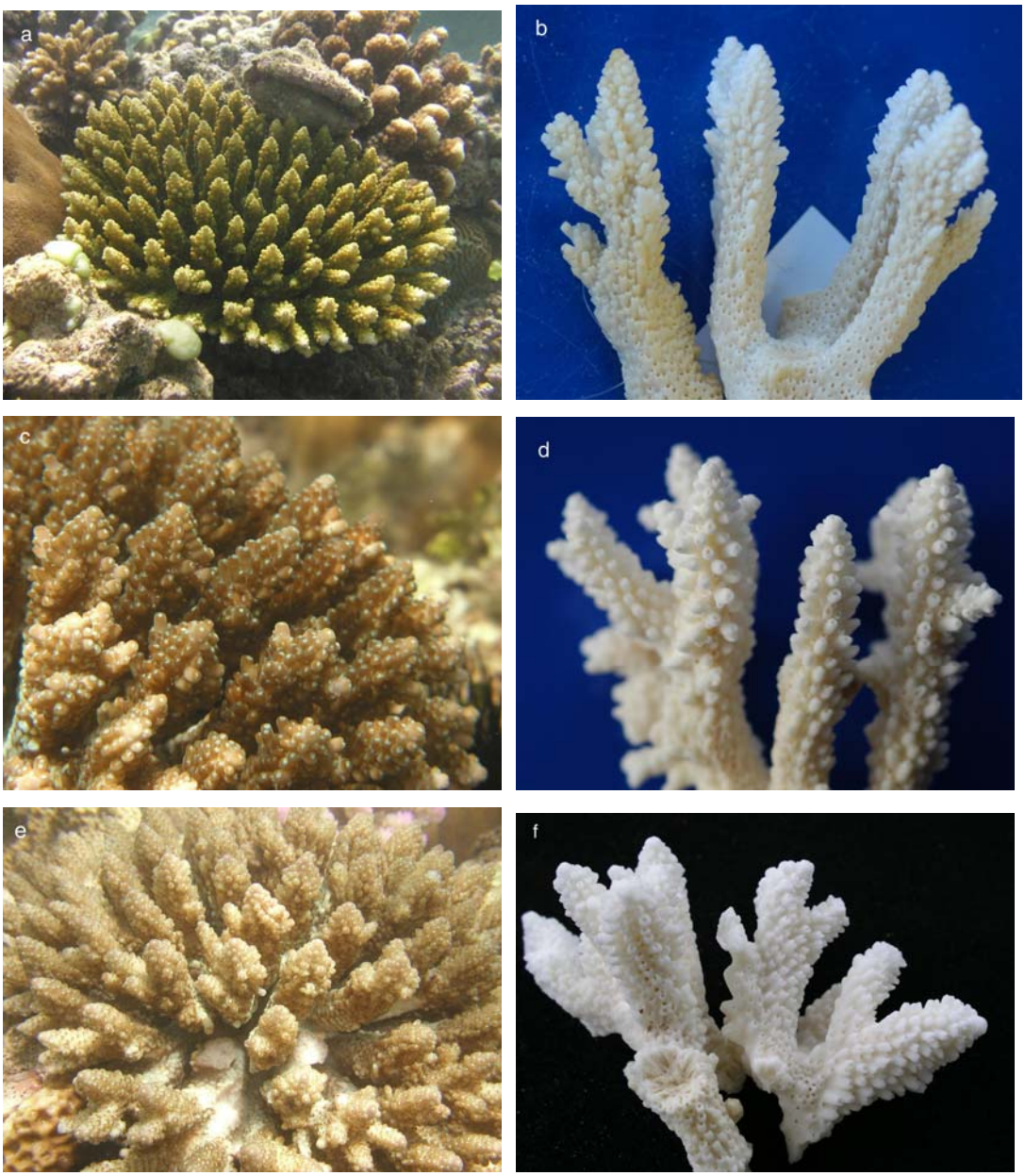

Figure 3.3: Live colonies and branches showing the skeletal structure of *Acropora valida* (a-b), *A. secale* (c-d) and *A. lutkeni* (e-f).

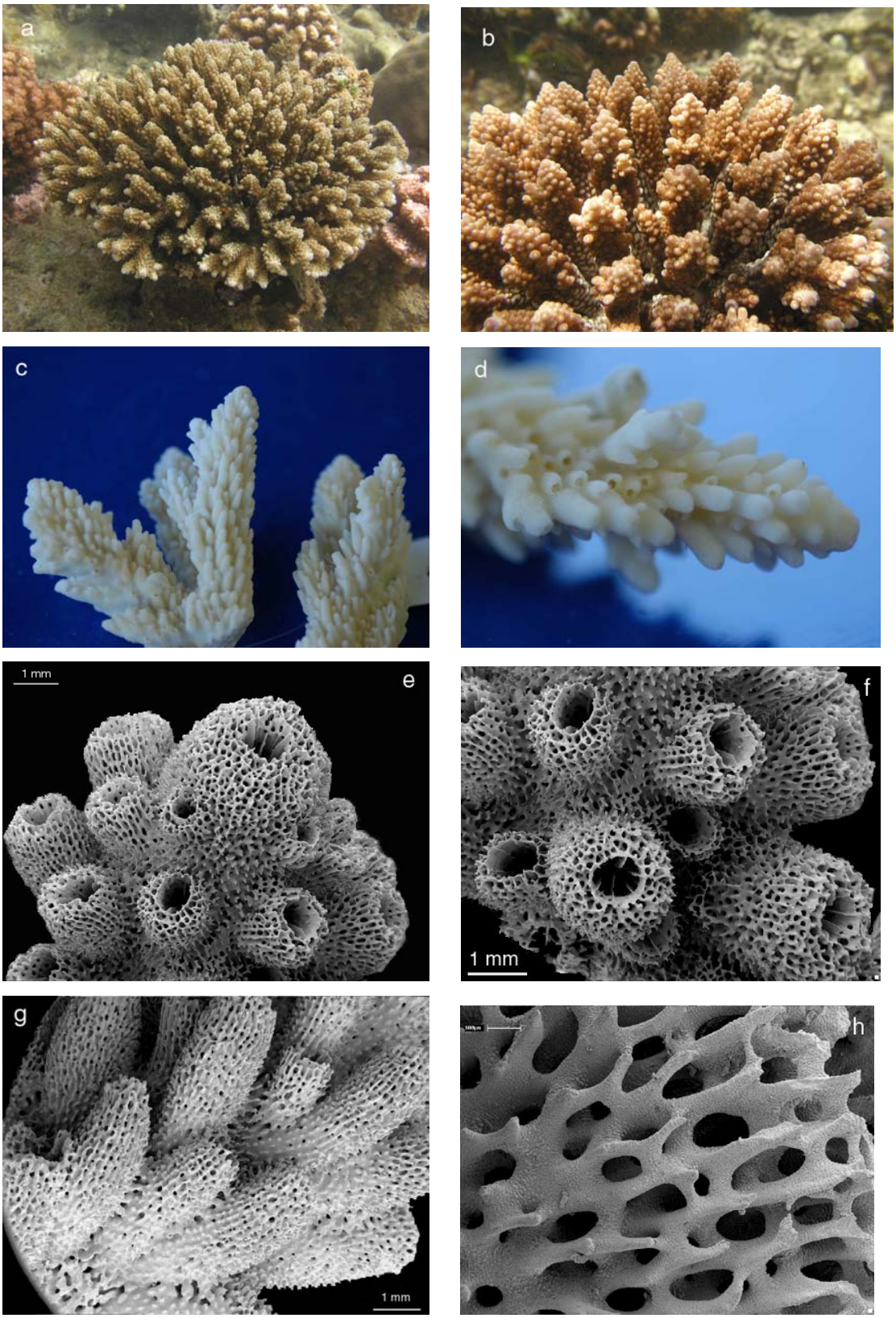

Figure 3.4: *Acropora* sp.1. Live colony (a-b), portion of colony (c-d); electron micrograph showing axial and radial corallites (e-g) and coenosteum on radial corallites (h).

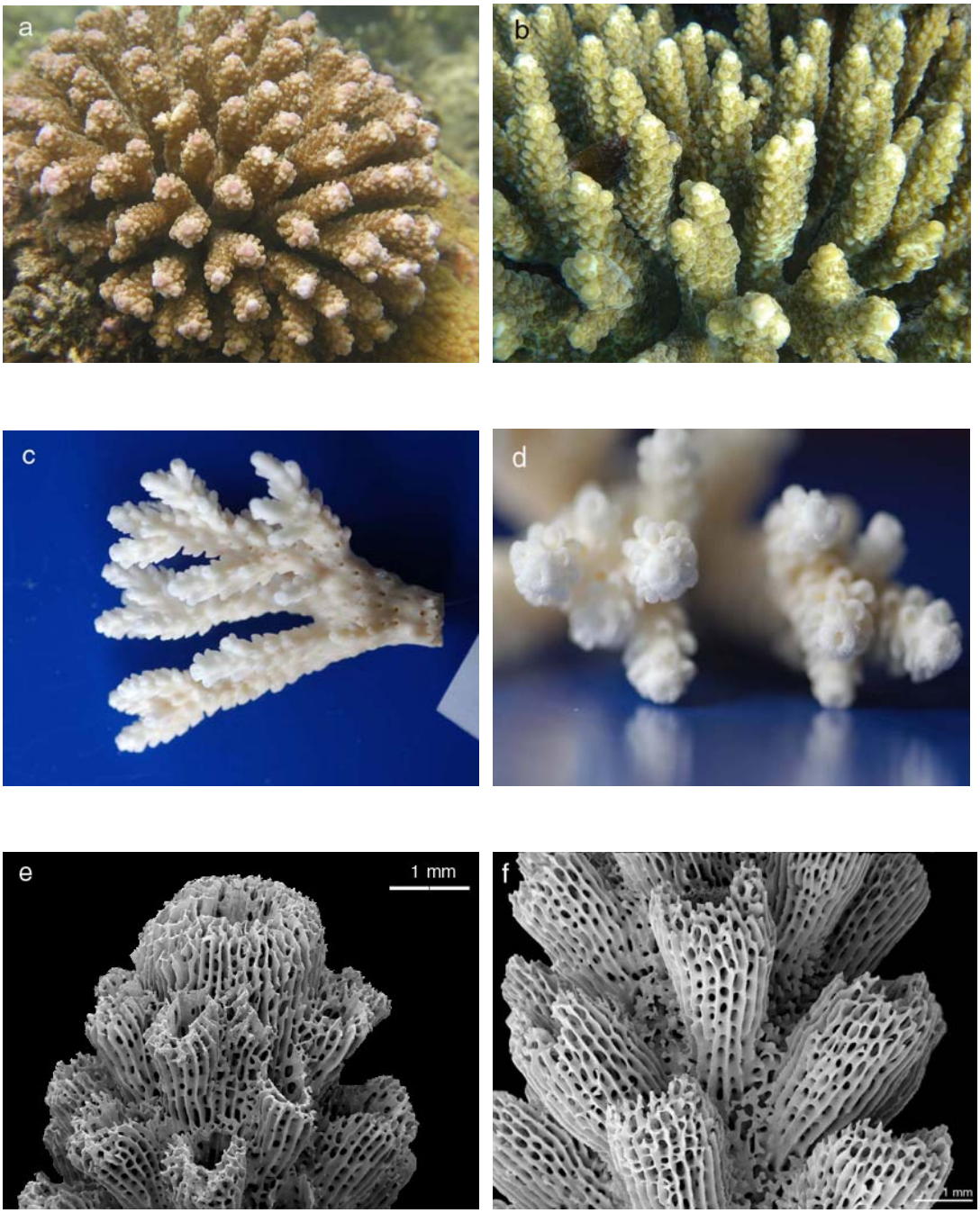

Figure 3.5: *Acropora mossambica*. Live colony (a-b), portion of colony (c-d), and scanning electron microscope images of axial and radial corallites at branch tip (e-f).

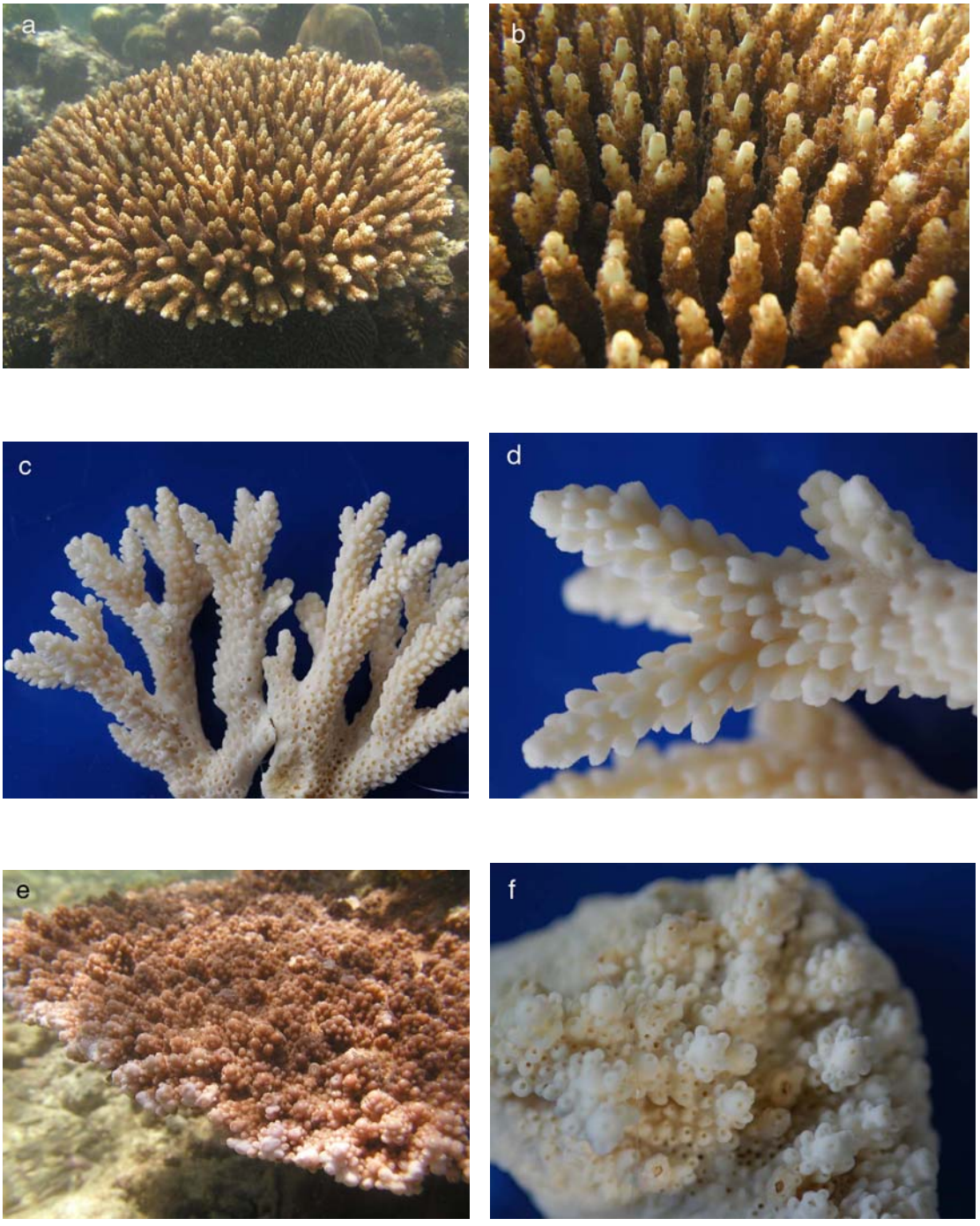

Figure 3.6: *Acropora sordiensis*: live colony (a-b), portion of colony (c-d). *Acropora branchi*: live colony (e) and axial and radial corallites (f).

CHAPTER 4: UNDERSTANDING PHENOTYPIC VARIATION IN *PLATYGYRA DAEDALEA* THROUGH MORPHOMETRIC AND GENETIC STUDIES.

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Declaration of authorship:

Components of this chapter relating to coral morphometrics were done in their entirety by S. Mangubhai, and components relating to coral genetics were done by P. Souter, in partial fulfilment of their respective PhDs. S. Mangubhai led the writing of the paper, and K. Miller (University of Tasmania) and D. Obura (CORDIO East Africa) reviewed the manuscript prior to submission to Marine Ecology Progress Series. The relative contributions of the three authors to the manuscript are indicated below.

Conception of the study:	SM (50%), PS (50%)
Design of the study:	SM (50%), PS (50%)
Collection of data:	SM (50%), PS (50%)
Analysis of data:	SM (50%), PS (35%), MG (15%)
Interpretation of data:	SM (50%), PS (40%), MG (10%)
Conclusions:	SM (50%), PS (40%), MG (10%)
Writing up of paper:	SM (70%), PS (30%)

4.1 Abstract

High intraspecific variability and lack of adequate field descriptions or distinguishing skeletal features has made identification of the scleractinian coral *Platygyra daedalea* challenging. This species displays a number of distinct morphological types that exist in sympatry on lagoonal reefs in Kenya and which often cannot be separated by field observations. To better understand how morpholgical and genetic variations were related, morphometric and molecular techniques were used to examine phenotypic variation in *P. daedalea*. A canonical discriminant analysis of measurements of ten skeletal characters confirmed the existence of two morphotypes. No single diagnostic trait to distinguish between the two morphotypes, though a combination of four characters separated them. A mathematical equation is presented to separate colonies into the two morphotypes, where field identification is not possible. Genetic differentiation was studied using five microsatellite loci and sequence analysis of the internal transcriber spacer (ITS1 and ITS2) and 5.8S region of the nuclear ribosomal RNA gene. AMOVA of the microsatellite data and the ITS sequence data showed significant genetic differences between the two morphotypes. However, phylogenetic analysis of ITS sequences showed no evidence of sequence divergence between morphotypes, which suggests that they share a gene pool, or that genetic divergence is a recent event. The paper concludes that the occurrence of distinct morphotypes is a characteristic of *P. daedalea* and that there does appear to be a genetic basis for separating morphotypes. However, genetic differences in *P. daedalea* could only be detected when combined with morpholometric data.

4.2 Introduction

Traditionally, the species unit has formed the basis for understanding ecology, evolutionary biology and biogeography. However, over the last couple of decades the increasing inclusion of novel molecular techniques in phylogeny has led to several cases where current classifications have been brought into question. Well-established species with clear differences in morphology and ecology may be almost indistinguishable at a genetic level. For example, the specious birds of prey the Old World buzzards (genus *Buteo*) includes a plethora of species and subspecies based on variable characters such as plumage colour and body size, but almost no sequence variability was found in the pseudo-control region of the mitochondrial DNA (Kruckenhauser et al. 2003). In contrast, there are cases where conservative morphological taxonomy has underestimated species diversity, such as in the deep-sea mussel *Acharax* sp., which was thought to be a single species until molecular studies allowed it to be separated into two distinct genetic clusters (Neulinger et al. 2006). In scleractinian corals the high degree of intraspecific phenotypic variability makes the taxonomic resolution of species subjective in the field (Veron 2000). Corals show morphological plasticity in response to their habitat and environment variables (Foster 1979; Lang 1984). Field identification is further confounded by the potential for some species of coral to cross-fertilize (Willis et al. 1997) and form viable hybrids with distinct morphologies (Vollmer and Palumbi 2002) or to form distinct morphological types ('morphotypes') within a species (Miller 1994).

Scleractinian coral taxonomy has been based on macroscopic and microscopic skeletal morphology (Vaughan and Wells 1943; Veron et al. 1977; Wallace 1999) on the premise that morphological discontinuities equate to species divisions. While morphometric approaches have been successful in distinguishing many genera and species (e.g. Wallace 1974; Veron and Wallace 1984), difficulties have arisen in their applicability to corals belonging to the families Faviidae and Poritidae, where many of the skeletal characteristics overlap between different species from similar or different habitats (Wijsman-Best 1974; Brakel 1977; Veron et al. 1977; Veron 2000). Genetic studies in some cases have supported original classifications based on morphology (Ayre et al. 1991; Garthwaite et al. 1994; Maté 2003) while in others, they have led to the separation of morphological groups into distinct species (Stobart and Benzie 1994;

Stobart 2000). Hence, the integration of morphometric and molecular studies has not consistently demonstrated whether morphological species of corals should be separated or amalgamated.

High intraspecific variation has been found in *Platygyra daedalea* on the Great Barrier Reef (GBR) where seven morphotypes were described by Miller (1994), two of which differed significantly in their skeletal characters to argue for separation into distinct morphological species. Allozyme electrophoretic surveys of *P. daedalea, P. sinensis* and *P. pini* at nine loci showed no relationship between genotype and morphological groupings at the species or intraspecies level, suggesting morphological species of *Platygyra* share a common gene pool (Miller 1992; Miller and Benzie 1997). In contrast, a study in Hong Kong on *P. pini* and four morphotypes of *P. sinensis* found genetic differences between the two species using ITS1, 5.8S and partial ITS2 rRNA sequence analysis, but not between morphotypes, with no diagnostic characters and clear groupings found on morphological traits (Lam and Morton 2003). These conflicting results suggest that the use of more variable or rapidly evolving molecular markers may be more appropriate for distinguishing between similar species, and even more so when comparing two morphotypes of the same species. It may also simply reflect the difficulties associated with field identification of these species.

Of the eight species of *Platygyra* that have been recorded in Kenya, *P. daedalea* is the dominant species found in lagoonal and fringing reefs with a wide distribution along the coast (D. Obura, unpubl. data). It is an important species in Kenya, particularly since it has shown some resistance to mass bleaching events, such as the one in the Western Indian Ocean during the 1997-98 El Niño Southern Oscillation (Wilkinson 2000; Obura 2001b). Colonies within the lagoon are massive, often hemispherical in form and show a variety of field characters. At the colony level, there is consistency in growth form but at the corallite-level colonies vary considerably in outward appearance, for example in septal shape, wall height, wall slope and the length and width of valleys (pers. obs.).

Detailed skeletal or molecular studies on corals for routine ecological studies are time-consuming, costly and not practical. Most researchers rely heavily on field

guides so it is important to define the variety of physical features a species such as *P. daedalea* displays in different localities to investigate whether specific morphotypes do exist, their potential ecological role, and if there is a genetic basis for separating them. Where intermediate forms exist, quantitative methods are needed that are less subjective and can distinguish colonies into specific morphotypes. Examining relationships between field and skeletal morphologies and genetic traits, can provide a better understanding of intraspecific variation and taxonomic boundaries in *P. daedalea* and hence reduce the possibility of taxonomic error (Miller 1992, 1994). The main aims of this chapter are to:

1) identify intraspecific morphological variation in *P. daedalea,* expressed in both the field observable traits and skeletal morphology, and to determine its relationship with genotypic traits;
2) develop a methodology for distinguishing different forms of *P. daedalea* into specific morphotypes; and
3) assess the level of molecular distinction between morphotypes using microsatellite markers and sequence variation at two ITS regions of the rRNA gene.

4.3 Methods

4.3.1 Field identification

Adult colonies of *P. daedalea* were identified in the field in accordance with Veron et al. (1977) and Veron (2000), at three patch reefs in the Mombasa Marine National Park and Reserve between 2003 - 2005 (see Chapter 2). There were 39 corals selected at Coral Gardens, 48 at Nyali Reef and 46 at Kijembe Reef, with the aim of including the full range of phenotypic traits or 'morphological varieties' observed in the lagoon. Only four characters, wall height, septa slope, septa shape and the prominence of the wall relative to the valley, were useful in distinguishing corals into groups recognisable in the field, and on this basis two distinct morphotypes were identified *a priori*:

(1) Prominent valley (PDV) – colonies have septa of mixed sizes and spacing, with short to medium walls that slope, and valleys that are more prominent (and appear wider) than the walls. While colour is not a useful distinguishing trait, in many instances this morphotype has brown walls and green valleys (Fig. 4.1a-b).

(2) Straight-walled (PDSW) – colonies have septa of equal size and even spacing, with tall and straight walls, such that the walls are more prominent (and partially hide) the valleys. Growth form is more consistent in this morphotype, is mostly hemispherical, and in most instances wall and valley colours are similar in colour (beige/cream), with a distinctive ridge forming at the top of the wall (Fig. 4.1c-d).

The remaining corals had field characters that were a mixture of those of PDV and PDSW morphotypes, and these were classified as 'intermediate forms' and subdivided into three smaller groups: E - uneven septa, wall either short or medium in height, walls and valleys equally prominent; F - even septa, walls straight and medium height, wall equal or more prominent than valley; and H - the remaining corals with a mix of many characters that did not fit into larger groupings. Of the 133 colonies sampled, 27 were identified in the field and by photographs as PDV, 18 as PDSW, and 88 as intermediate forms.

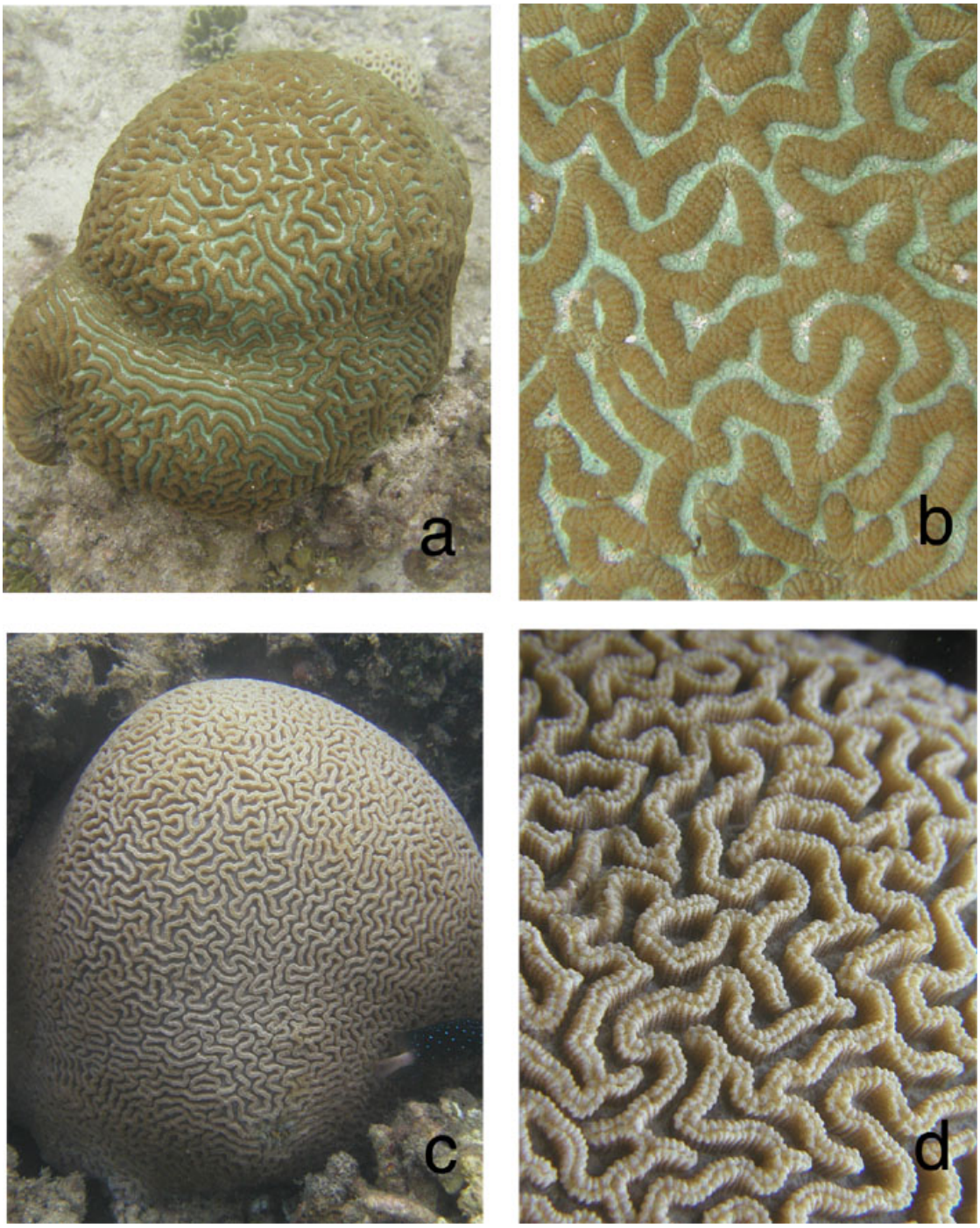


Figure 4.1: *Platygyra daedalea* morphotypes found in Kenyan lagoonal reefs. a-b: prominent valley (PDV), c-d straight-wall form (PDSW).

4.3.2 Skeletal characters

Samples for the morphometric analysis of the skeletons were approximately 10 x 10 cm, and were removed from colonies using a hammer and chisel. Samples were taken away from injured areas and the growing edge of the colonies, which can have atypical skeletal characters (Miller 1994), labelled, then soaked in diluted household bleach for 2-3 days until the tissues had been removed, washed in fresh water and dried. Nine skeletal characters defined by Miller (1994) were selected for this study: valley length (VL), valley width (VW), valley depth (VD), columella width (CW), septa thickness (ST), theca thickness (TT), exertness of septa (ES), polyp area (PA) calculated as the valley area divided by the number of polyp mouths in the valley, and number of septa per cm length of theca (SCM) (Fig. 4.2). A tenth character, wall width (WW), defined as the length of individual septa that formed the width of a wall, was also used (Fig. 4.3). Numerical values were averaged across a minimum of five (and where time permitted ten) measurements taken randomly on the skeletal piece under a stereomicroscope with a calibrated eyepiece micrometer. Valley length and polyp area were measured from photographs of the colony (with a ruler in the frame) and in the software program ImageJ 1.32j.

All analyses were performed on the mean values of the skeletal characters measured on each colony. Only colonies that were clearly identified in the field as PDV (n = 27) or PDSW (n = 18) were included in morphometric analyses to distinguish these morphotypes. T-tests were done to examine differences between PDV and PDSW for each of the ten characters, and all p-values <0.05 were considered significant. A canonical discriminant analysis (CDA) was performed on the ten skeletal characters to determine if the characters separated the two morphotypes and if so, which best discriminated between the two. All characters were normally distributed except for PA, which had slightly skewed data ($p < 0.01$, Kolmogorov-Smirnov test). Given that CDA is robust to deviations from normality, the data were treated as normally distributed for the analysis. The CDA generated a function to produce discriminant scores, which were then used to predict how closely related the remaining intermediate forms were to PDV or PDSW. All statistical analyses were done in SPSS 11.0 for Windows.

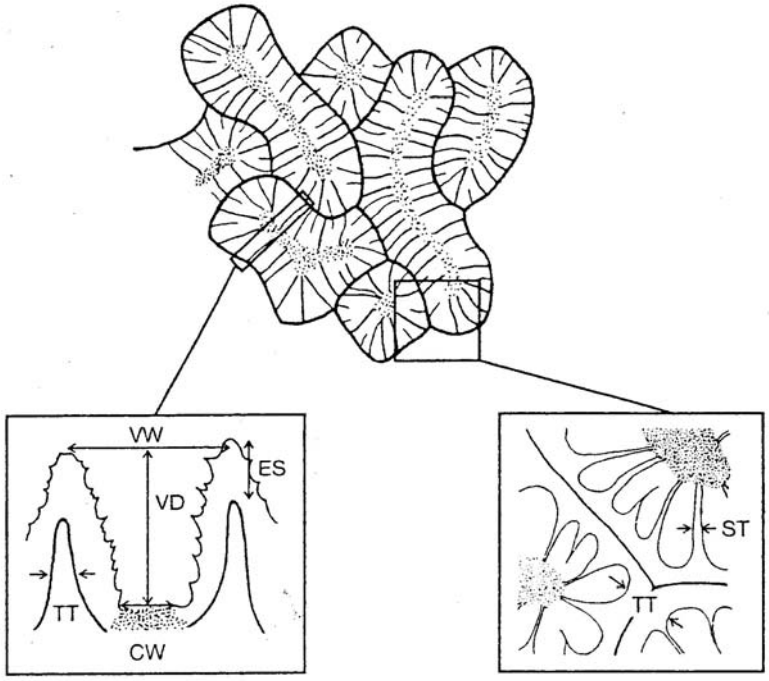


Figure 4.2: Diagrammatic representation of skeletal characters measured for morphometric analyses (Fig. 1 in Miller 1994). Names and descriptions of the characters are provided in section 4.3.2. Used with permission from author.

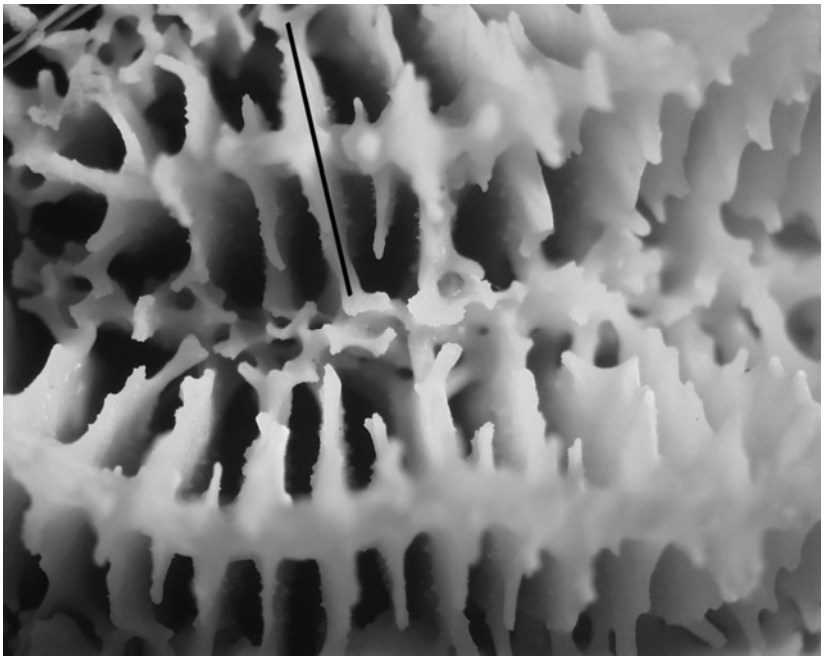


Figure 4.3: Skeleton of *Platygyra daedalea*. The black line indicates how wall width (WW) was measured.

4.3.3 Genetics

A total of 69 colonies of *P. daedalea* were selected for genetic analyses in May 2005. At the time of collection, morphometric analyses of the skeletons had not been completed and colonies were identified in the field as 25 PDV, 5 PDSW and 39 intermediate forms. Following morphometric analyses, genetic samples were labelled as follows: 59 PDV (Coral Gardens = 21, Nyali Reef = 20, Kijembe Reef = 18) and 10 PDSW (Coral Gardens = 4, Nyali Reef = 6). Small pieces, approximately 1 cm^2, were removed from the 69 colonies using a hammer and chisel and placed in separate labelled zip-lock bags. The samples were subsequently transferred into 10 ml centrifuge tubes filled with 70% ethanol and kept at ambient temperature until transported back to the laboratory.

DNA was extracted using the Qiagen® DNEasy kit according to the protocol for rodent tails. Fragments were placed directly into lysis buffer and kept in a water bath at 50 ºC overnight. A fragment of nuclear ribosomal DNA (rRNA) that has been used in a number of genetic studies of scleractinian corals (Takabayashi et al. 1997; Lam and Morton 2003), was amplified using the coral specific forward primer A18S (Hendriks et al. 1990, GenBank accession number X53498), and a universal reverse primer ITS4. PCR products were purified and sequenced by Macrogen Inc., Korea using the same primers as had been used for the PCR reaction.

Given that microsatellite loci are more polymorphic and evolve more rapidly than other DNA such as rDNA (Baker 2000), they may show a higher degree of divergence between morphotypes or potentially unique alleles, provided there is some reproductive barrier in place. Five fluorescent labelled microsatellite primers developed for *Platygyra* species (Miller and Howard 2004) were used for this study. PCR products as well as positive and negative controls were genotyped on an ABI 3700 capillary sequencer (Applied Biosystems) using a Gene Scan-500 Rox size standard provided by ABI, and visualised using GeneMapper 3.7. One microsatellite locus, Pd29, was found to be monomorphic in this data set and was subsequently excluded from analysis.

The ITS rRNA sequences were aligned manually using the programme BioEdit 7.0 and exported to the programme MEGA 3.1, which was used to reconstruct a phylogeny of the individuals based on the Maximum Parsimony optimality criterion with heuristic search. To align our genetic samples with a previous study of *Platygyra* species from Hong Kong, sequences of each morphotype of *P. sinensis* (GenBank accession numbers AF481885, AF481888, AF481895) and *P. pini* from the same subfamily (GenBank accession number AF481902) (Lam and Morton 2003) were included. *Montastrea franksi* which belongs to the same family but different subfamily (GenBank accession number AB065349) was used as an outgroup. Branch support levels were estimated using 1000 bootstraps. Sequence divergence was estimated using Kimuras 2-parameter model.

To examine genetic differences between the two morphotypes both within each site and after pooling the sites, and to assess the difference between the study sites with morphotypes pooled, an Analysis of Molecular Variance (AMOVA) was done using the programme Arlequin using both ITS and microsatellite data. The genetic distance method used by the AMOVA was pair-wise population sub-division (F_{ST}) which was estimated according to Cockerham and Weir (1984). The significance values were calculated using 20 000 permutations.

As PDV was found to be phenotypically more variable, we investigated whether this variability was reflected at the molecular level by assessing average molecular diversity over loci for each morphotype (using Arlequin), in accordance with Tajima (1983, 1993). Hardy-Weinberg equilibrium tests were performed to gauge population structures, and assignment tests were conducted on the log-likelihood of individual genotypes being classified correctly as PDV or PDSW, as predicted by the CDA. The significance values for the Hardy-Weinberg tests and F_{ST} values were calculated using permutation tests (Laval and Schneider 2005).

The programme Structure 2.0 was used to examine possible subpopulations by assigning individuals to clusters according to their four-loci microsatellite genotypes. The underlying hypothesis was that the sampled individuals should cluster into the two morphotypes or alternatively into the three sample sites. A series of analyses at a range of K-values (1-4) was done to ascertain the most probable number of clusters,

where K is the inferred numbers of sub-populations in the data set. A burn-in of 25 000 and a 250 000 run length was used.

4.4 Results

4.4.1 Morphometrics

A comparison of mean values and their ranges for PDV and PDSW for each of the ten skeletal characters showed that there was no single diagnostic character suitable for separating the morphotypes (Table 4.1). T-tests showed significant differences between six of the ten characters, PA, SCM, VD, VW, WW and VL, for the two morphotypes (Table 4.1).

A stepwise CDA identified the four skeletal variables SCM, WW, PA and ST as the best set of predictors of membership in the two groupings PDV and PDSW. One discriminant function was produced with an eigenvalue of 1.806, which accounted for 100% of the variance among the four variables. Discriminant scores for the function were highly correlated with the groupings ($r^2 = 0.64$). Standardised coefficients showed all four characters contributed to the discriminant function in roughly equal portions, with SCM being inversely related to the other three characters (Table 4.2).

A pooled within-groups covariance matrix classification procedure for the two morphotypes was done, where membership in groups was based on prior probabilities that took into account different group sizes. The classification procedure showed that 26 (96.3%) colonies of PDV and 15 colonies of PDSW (83.3%) were correctly identified (Table 4.3). Overall, 41 of the 45 of colonies assigned to one of the two morphotypes (91.1%) were correctly identified. Cross-validation (where each colony in the analysis is classified by the functions derived from all colonies other than that colony) was also performed to test if the original classification procedure provided 'overly optimistic' estimates of group membership. The test showed there was little difference between the original and cross-validation classification (i.e. only one coral changed its grouping), and therefore the original classification scheme was robust and the number of variables used in the model were correct (Table 4.3).

Table 4.1: The mean values of ten skeletal characters measured for all colonies of *Platygyra daedalea* and for the morphotypes PDV and PDSW. Ranges are indicated in parentheses. P-values were generated by F-statistics for comparisons of PDV and PDSW. All measurements are in mm except polyp area which is in cm^2.

Character	Code	*P. daedalea*	PDV	PDSW	p-value
No. septa cm^{-1} length	SCM	12.9	13.4	11.2	< 0.001
		(8.8 - 15.7)	(11.0 - 14.9)	(8.8 - 13.4)	
Wall width	WW	4.0	3.7	4.4	< 0.001
		(2.9 – 5.1)	(3.2 - 4.3)	(3.8 - 5.1)	
Polyp area	PA	11.4	9.7	15.4	< 0.001
		(6.4 - 28.7)	(6.6 - 12.3)	(10.4 - 28.7)	
Valley depth	VD	4.3	4.0	5.2	< 0.001
		(2.7 – 7.2)	(3.0 - 6.4)	(3.4 - 7.2)	
Valley width	VW	5.6	5.4	6.2	< 0.001
		(3.9 – 7.2)	(4.1 - 7.1)	(5.5 - 7.2)	
Valley length	VL	5.9	5.5	7.3	0.018
		(1.4 - 12.1)	(1.6 - 11.6)	(2.2 - 11.8)	
Corallum width	CW	1.1	1.1	1.1	0.055
		(0.8 – 1.5)	(0.8 - 1.4)	(0.9 - 1.4)	
Septa thickness	ST	0.2	0.2	0.2	0.097
		(0.1 – 0.4)	(0.1 - 0.2)	(0.1 - 0.4)	
Theca thickness	TT	0.9	0.9	0.1	0.134
		(0.5 – 1.7)	(0.6 - 1.3)	(0.5 - 1.2)	
Exertness of septa	ES	1.0	1.0	0.8	0.162
		(0.3 – 2.4)	(0.4 - 2.0)	(0.3 - 1.5)	
N		133	27	18	

Table 4.2: The unstandardised and standardised discriminant function coefficients generated by the CDA for PDV and PDSW colonies.

Characters	Unstandardised	Standardised
WW	1.678	0.578
ST	10.090	0.424
PA	0.122	0.423
SCM	-0.319	-0.361
Constant	-5.903	

Table 4.3: The percentage of corals correctly and incorrectly classified into the two morphotypes by the canonical discriminant analysis. Numbers of corals are indicated in parentheses.

Classification	Morphotype	Correct	Incorrect	Overall success (%)
Original	PDV	96.3 (26)	3.7 (1)	91.1 (45)
	PDSW	83.3 (15)	16.7 (3)	
Cross-validated	PDV	96.3 (26)	3.7 (1)	88.9 (45)
	PDSW	77.8 (14)	22.2 (4)	

A discriminant function coefficient matrix was produced from the CDA solution on the four diagnostic variables (Table 4.2), and the unstandardised coefficient values were used to calculate the discriminant score (DS) for each intermediate form colony using the equation below:

$$DS = -5.903 + (WW \times 1.678) + (ST \times 10.09) + (PA \times 0.122) - (SCM \times 0.319)$$

Unstandardised coefficients were selected to enable the function to be applicable to new data using raw variables. A bi-plot of the discriminant scores for PDV, PDSW and intermediate forms was produced (Fig. 4.4). The four incorrectly grouped colonies (identified by classification procedure) were responsible for observable overlap between morphotypes. Once colonies were reassigned to the group designated by the classification procedure, it was clear that all negative discriminant scores corresponded to PDV, and all positive scores corresponded to PDSW, and there was not a large gap between the two morphotypes' scores (Fig. 4.4).

Discriminant scores calculated for each intermediate form showed 78.4% of colonies to be PDV and 21.6% to be PDSW (Table 4.4). Almost all form E colonies belonged to PDV (92.3%) and only two colonies were misidentified in the field. By contrast, colonies belonging to forms F and H were more difficult to classify into the two morphotypes with accuracy, based on field identifications alone (Table 4.4). The inclusion of form E with PDV means that the field description for PDV should read "colonies have septa of mixed sizes and spacing, with short to medium walls that slope, and valleys that are more prominent (and appear wider) **or are equal to** the

walls". These results show PDV to be the dominant morphotype in Kenyan lagoonal reefs, with 73.7% of all corals in this study belonging to this group.

Table 4.4: The percentage of intermediate forms of *Platygyra daedalea* classified into the two morphotypes. Numbers of corals are indicated in parentheses.

Group	PDV	PDSW
E	92.3 (24)	7.7 (2)
F	76.9 (20)	23.1 (6)
H	69.4 (25)	30.6 (11)
Overall	78.4 (69)	21.6 (19)

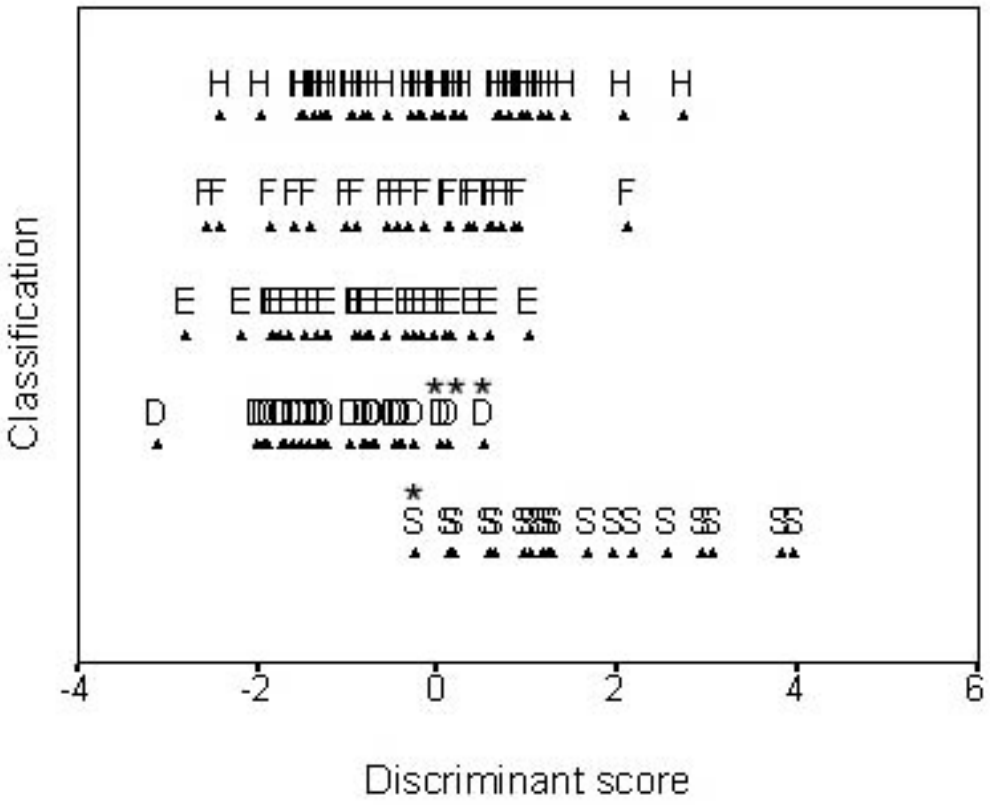


Figure 4.4: *Platygyra daedalea* groupings by discriminant scores. S: PDSW, D: PDV, E, F, H: intermediate forms. Asterisks are indicated above morphotypes identified by the CDA classification procedure to be assigned to the wrong group.

4.4.2 ITS sequencing

The rRNA fragment was successfully sequenced to include the ITS1, 5.8S and the complete ITS2 region in 52 individuals, of which 10 were classified as PDSW and 42 as PDV by the CDA. The remaining 17 individuals (16 PDV and 1 PDSW), showed poor or incomplete sequences and were excluded from further analysis. No specific morphotype or sample site was dominant among the excluded genetic samples.

The sequence aligned 639 positions of which 72 were variable and 29 were potentially parsimony informative. Cloning was not performed as we found no evidence of sequence heterogeneity at any of the parsimony informative sites that were used to infer the phylogenetic tree. The complete sequences contained less than 2% ambiguous sites. The ITS1 region had an average length of 209 bases and varied between 207 and 210. One colony from Kijembe Reef had an additional insertion of 18 bases. The 5.8S gene comprised of 168 positions and the ITS2 region varied between 210 and 218 positions. A total of 31 haplotypes were found among the samples. There were 9 haplotypes among 10 individuals of PDSW and 22 haplotypes among 40 individuals of PDV, with no identical haplotypes shared between the two morphotypes. Parsimony tests were constructed for the complete rDNA sequence. The average nucleotide substitution per site, measured as Kimura's 2-parameter mean distance, was 0.018 ± 0.003 between PDV and PDSW, and 0.020 ± 0.005 between Kenyan samples and the *P. sinensis* sequences derived from GenBank. No inferred parsimonious tree grouped PDV and PDSW separately, nor did it separate them from sequences of *P. sinensis* (Fig. 4.5).

Contrary to the phylogenetic analysis, AMOVAs carried out on the sequence data revealed a significant genetic difference between PDV and PDSW where 22% of the genetic variation was explained by the difference between the two morphotypes when treating all sampling sites as one population ($F_{ST} = 0.20$, $p = 0.017$). There was no genetic structure between populations at the different sites ($p = 0.604$).

4.4.3 Microsatellites

Analysis of the microsatellite data revealed a slight difference in genetic diversity measured by expected heterozygosity (Hs) over loci between the two morphotypes (PDV 0.26 ± 0.184, PDSW 0.37 ± 0.24). Two of five loci had significant excesses of heterozygotes in PDV, whereas all loci were in Hardy-Weinberg equilibrium in PDSW. In concordance with the ITS sequence analysis, AMOVAs showed significant subdivisions both between morphotypes within sites (F_{ST} = 0.055, p = 0.016) as well as between morphotypes when pooling sampling sites (F_{ST} = 0.020, p = 0.040). When doing the AMOVA on each locus separately it becomes apparent that this difference is caused by a significant differentiation at one locus, Pd 48 (F_{ST} = 0.335, p < 0.0001). None of the other loci showed signs of differentiation. No significant difference was found between sampling sites when pooling morphotypes (F_{ST} = -0.041, p = 0.60), nor between sites within each morphotype (PDSW F_{ST} = -0.15, p = 0.89 and PDV F_{ST} = 0.001, p = 0.30).

An assignment test performed in the programme Arlequin on the log-likelihood of individual multiloci genotypes correctly assigned 87% of the colonies to the same morphotype designated by the morphometric analysis (94% of PDV and 63% of PDSW) (Fig. 4.6). Six of the nine individuals that were assigned to a different genetic morphotype than the morphometric morphotype, were originally classified as intermediate forms in the field.

When using only microsatellite genetic data and no prior information on morphotypes the Bayesian population cluster analysis failed to assign any individuals to specific clusters and the maximum likelihood values was almost identical for models of K = 1 to K = 4 (where K = the inferred number of subpopulations in the data set). The programme Structure was also unable to assign the 39 colonies identified as intermediate forms in the field to either of the two morphotypes, when using the microsatellite genotypic information of colonies classified in the field as PDV or PDSW. However, after the genetic samples were relabelled following morphometric analysis, the model for K = 2 had the highest maximum likelihood and the programme successfully assigned 98% of PDV and 97% of PDSW to the correct morphotype.

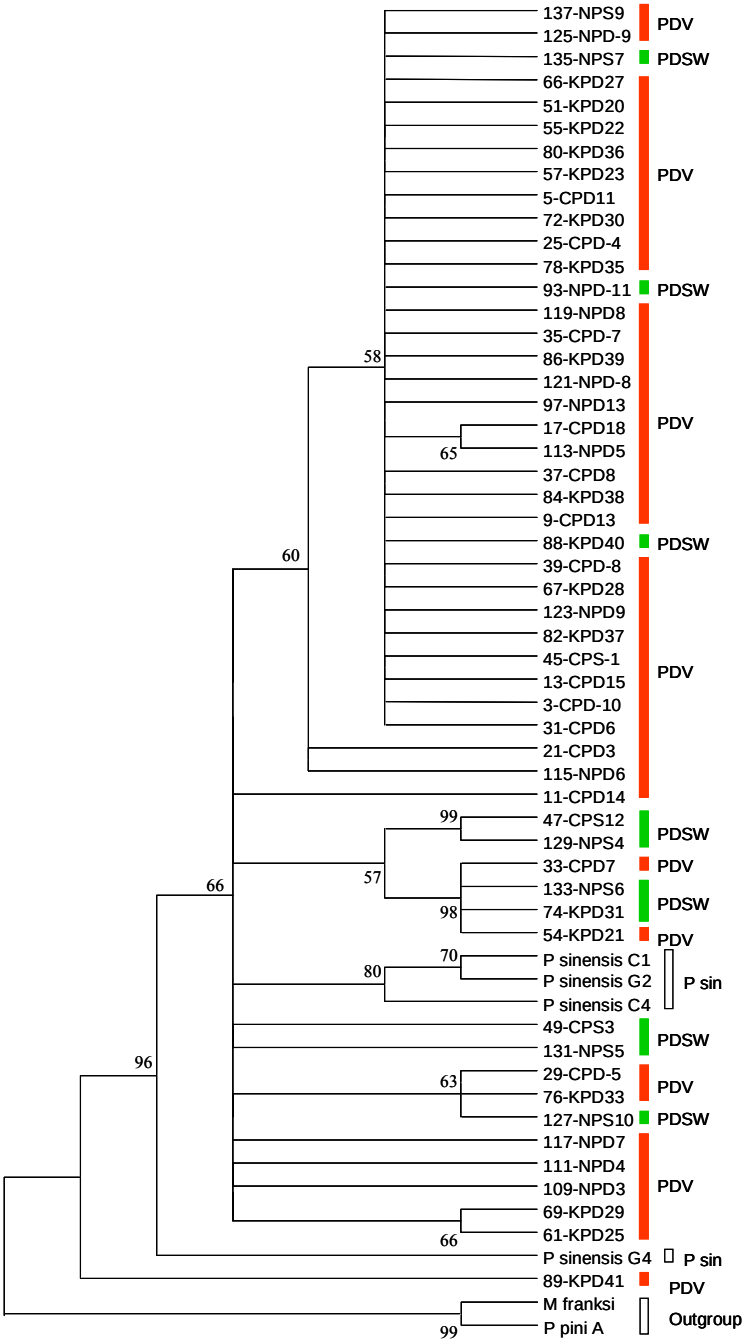


Figure 4.5: Maximum Parsimony tree of complete gene ITS-1 + 5.8S + ITS-2. Individual samples are named according to sample site and field identification (CPD/S – Coral Gardens PDV/PDSW; NPD/S – Nyali PDV/PDSW; KPD/S – Kijembe PDV/PDSW).

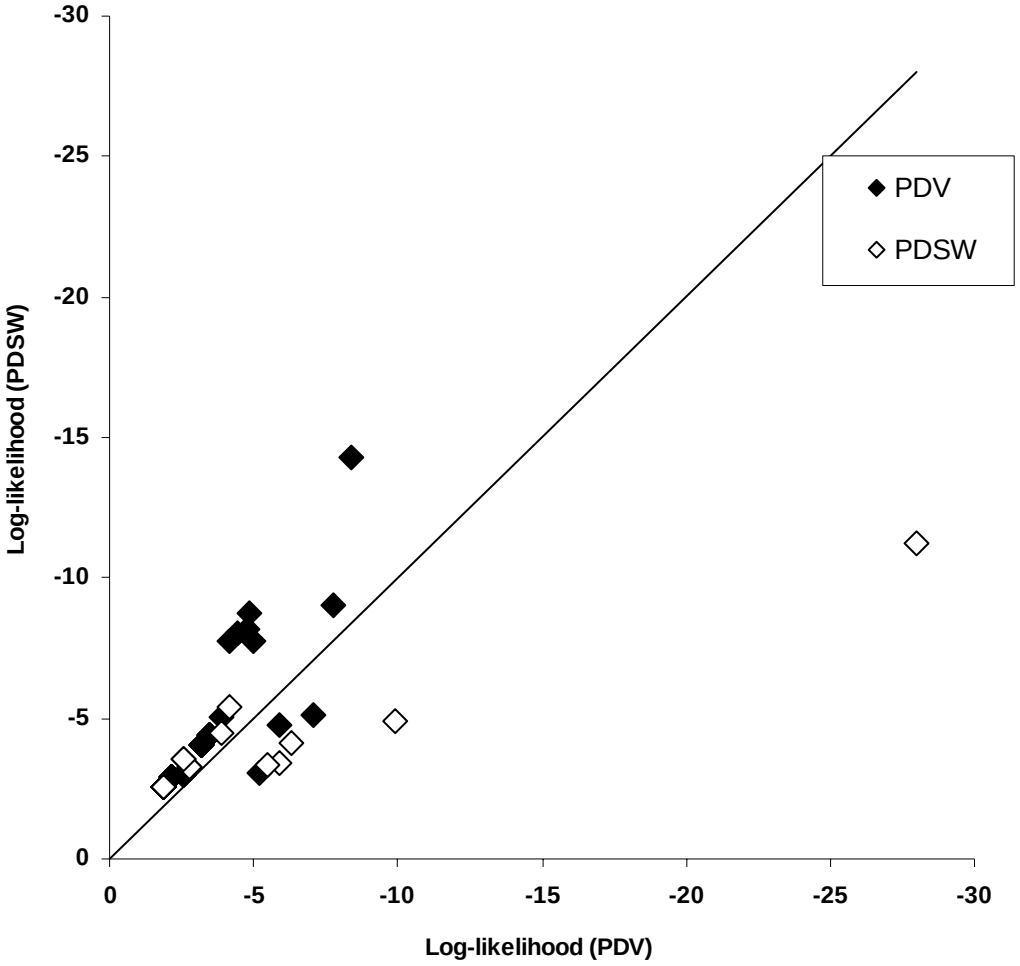


Figure 4.6: Assignment tests on the log-likelihood of individual genotypes being classified correctly as morphotypes PDV or PDSW as predicted by the CDA.

4.5 Discussion

Intraspecific phenotypic variability in scleractinian corals occurs in response to environmental variables (Wijsman-Best 1974; Foster 1980; Willis 1985) and genetic differences (Willis 1985; Willis and Ayre 1985) or a combination of both (Foster 1979; Miller 1992). In Kenya, two morphotypes of *Platygyra daedalea* were identified in a single lagoonal habitat type, and these observations were confirmed through morphometric studies. PDV was the dominant morphotype in the lagoon comprising 73.7% of the colonies sampled. Skeletal variation was continuous between the two morphotypes and while there was no single diagnostic trait that could be used to distinguish between PDV and PDSW, there were significant differences in six of the ten skeletal characters measured. These findings contrast with those of Miller (1994) who found that significant differences could only be detected between morphological species on the GBR when the nine skeletal characters were considered simultaneously.

With the exception of polyp area and valley length, the mean skeletal measurements and their ranges were consistent with those reported for *P. daedalea* on the GBR (Miller 1994). The narrower range in values for polyp area and valley length in Kenyan colonies most likely reflects the selection of one habitat type for this study, compared to four in the GBR study. The overlapping ranges in mean measurements between the different GBR morphotypes means it is not possible to determine if PDV and PDSW correspond to any of those described by Miller (1994), without running a CDA with the data from both regions. Valley length has been used to differentiate between species of *Platygyra* (Veron et al. 1977; Veron 2000) but was not found to be a useful trait for distinguishing Kenyan colonies, which have valley lengths comparable to *P. ryukyuensis* and *P. pini* on the GBR (Miller 1994).

The field descriptions for PDV and PDSW, and the CDA-generated mathematical equation presented in this paper can be used by other researchers in Kenya separately, or in combination, to assign *P. daedalea* colonies to one of the two morphotypes. Measurements of four skeletal characters were adequate to distinguish between morphotypes. The CDA classification procedure is currently under-utilised by

taxonomists and this study has shown its value in separating morphotypes that have overlapping skeletal characters, such as corals belonging to the Family Faviidae.

Phylogenetic analysis of the rRNA ITS sequences revealed no consistent grouping pattern of the two morphotypes of *P. daedalea* in Kenya (Fig. 4.5). However, both microsatellite data as well as the sequence data indicate that there is a small but significant genetic difference between the two morphotypes, but not between study sites, indicating that morphotypes are more genetically separated than sampling sites within the Mombasa Marine National Park and Reserve. In addition, ITS sequence data indicate that these 52 samples of *P. daedalea* are genetically indistinguishable from published sequences from four genetic clusters of *P. sinensis* from Hong Kong (Lam and Morton 2003), raising the issue of the taxonomic status of the *P. daedalea*/*sinensis* species complex or the validity of using ITS sequences to separate species.

An earlier study of the phylogenetic relationships between species of *Platygyra* used allozymes as genetic markers and found morphological but no clear genetic differences between species (Miller and Benzie 1997). As it is often assumed that allozymes are non-neutral markers, and therefore under direct influence of stabilising selection they have relatively low mutation rates (Hartl and Clark 1997). Also, most mutations that occur in allozyme markers are silent and as such will not cause a difference in motility on an electrophoretic gel and hence not be noted. This will decrease the signals of divergence and increase the chances of not detecting a genotypic difference that may exist.

In contrast, ITS sequencing found genetic distinctions but no clear morphological clustering between *P. sinensis* and *P. pini* in Hong Kong (Lam and Morton 2003), while the current study found morphological differences but no clear genetic differences using both ITS sequences and microsatellites. The lack of morphological clustering in the Hong Kong study may be attributable to their method of choice for morphometric analysis, which differed from the CDA used by Miller (1994) and in the present paper. Based on these three studies, it appears that the ITS region does display enough divergence to be useful at the species level, but may not be variable

enough to detect genetic differences between morphotypes with a current or recently shared gene pool.

The ITS sequences presented in this paper show a high level of diversity with a large proportion of unique haplotypes, consistent with other studies of corals (van Oppen et al. 2002; Marquez et al. 2003; Fukami et al. 2004). The rate of evolution of nuclear rRNA is believed to allow for differences between species to accumulate through genetic drift, while maintaining similarities between populations within species (Hillis and Dixon 1991). The use of ITS sequences for phylogenetic and population genetic studies of corals has been questioned based on evidence that corals display a faster rate of speciation than the concerted evolution of the rDNA, resulting in shared ancient rDNA lineages which would obscure processes such as introgressive hybridisation (Vollmer and Palumbi 2004). However, in the present study the combined results from the analysis of microsatellites and rDNA sequences support the existence of two morphotypes of *P. daedalea* that have evolved and exist in sympatry. While it is not possible to distinguish between these morphotypes using molecular markers alone, in combination with morphological data a significant genetic division is apparent. We used only four variable microsatellite loci, hence additional variable markers would probably improve the chances of discriminating between the two morphotypes based on genetics alone. Individual AMOVA of each microsatellite loci show that one locus, Pd 48, is solely responsible for the inferred differentiation. Hence it maybe speculated that this locus in linked to a gene that is under differential selection in the two morphotypes.

It is not clear how morphological boundaries are maintained in *Platygyra* species or morphotypes, with earlier studies showing there are no apparent gamete-level barriers to fertilisation between species on the GBR (Miller and Babcock 1997). A recent study in Kenya suggests the timing and duration of gametogenic cycles for PDV and PDSW are similar to each other, with both morphotypes capable of biannual spawning at similar times in August/September and February/March each year (see Chapter 5).

With regards to diversity and variability, PDSW was found to be more genetically diverse (Hs), was in Hardy-Weinberg equilibrium at all microsatellite loci and displayed a far greater proportion of unique haplotypes in the ITS region. It was also

more difficult to correctly assign to a morphotype using microsatellite markers. Although it is possible that the prevalence of unique haplotypes is a result of the small sample size of PDSW, it may be speculated that these two morphotypes share a recent ancestral past and that PDSW is the more ancestral type. Despite being less genetically diverse, PDV is more prevalent and phenotypically diverse, and if it has a selective advantage over PDSW in the sampled environment it may have evolved assortative mating mechanisms within its morphotype allowing for maintenance of morphological boundaries. However, due to the limited sample size and overall low polymorphism of the microsatellite loci included in the study, the genetic data should be interpreted with caution.

Morphotypes have now been identified in *Platygyra* in three different locations in the Indo-Pacific and the Western Indian Ocean, and appear to be a characteristic of this genus, though it is not known if morphotypes exist in all *Platygyra* species. At present, it is not known why PDV is more prevalent than PDSW in the lagoon, and whether this prevalence extends to deeper waters of the fringing reef and further along the East African coast. Given the prevalence of morphotypes in this genus, the next logical step would be to determine whether there are ecological differences between morphotypes in *P. daedalea*. For example, is one morphotype more resilient to bleaching or other forms of stress than the other, and does the prevalence of PDV in Kenya reflect differences in responses to bleaching. Therefore, further studies are required to understand the role of different morphotypes, and whether there are costs, benefits and limits to phenotypic plasticity that have ecological and evolutionary consequences.

CHAPTER 5: PATTERNS OF GAMETOGENESIS, SPAWNING AND FECUNDITY IN THE THREE FAVIID SPECIES

5.1 Introduction

The reproductive biology and seasonality of three scleractinian corals, *Echinopora gemmacea* (Lamarck 1816), *Platygyra daedalea* (Ellis and Solander 1786) and *Leptoria phrygia* (Ellis and Solander 1786), belonging to the Family Faviidae (Gregory 1900), were studied in the Mombasa Marine National Park and Reserve in Kenya. These species were selected because they are abundant and widespread in the Mombasa lagoon, often dominating the reef landscape (see Chapter 2), and are generally found throughout the Kenyan and wider East African coast (D. Obura, unpubl. data). All studies to date from other regions have found these three species to be simultaneous hermaphrodites that broadcast spawn gametes for external fertilisation and development (see reviews by Fadlallah 1983; Harrison and Wallace 1990; Richmond and Hunter 1990).

Leptoria phrygia is a massive coral distinguished by the presence of highly meandroid corallite valleys, with septa that are evenly spaced and of equal size. Colonies are mostly brown or green in Kenya, with walls and valleys of contrasting colour. The species is widely distributed throughout the Indo-Pacific and occurs across a wide range of habitats (Veron 2000). The timing and length of gametogenesis have been described for *L. phrygia* at Heron Island reef, southern GBR (Kojis and Quinn 1982) and on reefs adjacent to Return to Paradise Beach on Upolu and Matautu Bay on Savai'i, Western Samoa (Mildner 1991). Heron Island reef has a mean annual sea temperature range of about 6 ºC, while Western Samoa has a narrow range of 2.5 ºC. At both locations, *L. phrygia* undergoes a single annual gametogenic cycle that terminates in the synchronous release of gametes during summer. On the GBR, spawning occurs in November or December on the 5th night after full moon (AFM) with gametes being released 3-4 hours after sunset (Kojis and Quinn 1982; Willis et al. 1985; Babcock et al. 1986). In Western Samoa, spawning occurs around the 6th or 7th night AFM in November or December (Mildner 1991).

Echinopora gemmacea is an encrusting coral distinguished by plocoid corallites with thick, exert, irregularly arranged septa. Colonies are brown and cream, sometimes with light purple centres forming around the polyp mouths. The species is widely distributed in the Indo-Pacific and is found mainly in protected reef environments (Veron 2000). *Echinopora gemmacea* can be difficult to separate from *E. hirsutissima* in the field, which is less common in Kenya and is distinguished by the presence of densely covered thick spinules throughout the coenosteum (Veron et al. 1977; Veron 2000). Broadcast spawning has been recorded in *E. gemmacea* on the GBR (4^{th} and 5^{th} nights AFM, Babcock et al. 1986) and in Japan (5^{th} night AFM, Hayashibara et al. 1993). However, there are no published data available on the pattern, duration and timing of gametogenesis in this species, though gametogenic data are available for *E. lamellosa* in northern and southern Taiwan (Fan and Dai 1995)**.** In Taiwan *E. lamellosa* undergoes a single cycle of gametogenesis that occurs over 4-6 months commencing in April and terminating in split-spawning over 2-3 months in the summer and autumn between July – October (Fan and Dai 1995).

Taxonomic descriptions of *Platygyra daedalea* have been provided in Chapter 4. Broadcast spawning has been recorded in *P. daedalea* on the GBR (4^{th} - 7^{th} nights AFM, Willis et al. 1985; Babcock et al. 1986), Akajima (8^{th} night AFM, Hayashibara et al. 1993) and Shikoku (10^{th} night AFM, van Woesik 1995) Islands in Japan, in southern Taiwan (6^{th} night AFM, Dai et al. 1992) and in Kuwait (4^{th}-5^{th} nights AFM, Harrison 1995). Biannual cycles of gametogenesis were recorded in *P. daedalea* in northern Papua New Guinea (PNG) (Oliver et al. 1988), but data were not provided on the pattern and timing of gametogenic cycles in this location. On the central GBR, Babcock (1986) documented a single annual cycle of gametogenesis in *P. sinensis* that occurred over 6 months commencing in late April or May and terminating in synchronous spawning in October or November. Guest (2004) documented reproductive patterns in *Platygyra* sp. from March 2001 - April 2002 in Singapore, and found oocytes present in randomly selected colonies for 6-9 months of the year between August - April. Taxonomic complexities inherent in this genus (Miller 1992, 1994; Mangubhai et al. (in press); Chapter 4) meant that there were potentially two morphospecies present in the Singapore study, which most closely resembled *P. pini* and *P. verweyi*, though some samples also showed characteristics of *P. ryukyuensis*.

Preliminary results on the timing of spawning in *E. gemmacea* and *P. daedalea* were published in Mangubhai and Harrison (2006). Following a detailed morphometric and genetic study, Mangubhai et al. (in press; see also Chapter 4) determined that corals identified as *P. sinensis* in Mangubhai and Harrison (2006) were all *P. daedalea,* comprising two morphotypes, 'prominent valley' (PDV) and 'straight-walled' (PDSW). These changes are reflected in this thesis.
The main aims of this chapter are to:

1) describe the pattern, duration and timing of gametogenesis in three faviid species;
2) determine the level of spawning synchrony within and among species;
3) quantify and compare fecundity of faviids in Kenya with other geographical regions; and
4) examine the relationship between gametogenic cycles and spawning times and environmental parameters.

5.2 Methods

5.2.1 Field collection

Ten permanent colonies of *E. gemmacea* and 20-22 colonies of *P. daedalea* were marked at Coral Gardens and Nyali Reef in April 2003 and at Kijembe Reef in August 2004, and 10 colonies of *L. phrygia* were marked at Nyali Reef in August 2004 (Table 5.1). A different site was selected for sampling *E. gemmacea* and *P. daedalea* in the second study year to enable the sampling of sufficient numbers of new colonies. Given no site differences were found in the first year (Mangubhai and Harrison 2006) and that Kijembe Reef is only 250 m north of Nyali, there are unlikely to be site differences in the pattern of gametogenesis or spawning. Morphometric analysis of *P. daedalea* identified 19 of the colonies at Coral Gardens to be morphotype PDV and 3 to be morphotype PDSW (see Chapter 4). At Nyali Reef, 12 colonies were PDV and 8 were PDSW, while at Kijembe Reef 15 colonies were PDV and 5 were morphotype PDSW.

Sampling in the first reproductive season extended for 14 months from April 2003 - May 2004, and in the second season for 10 months from August 2004 - May 2005. Large adult colonies >35 cm maximum diameter (Table 5.1) were selected to ensure repeated sampling did not remove more than 15% of tissue biomass from any individual colony. Colonies sampled were separated by at least 2 m and individual features were closely examined during selection to ensure that colonies were distinct in their physical characteristics and whole (i.e. not fragments), and were therefore likely to be genetically distinct. Samples were collected on snorkel at low tide using a hammer and chisel, and placed in labeled perforated plastic bags to allow seawater to penetrate the samples. Each sample measured approximately 4 x 4 cm and collections were focused where possible, on areas of the colonies with natural 'mounds' for ease of collection and to minimise damage. Subsequent samples were separated by 10-15 cm to avoid collecting tissue that might be allocating resources away from reproduction and towards the healing of lesions (Oren et al. 2001; Van Veghel and Bak 1994; Hall 1997). Samples were not taken near the margins of colonies where polyps may be sterile or have a lower fecundity than the rest of the colony (Szmant 1986, 1991; Chornesky and Peters 1987; Soong and Lang 1992; Sakai 1998).

Table 5.1: The number of permanently marked colonies (n) of each species and their mean maximum diameter (cm) at the three study sites. Season: 1 = April 2003 - May 2004, 2 = August 2004 – May 2005. Sites: CG = Coral Gardens, NR = Nyali Reef, KR = Kijembe Reef.

Species	**Site**	**Season**	**n**	**Colony sizes**			
				mean	**sd**	**max**	**min**
E. gemmacea	CG	1	10	66.2	24.8	120	40
	NR	1	10	81.7	17.0	115	58
	KR	2	10	73.5	19.1	103	44
P. daedalea	CG	1	22	59.6	16.3	108	36
	NR	1	20	69.4	24.4	140	42
	KR	2	20	79.7	18.4	112	54
L. phrygia	NR	2	10	81.7	10.3	102	68

In the first reproductive season, samples of *P. daedalea* were initially collected every 1-2 months, and then at 2-3 week intervals closer to the predicted period of spawning,

while *E. gemmacea* was sampled at monthly intervals throughout the study. Corals selected for the second reproductive season were sampled less frequently during the early parts of the gametogenic cycle, and then at two week, one week and 3-4 day intervals closer to the predicted period of spawning. The overall number of samples collected depended on size, with smaller colonies being sampled less frequently to minimise tissue loss and to reduce stress to the corals.

The timing and frequency of collections in the second reproductive season was based on spawning periods recorded in the previous season (Mangubhai and Harrison 2006), giving due consideration to the season and month, lunar phase and the size and maturity of oocytes observed in the field. No colonies were sampled in the southeast monsoon months June and July during the two-year study because strong winds and rough seas made it difficult to access the sites on a regular basis. Once a colony had spawned, 1-2 additional samples were taken 1-2 weeks later to determine whether any 'unspawned' oocytes remained in the colony and whether there was any evidence of post-spawning brooding of retained eggs (Sakai 1997; Nozawa and Harrison 2005). Those samples with pigmented oocytes were considered to have maturing oocytes, and in faviid species pigmentation appears 4-6 weeks prior to spawning (Babcock et al. 1986). When the first mature oocytes were observed in the field, an additional 10-38 colonies of each species were identified and marked at the sites to provide more extensive data on the timing of spawning and intra- and inter-specific spawning synchrony. These 'additional' colonies were also compared with 'permanent' colonies to determine whether repeated sampling had any adverse effects on coral reproduction. Samples were collected and processed in the laboratory in the same manner as those collected for gametogenic analysis. This overall sampling strategy enabled reproduction to be followed in individual colonies as well within the wider population.

5.2.2 Laboratory preparation of samples

Samples were transported to the laboratory immediately after returning from each sampling trip, where they were initially examined alive under a dissecting microscope and the presence or absence of gametes, their approximate size (i.e. small, medium or large) and colour were recorded. Reproductive condition was divided into three

categories: ‘mature’ if oocytes were pigmented, ‘immature’ if oocytes were smaller and pale or white, and ‘empty’ if oocytes were too small to view with the naked eye (Oliver et al. 1988; Baird et al. 2002; Mangubhai and Harrison 2006). These categories were used to give a broad indication of the likely timing of spawning (i.e. within weeks or months), so that sampling times could be adjusted accordingly. However, not all oocytes within a colony become pigmented prior to spawning (Mangubhai and Harrison 2006), and the reproductive status of each colony was confirmed through tissue dissection. Spawning was inferred from the disappearance of mature gametes between sampling periods, and the absence of brooded planulae or embryos.

Following initial microscopic examination, samples were fixed in 10% formalin in seawater for at least 48 hours, then rinsed in fresh water and transferred to a solution of 0.5-5% hydrochloric acid (HCl) for 2-3 weeks, or until samples had decalcified. It was important to wash coral samples prior to transfer to HCl to reduce the quantity of the toxic bi-product dichlorodimethylether (CH_2ClOCH_2Cl) produced by the reaction of formalin and acid (Buijs, pers. comm.). Samples were decalcified initially using a lower concentration of HCl (0.5-1%) to minimise tissue damage during the initial release of hydrogen gas, and then the acid concentration was increased as the decalcification process proceeded. Hydrochloric acid solutions were changed every 1-2 days as required, until the skeleton had dissolved. The tissue remaining following decalcification was rinsed in fresh water and preserved in 70% ethanol.

5.2.3 Microscope analysis

Decalcified samples were placed on a dark-coloured petri dish and five polyps were randomly selected and removed under a dissecting microscope using fine forceps. Sub-sampling of mesenteries varied depending on the genus and its reproductive and tissue morphology. In *E. gemmacea,* eight mesenteries (four long and four short) were randomly sub-sampled from each polyp. In *P. daedalea* and *L. phrygia*, polyps shared mesenteries and therefore a portion of the tissue surrounding five randomly selected polyp mouths was removed by tearing along the wall ridge, and eight mesenteries were randomly sub-sampled.

Polyps were dissected by gently tearing apart the tissue with fine-tipped forceps, starting from the mouth and extending down the pharynx to expose the mesenteries beneath (after P. Harrison, pers. comm.). Where necessary, tissue was held apart by entomological dissection pins (Size OOO) to give a flat plane. On each mesentery, the total number of oocytes was recorded, and the maximum length and perpendicular width of up to six randomly selected oocytes were measured using a calibrated eyepiece micrometer. Spermaries are intermingled with oocytes, so the combined 'oocyte-spermary' or 'gonad' mass was also measured, and mean diameters for oocytes and gonad mass were obtained by averaging the length and width measurements. This method, rather than histological sectioning, enabled all oocytes in a polyp or mesentery to be counted rather than a sub-sample, and hence is a more accurate measure of fecundity.

5.2.4 Estimating fecundity

To compare reproductive effort between faviids, coral fecundity was calculated as the number of oocytes per cm^2 of tissue. Fecundity was analysed using samples of corals collected for gametogenesis that were reproductively mature. The method for recording the number of oocytes per mesentery was described in section 5.2.3.

In *E. gemmacea*, the mean number of mesenteries per polyp was determined by counting the total number of mesenteries in 5 or 10 polyps (if time permitted), randomly selected from tissue samples collected from 5 colonies at Coral Gardens and at Nyali Reef, and 20 colonies at Kijembe Reef. Preliminary observations suggested that smaller polyps did not produce eggs, and hence the maximum diameter across the mouth of the polyp and the proportion of mesenteries with oocytes was recorded for each polyp. The number of polyps per 5 cm^2 was determined by photographs taken *in situ* using a digital underwater camera (Olympus 4040), and counting the number of polyps within a 5 x 5 cm square frame held against the colony surface. Ten replicate photographs were taken of each of the permanent colonies at Coral Gardens and Nyali Reef, but time constraints prevented any photographs being taken of colonies at Kijembe Reef.

In *P. daedalea,* five pieces of the tissue surrounding 2-8 polyp mouths were randomly selected from mature samples from 10 colonies at Coral Gardens and at Nyali Reef, and 20 colonies from Kijembe Reef. In *L. phrygia,* tissue samples were selected from the 10 permanent colonies at Nyali Reef. The length and width of the tissue was measured under a stereomicroscope with a calibrated eyepiece micrometer to obtain tissue area, and the total number of mesenteries was counted.

Fecundity in *E. gemmacea* was calculated by equation (1), and in *P. daedalea* and *L. phrygia* by equation (2) as follows:

$$F = (O_l + O_s) \times (M/2) \times (P/5) \times \%P \qquad (1)$$

$$F = O \times M / (T_l \times T_w) \times \%M \qquad (2)$$

F = fecundity, measured as the number of oocytes per cm^2
O = mean number of oocytes per mesentery (l = long, s = short mesentery)
M = number of mesenteries
P = number of polyps recorded in 5 cm^2 frame
%P = proportion of polyps with mature oocytes just prior to spawning
T = tissue dimensions (l = length, w = width)
%M = proportion of mesenteries with mature oocytes just prior to spawning

5.2.5 Spawning in aquaria

Two colony fragments of *L. phrygia* and four fragments of *E. gemmacea* (approximately 15 x 15 cm) were collected from Nyali Reef on 29 December 2004 and 26 February 2005, respectively. They were maintained separately in small aquaria for 4-5 days, with a manually-controlled flow-through seawater system. Full seawater exchange was done 3-5 times per day and within 1-2 hours of spawning. For a maximum of five consecutive nights coral fragments were examined every half hour from 18:00 (just prior to sunset) to 23:00 hours or until spawning ceased, using a torch covered with red cellophane to avoid causing the light-sensitive faviids from contracting and therefore delaying or preventing spawning (P. Harrison, pers. comm.). Information was recorded on the timing of 'setting', (i.e. when the egg-sperm bundles

are formed and then held in the oral cavity prior to release), the onset and duration of spawning, and the method of gamete release. In this thesis, the convention of numbering lunar days is in accordance with Atoda (1947a) and Stimson (1978), where new moon is lunar day 0, second lunar quarter commences on lunar day 8, full moon is lunar day 15, and the fourth or last quarter commences on lunar day 22.

5.2.6 Environmental parameters

Temperature loggers with internal sensors (HOBO StowAway TidbiT) were deployed at Coral Gardens from May 2003 – June 2004 and at Nyali Reef from April 2003 – December 2005, within close proximity to marked corals at 0.5 m low water spring tide level. The loggers were covered in electrical tape to prevent direct fouling or damage to the two nodes, and were attached to the substrata using plastic-sheathed electrical wiring. Temperature readings were taken every hour and the data downloaded every 6-12 months. Mean weekly temperatures were calculated.

Salinity and turbidity readings were done from February 2003 – February 2005 during most field sessions, at the lowest part of the low tide. Water samples were collected in a 75 ml container and salinity was measured to the nearest parts per thousand (‰) in the laboratory using a refractometer, while water turbidity was assessed using a secchi disk, to measure secchi disk depth to the nearest 0.1 m. Tidal data were obtained from the annual Ports Authority publication, which lists tides at Kilindini (4º04’S, 39º40’E) adjacent to the Port of Mombasa, which is about 2.8 km south of Nyali Reef.

5.2.7 Statistical analyses

Data were statistically analysed using the SPSS for Windows (version 11, 2001). A two-factor analysis of variance (ANOVA) was used to test for significant effects of, and interactions between sites, and the impact of collection (permanent versus additional colonies) on mean gamete diameter and number of oocytes on mesenteries. A Levene test for homogeneity of variances was done to test the assumption that variances of the groups are all equal, and data were log-transformed where required. Where differences occurred among the means, post-hoc range tests and pairwise multiple comparisons were done to determine which means differed significantly.

Independent t-tests were used to test for significant differences in the mean number of oocytes and the mean oocyte and gonad mass diameter between: (a) short and long mesenteries in *E. gemmacea*; (b) consecutive reproductive seasons; and (c) minor and major spawning events in *P. daedalea*. A Mann-Whitney U non-parametric test was used to detect differences in the percentage of mesenteries participating in reproduction between minor and major spawning events. All p-values below 0.05 were considered statistically significant.

5.3 Results

5.3.1 Reproductive pattern

Echinopora gemmacea, Platygyra daedalea and *Leptoria phrygia* were simultaneous hermaphrodites, with both mature oocytes and spermaries observed together in polyps prior to gamete release (Fig. 5.1-5.2). While spawning was not observed directly in the field, the disappearance of mature oocytes and spermaries from consecutive samples taken a few days to a few weeks apart and observations of spawning by colonies of *L. phrygia* and *E. gemmacea* kept in aquaria, indicates these species are broadcast spawners. Further evidence is provided by the lack of planulae in the 1041 samples examined.

5.3.2 Arrangement of gonads

All three faviids had oocytes and spermaries intermingled within the mesogloea of the same mesentery. In *E. gemmacea* polyps there was an alternation of long and short mesenteries, with shorter ones located closer towards the mouth and longer ones extending oral-aborally into the skeletal framework of the colony (Fig. 5.1). In contrast, the mesenteries of *P. daedalea* (Fig. 5.2) and *L. phrygia* were continuous between polyp mouths with generally two mesenteries present in each interseptal lobe. Oocytes appeared to develop mainly on only one of each pair of mesenteries in *L. phrygia*, though this pattern was not consistent throughout all samples and may reflect space constraints in individual interseptal lobes.

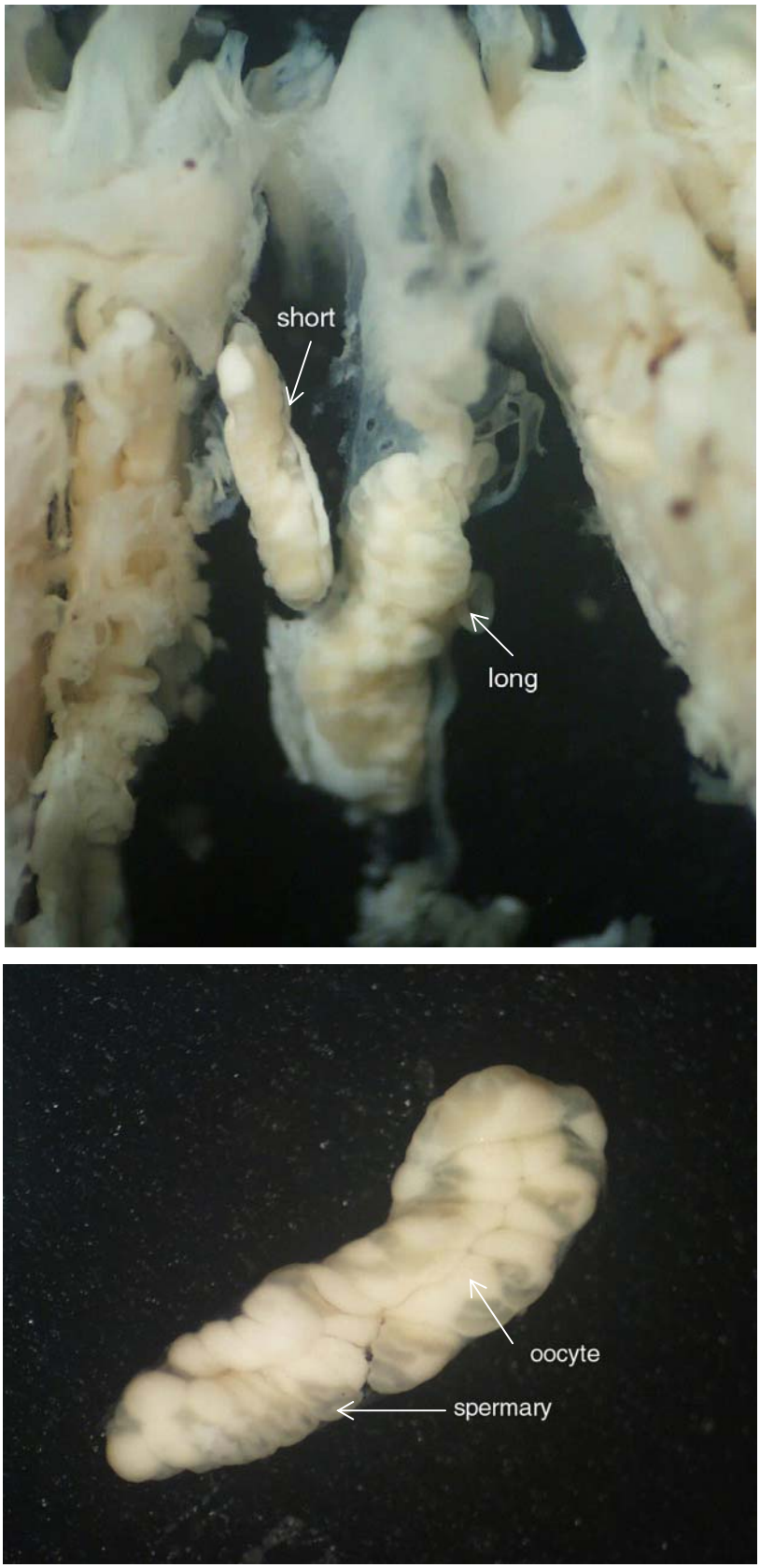


Figure 5.1: Photographs showing the arrangement of mature oocytes and spermaries on long and short mesenteries (above) and the structure of the gonad mass (below) in *Echinopora gemmacea.*

Figure 5.2: Photographs showing the arrangement of mature oocytes and spermaries along two adjacent mesenteries in *Platygyra daedalea*.

5.3.3 Gametogenesis

5.3.3.1 Echinopora gemmacea

Echinopora gemmacea had a single annual cycle of gametogenesis, with oogenesis occurring for 4-6 months from November to April and spermatogenesis occurring for 3-4 months from January to April (Fig. 5.3). Oogenesis preceded spermatogenesis by 1-2 months. Patterns of oogenesis and spermatogenesis were consistent between consecutive reproductive seasons with gametes reaching maturity at approximately the same time between February - April in 2004 and 2005. There was a quiescent non-reproductive period of 6 months between gametogenic cycles. The smallest detectable oocyte had a mean diameter of 28.6 µm indicating that oogenesis had probably started at least a few weeks before those samples were taken in November 2003. The mean diameter of oocytes and the gonad mass at maturity were 168.5 µm (sd = 22.6) and 1272.4 µm (sd = 291.0), respectively (Table 5.2).

Table 5.2. The mean diameter of mature oocytes and gonad mass of *Echinopora gemmacea, Platygyra daedalea* and *Leptoria phrygia* recorded in each reproductive season and overall for the two-year study. PDV = *P. daedalea* prominent valley, PDSW = *P. daedalea* straight-wall morphotypes. Reproductive season: 1 = April 2003 - May 2004, 2 = August 2004 - May 2005.

Species	**Season**	**n**	**Mature oocyte**		**Mature gonad mass**	
			mean	**sd**	**mean**	**sd**
E. gemmacea	All	40	168.5	(22.6)	1272.4	(291.0)
L. phrygia	All	13	239.1	(45.7)	1317.1	(250.6)
P. daedalea (all)	All	122	258.5	(25.3)	1532.7	(382.4)
PDV	All	91	259.0	(26.1)	1550.3	(368.2)
PDSW	All	31	257.2	(23.2)	1481.1	(423.6)
E. gemmacea	1	20	162.0	(14.5)	1253.2	(201.7)
	2	20	175.0	(27.4)	1291.7	(363.8)
P. daedalea (all)	1	79	251.3	(24.3)	1586.0	(370.9)
	2	43	271.9	(21.7)	1434.9	(388.1)
PDV	1	62	250.7	(24.9)	1574.1	(366.9)
	2	29	276.8	(18.8)	1499.4	(372.0)
PDSW	1	17	253.5	(22.4)	1629.3	(393.3)
	2	14	261.6	(24.4)	1301.1	(400.1)

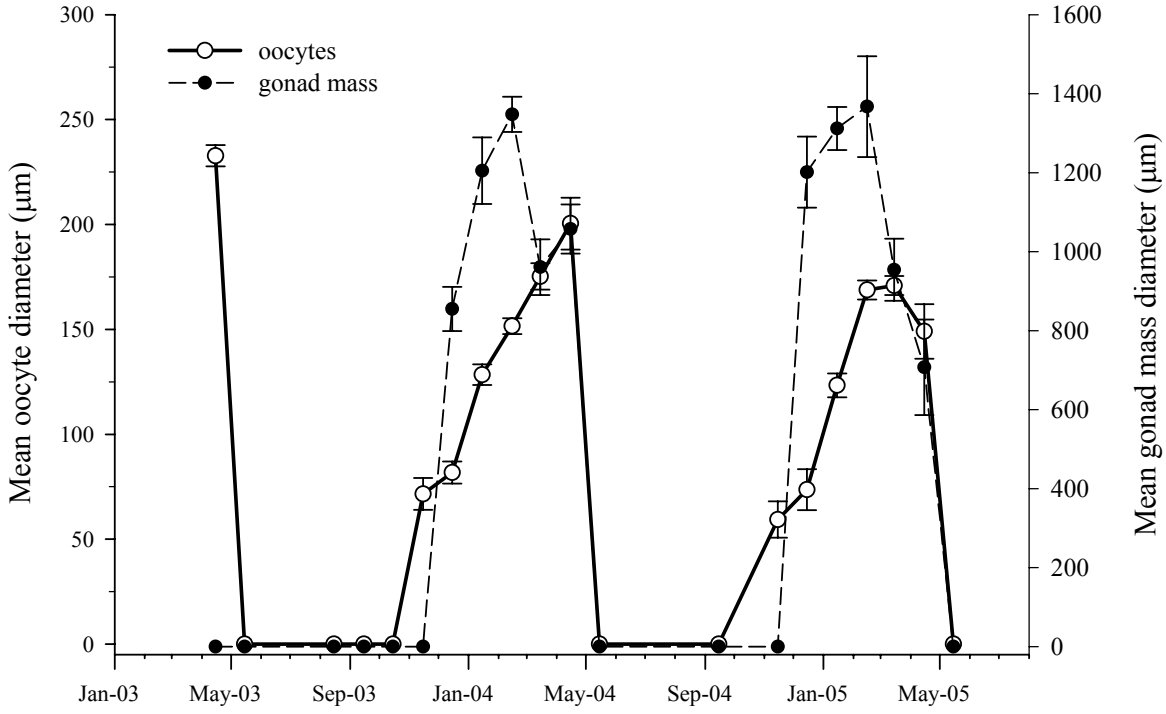


Figure 5.3: *Echinopora gemmacea*. Seasonal changes in mean oocyte (left y-axis) and gonad mass (right y-axis) diameter of permanent colonies at Coral Gardens and Nyali Reef in April 2003 - May 2004 (n = 20), and at Kijembe Reef in August 2004 - May 2005 (n = 10). Mesenteries that did not have gametes present were omitted when calculating mean sizes, and therefore the sizes in the graph represent actual sizes. Error bars are standard errors.

The mean proportion of mesenteries with gametes increased over time with approximately 77% of all mesenteries having gametes just prior to spawning in February, in both reproductive seasons (Fig. 5.4). In March 2004 and 2005, the mean proportion of mesenteries with gametes decreased to <50% and reflects the occurrence of both split-spawning of the population and partial spawning within individual colonies (see section 5.3.4). In April 2003, unusually large mature oocytes were present in samples with no associated spermaries (Fig. 5.3-5.4).

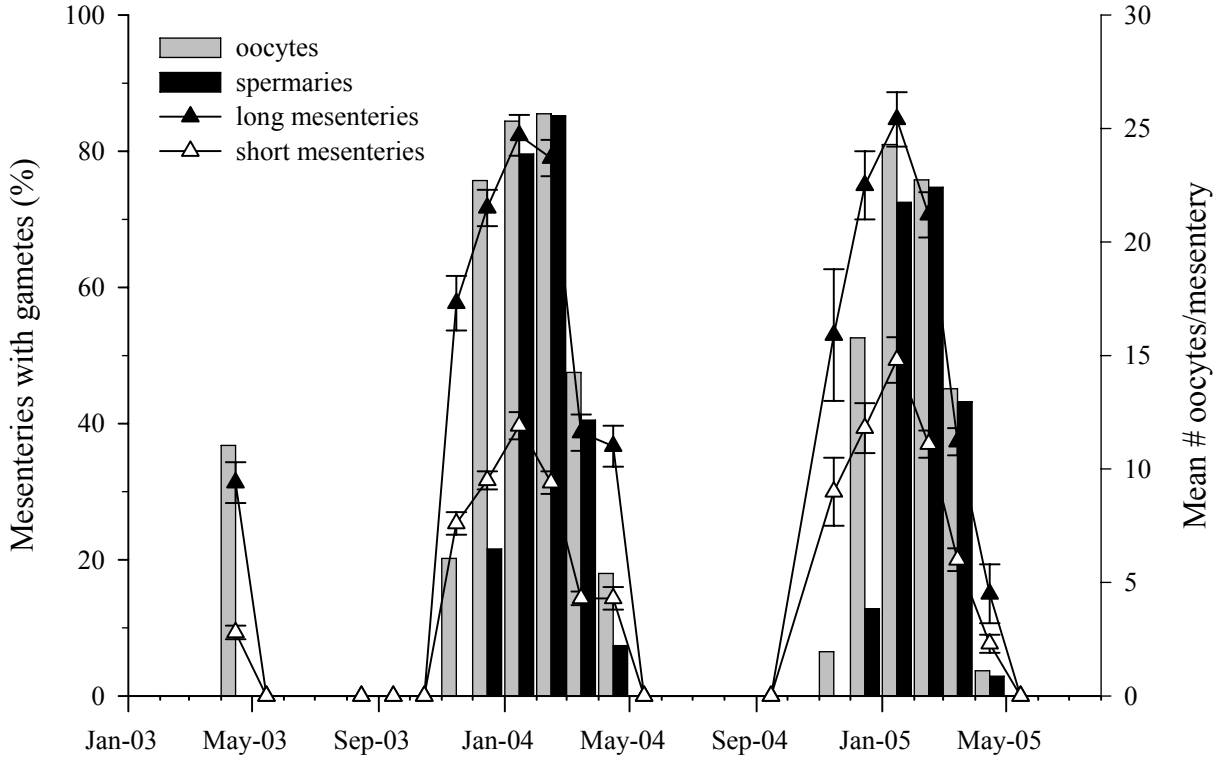


Figure 5.4: *Echinopora gemmacea*. Seasonal changes in the mean proportion of mesenteries with oocytes and spermaries (bars) and mean number of oocytes per mesentery (line) at Coral Gardens and Nyali Reef in April 2003 - May 2004 (n = 20), and at Kijembe Reef in August 2004 - May 2005 (n = 10). Error bars are standard errors.

While the number of oocytes per mesentery varied during the study, ranging from 0-48 and 0-72 in short and long mesenteries, respectively, the trend in both years was for an increase in the number of oocytes present as oogenesis progressed (Fig. 5.4). The mean number of oocytes per mesentery was significantly different between short and long mesenteries at maturity (short = 7.8, long = 18.0, $F_{(1, 58.1)} = 18.509$, $p < 0.001$, Table 5.3), though both underwent similar patterns of gametogenesis over time. A small reduction in the mean number of oocytes per mesentery occurred between January - February, just prior to spawning, suggesting some resorption of oocytes may have occurred (Fig. 5.4).

T-tests showed there were no significant differences in the mean oocyte diameter between short and long mesenteries ($F_{(1, 78)} = 0.312$, $p = 0.941$), but there was a difference in gonad mass diameter between mesentery types ($F_{(1, 78)} = 3.117$, $p < 0.001$) (Table 5.3). There were no significant differences in the mean diameter of oocytes ($F_{(1, 29.6)} = 7.39$, $p = 0.073$) or gonad mass ($F_{(1, 30.4)} = 9.533$, $p = 0.678$), or the mean number of oocytes per mesentery ($F_{(1, 33.2)} = 5.977$, $p = 0.738$) between the two reproductive seasons.

Table 5.3: The mean diameter of mature oocytes and gonad mass (μm) and the mean number of oocytes found on short and long mesenteries in *Echinopora gemmacea.* T-test results for significant differences between short and long mesenteries are shown.

Gamete	Type	n	mean	sd	p-value
Oocyte diameter	long	40	168.6	22.5	0.941
	short	40	168.2	23.5	
Gonad mass diameter	long	40	1587.7	345.3	< 0.001
	short	40	956.8	267.3	
# oocytes	long	40	18.0	7.6	< 0.001
	short	40	7.8	3.9	

5.3.3.2 Platygyra daedalea

Results for *P. daedalea* are presented for the two morphotypes PDV and PDSW, identified in Kenyan lagoonal reefs (see Chapter 4). Different colonies of *P. daedalea* showed either a single annual cycle of gametogenesis and spawning, or two gametogenic cycles per year and biannual spawning.

The majority of *P. daedalea* studied (84%, n = 62) showed a single annual gametogenic cycle. Morphotypes PDV and PDSW had similar gametogenic cycles with oogenesis occurring for 6-7 months from September - March, and spermatogenesis occurring for 5 months from November - March (Fig. 5.5). There was a quiescent non-reproductive period of 4 months between gametogenic cycles for

colonies with only one gametogenic cycle per year. Patterns of oogenesis and spermatogenesis were consistent between the two reproductive seasons, with gametes reaching maturity at approximately the same time in February - March in 2004 and 2005. The pattern, timing and duration of gametogenesis were generally consistent between years. The mean diameter of *P. daedalea* oocytes and gonad mass at maturity were 258.5 µm (sd = 25.3) and 1532.7 µm (sd = 382.4), respectively (Table 5.2).T-tests found no significant differences between the morphotypes PDV and PDSW in regards to mean oocyte ($F_{1,120}$=0.906, p=0.728) or gonad mass diameter ($F_{1,120}$=1.559, p=0.386) or the mean number of oocytes per mesentery ($F_{1,41.2}$=5.794, p=0.894) at maturity. One difference noted between the two reproductive periods was the presence of immature oocytes (mean diameter PDV = 125.8 µm, PDSW = 106.3 µm) in August 2003 samples from 13 colonies, while no gametes were present in corresponding August 2004 samples (Fig 5.5). Three of the 13 colonies sampled in August 2003 had oocytes of >200 µm mean diameter on one mesentery, but without associated spermaries.

The number of oocytes recorded within mesenteries ranged from 0-40 during the study, with some reduction in the mean number of oocytes occurring in the 2-3 months prior to spawning. Two months prior to spawning, >98% of mesenteries in PDV and PDSW contained mature oocytes and spermaries (Fig. 5.6). The mean proportion of mesenteries declined more gradually in PDV and PDSW in the second reproductive season in February and March, and reflects the occurrence of both split-spawning of the population and partial spawning of individual colonies over consecutive lunar months (see section 5.3.4). In a small number of colonies in 2004 (n = 3) and 2005 (n = 6), 3-7 large mature oocytes remained after spawning had occurred, of which <50% had associated spermaries (Fig 5.5). It is likely that after spawning, these unspawned gametes are reabsorbed by the colony. No unspawned mature gametes were found in any of the eight colonies exhibiting biannual spawning.

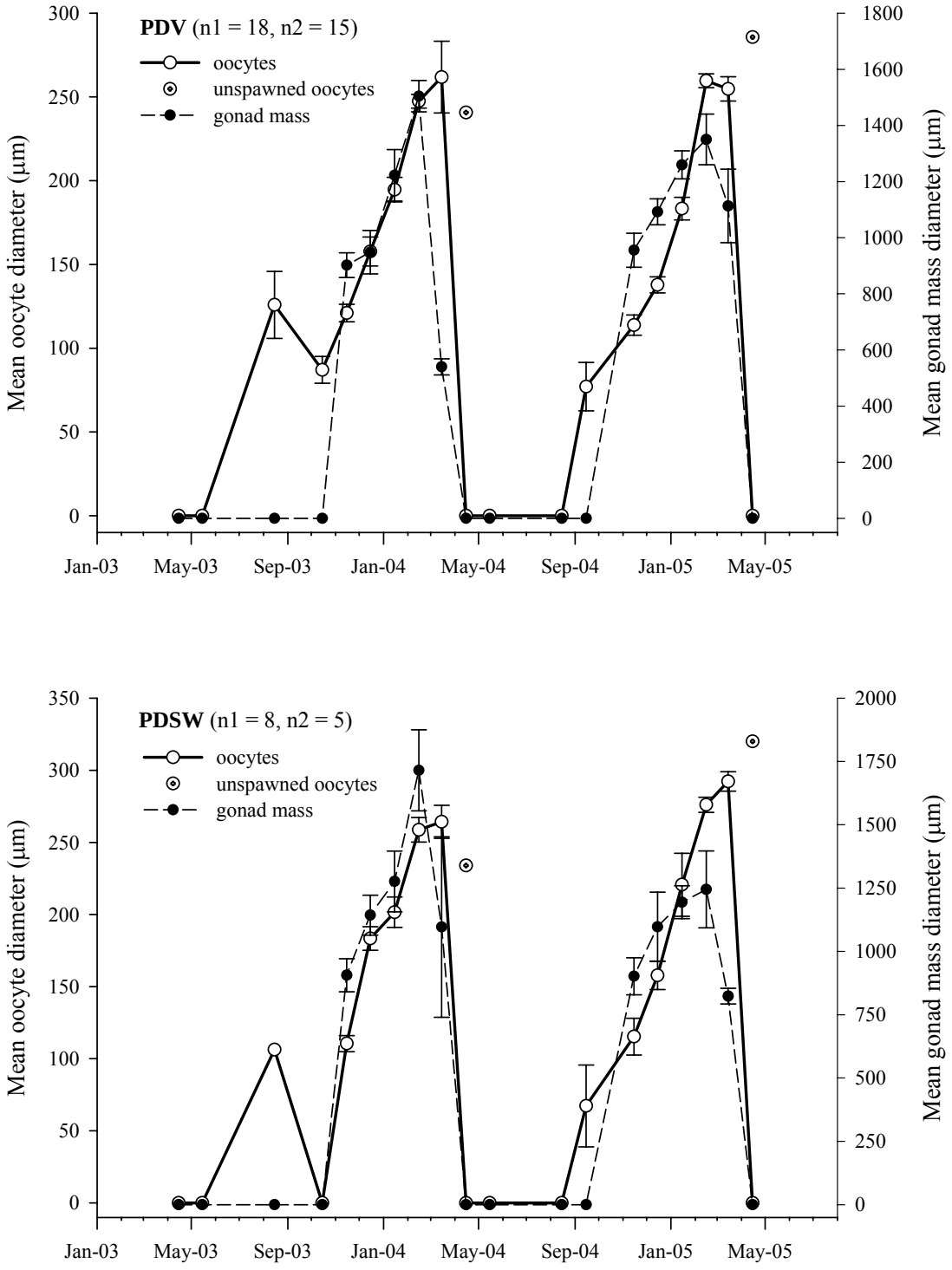


Figure 5.5: *Platygyra daedalea*. Seasonal changes in mean oocyte (left y-axis) and gonad mass (right y-axis) diameter of morphotypes PDV and PDSW, exhibiting annual spawning at Coral Gardens and Nyali Reef from April 2003 – May 2004 (n1), and Kijembe Reef from August 2004 – May 2005 (n2). Mesenteries that did not have gametes present were omitted when calculating mean sizes, and therefore the sizes in the graph represent actual sizes. Error bars are standard errors.

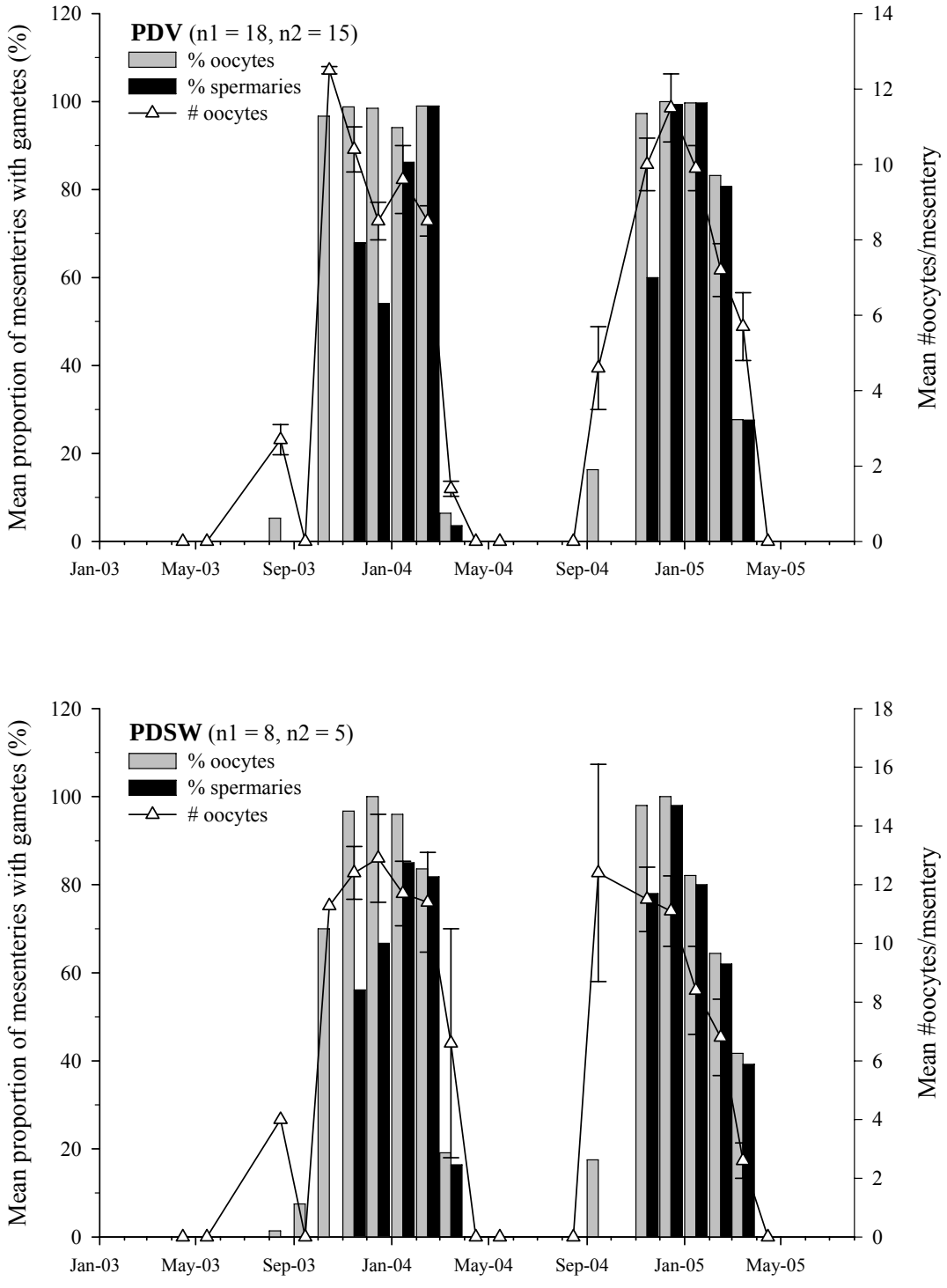


Figure 5.6: *Platygyra daedalea*. Seasonal changes in the mean proportion of mesenteries with oocytes and spermaries (bars) and mean number of oocytes per mesentery (line) in morphotypes PDV and PDSW exhibiting annual spawning at Coral Gardens and Nyali Reef from April 2003 – May 2004 (n1), and at Kijembe Reef from August 2004 – May 2005 (n2). Error bars are standard errors.

Biannual cycles of gametogenesis and spawning were recorded in seven permanent colonies of PDV from Coral Gardens and one colony from Nyali Reef (Fig. 5.7), and two colonies of PDSW from Coral Gardens, in the 2003 - 2004 reproductive season. Four of these eight colonies of the PDV morphotype from Coral Gardens and Nyali Reef that underwent biannual cycles in the 2003 - 2004 reproductive season, were resampled in August 2004 and found with mature gametes. None of the 20 permanent colonies at Kijembe Reef comprising both morphotypes showed biannual cycles of gametogenesis or spawning during the 2004 - 2005 reproductive season. Instead all of these colonies exhibited a single annual cycle of gametogenesis. Due to the low number of colonies of the PDSW morphotype exhibiting biannual cycles, graphical and statistical analyses for biannual gametogenesis and spawning have been limited to PDV colonies.

The presence of small oocytes in May 2003 (25.0-56.3 μm) from one colony of PDV, and the lack of an obvious quiescent period following the minor spawning in August and September 2003 indicates that gametogenic cycles may overlap within biannually spawning corals (Fig. 5.7). Monthly size-frequency distributions of oocytes in samples from May 2003 - September 2004 provides further evidence of overlapping gametogenic cycles in PDV (Fig. 5.8). Each monthly distribution represents the average frequencies of six size-classes of oocytes in the eight colonies sampled, with 'n' representing the number of colonies with gametes present. No graph is shown for May 2004 because gametes were absent from all eight colonies, and no samples were collected in June and July during the study. Graphs for August and September 2003 are similar to each other, with colonies showing oocytes at different developmental stages (i.e. across 4-5 size classes) but with >60% of gametes being of mature size (Fig. 5.8). From October 2003 to April 2004 there is a progressive shift towards the larger size classes, with almost none of the smaller size classes observed in February - April 2004 samples. Only one colony had oocytes in September 2004 and unlike the previous year, no smaller size classes were observed in this sample.

There was no significant difference detected in the mean proportion of mesenteries with oocytes ($p = 0.432$) or spermaries ($p = 0.895$), the mean oocyte ($F_{(1, 15)} = 0.024$, $p = 0.178$) or gonad mass diameter ($F_{(1, 11)} = 0.166$, $p = 0.685$), or the mean number of oocytes per mesentery ($F_{(1, 15)} = 0.682$, $p = 0.879$) at maturity, between the 2003 and

2004 minor spawning events. Hence, for subsequent comparisons with the major spawning, data from the two minor events were pooled. A Mann-Whitney U test found significantly fewer mesenteries of PDV had mature gametes prior to the minor spawning in 2003 (<31%) and 2004 (<34%) compared to major spawning in 2004 (>97%) ($p < 0.001$, Table 5.4, Fig. 5.9). The high proportion of mesenteries with gametes during major spawning (in 7 out of 8 colonies this was 100%), suggests that most individual polyps are capable of spawning biannually. Another notable difference between minor and major spawning events was that male reproductive output was lower during minor spawning, where only 36.9-59.2% (mean = 48.1%) of mesenteries with mature oocytes had associated spermaries (Fig. 5.9). Mean oocyte diameter did not differ significantly between minor and major spawning events ($F_{(1, 23)} = 1.306$, $p = 0.919$, Table 5.4). By comparison, both the mean gonad mass diameter ($F_{(1, 8.9)} = 4.510$, $p<0.01$) and the mean number of oocytes per mesentery ($F_{(1, 23)} = 5.228$, $p<0.001$) showed significant differences between spawning events, suggesting a greater investment of reproductive energy for the major spawning in the northeast (NE) monsoon season.

Table 5.4: The mean and standard deviations (in parentheses) for the proportion of mesenteries with gametes, diameter of oocytes and gonad mass and the number of oocytes per mesentery in *Platygyra daedalea* prominent valley morphotype, during minor and major spawning events at Coral Gardens and Nyali Reef. Tests for significant differences between spawning events are also shown.

Measurement	**Minor**	**Major**	**Test**	**p-value**
Mesenteries with oocytes	32.5% (25.3)	99.4% (1.8)	Mann-Whitney U	< 0.001
Mesenteries with spermaries	14.7% (14.2)	96.9% (7.0)	Mann-Whitney U	< 0.001
Oocyte diameter	258.9 µm (60.5)	256.5 µm (41.0)	T-test	0.919
Gonad mass diameter	745.9 µm (183.0)	1457.4 µm (397.3)	T-test	< 0.010
# oocytes	3.3 (1.8)	7.9 (3.8)	T-test	< 0.001

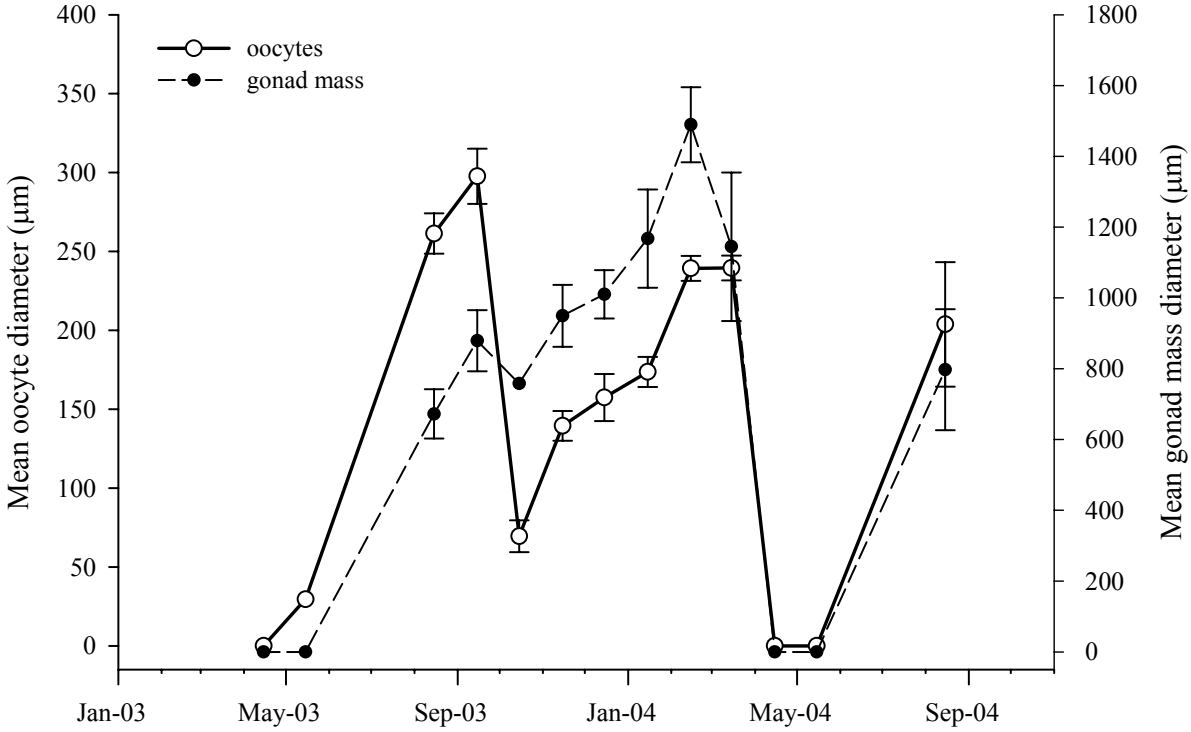
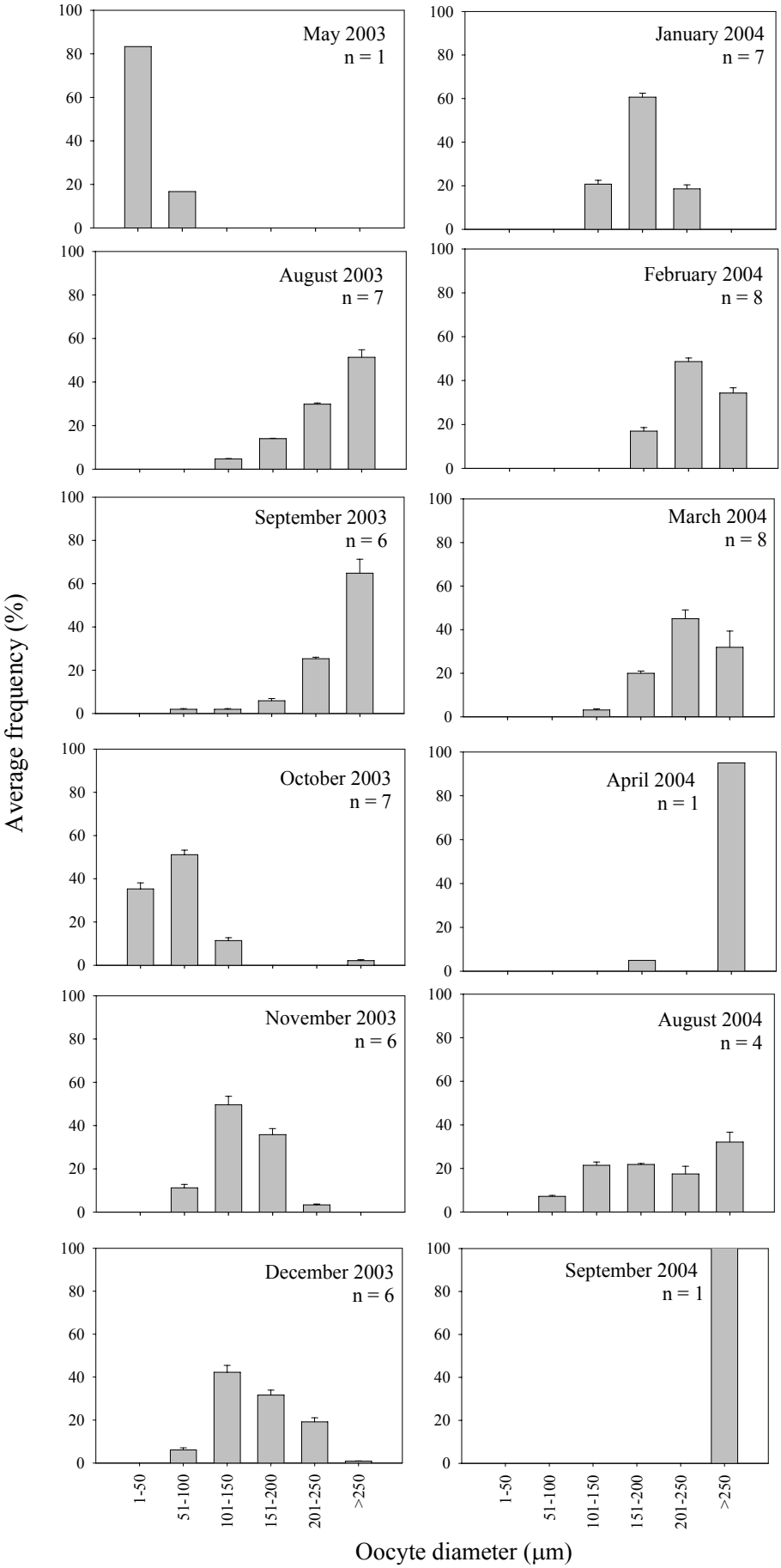


Figure 5.7: *Platygyra daedalea* prominent-valley morphotype. Seasonal changes in mean oocyte (left y-axis) and gonad mass (right y-axis) diameter of colonies exhibiting biannual spawning at Coral Gardens and Nyali Reef from April 2003 – August 2004. Mesenteries that did not have gametes present were omitted when calculating mean sizes, and therefore the sizes in the graph represent actual sizes. Error bars are standard errors. n = 8.

Figure 5.8 (overleaf): Average size-frequency distributions of oocyte diameters from *Platygyra daedalea* colonies (PDV morphotype) exhibiting biannual spawning at Coral Gardens and Nyali Reef, between May 2003 - September 2004. Eight colonies were examined each month (except in June-July in 2003 and 2004). No gametes were present in colonies in May 2004. n = number of colonies with gametes present. Error bars are standard errors.


May 2003
n = 1
January 2004
n = 7
August 2003
n = 7
February 2004
n = 8
September 2003
n = 6
March 2004
n = 8
October 2003
n = 7
April 2004
n = 1
November 2003
n = 6
August 2004
n = 4
December 2003
n = 6
September 2004
n = 1
Average frequency (%)
Oocyte diameter (µm)
1-50
51-100
101-150
151-200
201-250
>250

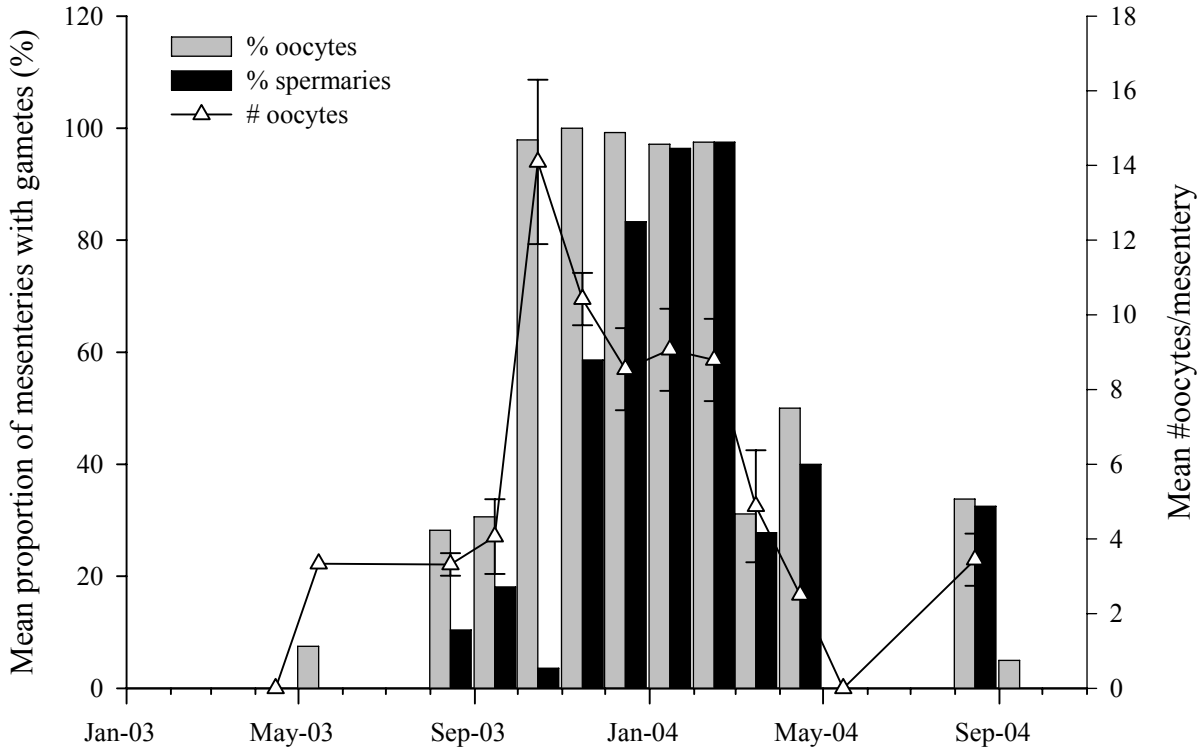


Figure 5.9: *Platygyra daedalea* prominent valley morphotype (PDV). Seasonal changes in the mean proportion of mesenteries with oocytes and spermaries (bars) and mean number of oocytes per mesentery (line) in colonies exhibiting biannual spawning at Coral Gardens and Nyali Reef from April 2003 – May 2004. Error bars are standard errors. n = 8.

5.3.3.3 Leptoria phrygia

Colonies of *L. phrygia* showed different patterns of gametogenesis during the sampling period from September 2004 - February 2005. A single cycle of gametogenesis was observed in all *L. phrygia* colonies during the sampling period. Samples collected in September 2004 already contained oocytes with a mean diameter of 87.6 μm, which suggested that oogenesis commenced some time prior to this month. Therefore, oogenesis occurred for approximately 6-7 months from August - February, and spermatogenesis occurred for 4-5 months from October - February (Fig.

5.10). While oogenesis commenced earlier than spermatogenesis, gametes reached maturity at approximately the same time in December 2004. Mean oocyte and gonad mass diameters at maturity were 232.8 μm (sd = 51.7) and 1239.0 μm (sd = 242.5), respectively (Table 5.2).

The mean number of oocytes per mesentery decreased progressively from 10.1 to 7.5 from September to December suggesting some resorption of oocytes may have occurred (Fig. 5.11). There was also a corresponding decrease in the mean proportion of mesenteries with oocytes from 92.1% in September to 77.1% just prior to the commencement of spawning following the full moon on 26 December 2004 (Fig. 5.12). The mean proportion of mesenteries with gametes decreased in January 2005 to <30% and reflects split-spawning within the population (see section 5.3.4). There was an increase in the proportion of mesenteries with oocytes observed between January and February 2005 from 30 to 50% (Fig. 5.11), and the range of oocyte sizes present in five of the ten colonies, particularly noticeable from December - January, suggested there may be two overlapping oogenic cycles occurring within some individual colonies. A closer examination of the gametogenic cycles of each of the ten colonies studied showed the following patterns: five colonies had one oogenic cycle throughout the study; the remaining five colonies had two oogenic cycles with spawning occurring in consecutive lunar months (December and January), with mature (and a small number of immature) oocytes present in three of these colonies in February 2005, after the second spawning had occurred. Not all mature oocytes in the second oogenic cycle had spermaries associated with them (Fig. 5.11), indicating that there is a much larger investment of reproductive effort in the first oogenic cycle.

Monthly size-frequency distributions of oocytes from May 2003 to September 2004 provided further evidence for overlapping oogenic cycles in *L. phrygia* (Fig. 5.12). Each monthly distribution represents the average frequencies of the four size-classes of oocytes in the ten sampled colonies, with 'n' representing the number of colonies with gametes present. Figure 5.12 shows a progressive change from a dominance of smaller size classes in September 2004 to larger size classes dominating in December 2004 and January 2005. Small size classes are present throughout the study period, suggesting that these oogenic cycles overlap for at least part of the gametogenic cycle.

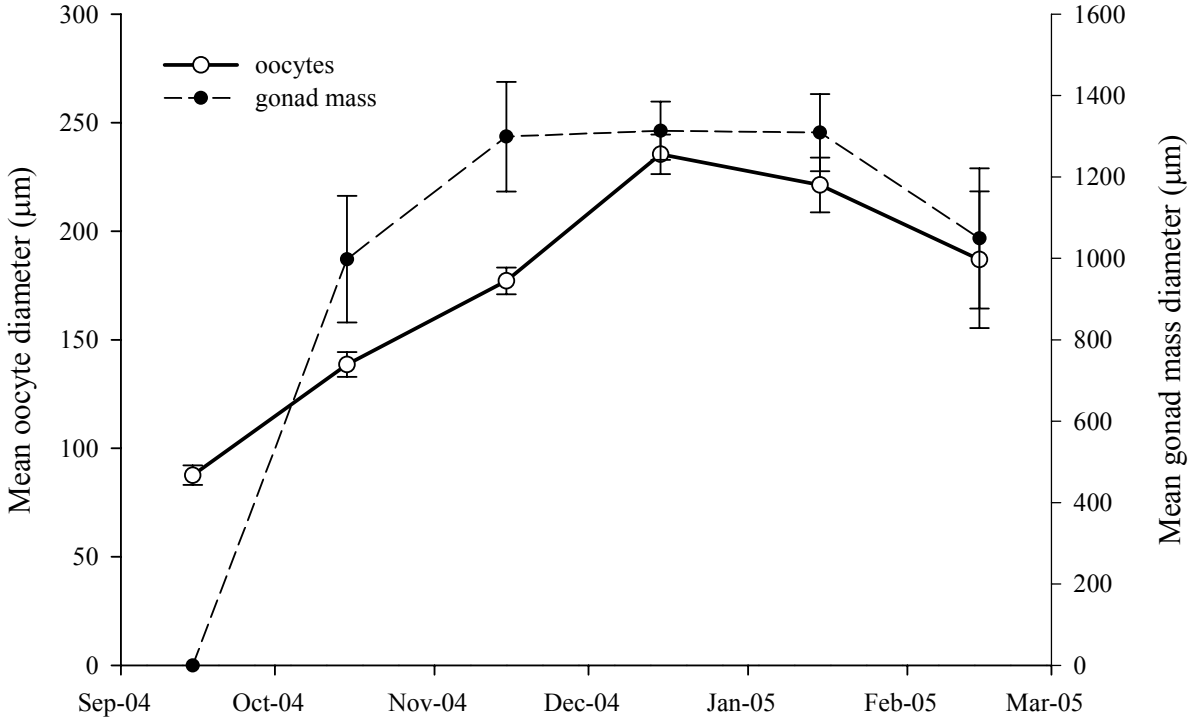


Figure 5.10: *Leptoria phrygia*. Seasonal changes in mean oocyte (left y-axis) and gonad mass (right y-axis) diameter at Nyali Reef. Mean diameter was calculated only on mesenteries with gametes present (therefore gamete sizes in the graph represents actual sizes). n = 10. Error bars are standard errors.

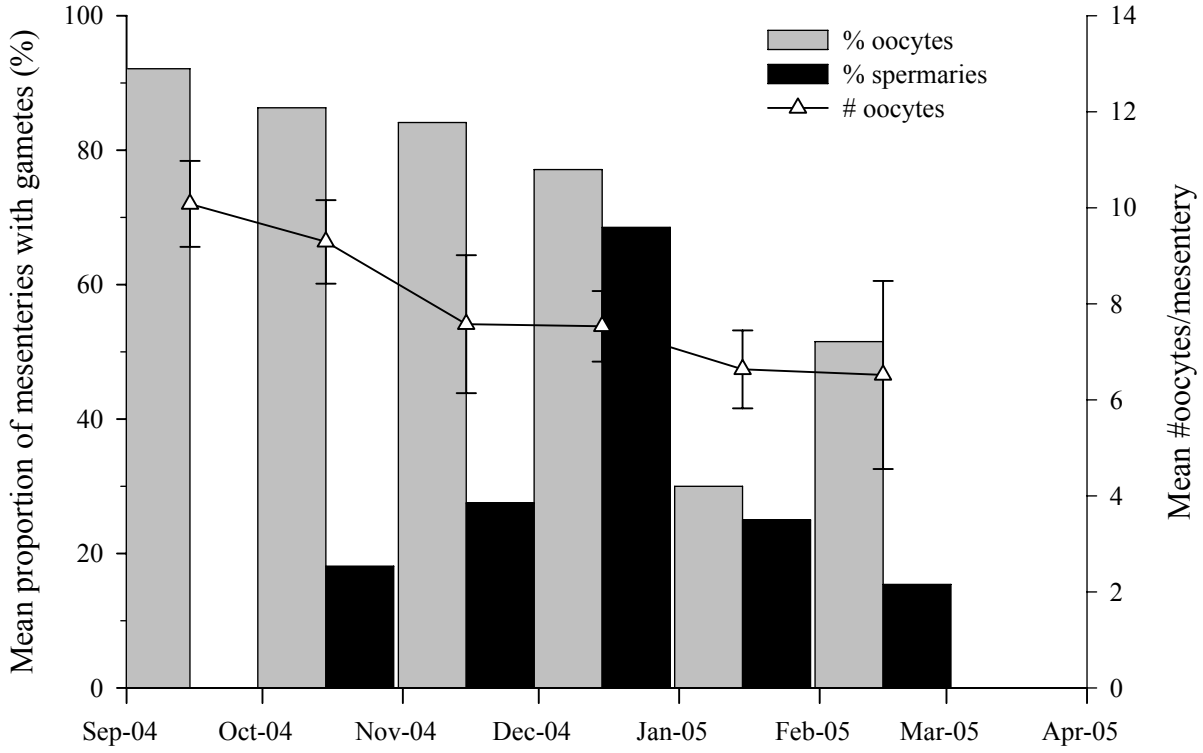


Figure 5.11: *Leptoria phrygia.* Seasonal changes in the mean proportion of mesenteries with oocytes and spermaries (bars) and mean number of oocytes per mesentery (line) at Nyali Reef (n = 10). Error bars are standard errors.

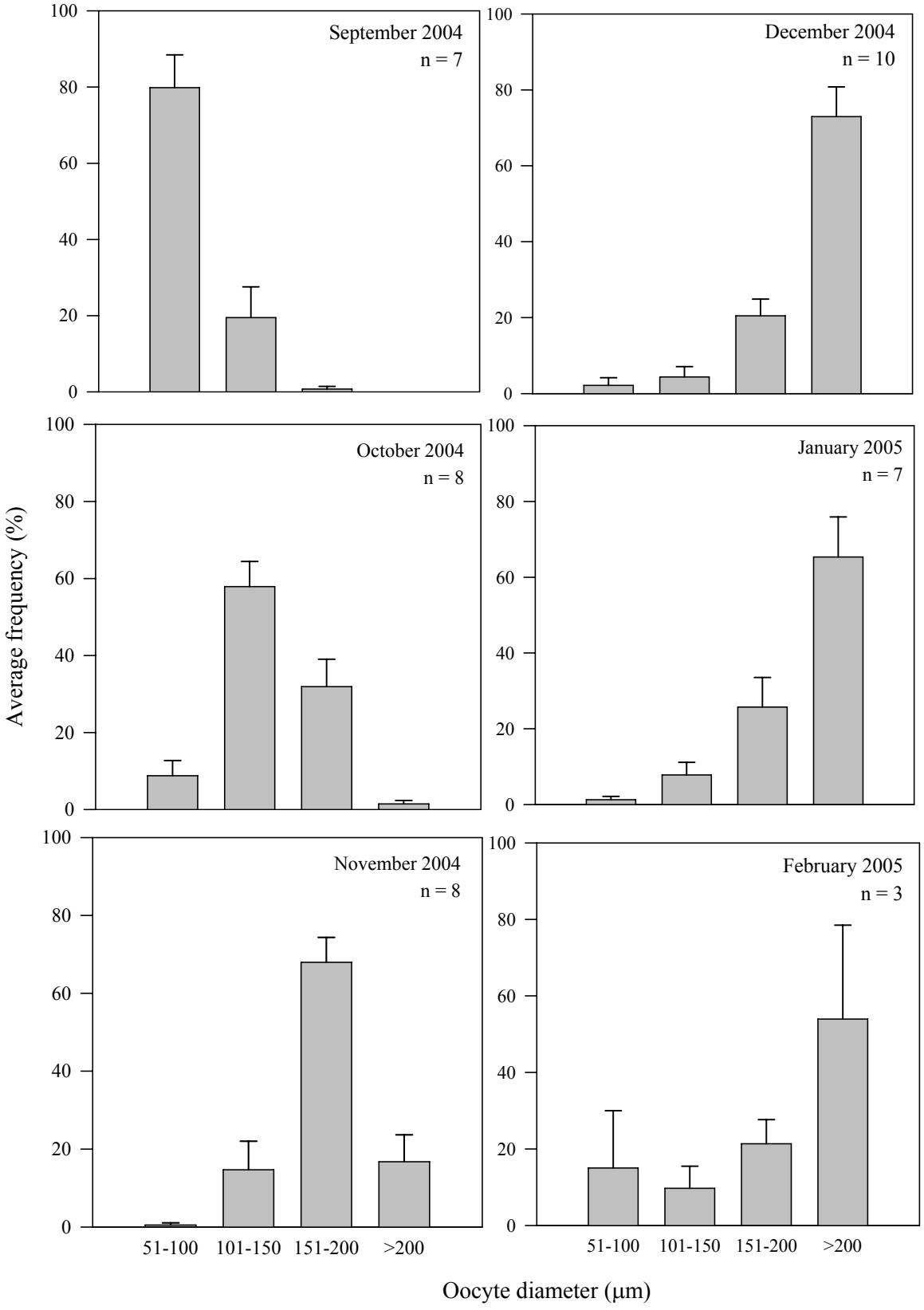


Figure 5.12: *Leptoria phrygia*. Average size-frequency distributions of oocyte diameters (>50 µm) at Nyali Reef from September 2004 - February 2005. n = number of colonies with gametes present. Error bars are standard errors.

5.3.4 Seasonality and the timing of spawning

5.3.4.1 Echinopora gemmacea

Mature gametes present in dissected polyps of *E. gemmacea* were not visible in the field or in fresh samples examined under a stereomicroscope. Spawning occurred during the NE monsoon and was split between February, March and April, and this pattern was consistent between study years (Table 5.5; Fig. 5.13; see also Fig. 3 in Mangubhai and Harrison 2006). Spawning periods in *E. gemmacea* overlapped with *P. daedalea* for the months of February and March in 2004 and 2005, and April in 2004, but did not overlap with the spawning period of *L. phrygia* (Table 5.5; Fig. 5.13). There were no differences in the spawning periods of *E. gemmacea* between the three study sites, and all marked colonies produced mature gametes in both years. Spawning records were not obtained for two marked colonies in 2005 which suffered 40-55% partial mortality from crown-of-thorns starfish (*Acanthaster planci*) predation 4-5 months prior to spawning, though oocytes and spermaries were observed in both colonies.

In 11 of the 21 colonies studied in 2005, spawning was inferred to have occurred during a 7-8 day period, and most likely between the full moon and last lunar quarter (Table 5.6; Fig. 5.13). Partial spawning was recorded in approximately 20% of the permanent colonies sampled in 2004 (n = 20) and in 2005 (n = 21). Data from three colonies that partially spawned in 2005, suggest that gametes were released over a number of consecutive nights, rather than during consecutive lunar months (Fig. 5.13). Spawning in 2004 is likely to have occurred over consecutive nights and lunar months. While spawning was not directly observed in this species, brown eggs were found floating on the water surface at 21:45 hours on 26 February 2005, two nights AFM, above two colonies held in aquaria. No samples were collected in the field on the 26 and 27 February, and therefore it is not possible to confirm if spawning coincided with spawning on the reef. However, the timing of spawning is consistent with the period in which spawning occurred in this species in 2005. The remaining two colonies in aquaria did not spawn and were returned to the sea five days later.

Table 5.5: The proportion of the population that spawned in each lunar month. Colonies that partially spawned are only listed once. Number of colonies are indicated in parentheses. ?: only mature samples observed, and spawning was inferred to have occurred after April full moon. '–': no sampling was done.

Year	Species	Dec	Jan	Feb	Mar	Apr
2004	*E. gemmacea*	0	0	5.3 (1)	57.9 (11)	36.8 (7)
	P. daedalea	0	0	5.3 (4)	93.4 (71)	1.3 (1)
2005	*E. gemmacea*	0	0	49.2 (9)	49.2 (9)	14.3 (3)?
	P. daedalea	0	0	75.0 (30)	25.0 (10)	0
	*L. phrygia**	78.6 (11)	21.4 (3)	0	-	-

Figure 5.13 (overleaf): Reproductive periods for marked colonies of faviids in Mombasa Marine National Park and Reserve from 2004-2005. Each line is a spawning record for a single colony. ●—○ = the period between the last sample date when gametes were present (closed symbol) and the subsequent sample date when gametes were absent (open symbol), ●—●—○ , ●—● ●—○ = the closed symbols in the middle represent the date(s) when some of the gametes had disappeared, indicating partial spawning occurred. Two ●—○ on a single line indicates colonies where mature and immature oocytes were observed (i.e. a range of oocyte size classes), and spawning was observed twice. Different symbols have been used to differentiate between *P. daedalea* morphotypes PDV (circles) and PDSW (triangles). ○= full moon, ● = new moon.

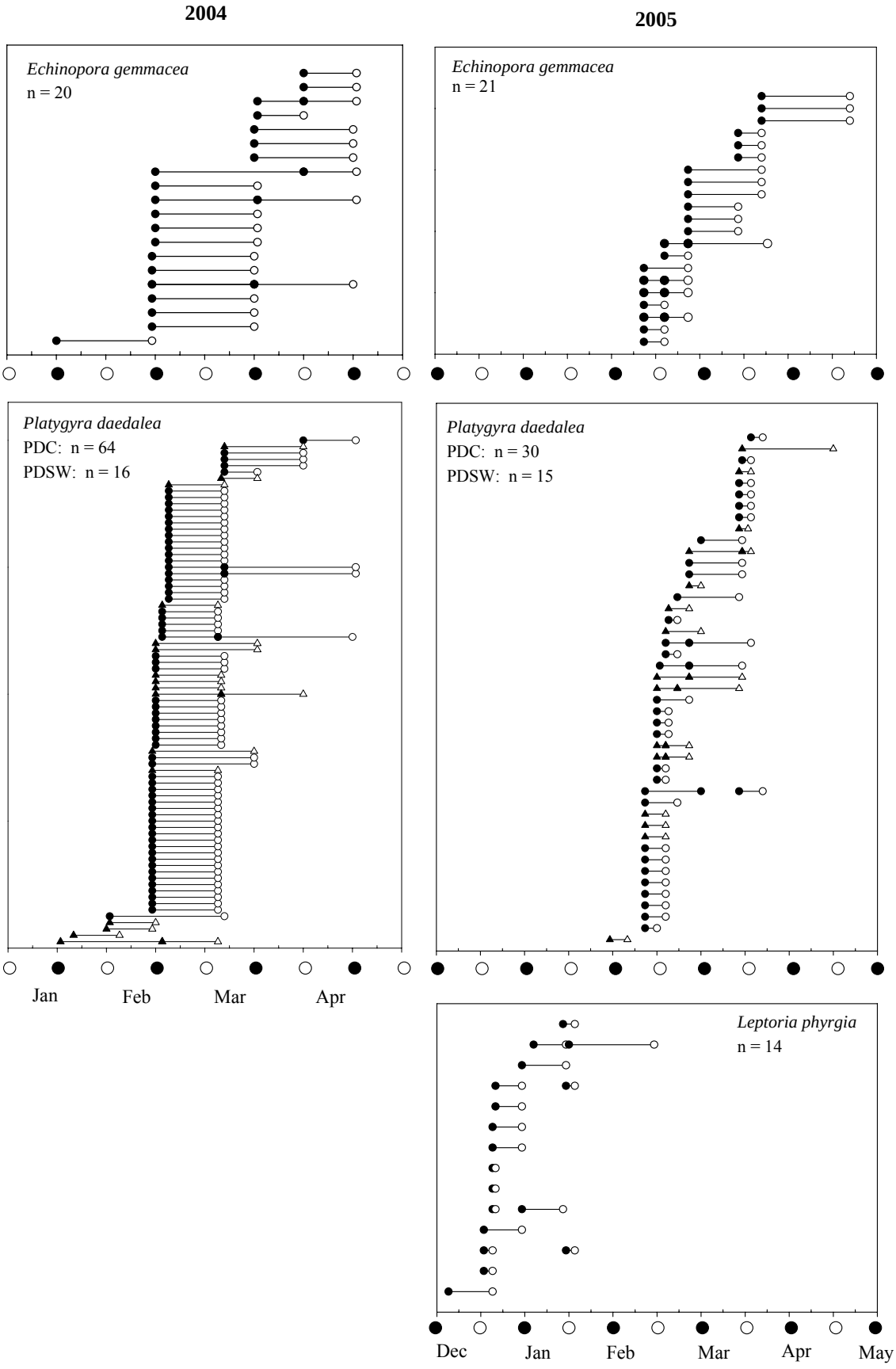

2004
2005
Echinopora gemmacea
n = 20
Echinopora gemmacea
n = 21
Platygyra daedalea
PDC: n = 64
PDSW: n = 16
Platygyra daedalea
PDC: n = 30
PDSW: n = 15
Leptoria phyrgia
n = 14
Jan
Feb
Mar
Apr
Dec
Jan
Feb
Mar
Apr
May

Table 5.6: The lunar phase when the last sample was observed (Moon-mat) and subsequent sample when gametes were absent (Moon-abs) from coral colonies containing mature gametes. Lunar days are divided into four lunar quarters: 1st = 0-7, 2nd = 8-14, 3rd = 15-21, 4th = 22-29, where lunar day 0 = new moon, and lunar day 15 = full moon. Data are shown for colonies with spawning periods inferred from samples taken over 10 days or less. Asterisks indicate when partial spawning occurred. Days = days between samples. Full moons were on 27 December 2004, and 25 January, 24 February, 26 March in 2005.

Species	n	Mature	Absent	Days	Moon-mat	Moon-abs	Lunar quarter
E. gemmacea	6	21-Feb-05	28-Feb-05	7	12	19	2nd/3rd
	3	25-Mar-05	2-Apr-05	8	14	22	2nd/3rd
	2	28-Feb-05	8-Mar-05	8	19	27	3rd/4th
	3*	28-Feb-05	8-Mar-05	8	19	27	3rd/4th
P. daedalea	1	9-Feb-05	15-Feb-05	6	0	6	1st
	11	21-Feb-05	28-Feb-05	7	12	19	2nd/3rd
	1	26-Feb-05	8-Mar-05	10	17	27	2nd/3rd
	1	25-Mar-05	28-Mar-05	3	14	17	2nd/3rd
	6	25-Mar-05	29-Mar-05	4	14	18	2nd/3rd
	1*	25-Mar-05	2-Apr-05	8	14	22	2nd/3rd
	4	25-Feb-05	28-Feb-05	3	16	19	3rd
	3	25-Feb-05	1-Mar-05	4	16	20	3rd
	1*	26-Mar-05	29-Mar-05	3	15	18	3rd
	1	29-Mar-05	2-Apr-05	4	18	22	3rd
	1	25-Feb-05	4-Mar-05	7	16	23	3rd/4th
	1	28-Feb-05	4-Mar-05	4	19	23	3rd/4th
	1	28-Feb-05	8-Mar-05	8	19	27	3rd/4th
	2*	28-Feb-05	8-Mar-05	8	19	27	3rd/4th
	1	1-Mar-05	4-Mar-05	3	20	23	3rd/4th
	1	1-Mar-05	8-Mar-05	7	20	27	3rd/4th
	1	8-Mar-05	12-Mar-05	4	27	1	4th/1st
L. phrygia	1	24-Jan-05	28-Jan-05	4	14	18	2nd/3rd
	2	28-Dec-04	31-Dec-04	3	16	19	3rd
	3	31-Dec-04	1-Jan-05	1	19	20	3rd
	2	31-Dec-04	10-Jan-05	10	19	0	3rd/4th
	2	1-Jan-05	10-Jan-05	9	20	0	3rd/4th

5.3.4.2 Platygyra daedalea

Pink mature oocytes of *P. daedalea* were observed in the field and in fresh samples examined under a stereomicroscope up to seven weeks prior to spawning. Major spawning in this species occurred during the NE monsoon, predominantly in February and March, and this pattern was consistent between study years (Table 5.5). Spawning was more synchronous in *P. daedalea* in the major spawning period in 2004, where 93.4% of the population spawned in March, compared to 75.0% of the population spawning in the major spawning period in February 2005.

There were no differences in the spawning periods between the three sites or between the two morphotypes PDV and PDSW, though it was noted that a small number of colonies of PDSW spawned early during the major spawning period in 2004 (Fig. 5.13). Minor spawning occurred during the southeast (SE) monsoon and was split between August and September in both study years, though one colony spawned as late as October in 2003 (Fig. 5.14). Fewer colonies spawned during the minor spawning in 2004 (12.5%, n = 64) compared to 2003 (19.2%, n = 73), while >97% spawned during the major spawning in 2004 (n = 82) and 2005 (n = 46). In three colonies, spawning was recorded in three consecutive spawning events – August 2003, February 2004 and August 2004, indicating that some colonies can spawn biannually over consecutive years.

Spawning was inferred to have occurred during a 3-8 day period in 33 of the 46 colonies studied in 2005 (Table 5.6). The majority of colonies spawned between full moon (lunar day 15) and the last lunar quarter (lunar day 22), with the data showing that the population spawned over more than one night and over consecutive lunar months (Table 5.6, Fig. 5.13). There were two notable exceptions. One colony of PDSW spawned in the first lunar quarter, between the new moon and lunar day 6, while a second colony spawned in the period around the new moon (between lunar day 27 and the following lunar day 1) (Table 5.6). Given that the population of *P. daedalea* spawned over more than one night, there is a high probability of an overlap with spawning nights for *E. gemmacea.* Spawning periods recorded for the two minor spawning events are too broad to make statements on timing in relation to lunar

periods for most colonies (Fig. 5.14). However, spawning occurred between full moon and new moon in one colony in August 2003 and in two colonies in September 2003, and between new moon and the next full moon in three colonies in August 2003.

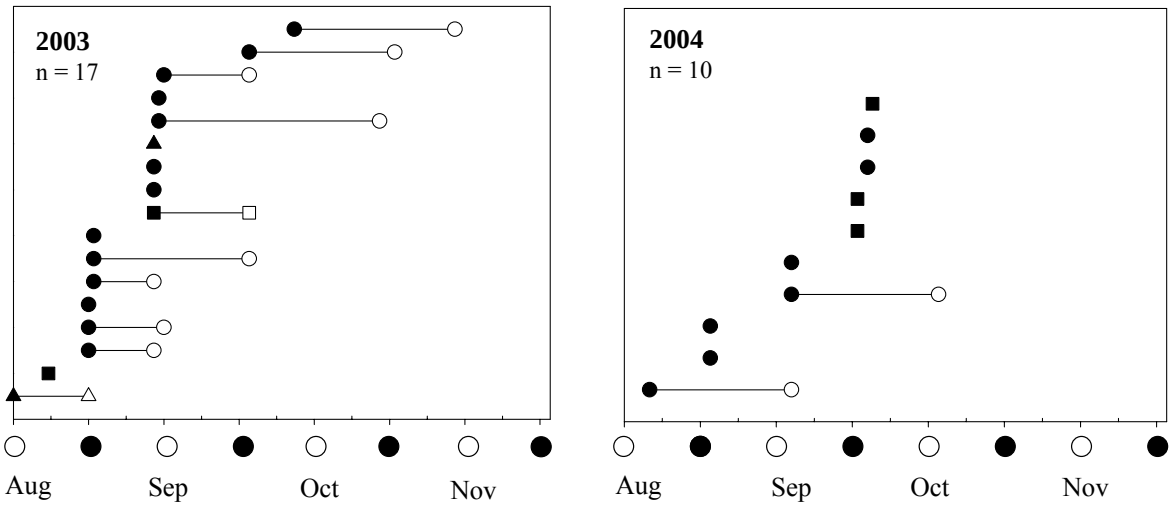


Figure 5.14: Reproductive periods for marked colonies of Platygyra daedalea during the minor spawning periods in 2003 and 2004. Each line is a spawning record for a single colony. ●—○ = the period between the last sample date when gametes were present (closed symbol) and the subsequent sample date when gametes were absent (open symbol). Data are presented for P. daedalea morphotypes PDV (circles), PDSW (squares) and unclassified colonies (inverted triangles). Symbols on their own indicate that mature samples were observed, but no subsequent samples were taken from that colony. ○= full moon, ●= new moon.

5.3.4.3 Leptoria phrygia

Pink mature oocytes of *L. phrygia* were observed in the field and in fresh samples examined under a stereomicroscope, up to 5.5 weeks prior to spawning. Spawning in this species occurred during the NE monsoon, predominantly in December and January, and did not overlap with spawning periods for *E. gemmacea* and *P. daedalea* (Fig. 5.13). Overlapping oogenic cycles in *L. phrygia* meant some colonies had immature oocytes that were retained and underwent further development, and reached maturity in February, though <20% of these had associated spermaries. There were no

differences in the spawning periods between Nyali and Kijembe Reefs, and 14 of the marked colonies (70%) spawned mature gametes in December 2003 - January 2004 (Table 5.5, Fig. 5.13). Of the six colonies that did not spawn during the sampling period, two had mature gametes in 8 of the 40 mesenteries sampled in December, but had no gametes in mesenteries in samples taken two weeks prior to this. It is not clear whether these colonies spawned earlier than the rest, or whether reproductive effort was much lower, and therefore highly variable between sample periods. No gametes were recorded in four colonies (20%), but because they were not sampled until December it is not possible to determine whether these colonies had spawned in November prior to sampling, or whether they did not produce gametes that year.

Spawning was inferred to have occurred during a 1-8 day period in 6 of the 14 colonies studied in 2005 (Table 5.6). In three colonies, spawning occurred on 31 December 2004, the 4th night AFM. In two other colonies spawning occurred in the period between the 1st and 3rd nights AFM. Therefore, spawning in *L. phrygia* is likely to occur over a number of consecutive nights.

Gametes were released in one aquarium colony at approximately 21:30 hours on the nights of the 30 and 31 December 2004, and 1 January 2005 with gamete 'setting' occurring an hour prior to release. However, spawning in this colony may have been induced by sampling stress because the colony from which the aquarium sample was removed did not spawn in the field until after the 10 January 2005. Compact positively buoyant bundles composed of eggs and sperm clusters were slowly extruded through the mouth (Type I spawning behaviour, Babcock et al. 1986), and floated immediately to the water surface where the water movement generated by the airstone caused bundles to slowly break apart, separating individual eggs and sperm clouds (Fig. 5.15).

Figure 5.15: Photographs showing ‘setting’ and spawning (above) and released egg-sperm bundles (larger spheres) and individual eggs (below) in *Leptoria phrygia*.

5.3.4.4 Environmental parameters

The annual range in mean weekly sea surface temperatures at Coral Gardens and Nyali Reef were similar and showed a marked seasonal pattern with temperatures ranging from 24.7-29.7 ºC, a difference of 5 ºC (Fig. 5.16). The highest temperatures were recorded during the NE monsoon months in March and April, and the lowest temperatures were recorded in the SE monsoon months of August and September, with the greatest fluctuations occurring over the summer between January and April (average minimum = 26.9 ºC; maximum = 29.6 ºC). The rapid drop in temperature between April and May is associated with the switch in the monsoon seasons from NE to SE, which occurred in early to mid-April during the two study years (Fig. 5.16).

Major spawning in the three faviid species occurred in the NE monsoon when temperatures reached their summer maximum averaging 28.3 ºC, and wind conditions were slow and steady and seas were calm. Minor spawning in *P. daedalea* occurred in the SE monsoon, when temperatures averaged 25.4 ºC (average minimum = 25.0 ºC, maximum = 26.5 ºC). While data were not available for the study years, averages from 1997 - 2003 indicate that solar radiation is highest during the major spawning in February and March, and is undergoing the steepest increase during the minor spawning in August and September (see Fig. 2.3, Chapter 2). Spawning coincided with periods of low rainfall, with the major spawning occurring just prior to peak rainfall on the coast (see Fig. 2.4, Chapter 2). Salinity was 35 ‰ at all sites and at all sampling times during the study. Turbidity varied between 4.9-15.3 m secchi depth during the study and was significantly correlated with tidal height ($F_{(1, 139)}$, $p < 0.001$), though the relationship was not strong ($r^2 = 0.17$). Sampling was not done during the main SE monsoon months of June and July when the prevailing winds are the strongest and sea conditions are the roughest, compared to other months of the year. However, turbidity ranges in May and August, were similar to those recorded in the NE monsoon months.

In Kenya, spring tides occur one or two days after the full and new moon and neap tides occur just after the second and last lunar quarter. Spawning in *P. daedalea* and *L. phrygia* in Kenya coincided with spring tides (Fig. 5.17). The spawning period for *E. gemmacea* was not sufficiently defined to depict the likely tidal regime.

In *L. phrygia* spawning occurred on the night of the 31 December 2004, as inferred by the disappearance of gametes from sequential samples taken from three colonies in the field. Spawning also occurred in one colony kept in the laboratory on the same night, around 21:30 hours, which coincided with the tide dropping to the second low tide of the day, when tidal mixing was likely to be minimal (Fig. 5.18). The difference in tidal height between 19:07 and 00:50 hours was on that night 2.1 m.

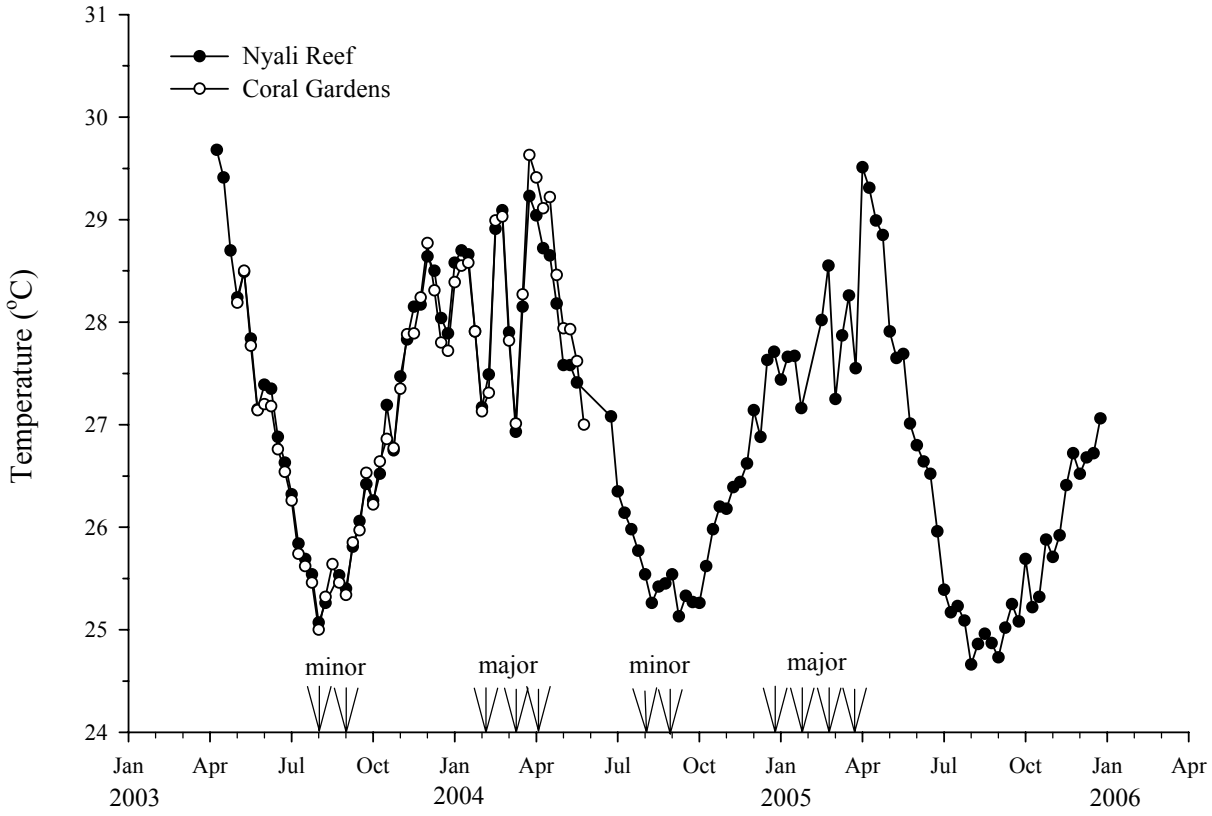


Figure 5.16: Mean weekly sea surface temperatures at Coral Gardens (white circle) from May 2003 – June 2004 and at Nyali Reef (black circle) from April 2003 - December 2005. Arrows indicate months when minor and major spawning occurred.

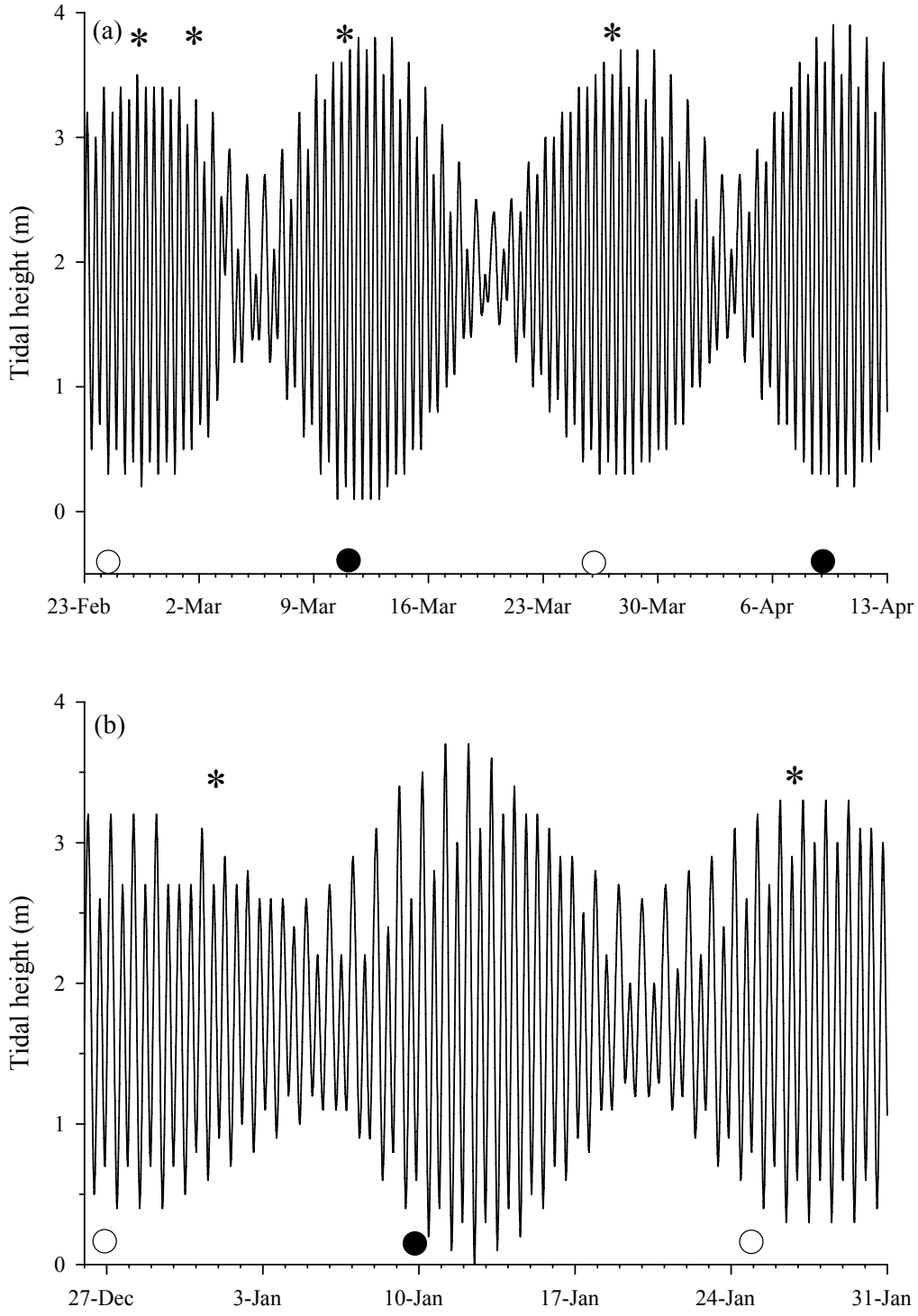


Figure 5.17: Tidal and lunar rhythms in Kenya during the summer spawning months in 2005. Asterisks indicate when spawning occurred in (a) *Platygyra daedalea* and (b) *Leptoria phrygia*. ○: full moon, ●: new moon.

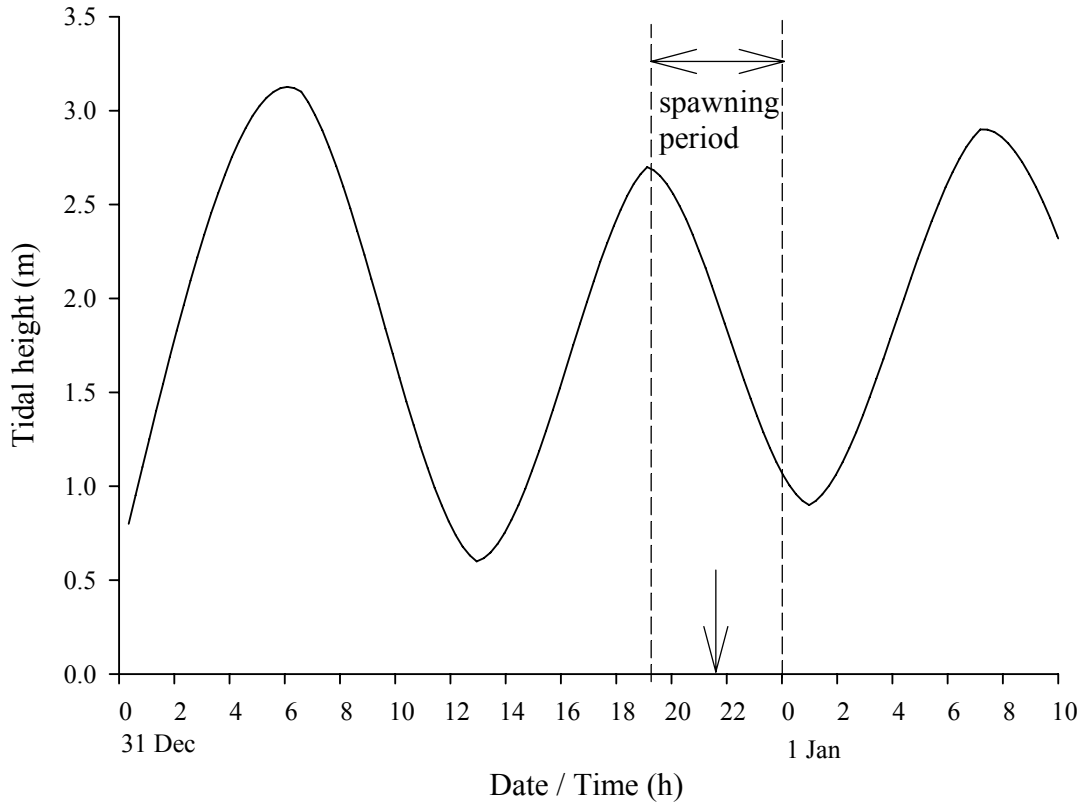


Figure 5.18: Tidal phase at Nyali Reef on 31 December 2004, the 4th night after full moon. 'Spawning period' marks the hours between sunset and midnight, and the arrow on the x-axis indicates the timing of spawning (21:30 hours) recorded in *Leptoria phrygia* held in an aquarium.

The timing of sunrise and sunset varies annually by 30 minutes in Kenya and there is little seasonal variation in daylength, with the greatest range being 10 minutes (Fig. 5.19). Major spawning occurred after the longest day period which coincides with the declining change in daylength, while minor spawning occurred before the shortest day period (Fig. 5.19).

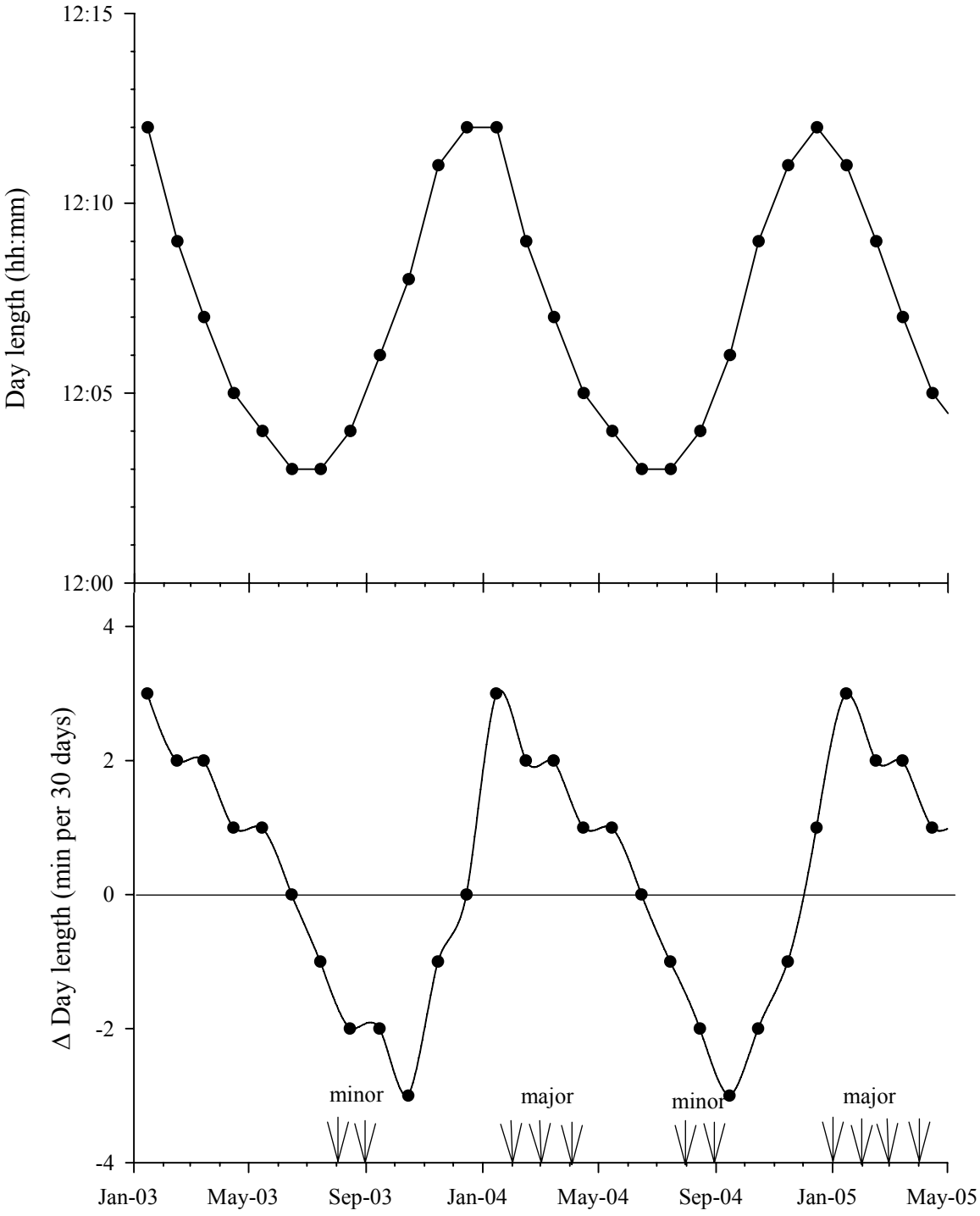


Figure 5.19: Seasonal variation in daylength in Kenya. Arrows indicate when spawning was recorded in *Echinopora gemmacea, Platygyra daedalea* and *Leptoria phrygia*. Daylength calculated from sunrise and sunset times from the internet (www.timeanddate.com/worldclock/astronomy.html) for Nairobi, Kenya.

5.3.5 Fecundity estimates for Kenyan faviids

Repeated sampling of permanent colonies for gametogenesis resulted in the removal of up to 12.6% (mean = 4.8%), 11.7% (mean = 4.4%) and 4.4% (mean = 1.9%) of living tissue from colonies of *E. gemmacea*, *P. daedalea* and *L. phrygia*, respectively. By contrast, up to 6% (mean = 1.8%) and 1.6% (mean = 1.3%) of living tissue was removed from additional colonies of *E. gemmacea* and *P. daedalea*, respectively, sampled briefly during the spawning periods. No data were collected for additional sampled colonies of *L. phrygia*. There were no significant differences in mean oocyte diameter or the mean number of oocytes per mesentery between permanent and additional colonies of *E. gemmacea* and *P. daedalea* ($p > 0.05$, Table 5.7-5.8). There was no interaction between sites and colony type (i.e. permanent versus additional) for both species.

The two-way ANOVA did, however, detect significant differences in both the mean oocyte diameter and mean number of oocytes per mesentery between sites for *P. daedalea*. A Tukey HSD post-hoc test found significant differences in the mean oocyte diameter between all three sites ($p < 0.05$), and significant differences between Nyali Reef and Kijembe Reef for the mean number of oocytes per mesentery ($p < 0.05$). There were no site differences for *E. gemmacea.* The mean, standard deviation, minimum and maximum values for both oocyte parameters (i.e. diameter and number) for *P. daedalea* at each of the sites, are provided in Table 5.9.

Table 5.7: Results of a two-way ANOVA to test for potential impacts of repeated sampling on mean oocyte diameter and the mean number of oocytes per mesentery in *Echinopora gemmacea.* Type: permanent versus additional colonies. Data for mean oocyte diameter did not meet the assumption for equal variances, and hence data were log (x+1) transformed.

Source	SS	df	MS	F	p-value
Ln (Oocyte diameter)					
Type	6.7×10^{-3}	1	6.7×10^{-3}	0.365	0.547
Site	2.8×10^{-2}	2	1.4×10^{-2}	0.751	0.475
Type*Site	3.2×10^{-5}	1	3.2×10^{-5}	0.002	0.967
Number of oocytes/mesentery					
Type	10.6	1	10.6	0.163	0.687
Site	44.8	2	22.4	0.344	0.710
Type*Site	0.6	1	0.6	0.009	0.926

Table 5.8: Results of a two-way ANOVA to test for potential impact of repeated sampling on mean oocyte diameter and the mean number of oocytes per mesentery in *Platygyra daedalea.* Type: permanent versus additional colonies.

Source	SS	df	MS	F	p-value
Oocyte diameter					
Type	279.8	1	279.8	0.546	0.461
Site	16 835.8	2	8417.9	16.422	< **0.001**
Type*Site	2336.1	2	1168.0	2.279	0.107
Number of oocytes/mesentery					
Type	2.2×10^{-4}	1	2×10^{-4}	0.000	0.997
Site	89.5	2	44.7	3.869	< **0.050**
Type*Site	29.802	2	14.9	1.289	0.279

Table 5.9: The mean oocyte diameter and mean number of oocytes per mesentery in *Platygyra daedalea* at the three study sites.

	n	Oocyte diameter				No. oocytes/mesentery			
		mean	sd	min	max	mean	sd	min	max
Coral Gardens	34	241.5	22.8	203.1	311.1	8.1	3.4	1.9	16.0
Nyali Reef	46	271.9	22.3	219.1	312.4	7.5	2.9	2.8	14.8
Kijembe Reef	45	257.8	23.3	204.3	340.2	9.4	3.8	2.4	18.2

Estimates of fecundity for the three faviid species were calculated as the number of oocytes per cm^2. Fecundity in *P. daedalea* was consistent within colonies with >99% of all mesenteries containing oocytes at maturity in both years (Fig. 5.6 and 5.9), compared to *L. phrygia* which was more variable and averaged 77% (Fig. 5.11). Fecundity in *E. gemmacea* was also variable with not all polyps producing oocytes, and additional studies were done to quantify this variation. These studies showed there was not a strong relationship between the mean oocyte diameter and the mean number of oocytes per mesentery in *E. gemmacea* ($r^2 = 0.11$, Fig. 5.20), but there was a stronger relationship between polyp diameter and the number of oocytes ($r^2 = 0.41$, Fig. 5.21). The majority of the 250 *E. gemmacea* polyps dissected (97.2%) had either oocytes present on all mesenteries or no oocytes suggesting that if a polyp was participating in reproduction, it invested effort into all mesenteries rather than a portion of them. Polyps with a smaller diameter, particularly those <0.3 cm, were less likely to produce oocytes than those that were larger, and all polyps greater than 0.6 cm were gravid (Fig. 5.22). Overall, it was estimated that 22% of all *E. gemmacea* polyps sampled were not participating in reproduction. Similar data could not be calculated for *P. daedalea* and *L. phrygia* because these species are meandroid, and therefore mesenteries are continuous between polyp mouths.

Echinopora gemmacea, *P. daedalea* and *L. phrygia* had an annual average fecundity of 4237, 671 and 644 oocytes cm^{-2}, respectively (Table 5.10). *Platygyra daedalea* was less fecund than *L. phrygia* during the major spawning period (589 oocytes cm^{-2}), but its total annual fecundity was slightly higher with the inclusion of the oocytes produced during the minor spawning (82 oocytes cm^{-2}). While *E. gemmacea* produced the smallest oocytes at maturity compared to the *L. phrygia* and *P. daedalea*, its estimated fecundity was approximately six times higher than the other two species (Table 5.10). It is also important to note that fecundity in marginal polyps was not quantified in any of the species, and therefore fecundity estimates may be higher than actual values. Total oocyte biomass in *E. gemmacea, P. daedalea* and *L. phrygia* was 13.9, 6.1 and 4.6 mm^3 cm^{-2}, respectively (Table 5.10). Total oocyte biomass was higher in *P. daedalea* than *L. phrygia* during major spawning as well as annually.

Table 5.10: Comparative mean fecundity (per cm^2) for three Kenyan faviid species. Total oocyte biomass (mm^3 cm^{-2}) was calculated by multiplying the mean fecundity by the oocyte diameter (see Table 5.2) transferred to a sphere. Fecundity during major and minor spawning, as well as annual fecundity are shown for *Platygyra daedalea*. s = short, l = long mesenteries (mes).

Species	Oocytes/ mes	Mes/ polyp	Polyps / 5cm^2	Mes/ cm^2	% Fecund	Fecundity	Biomass/ cm^2
E. gemmacea	18^s, 7.8^l	33.7	63.8	-	0.78	4237	13.9
L. phrygia	5.8	-	-	144.3	0.77	644	4.6
P. daedalea							
major	7.9	-	-	75.3	0.99	589	5.3
minor	3.3				0.33	82	0.8
annual						671	6.1

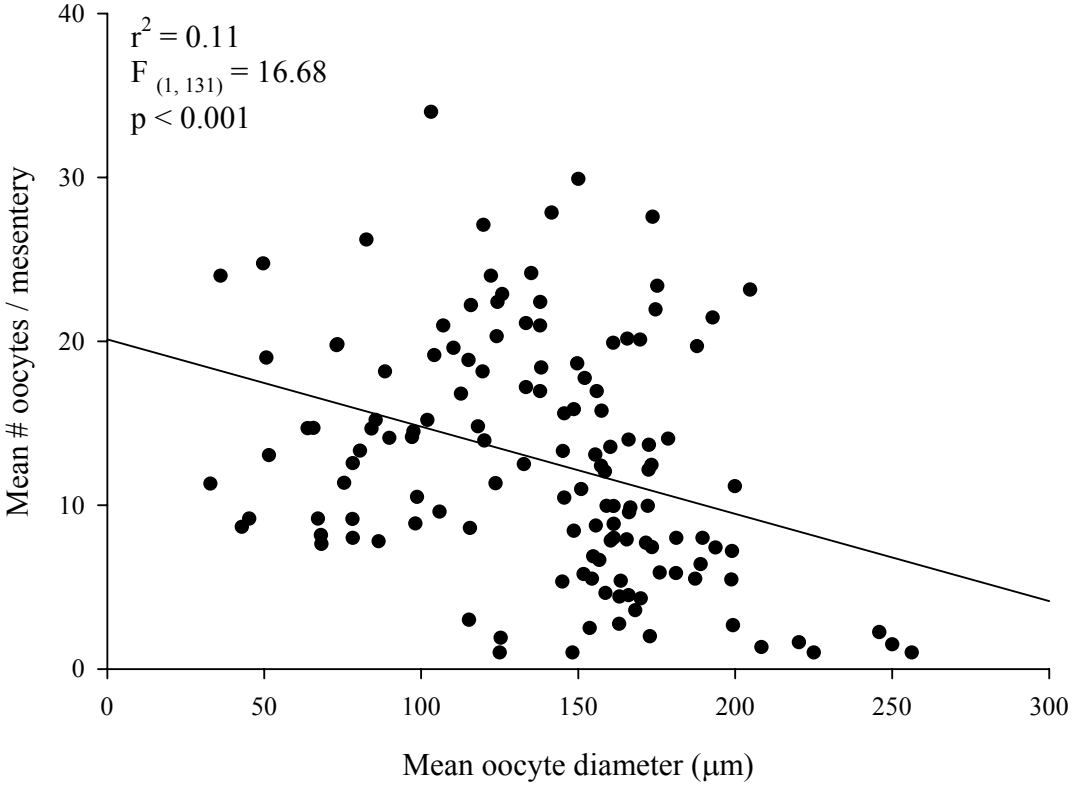


Figure 5.20: Relationship between oocyte size and number of oocytes in *Echinopora gemmacea* mesenteries.

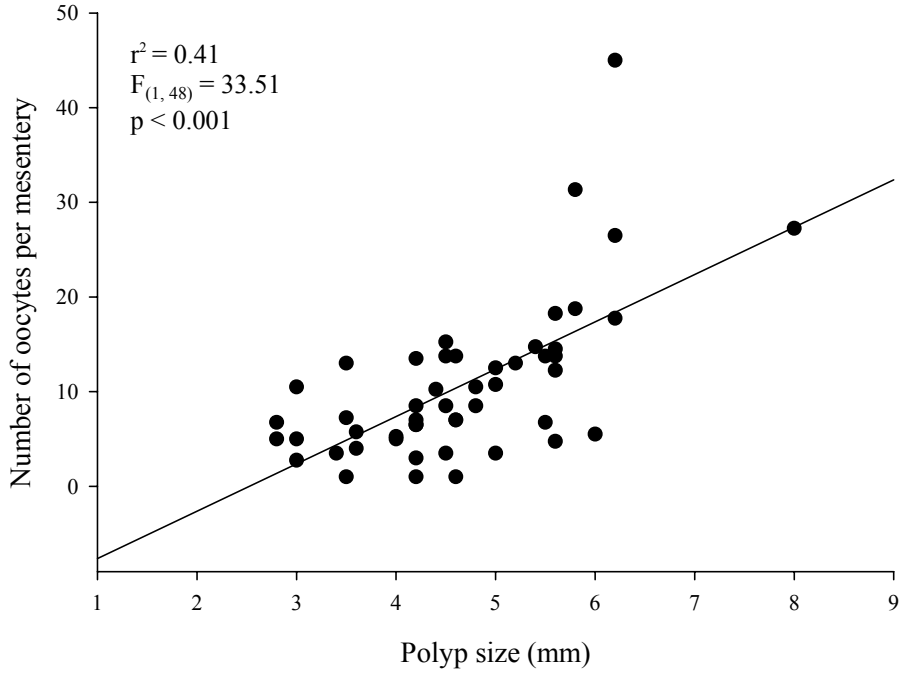


Figure 5.21: Relationship between polyp size (measured as polyp diameter) and the mean number of oocytes per mesentery in *Echinopora gemmacea*.

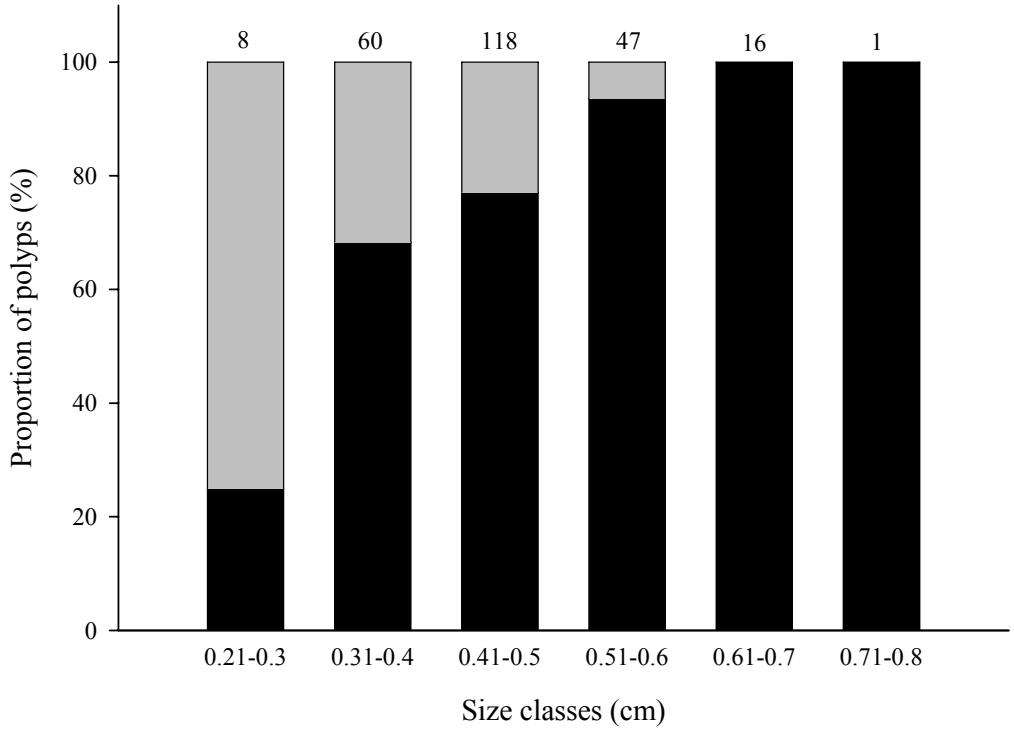


Figure 5.22: The proportion of polyps in different size classes that were gravid (black) and non-reproductive (grey) in *Echinopora gemmacea*. The number of polyps sampled in each size class is indicated at the top of each bar. A total of 250 polyps were sampled.

5.4 Discussion

5.4.1 Reproductive patterns

Echinopora gemmacea, *Platygyra daedalea* and *Leptoria phrygia* are simultaneous hermaphrodites in Kenya, with protogynous gamete development with oocytes and spermaries intermingled on the same mesentery. These sexual patterns predominate in the Family Faviidae and have been recorded in many other species (Harrison 1985), for example, *Favites abdita* (Kojis and Quinn 1982), *Favia favus* (Harriott 1983a), *Goniastrea aspera* (Babcock 1984; Sakai 1997), *Montastrea annularis* (Szmant 1991; Van Veghel 1994), *Cyphastrea microphthalma* (Shlesinger et al. 1998) and *Echinopora lamellosa* (Fan and Dai 1995). All three faviid species studied are broadcast spawners as evidenced by: (a) the presence of mature pigmented oocytes and large spermaries in polyps, and the absence of gametes in subsequent samples taken 1-8 days later; (b) spawning observed in colonies of *E. gemmacea* and *L. phrygia* held in aquaria; and (c) the lack of planulae in >1000 samples, including samples taken 1-2 weeks following spawning.

5.4.2 Gametogenesis

While the onset of gametogenesis varied between individual colonies by up to a few weeks, the populations of each species became more synchronised as gametogenesis progressed, with rapid gamete maturation in the 1-2 months prior to spawning. Mature gametes were seen up to seven weeks prior to spawning, which is consistent with faviids (4-6 weeks) on the GBR (Babcock et al. 1986). There was no relationship between the latitude of study sites (across a range of regions), and the length of the gametogenic cycles, the number of spawning months or the size of the oocytes at maturity of faviid species studied (Table 5.11).

Each of the three species studied in Kenya had key features in their gametogenic cycles that differed from each other. *Echinopora gemmacea* had a single annual cycle of gametogenesis while *P. daedalea* colonies had either annual or biannual cycles. In contrast, a single annual period of gametogenesis was recorded in *L. phrygia* with two cycles of oogenesis and multiple maturation and spawning events.

Table 5.11: Comparison of reproductive characteristics of broadcast spawning scleractinian corals from the Family Faviidae in order of latitude, from north to south. '-' indicates no information available. *: both broadcast spawning and brooding were recorded. #: maximum oocyte diameter measured.

Region	Location	Lat	Species	Sex	Length of gametogen.	Spawn. months	Spawning period	Egg size	No. cycles	Source
Atlantic	Bermuda	32ºN	*Diploria strigosa*	H	8-9 mo	1-2 mo	Jul-Aug	440	1	Wyers 1985
Red Sea	Gulf of Eilat	29ºN	*Favia favus*	H	6-7 mo	2 mo	Jul-Aug	395#	1	Shlesinger & Loya 1985; Shlesinger et al. 1998
Red Sea	Gulf of Eilat	29ºN	*Cyphastrea micropthalma*	H	7 mo	1 mo	Aug	290#	1	Shlesinger et al. 1998
Red Sea	Gulf of Eilat	29ºN	*Goniastrea retiformis*	H	5 mo	1 mo	Aug	315#	1	Shlesinger & Loya 1985; Shlesinger et al. 1998
Red Sea	Gulf of Eilat	29ºN	*Platygyra lamellina*	H	6-7 mo	2 mo	Jul-Aug	370#	1	Shlesinger & Loya 1985; Shlesinger et al. 1998
Red Sea	Gulf of Eilat	29ºN	*Favites pentagona*	H	8-9 mo	1 mo	Apr	240#	1	Shlesinger et al. 1998
Indo-Pacific	Okinawa	26ºN	*Goniastrea aspera**	H	4-5 mo	2 mo	Jun-Jul	370	1	Sakai 1997
Indo-Pacific	N. Taiwan	25ºN	*Echinopora lamellosa*	H	4-5 mo	1-2 mo	Jul-Aug	258	1	Fan & Dai 1995
Indo-Pacific	S. Taiwan	21ºN	*Echinopora lamellosa*	H	4-6 mo	1-2 mo	Aug-Oct	215	1	Fan & Dai 1995
Atlantic	Puerto Rico	18ºN	*Montastrea annularis*	H	4 mo	1-2 mo	Aug-Sep	300	1	Szmant 1986, 1991
Atlantic	Puerto Rico	18ºN	*Montastrea cavernosa*	G	10-11 mo	2-3 mo	Jul-Sep	350	1	Szmant 1986, 1991
Atlantic	Puerto Rico	18ºN	*Diploria strigosa*	H	6-7 mo	1 mo	Aug	400	1	Szmant 1986
Atlantic	Jamaica	17ºN	*Montastrea annularis*	H	4-5 mo	1-2 mo	Aug-Sep	535	1	Mendes & Woodley 2002
Atlantic	Curaçao	12ºN	*Montastrea annularis*	H	5-6 mo	2 mo	Sep-Oct	225	1	Van Veghel 1994
Atlantic	Colombia	11ºN	*Montastrea cavernosa*	G	11 mo	2-3 mo	Aug-Oct	346	1	Acosta & Zea 1997
WIO	**Kenya**	**4ºS**	***Echinopora gemmacea***	**H**	**4-6 mo**	**3 mo**	**Feb-Apr**	**169**	**1**	**This study**
WIO	**Kenya**	**4ºS**	***Leptoria phrygia***	**H**	**6-7 mo**	**2 mo**	**Dec-Jan**	**239**	**1**	**This study**
WIO	**Kenya**	**4ºS**	***Platygyra daedalea***	**H**	**6-7 mo**	**2-3 mo**	**Feb-Apr**	**259**	**1, 2**	**This study**
Indo-Pacific	GBR	14ºS	*Favia favus*	H	6-7 mo	1-2 mo	Dec	500#	1	Harriott 1983
Indo-Pacific	W. Samoa	15ºS	*Leptoria phrygia*	H	8 mo	1 mo	Nov/Dec	450	1	Mildner 1991
Indo-Pacific	GBR	19ºS	*Goniastrea aspera*	H	6 mo	1 mo	Oct	350	1	Babcock 1984
Indo-Pacific	GBR	23ºS	*Favites abdita*	H	8 mo	1 mo	Nov	394	1	Kojis & Quinn 1982
Indo-Pacific	GBR	23ºS	*Leptoria phrygia*	H	8 mo	1 mo	Dec	421	1	Kojis & Quinn 1982
Indo-Pacific	GBR	23ºS	*Goniastrea favulus*	H	9 mo	1 mo	Nov	510	1	Kojis & Quinn 1981

The period of gametogenesis was shorter in *E. gemmacea* (4-6 months) compared to the other two faviid species, but was of similar length to gametogenic cycles in *E. lamellosa* in northern and southern Taiwan (Fan and Dai 1995). Mature oocytes of *E. gemmacea* were much smaller than in *E. lamellosa* (which averaged 215-300 μm in Taiwan) and other faviids studied to date (see Table 5.11), which explains why mature gametes could not be seen in fractured samples in the field. The presence of unusually large mature oocytes in *E. gemmacea* without associated spermaries recorded in tissue samples in April 2003 (Fig. 5.3), may have been caused by mild bleaching that occurred between late February to June 2003. During this period most colonies of *E. gemmacea* had pale tissue ranging from 10-80% but no colonies fully bleached (unpubl. data). Coral bleaching has been shown to reduce fecundity and fertilisation rates in some corals (Ward et al. 2002; Omori et al. 2001; Baird and Marshall 2002), but little is known about the effects of mild-bleaching or shorter bleaching events on coral reproduction.

While single annual gametogenic cycles dominated in *P. daedalea*, biannual gametogenic cycles occurred in a few colonies of both morphotypes (PDV and PDSW) and were observed in consecutive years. During the minor spawning period, oogenic cycles overlapped in biannually spawning colonies for at least 2 months prior to gamete release. Oliver et al. (1988) also observed mature gametes in tagged colonies of *P. daedalea* at two distinct time periods (March and September/October) in Madang, PNG, which indicates that some colonies of this species spawn biannually in at least two regions. Madang (5ºS) is at a similar latitude to Kenya (4ºS). *Platygyra* sp. (with field characteristics of *P. pini* and *P. verweyi*) was also observed with mature gametes on equatorial reefs in Singapore (1ºN) in November and March/April indicating that biannual spawning occurs (Guest 2004). However, gametogenesis was not followed in individual colonies in the study in Singapore and therefore it is not known whether individual colonies have biannual cycles of gametogenesis or whether coral populations split-spawn at different times of the year (Guest 2004). These three studies indicate that at least some colonies of *P. daedalea* and possibly some congeners are capable of biannual spawning in equatorial regions over a long longitudinal range. Interestingly, the periods when minor and major spawning occurs in Kenya and PNG are similar, suggesting that the length and timing of gametogenic cycles are fairly consistent within *P. daedalea*.

In Kenya, reproductive effort in *P. daedalea* differed between major (summer) and minor (winter) spawning. Not all colonies in the population reproduced biannually (<20%), and during minor spawning not all mesenteries produced oocytes (32.5%) and less than half of the mature oocytes had associated spermaries (48.1%). The average number of oocytes per mesentery was significantly less during minor (3.3 oocytes) compared to major spawning (7.9 oocytes). Colonies that spawned biannually in the first reproductive season were also observed with mature gametes the following year. However, it is not known whether individual corals consistently spawn annually or biannually, or whether it is pre-determined for the individual colony or induced by environmental conditions.

A similar pattern is seen in *Montipora digitata* at Magnetic Island reef, GBR, which has biannual cycles of gametogenesis but fewer members of the population spawn in autumn (25% less) compared to spring (Stobart et al. 1992). While a greater proportion of the population spawn in autumn on the GBR compared to winter spawning in Kenya, autumn spawning was more temporally variable (Stobart et al. 1992) and was not detected by an earlier year-long study at the same site (Heyward and Collins 1985). This temporal variability between minor spawning events is also apparent in Kenya, with none of the 20 colonies repeated sampled in the second study year undergoing biannual gametogenic cycles and mature gametes were recorded in 12.5% of additional colonies sampled in August-September 2004, compared to 19.2% in the previous year. Similar to *P. daedalea* in Kenya, reproductive output was lower on the GBR during minor spawning with not all polyps of *M. digitata* containing gametes (approximately two thirds), and only half the number of oocytes or less were produced per polyp (Stobart et al. 1992). Biannual spawning was also recorded in the congeners *M. aequituberculata* and *M. peltiformis* in the same study (Stobart et al. 1992).

It is not known why some colonies of *P. daedalea* complete two cycles of gametogenesis, while other colonies and *E. gemmacea*, *L. phrygia* and three species of *Acropora* (see Chapter 6) complete one gametogenic cycle each year in Kenya. It is also unclear how successful the minor spawning is, when only a small proportion of the population participate in the event, and those that do, have a reduced reproductive

output. In August 2003, some *P. daedalea* colonies had medium to large immature oocytes without associated spermaries suggesting a second cycle of gametogenesis commenced in some polyps prior to minor spawning, but was not completed. It is likely that these oocytes did not reach maturity in time and were reabsorbed by the colony. Resorption of unspawned gametes has been recorded in other coral species (Szmant-Froelich et al. 1980; Harriott 1983a; Wyers 1985; Sier and Olive 1994; Mendes and Woodley 2002; Neves and Pires 2002). It is not understood why some corals invest in biannual spawning while the majority of hermaphroditic broadcasters do not. Biannual spawning may occur as a result of different species allocating their resources between reproduction and growth, or alternatively, it may be a way to minimise the risk of a catastrophic event destroying the annual reproductive efforts of a species (Harrison et al. 1984; Richmond and Hunter 1990; Stobart et al. 1992). While reproductive effort was much less, advantages to minor winter spawning may be less competition for space among settling spat, which could lead to higher recruitment success (Shlesinger and Loya 1985; see Chapter 7).

The length of gametogenesis in *L. phrygia* in Kenya (6-7 months) is fairly similar to records for this species on the GBR and in Western Samoa (7-8 months, Kojis and Quinn 1982; Mildner 1991). However, overlapping oogenic cycles have not previously been recorded in *L. phrygia* in other parts of the world. Unlike the pattern observed in biannually spawning *P. daedalea* where different oocyte size classes were only present for 2-3 months, small size classes were present in *L. phrygia* throughout most of the study period (particularly from December to January), suggesting that there are at least two oogenic cycles which terminated in spawning within 1-2 months of each other (Fig. 5.12-5.13). Not all individuals had overlapping oogenic cycles, and it is not known whether it is pre-determined for the individual or induced by environmental conditions. Overlapping oogenic cycles have been recorded in gonochoric *Turbinaria mesenterina* on the GBR (Willis 1987 cited in Harrison and Wallace 1990) and solitary corals from temperate regions (Szmant-Froelich et al. 1980; Fadlallah 1982; Fadlallah and Pearse 1982a, 1982b; Goffredo et al. 2002, 2006).

The presence of mature oocytes without associated spermaries in some January and February samples of *L. phrygia*, suggest that reproductive effort is not equal across

consecutive oogenic cycles, with a larger investment of energy into the main cycle. Unfortunately, collections of *L. phrygia* had to be stopped earlier than planned during the study, and therefore it is not known whether mature gametes present in February samples were successfully released. Szmant et al. (1980) noted that while gametes formed during a second cycle of gametogenesis in *Astrangia danae,* they were absorbed before they reached maturity. However, under favourable conditions when polyps were maintained and fed in the laboratory, *A. danae* was capable of year-round spawning (Szmant et al. 1980). Similarly *L. phrygia* may be able complete more than one successive oogenic cycle if conditions are favourable, and may halt development and reabsorb gametes if conditions become less favourable. However, further research is needed to substantiate this hypothesis, and to determine the exact number of oogenic cycles *L. phrygia* has in Kenya, and how many of them result in successful spawning.

5.4.3 Spawning patterns

Echinopora gemmacea, *L. phrygia* and the majority of *P. daedalea* colonies spawned during the NE monsoon season over a 4-month period between late December to April in 2005 (Table 5.5). This contrasts with *Acropora* species which spawned over a 7-month period in Kenya, suggesting that interspecific spawning synchrony is tighter in faviids than acroporids (Mangubhai and Harrison 2006; see also Chapter 6). Differences in spawning synchrony between faviids and acroporids has also been recorded at equatorial reefs in PNG and Singapore as well as higher latitude reefs in Japan, suggesting that this is a feature of the two families in some locations, rather than a latitudinal gradient (Oliver et al. 1988; Hayashibara et al. 1993; Guest 2004).

The populations of the three faviid species split-spawned over 2-3 consecutive lunar months, and this pattern was consistent with *E. gemmacea* and *P. daedalea* between study years. These findings suggest that split-spawning is a phenomenon that results in a protracted breeding season in Kenya, and is not just a response to a shift in the lunar phase as occurs on the GBR (Willis et al. 1985). Similarly, split-spawning of faviids has been recorded at Akajima Island, Japan extending over 2-3 consecutive lunar months and during consecutive years (Hayashibara et al. 1993). Split-spawning

also occurred during minor spawning in *P. daedalea* in August and September, with one colony spawning as late as October in 2003 in Kenya.

Partial spawning was also recorded in individuals of *E. gemmacea* and *P. daedalea* in 2004 and 2005, over consecutive nights as well as during consecutive lunar months (Fig. 5.13). Partial spawning was recorded in 20 of the 166 (12%) *E. gemmacea* and *P. daedalea* colonies studied during the two-year study. Data from different regions around the world suggest that partial spawning by individuals is less common, and the extent to which it occurs and its causative factors are not currently understood. Partial spawning over a period of up to three consecutive lunar months has been recorded in *Montastrea cavernosa* (Acosta and Zea 1997) and *M. faveolata* (Bastidas et al. 2005) in the Caribbean, and in *Astreopora myriophthalma*, *Lobophyllia hemprichii* and *Merulina ampliata* at high-latitude reefs in Western Australia (Babcock et al. 1994). A study in Venezuela showed partial spawning occurred in some individual colonies of *Montastrea faveolata* and *Eusimilia fastigiata* during consecutive nights as well as during lunar months (Bastidas et al. 2005).

The three species studied showed varying degrees of isolation or synchrony in their spawning periods. *Leptoria phrygia* was temporally isolated from the other two species, with spawning in the population occurring earlier, during lunar cycles in December and January. In contrast, there was a clear overlap in the spawning period between *E. gemmacea* and *P. daedalea* for the months of February and March in both study years. These results are slightly different to spawning patterns on the GBR where all three species show greater interspecific synchrony, spawning in the same month and between 4-7 nights AFM (Willis et al. 1985; Babcock et al. 1986).

The exact night of spawning was recorded for three colonies of *L. phrygia* (4^{th} night AFM), and in a further three colonies spawning was inferred from the disappearance of gametes from sequential samples and narrowed to a 3-4 day interval (Table 5.6) In *P. daedalea* spawning times for 37 colonies (inferred from the disappearance of gametes from sequential samples) were narrowed to a 3-8 day interval. Although two colonies of *P. daedalea* spawned around the time of the new moon in 2005, the majority of colonies for the three species concentrated their reproductive effort between full moon and the last lunar quarter (Table 5.6 and Fig. 5.13). The spawning

periods recorded for each species suggest that spawning occurred over more than one consecutive night, and therefore it is likely that a portion of the populations of *E. gemmacea* and *P. daedalea* spawned together on the same night or nights in February and March. Mature gametes were also recorded in one *Hydnophora exesa*, two *Turbinaria mesenterina*, three *Favites pentagona* and three colonies of *Astreopora listeri* at Nyali Reef on 31 December 2004, as well as in *Acropora* species sampled from December to April (see Chapter 6). These spawning data provide strong evidence that some degree of reproductive seasonality and multispecific spawning are features of Kenyan reefs.

5.4.4 Environmental parameters

Echinopora gemmacea, *L. phrygia* and the majority of *P. daedalea* colonies spawned when sea surface temperatures were at their highest (averaging 28.3 ºC), wind conditions were calm and steady and seas were slight. This suggests that the two monsoon seasons along the East African coast strongly influence the reproductive patterns of faviid corals in Kenya. The sea surface temperature fluctuated in the summer months of January – April at the study sites, ranging from 26.9-29.6 ºC. The most likely explanation for this is that the shallow depth of the lagoon makes it susceptible to temperature fluctuations association with cloud cover and prevailing wind conditions.

There was no clear relationship between spawning in the three faviid species and the timing of solar radiation maxima in Kenya. Spawning occurred in *L. phrygia* prior to the solar radiation maximum in February/March, while spawning in *E. gemmacea* and *P. daedalea* occurred during this maximum period. Minor spawning in *P. daedalea* occurred when sea surface temperatures were lowest and averaged 25.4 ºC, and when solar radiation was rapidly rising just prior to the October/November maximum.

Spawning in Kenya occurred around the time of spring tides, or soon after, which is similar to southern Western Australia (Babcock et al. 1994) and contrasts with the primarily neap tide spawning on the GBR and northern Western Australia (Willis et al. 1985; Babcock et al. 1986; Simpson 1985, 1991). Spawning recorded in *L. phrygia* and *Acropora* species (see Chapter 6) in aquaria suggest that spawning occurred

during ebb tide, three hours prior to low tide. Spring low tides usually result in the water in the Mombasa lagoon being isolated from oceanic waters due to the presence of the fringing reef. Tidal mixing 1.5-2 hours either side of low tide is usually minimal and may decrease gamete dilution and enhance fertilisation during this period (Harrison and Wallace 1990). Two hours after low tide, the current usually increases as the lagoon begins to fill, and this may promote the dispersal of gametes within the lagoon providing a 12-hour window for fertilisation and early embryo development before they are potentially swept out to sea during the following daylight ebb tide.

Spawning also coincided with the period of lowest rainfall along the Kenyan coast and prior to the period of peak annual rainfall (see Fig 2.4, Chapter 2), which is consistent with predictions by Mendes and Woodley (2002) that spawning occurs before periods of heavy rainfall. Both major and minor spawning in *P. daedalea* occurred when rainfall was lowest, hence avoiding periods of potentially low salinity which may be harmful to gametes (Richmond 1993; Harrison 1995). However, rainfall is unlikely to be one of the major proximate cues governing the timing of spawning events in Kenya given its variability from year to year, though it may have an interactive effect with more reliable cues such as sea surface temperatures and changes in the monsoon season.

Observations of spawning in aquaria in *E. gemmacea* and *L. phrygia* as well as acroporids (see Chapter 6) suggest that spawning occurs after the onset of darkness, which is consistent with observations in most parts of the world (Harrison and Wallace 1990). Nocturnal spawning is likely to enhance the survival of gametes, through avoidance of predation by visual feeders such as planktivorous fish (Harrison et al. 1984; Babcock et al. 1986), and reducing the damaging impacts of UV light on gametes and developing embryos (Wellington and Fitt 2003).

Seasonal variation in daylength is less pronounced at the equator, varying by ten minutes in Kenya, and hence it is not known whether these changes are too small to play a role in the timing of maturation of gametes or timing of spawning events. However, seasonal variation in the changes in daylength, the largest of which coincides with the equinoxes in September and March did coincide with the timing of maturation and spawning in faviids in Kenya. This suggests that changes in

photoperiod, albeit slight, may play a role for some species or groups of species on equatorial reefs, and is consistent with findings by Borchert et al. (2005) studying synchronous flowering in Amazonian tropical trees at the equator. Borchert et al. (2005) suggested that in the equatorial regions (with low climatic variability), the greatest changes in daylength occur only around the equinoxes or solstices, and that these are sufficient to induce flowering in tropical rainforests. Manipulative experimentation is required to confirm the role of photoperiod and temperature changes in determining the timing of coral reproduction on equatorial reefs such as Kenya.

5.4.5 Reproductive output

A number of studies have shown that the removal of tissue and underlying skeleton from reef corals may have a negative impact on their reproduction, particularly in the area immediately adjacent to the lesion where coral fecundity may be reduced (Van Veghel and Bak 1994; Hall 1997; Oren et al. 2001). In this study, the removal of 11.7-12.6% of living tissue biomass through repeated sampling of permanent colonies of *E. gemmacea* and *P. daedalea* did not result in significant differences in oocyte diameter or number of oocytes per mesentery, when compared to additional colonies sampled briefly (1.6-6% of tissue removed). Therefore, it is unlikely that repeated sampling affected the quality of the data collected, particularly on coral fecundity. As indicated previously, large colonies were chosen for repeated sampling to avoid biomass reduction confounding the data, and samples were separated by 10-15 cm of living tissue to avoid sampling near damaged areas, which might have biased the results. The majority of lesions in *E. gemmacea* healed within 1-1.5 years and could not be distinguished from the rest of the colony, while in *P. daedalea* lesions had only partially healed after 1.5 years (unpubl. data).

Fecundity was calculated as the number of oocytes per cm^2 of tissue, because it enabled comparisons among species that differed anatomically and allowed comparisons with corals from other geographic regions (reviewed in Harrison and Wallace 1990). Fecundity was six times higher in *E. gemmacea* compared to *P. daedalea* and L. *phrygia*, and is possibly the highest recorded thus far, for any faviid (Table 5.12). All three species had smaller oocyte diameters in Kenya compared to

other parts of the world. For example, mean oocyte diameter in *L. phrygia* was 239 µm compared to 421 and 450 µm recorded on the GBR and in Western Samoa, respectively (Kojis and Quinn 1982; Mildner 1991).

This study highlighted four factors that are important to take into consideration when calculating fecundity: (a) polyp anatomy; (b) size of polyps; (c) proportion of mesenteries with mature gametes; and (d) number of reproductive cycles per year. The arrangement of mesenteries in *E. gemmacea* resulted in significant differences in the number of oocytes present on short and large mesenteries at maturity. While there was no strong relationship between polyp size and the number of oocytes present on mesenteries, small polyps were generally sterile (Fig 5.22). Szmant-Froelich (1985) found small newly budded polyps were often sterile in *Montastrea annularis*, and it has been suggested that this may be related to the species extratentacular mode of budding (Harrison and Wallace 1990). Sakai (1998) found polyps in *Goniastrea aspera* formed by extratentacular budding were initially immature compared to those formed by intratentacular budding within the same colony. Extratentacular budding was common in *E. gemmacea* in Kenya, often occurring throughout the colony (pers. obs), and smaller polyps formed in this manner may be directing energy towards growth rather than reproduction.

The proportion of mesenteries with mature gametes varied between species. During the major spawning, >99% of mesenteries of *P. daedalea* had gametes, compared to 77% and 78% in *L. phrygia* and *E. gemmacea,* respectively. Therefore, fecundity could be over-estimated if these percentages are not taken into account. Lastly, the number of mature gametes produced during multiple spawning events needs to be taken into consideration when calculating annual fecundity. *Platygyra daedalea* were less fecund than *L. phrygia* during the major spawning, but its overall annual fecundity was slightly higher once the minor spawning was included in annual estimates.

Differences in mean oocyte size were observed in *P. daedalea* between the three sites, despite their proximity to each other. The mean number of oocytes per mesentery also differed between Nyali and Kijembe Reefs which were separated by 250 m in the National Reserve, but neither parameter showed differences with Coral Gardens (in

the National Park) which was 10 km north. Therefore, differences between sites are unlikely to be attributable to their management status. It is not known what caused these site differences given that no corresponding variability was found in *E. gemmacea*. While fecundity can vary over the lifetime of a coral and with age (Szmant-Froelich 1985), all corals were about the same size and showed no evidence of partial mortality or stress, which can have a negative effect on fecundity (Kojis and Quinn 1984). The largest stress that occurred during the study was mild bleaching observed in early 2003. However, bleaching did not affect the oocyte size or numbers at maturity in the 2004 reproductive season, and therefore site differences are unlikely to be attributable to this stress (unpubl. data).

Variation in polyp fecundity has been recorded in some coral species. For example, population differences were recorded in *Goniastrea aspera* and *G. favulus* on the central and southern GBR (Kojis and Quinn 1981a; Babcock 1986), and in *Stylophora pistillata* in the Red Sea (Rinkevich and Loya 1987). There was no difference in the mean oocyte or gonad mass diameter or number of oocytes per mesentery between the two morphotypes, and therefore site differences do not reflect the relative proportion of each morphotype at individual sites. Therefore, the differences observed in mean oocyte diameter and number of oocytes per mesentery between the different sites in the Mombasa lagoon may simply reflect variability that is inherent in *P. daedalea*.

Table 5.12: Comparisons of fecundity and mean oocyte size (μm) recorded in broadcast spawners in the Family Faviidae at different geographic locations. *: maximum diameter measured. H: hermaphroditic, G: gonochoric.

Species	Location	Lat	Type	Size	Oocytes/cm^2	Reference
Echinopora gemmacea	**Kenya**	**4ºS**	**H**	**169**	**4237**	**This study**
Montastrea annularis	Puerto Rico	18ºN	H	300	1368	Szmant 1986
Goniastrea aspera	GBR	19ºS	H	350	1931	Babcock 1984
Goniastrea aspera	GBR	19ºS	H	360	935	Babcock 1988
*Favia favus**	GBR	14ºS	H	500	764	Harriott 1983
Platygyra daedalea	**Kenya**	**4ºS**	**H**	**259**	**671**	**This study**
Leptoria phrygia	**Kenya**	**4ºS**	**H**	**239**	**644**	**This study**
Montastrea cavernosa	Puerto Rico	18ºN	G	350	576	Szmant 1986
Diploria strigosa	Puerto Rico	18ºN	H	400	486	Szmant 1986
Goniastrea favulus	GBR	23.5ºS	H	510	420	Kojis & Quinn 1981
Goniastrea favulus	GBR	19ºS	H	420	360	Babcock 1988
Platygyra sinensis	GBR	19ºS	H	405	350	Babcock 1988
Diploria strigosa	Bermuda	32ºN	H	440	350	Wyers 1985

CHAPTER 6: PATTERNS OF GAMETOGENESIS AND SPAWNING IN THE GENUS *ACROPORA*

6.1 Introduction

Patterns of gametogenesis and spawning in the genus *Acropora* were studied in the Mombasa Marine National Reserve in Kenya. This genus was selected because of its ecological importance, abundance and diversity on tropical reefs, and its wide distribution in the Western Indian Ocean (Sheppard 1987; Wallace 1999; Veron 2000). *Acropora* species are recognised as important components in the recovery of coral reefs following disturbances such as outbreaks of crown-of-thorns starfish (*Acanthaster planci*) and cyclones, because of their role as early colonisers of reefs and their rapid growth rate, relative to other genera (Pearson 1981; Wallace 1999). It is, however, one of the more susceptible genera to coral bleaching, and high mortalities of up to 100% were recorded in Kenya following the 1997-98 mass bleaching event (Obura et al. 2000b), and the subsequent recovery of *Acropora* species has been slow (see Chapter 7).

With the exception of species belonging to the subgenus *Isopora,* which brood planulae (Kojis 1986a, 1986b), most studies have found *Acropora* species to be simultaneous hermaphrodites that broadcast spawn gametes for external fertilisation and development (reviewed by Fadlallah 1983; Harrison and Wallace 1990; Richmond and Hunter 1990). *Acropora* species usually undergo a single annual cycle of gametogenesis with oogenesis preceding spermatogenesis by 5-8 months, and both oocytes and spermaries develop rapidly and mature synchronously in the 1-2 months prior to spawning (Wallace 1985a; Babcock et al. 1986). Following spawning, there is a quiescent non-reproductive period of 3-4 months before gametogenesis commences again (Wallace 1985a; P. Harrison, unpubl. data).

Biannual gametogenic cycles are rare, but were recorded in *A. hyacinthus, A. gemmifera* and a branching morphotype of *A. humilis* on reefs in Western Samoa (Mildner 1991), and in *A. formosa* and *A. hyacinthus* on reefs in northern Papua New Guinea (PNG) (Oliver et al. 1988). In contrast, individual colonies of *A. samoensis*

and *A. cytherea* on reefs in the Dampier Archipelago, Western Australia underwent a single annual cycle of gametogenesis but the population spawned biannually, with individual colonies releasing gametes in either October or March, with no significant differences recorded in the reproductive output of corals between the two spawning events (Rosser 2005).

Multispecific spawning of *Acropora* assemblages have been described predominantly in the Indo-Pacific (see reviews by Harrison and Wallace 1990; Richmond and Hunter 1990) and are sometimes less synchronous than faviid and other massive species, with a higher degree of split-spawning over different lunar months, suggesting this may be a feature of the reproductive biology of *Acropora* in some locations (Oliver et al. 1988; Hayashibara et al. 1993; Baird et al. 2002; Wilson and Harrison 2003). The level of spawning synchrony in *Acropora* assemblages varies between regions but direct comparisons are difficult because: the length of studies varies with most studies collecting data only around the main spawning events, the number of species sampled differs between studies, and in some cases different methods are used. On the central GBR, the majority of *Acropora* species release gametes during mass spawning events following full moon periods in the austral late spring to early summer and is consistent between years (Harrison et al. 1984; Willis et al. 1985; Babcock et al. 1986). Some *Acropora* species on the GBR may, however, split their spawning effort over a number of consecutive lunar cycles, or may spawn over non-consecutive months or at different times of year (Wallace 1985a; Willis et al. 1985; Wolstenholme 2004). On the southern GBR the lunar timing of mass spawning in *Acropora* species is less consistent between years, with spawning commencing sometime between the 3rd to 10th nights after full moon (AFM) (P. Harrison, pers. comm.).

At Akajima Island, Japan *Acropora* are less synchronous among species, spawning between the 3rd night before to the 7th night AFM over a 4-month period, but there is synchrony within species, which generally spawn over 1-2 nights over 1-2 months (Hayashibara et al. 1993). By contrast, the six *Acropora* species that dominated study sites in the Gulf of Eilat, northern Red Sea spawned in different seasons, months and lunar phases, so that there was little or no overlap in spawning between species (Shlesinger and Loya 1985; Shlesinger et al. 1998).

Preliminary results on the timing of spawning in *Acropora* species in Kenya were published in Mangubhai and Harrison (2006). The names of two species have been changed since the publication of that paper, and are reflected in this thesis. *Acropora* cf. *appressa* has been changed to *A. sordiensis* (Riegl 1995) and *Acropora* sp.A has been identified as *A. mossambica* (Riegl 1995) (see Chapter 3). Corals collectively referred to as the *Acropora nasuta* group in Mangubhai and Harrison (2006) were thought to be *A. valida, A. secale* and a number of 'intermediate' morphs. Taxonomic resolution has confirmed these morphological groupings and colonies previously identified as intermediate morphs are referred to as *Acropora* sp.1 in this thesis (see Chapter 3).

Despite the abundance and diversity of *Acropora* species on tropical reefs and the ease of studying them (i.e. without the need for complex histological processing), there have been very few studies that have described gametogenic cycles in this genus. The main aims of this chapter are to:

1) describe the pattern, duration and timing of gametogenesis in three locally abundant species of *Acropora* - *A. tenuis, A. valida* and *Acropora* sp.1;
2) determine the level of spawning synchrony within and among species; and
3) examine the relationship between gametogenic cycles and spawning times and environmental parameters.

6.2 Methods

6.2.1 Field collection

A total of 401 colonies were marked and sampled for this study, comprising 53 'permanent' and 348 'additional' colonies. Ten permanent colonies of *A. tenuis* and 20 colonies of the *Acropora nasuta* group (*sensu* Wallace 1999) were repeatedly sampled at Nyali Reef from April 2003 and at Kijembe Reef from September 2004, to determine patterns of gametogenesis. A different site was selected for sampling in the second study year because of the low abundance of adult *Acropora* species at Nyali Reef, and patch reefs in general in the Mombasa lagoon. It was assumed that because

Nyali and Kijembe Reefs were within close proximity to each other (see Chapter 2), spawning patterns were unlikely to differ between sites. No sampling was done at Coral Gardens because of the very low abundance and diversity of adult *Acropora* species at this site. Adult colonies >20 cm maximum diameter (Table 6.1) were selected to ensure repeated sampling did not remove more than 10-20% of the branches from any individual colony. Colonies sampled were separated by >1-2 m where possible, and individual features were closely examined during selection to ensure that colonies were whole (i.e. not fragments) and therefore likely to be genetically distinct.

Taxonomic resolution of the *A. nasuta* group found the permanent colonies were comprised of the following species: 18 *Acropora* sp.1, 15 *A. valida*, 1 *A. secale* and 1 *A. lutkeni* (Table 6.1). The remaining five colonies died from crown-of-thorns starfish predation before they could be identified, and were not replaced. Three colonies of *A. tenuis* died between November – December 2003 from unknown causes, and were replaced by three new colonies. Sampling in the first reproductive season extended for 14 months from April 2003 – May 2004, and sampling in the second season extended for 9 months from September 2004 – May 2005. Five *A. tenuis*, five *A. valida* and six *Acropora* sp.1 tagged in the first reproductive season were also re-sampled in August 2004 to provide 17 months of data for these colonies.

Table 6.1: The number of permanently marked colonies (n_{perm}) of each species and their mean maximum diameter (cm) at the two study sites. Season: 1 = April 2003 – May 2004 at Nyali Reef; 2 = August 2004 – May 2005 at Kijembe Reef. n_{add} = number of additional colonies sampled for each species.

Species	**Season**	**n_{perm}**	**n_{add}**	**Colony sizes**			
				mean	**sd**	**max**	**min**
A. tenuis	1	10	12	25.4	5.1	34	20
	2	10	10	32.3	6.9	46	21
A. valida	1	5	19	37.8	10.9	56	27
	2	10	15	42.1	9.6	54	29
Acropora sp.1	1	8	22	41.1	7.1	48	30
	2	10	7	39.8	7.0	56	32

Samples were collected on snorkel as described in section 5.2.1. A single branch measuring 5-10 cm was removed during each collection period. Collections were made away from the growing edge of colonies to avoid sampling areas likely to be allocating resources towards growth rather than reproduction, or that may be competing with adjacent colonies and therefore may have a lower fecundity (Wallace 1985a; Rinkevich and Loya 1985). In the first reproductive season, samples of *A. tenuis, A. valida* and *Acropora* sp.1 were initially collected every 1-2 months, and then at 2-3 week intervals closer to the predicted period of spawning. Corals selected for the second reproductive season were initially sampled every 1-2 months, and then at 2 week, 1 week and 1-4 day intervals, closer to the predicted period of spawning. The overall number of branches collected depended on the size of the colony, with smaller colonies being sampled less frequently, to minimise losses in tissue biomass and to reduce stress to the corals.

The timing and frequency of collections in the second reproductive season was based on spawning periods recorded in the previous season (Mangubhai and Harrison 2006), giving due consideration to the season and month, lunar phase and the size and maturity of oocytes observed in the field. No colonies were sampled in the southeast monsoon months June and July during the two-year study because strong winds and rough seas made it difficult to access the sites on a regular basis. Once a colony had spawned, 1-2 additional samples were taken 1-2 weeks later to determine whether any 'unspawned' oocytes remained in the colony, and whether there as any evidence of post-spawning brooding of remaining eggs (Sakai 1997). Similar to the faviid species studied, those samples with pigmented oocytes were considered to have maturing oocytes, and in *Acropora* species pigmentation appears about 3 weeks prior to spawning (Harrison et al. 1984; Babcock et al. 1986). This strategy enabled reproduction to be followed in individual colonies as well as within the wider population.

To determine the timing of spawning and the level of synchrony within and among *Acropora* species, colonies of a wide range of species were marked in September and October at Nyali Reef in 2003, and at Kijembe and Mamba Reefs in 2004. The number of corals marked for each species depended on their relative abundance at sites, and colonies ranged in size from 15-80 cm maximum diameter (mean = 30.9

cm, sd = 10.8). A total of 117 colonies were marked at Nyali Reef in 2003, and 73 colonies were marked both at Kijembe and at Mamba Reefs in 2004. Prior to predicted spawning, additional colonies of *A. tenuis, A. valida* and *Acropora* sp.1 were also marked at Nyali Reef in 2003 and at Mamba Reef in 2004, to gather more extensive data on the timing of spawning and the level of intra- and inter-specific spawning synchrony occurring (Table 6.1). Sixty colonies (12 species) sampled between September 2003 – May 2004 at Nyali Reef, were re-sampled in August 2004 to look for evidence of winter spawning.

6.2.2 Laboratory preparation of samples and microscope analysis

Tissue samples of *Acropora* species were transported alive to the laboratory immediately after returning from each sampling trip, and their reproductive condition was assessed in accordance with the three categories (i.e. mature, immature and absent) defined in section 5.2.2. Tissue samples were then fixed, decalcified and preserved in the same manner described in section 5.2.2. Decalcified branch samples were placed on a dark-coloured petrie dish and five polyps were randomly selected from the centre of the branch and removed under a dissecting microscope using fine forceps (after Wallace 1985a). Polyps at the branch tip were avoided as polyps may be sterile or sub-fecund (Wallace 1985a). The total number of oocytes was recorded, and the maximum length and perpendicular width of up to six randomly selected oocytes were measured on each mesentery using a calibrated eyepiece micrometer. This method, rather than histological sectioning, enabled all oocytes in a polyp to be counted rather than a sub-sample, and hence is a more accurate measure of fecundity. In 66 colonies (11 species), the length of the sterile zone at the branch tip was measured under a dissecting microscope.

6.2.3 Spawning in aquaria

Branches of nine species (*Acropora* sp.1, *A. divaricata, A. humilis, A. mossambica, A. samoensis, A. secale, A. sordiensis, A. tenuis* and *A. valida*) were maintained and monitored in separate aquaria for 3-4 days from December 2004 – March 2005, as described in section 5.2.5. *Acropora* species are very sensitive to stress which may cause colonies to release oocytes prematurely (P. Harrison, pers. comm.). Hence,

during transportation particular care was taken to ensure coral branches were submerged in seawater at all times and were not allowed to touch each other to avoid abrasions, and examinations at night were made using a torch covered with red cellophane. Information was recorded on the timing of 'setting', (i.e. when the egg-sperm bundles are formed and then held in the oral cavity prior to release), the onset and duration of spawning and the method of gamete release. Where spawning in aquaria occurred, field samples were collected from the same colony the next day to confirm spawning in the field. As stated in section 5.2.5, the convention of numbering lunar days in this thesis is in accordance with Atoda (1947a) and Stimson (1978).

6.2.4 Environmental parameters

A complete description of the methods used for measuring environmental parameters have been provided in section 5.2.6. Sea surface temperature readings were taken every hour by temperature loggers deployed at Coral Gardens from May 2003 – June 2004 and at Nyali Reef from April 2003 – December 2005, and weekly averages calculated. Salinity and turbidity readings were done from February 2003 – February 2005 during most field sessions, and tidal data were obtained from the annual Ports Authority publication.

6.3 Results

6.3.1 Reproductive pattern

All *Acropora* species studied in Kenya were simultaneous hermaphrodites, with both mature oocytes and spermaries observed together in polyps prior to gamete release. While spawning was not observed directly in the field, observations of spawning in aquaria of 14 colonies of *Acropora* comprising of 7 species, and the disappearance of mature oocytes and spermaries from consecutive samples taken a few days to a few weeks apart, indicates that these species are broadcast spawners. Furthermore, no planulae were recorded in the 1959 tissue samples (9795 polyps) examined.

6.3.2 Arrangement of oocytes and spermaries

A diagrammatic representation of the arrangement of mature oocytes and spermaries in *Acropora* polyps after dissection is shown in Figure 6.1. *Acropora* species had eight gravid mesenteries per polyp and mature spermaries and oocytes developed on separate mesenteries (Fig. 6.1-6.5). Large spermaries were larger in size than small spermaries, and long oocyte strings had more oocytes than short oocyte strings, and this pattern was consistent in all polyps of the 23 *Acropora* species studied. Oocytes were generally oval throughout the gametogenic cycle, though some became more irregular in shape as they grew depending on their position on a mesentery and space constraints within the polyp (pers. obs.; see also Fig. 6.3-6.5).

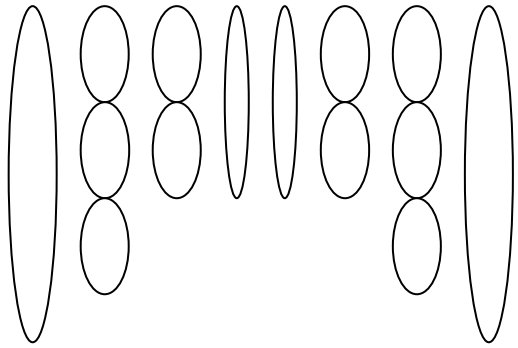


Figure 6.1: Diagrammatic representation of the arrangement of mature oocytes and spermaries in polyps of *Acropora* species after dissection, modified from Wilson (1998). S = large spermary, O = long oocyte string, o = short oocyte string, s = small spermary.

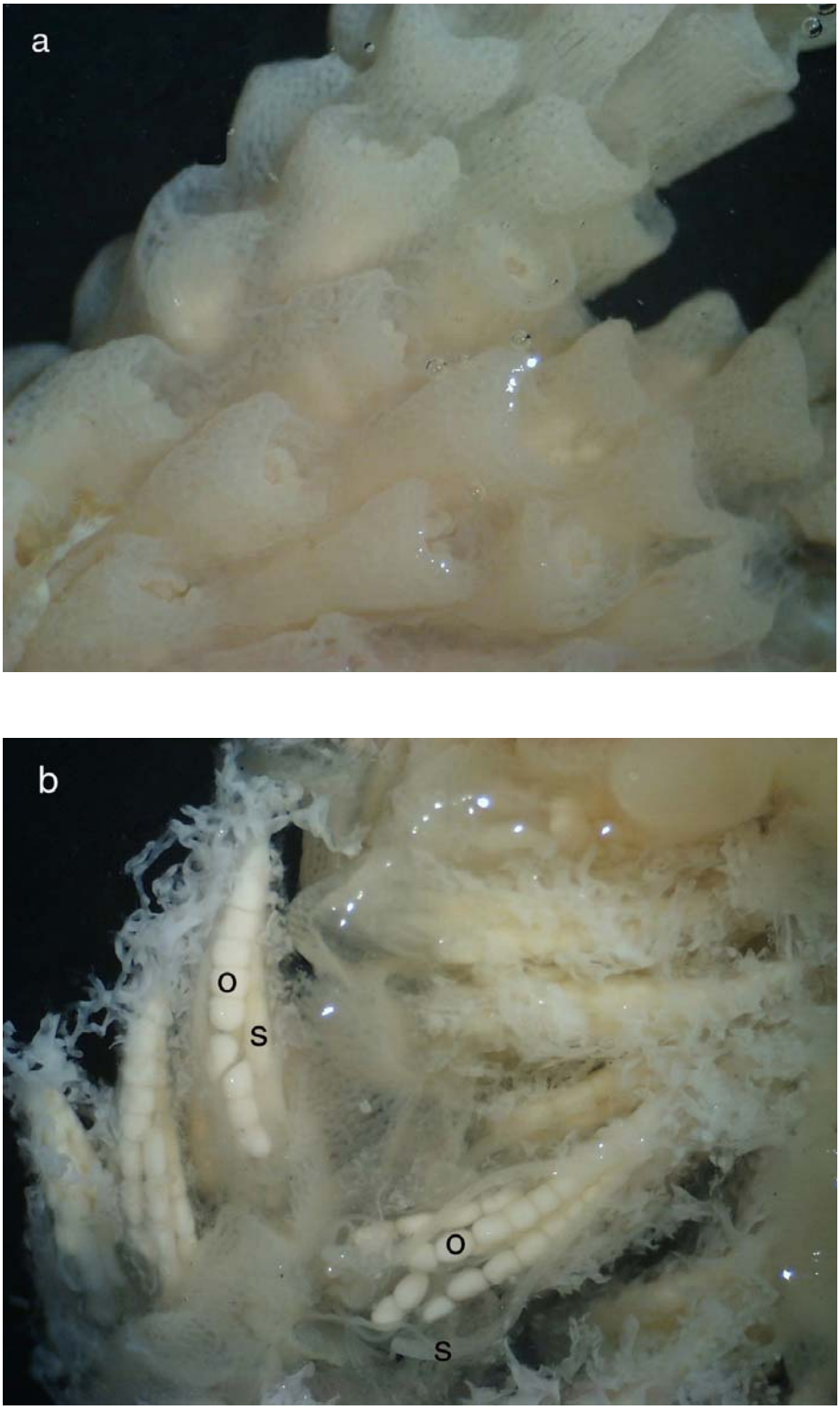


Figure 6.2: Photographs showing (a) the tissue that remains following decalcification of *Acropora tenuis*, and (b) the strings of oocytes (o) and spermaries (s) within individual polyps of *Acropora valida*.

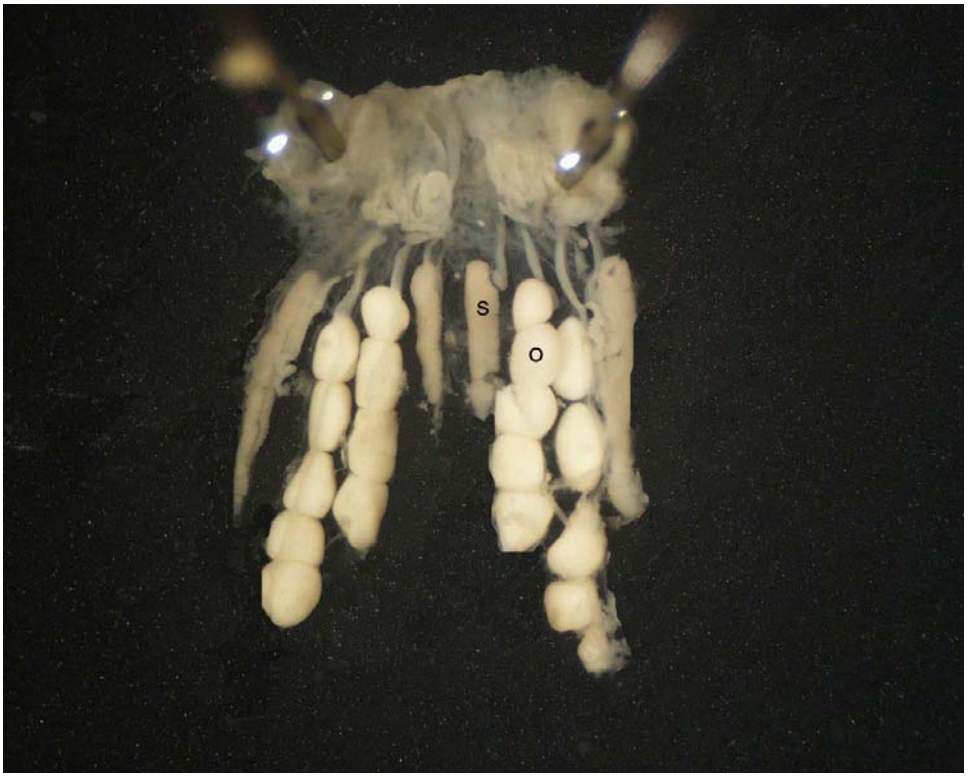


Figure 6.3: Arrangement of mature oocytes (o) and spermaries (s) on mesenteries in a polyp of *Acropora tenuis*, sampled on 21 February 2004. Spawning occurred between 21 February – 12 March 2004 in this colony.

Figure 6.4: Arrangement of mature oocytes (o) and spermaries (s) on mesenteries in a polyp of *Acropora valida* sampled on 27 February 2003. Spawning date not known.

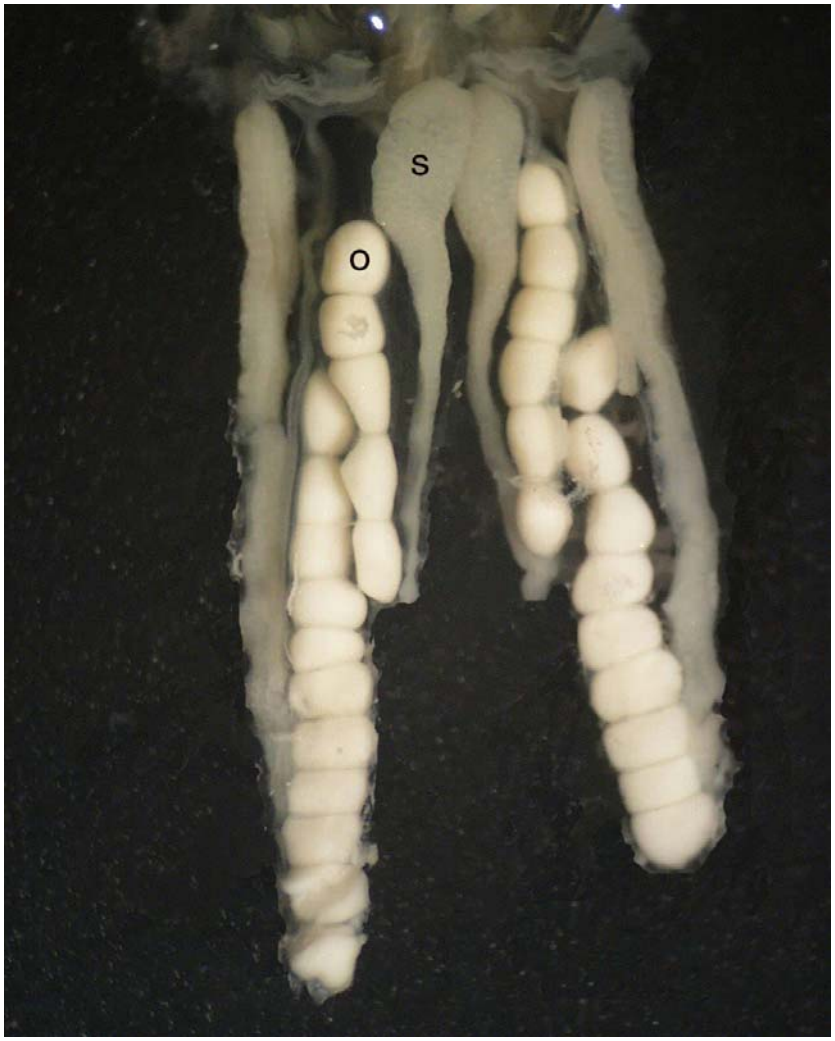


Figure 6.5: Arrangement of mature oocytes (o) and spermaries (s) on mesenteries in a polyp of *Acropora* sp.1, sampled on 21 February 2004. Spawning occurred between 12 March – 23 March 2004 in this colony.

6.3.3 Gametogenesis

Acropora tenuis and almost all colonies of *A. valida* and *Acropora* sp.1 had a single annual cycle of gametogenesis, with oogenesis preceding spermatogenesis by 4-6 months (Fig. 6.6-6.7). Patterns of oogenesis and spermatogenesis were consistent between consecutive reproductive seasons, with gametes reaching maturity between January - February in *A. tenuis*, and between December - February in *A. valida* and *Acropora* sp.1. There was no difference in the general pattern or the timing of oogenesis or spermatogenesis between *A. valida* and *Acropora* sp.1 (Fig. 6.7). At the population level (i.e. when individual colonies are averaged for the sampled

population), there was no obvious quiescent non-reproductive period between gametogenic cycles for the three species (Fig. 6.6-6.7). All three species underwent similar seasonal changes in the mean number of oocytes, with the numbers peaking in August/September in 2003 and in October in 2004, and with some reduction in oocytes numbers occurring during oogenesis (Fig. 6.8).

Seasonal changes in the mean diameter of mature oocytes and spermaries was plotted for individual colonies of *A. tenuis* (Fig. 6.9), *A. valida* (Fig. 6.10) and *Acropora* sp.1 (Fig. 6.11) sampled over 17 months to look at (a) variability in the length of oogenesis and spermatogenesis between colonies, (b) synchrony between colonies, and (c) to determine whether there was a quiescent period between gametogenic cycles for individual colonies. In *A. tenuis*, oogenesis occurred for 8-11 months between the period May – March, and spermatogenesis occurred for 3-4 months between the period December – March (Fig. 6.9). While the onset of gametogenesis varied between individual colonies by a few weeks, the population of *A. tenuis* became more synchronous as gametogenesis progressed, with rapid maturation in the 1-2 months prior to spawning. Quiescent non-reproductive periods occurred for a short period of 1-2 months between gametogenic cycles within colonies (Fig. 6.9), but as stated earlier, when the data are averaged for the sampled population, there is no obvious quiescent period (Fig. 6.6).

In *A. valida* and *Acropora* sp.1, oogenesis occurred for 11-12 months from April – March, and spermatogenesis occurred for 7-8 months from August – March. A very short quiescent non-reproductive period between gametogenic cycles was observed in some colonies that lacked oocytes for one or two sampling periods (Fig. 6.10-6.11). The onset of gametogenesis varied between individual colonies by a few weeks, and both oocyte and spermary maturation were fairly asynchronous in *A. valida* and *Acropora* sp.1 populations, compared to *A. tenuis*.

Biannual cycles of gametogenesis were recorded in one colony of *A. valida* and one colony of *Acropora* sp.1 (Fig. 6.12), which equates to 3.8% of the permanently marked colonies studied. Gametogenesis commenced in April (similar to colonies with a single cycle of gametogenesis), with mature oocytes and associated spermaries recorded in October 2003 in *A. valida*, and in November 2003 in *Acropora* sp.1 in

tissue samples. Mature pink oocytes were also observed in samples in the field in these two colonies during these two months. Mean oocyte and spermary diameter declined sharply by late November 2003, which suggests that both species spawned during this month (Fig. 6.12). Mean oocyte and spermary diameter then increased rapidly and mature gametes were recorded in late December 2003 in *A. valida*, and in February 2004 in *Acropora* sp.1. Spermaries did not develop in *A. valida* after November 2003, following the first spawning. The two species spawned at different times during the second spawning event, with *A. valida* releasing oocytes in January 2004, and *Acropora* sp.1 releasing gametes in late February 2004. There was no quiescent non-reproductive period between biannual gametogenic cycles in the colony of *Acropora* sp.1, but no gametes were recorded in the biannual spawning *A. valida* colony during the last sample taken in January 2004 (Fig. 6.12).

The smallest detectable oocyte in *A. tenuis, A. valida* and *Acropora* sp.1 had a mean diameter of 20, 37.5 and 33.3 μm, respectively, which were recorded near the commencement of their gametogenic cycles. The mean diameter of oocytes at maturity in *A. tenuis, A. valida* and *Acropora* sp.1 were 448.3 μm (sd = 81.2), 468.3 μm (sd = 87.4) and 479.5 μm (sd = 76.1), respectively (Table 6.2).

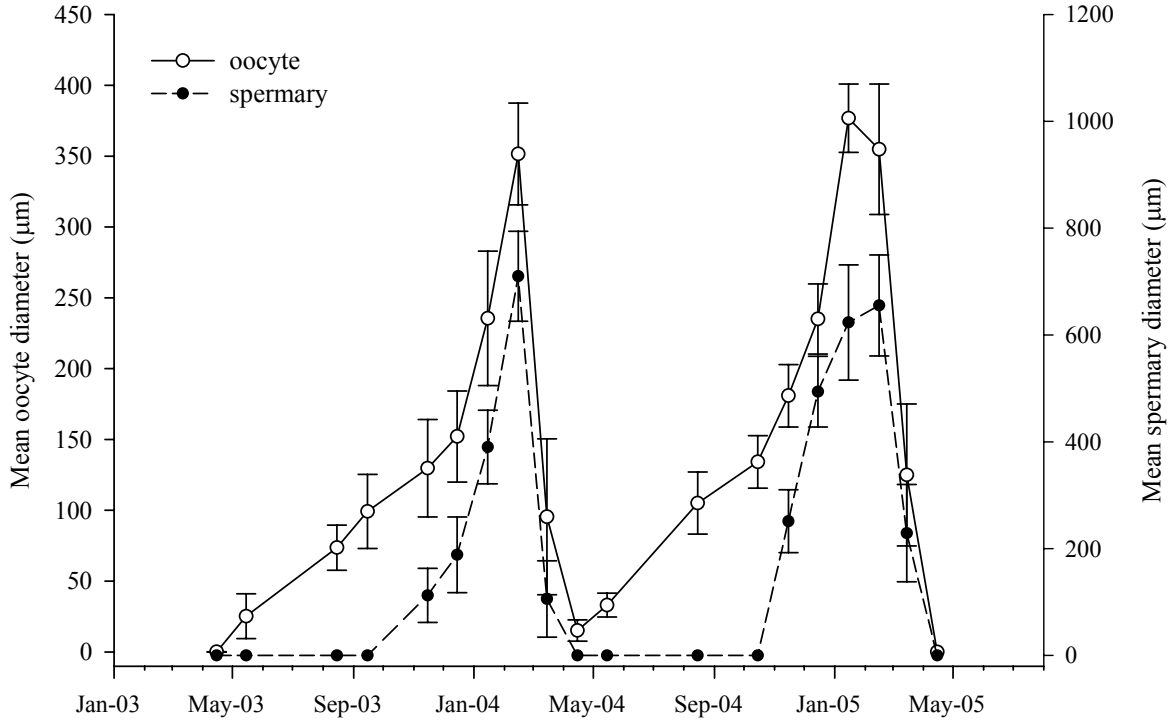


Figure 6.6: *Acropora tenuis*. Seasonal changes in mean oocyte (left y-axis) and spermary (right y-axis) diameter of permanently marked colonies at Nyali Reef in April 2003 – August 2004 (n = 9), and at Kijembe Reef in October 2004 – April 2005 (n = 10). Oocyte and spermary sizes were averaged for each month. Error bars are standard error.

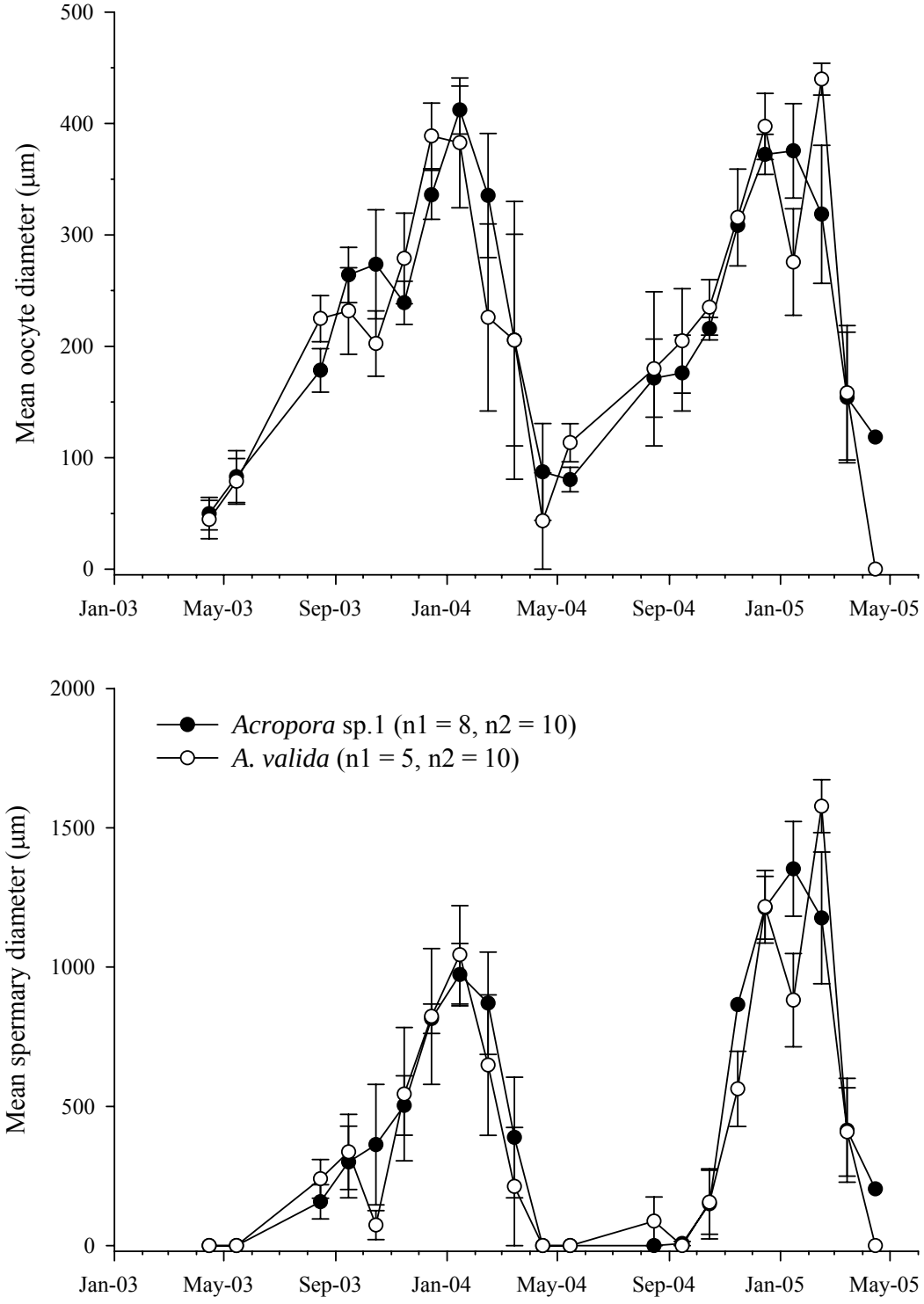


Figure 6.7: Seasonal changes in mean oocyte and spermary diameter of permanently marked colonies of *Acropora* sp. 1 and *A. valida* at Nyali Reef in April 2003 – August 2004, and at Kijembe Reef in September 2004 – April 2005. Gamete sizes were averaged for each month. n1 = number of colonies sampled in the first reproductive season, n2 = number of colonies sampled in the second reproductive season. Error bars are standard error.

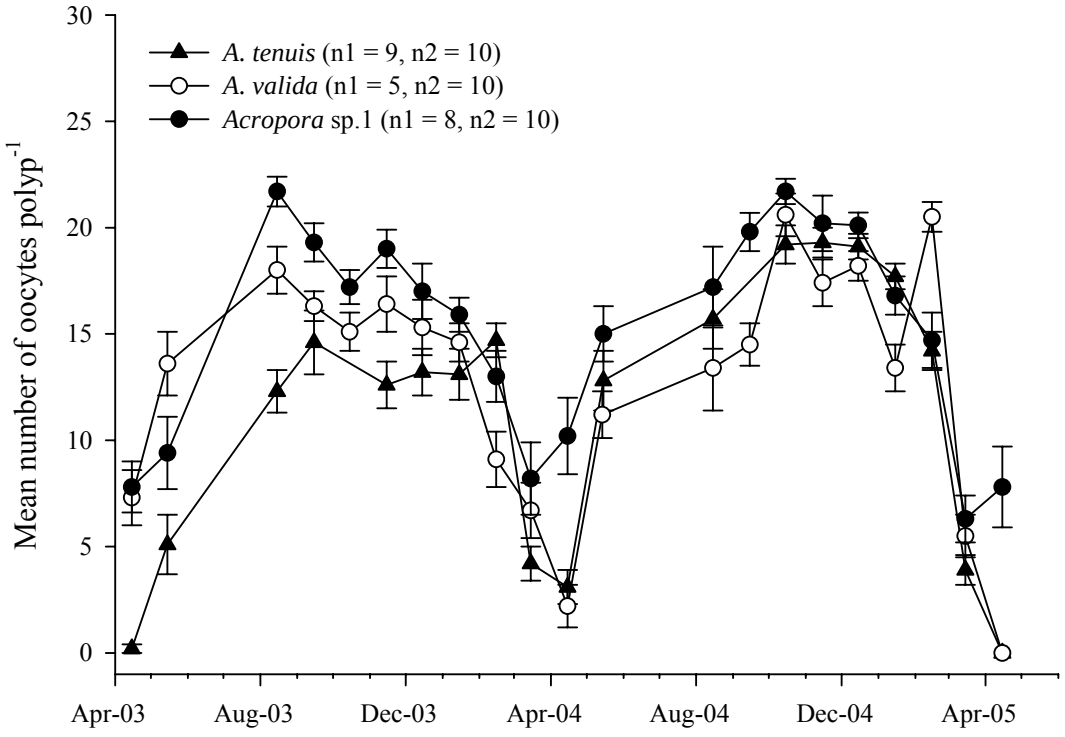


Figure 6.8: Seasonal changes in the mean number of oocytes in permanently marked colonies of *Acropora* species at Nyali Reef in April 2003 – May 2004, and at Kijembe Reef in August 2004 – April 2005. n1 = number of colonies sampled in the first reproductive season, n2 = number of colonies sampled in the second reproductive season. Error bars are standard error.

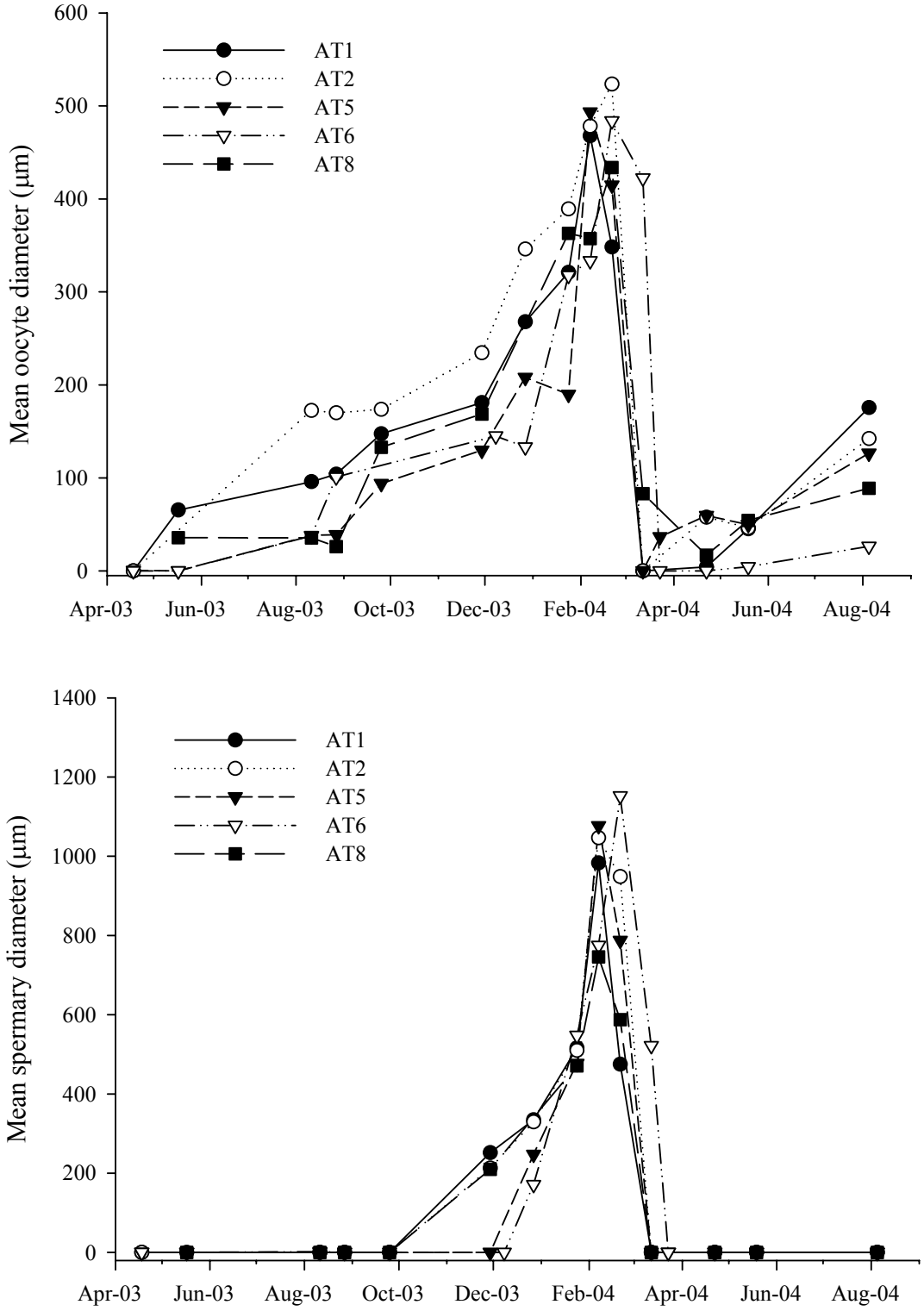


Figure 6.9: *Acropora tenuis*. Seasonal changes in mean oocyte and spermary diameter of five permanently marked colonies at Nyali Reef sampled over 17 months from April 2003 – August 2004. Error bars are standard error.

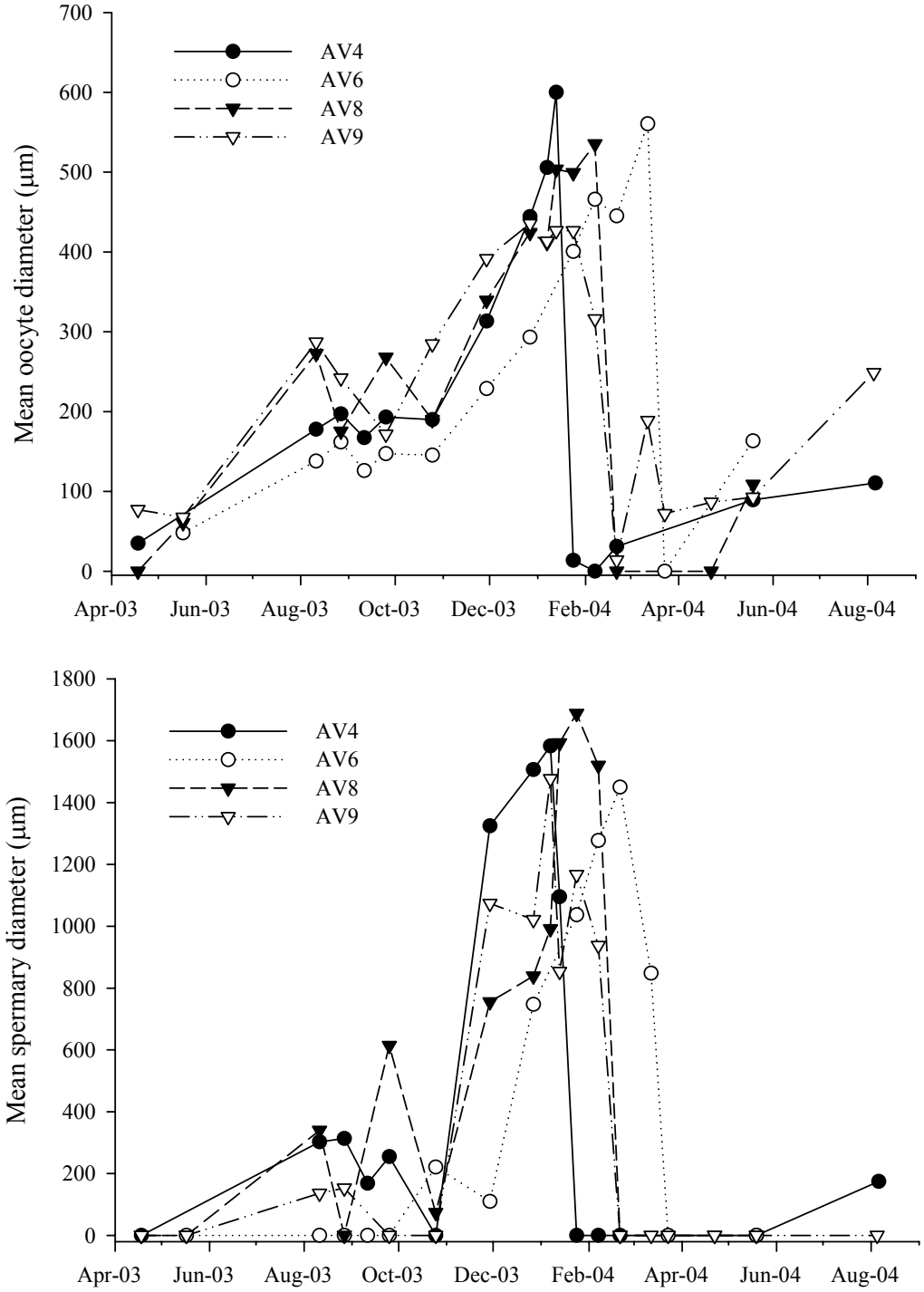


Figure 6.10: *Acropora valida*. Seasonal changes in mean oocyte and spermary diameter of four permanently marked colonies at Nyali Reef sampled over 17 months from April 2003 – August 2004. Error bars are standard error.

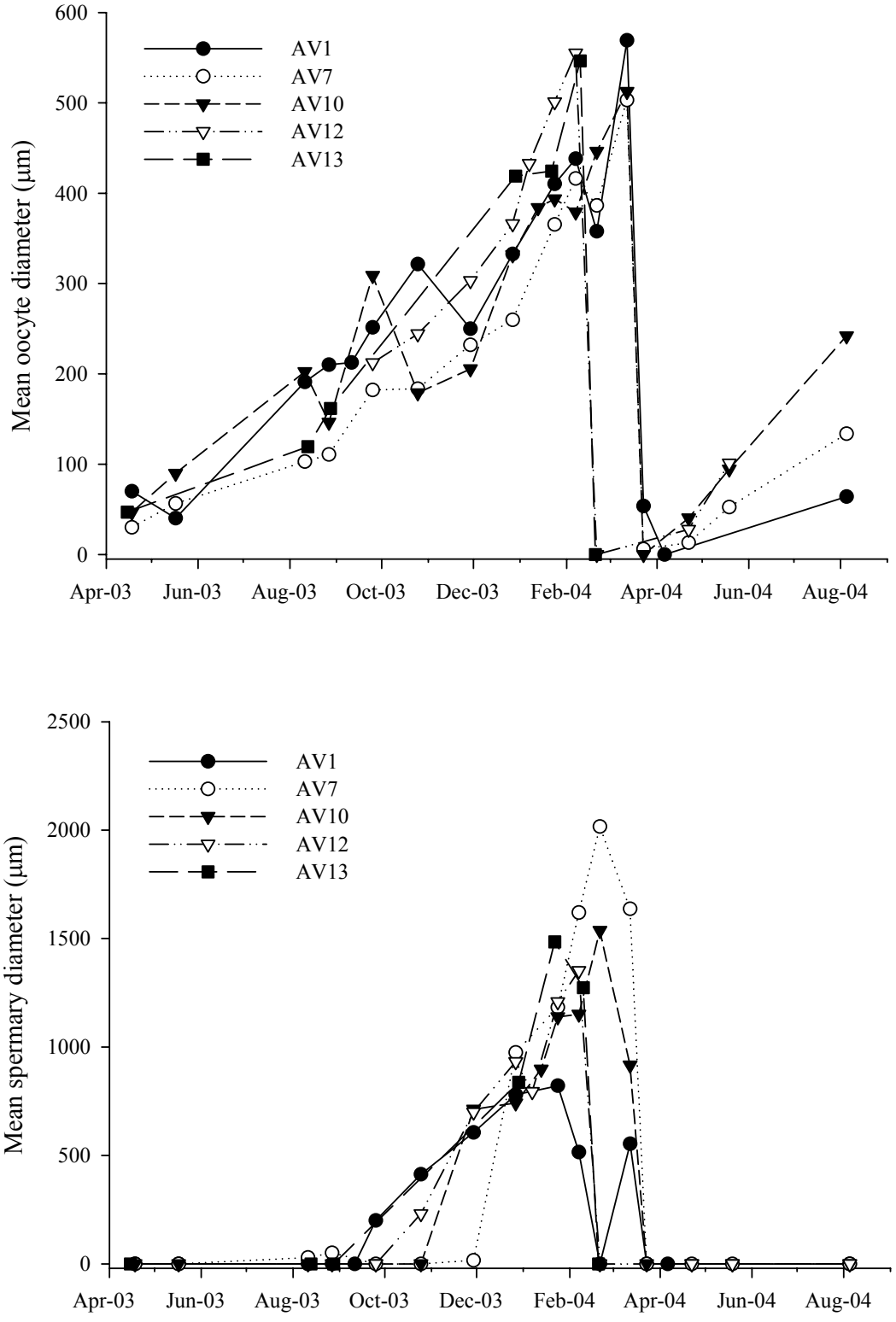


Figure 6.11: *Acropora* sp.1. Seasonal changes in mean oocyte and spermary diameter of five permanently marked colonies at Nyali Reef sampled over 17 months from April 2003 – August 2004. Error bars are standard error.

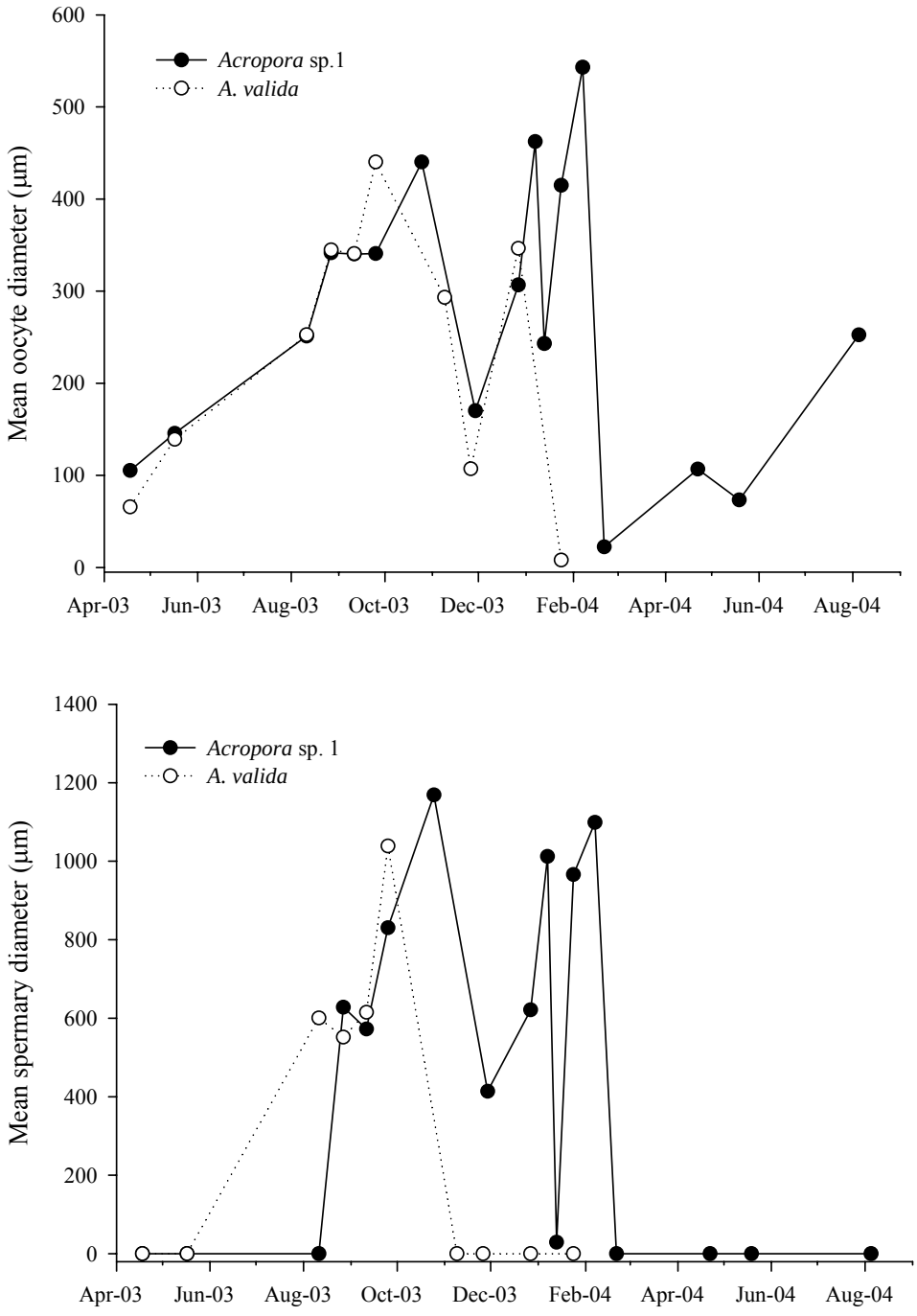


Figure 6.12: Seasonal changes in mean oocyte and spermary diameter of two permanently marked colonies of *Acropora* sp.1 and *A. valida* at Nyali Reef sampled over 17 months from April 2003 – August 2004 that spawned biannually. Error bars are standard error.

6.3.4 Fecundity, seasonality and the timing of spawning

6.3.4.1 Fecundity

Fecundity in *Acropora* species is usually expressed as the total number of oocytes polyp^{-1} (Wallace 1985a, 1999). In this study, *A. cytherea* had the lowest mean fecundity (6.9 oocytes polyp^{-1}), while *A. sordiensis* had the highest mean fecundity (21.5 oocytes polyp^{-1}) (Table 6.2). Mean oocyte diameter ranged from 404.4-557.5 µm (516.7-933.3 µm maximum diameter) and mean spermary diameter ranged from 445.0-1507.2 µm (Table 6.2). There was no relationship between mean oocyte diameter and fecundity ($F_{(1,17)} = 3.36$, $p = 0.085$, $r^2 = 0.16$), or between mean oocyte and mean spermary diameter ($F_{(1,17)} = 1.87$, $p = 0.189$, $r^2 = 0.10$) in *Acropora* species. However, there was a significant positive relationship between fecundity and mean spermary diameter ($F_{(1,17)} = 25.4$, $p < 0.001$, $r^2 = 0.60$). Gametes were absent in axial corallites, and the length of the sterile zone at the branch tip ranged from 0.3-2.2 cm and averaged 1.0 cm (± 0.4) in the 66 colonies (11 species) sampled. Sub-fecund radial corallites extended approximately 1-3 cm below the axial corallite (pers. obs.).

Mature pigmented oocytes were observed in the field and in fresh samples examined under a dissecting microscope, on average 2-3 weeks prior to spawning, though in some colonies mature oocytes were observed for 4-6 weeks prior to spawning. Pink and orange were the most common oocyte colour observed at maturity, though not all oocytes within a colony became pigmented prior to spawning (Table 6.2). Cerise-coloured oocytes were less common and were only recorded in *A. tenuis* and *A. subulata.* Mature white or pale oocytes were recorded in 12 (63.2%) of the 19 species, and in 55 (13.7%) of the 401 colonies studied. Oocyte colour was generally inconsistent among different colonies within species, and therefore did not provide a useful tool for identifying morphologically similar species.

Of the 192 colonies sampled at Nyali Reef in 2003 - 2004 (including permanently marked colonies), comprising 19 species, 146 (76.0%) were observed with mature gametes during the study. Of the remaining 46 colonies, 16 colonies did not produce gametes (8.3%), 8 colonies died (4.2%) from crown-of-thorns starfish predation,

damage from local fishers, mechanical damage during collection or unknown causes, and 22 colonies (11.5%) were observed with immature oocytes and spermaries but collections from these colonies had to cease before spawning occurred. Of the 209 colonies sampled at Kijembe and Mamba Reefs in 2004-2005 (including permanent marked colonies), comprising 17 species, 157 (75.1%) were observed with mature gametes during the study. Of the remaining 52 colonies, 17 colonies did not produce gametes (8.1%), 16 died (7.7%) from similar causes to those listed above for the previous year, and 19 (9.1%) were observed with immature oocytes and spermaries, but collections from these colonies had to cease before spawning occurred. Sixty colonies (12 species) marked at Nyali Reef in 2003 and re-sampled in August 2004, had only immature oocytes and no spermaries were recorded in tissue samples, suggesting winter spawning did not occur in these colonies.

6.3.4.2 Timing of spawning – lunar month

Figures 6.13 and 6.14 show the reproductive periods for *Acropora* species in the first reproductive season (2003 - 2004) and the second reproductive season (2004 - 2005), respectively, inferred from the disappearance of gametes from sequential tissue samples. Table 6.3 shows the proportion of the population (%) that spawned in each lunar month during the two study years. The number of colonies have been provided in the table so that actual numbers of colonies can be calculated if required.

Spawning in *Acropora* species was asynchronous, and extended over 7 months from October – April in both study years, with the majority of colonies (77-78%) releasing gametes between January – March (Fig. 6.13-6.14, Table 6.3). In 2004, the main spawning month was March with 35% of colonies releasing gametes in this month, while in 2005 the main spawning month was February with 42% of colonies releasing gametes. The greatest overlap in spawning of different species occurred in February, with 12 and 11 species releasing gametes in this month in 2004 and 2005, respectively (Table 6.3).

Table 6.2. The mean number of oocytes and the mean diameter of oocytes and spermaries in reproductively mature *Acropora* species (ordered in decreasing mean oocyte size). n1 = number of colonies sampled in the first reproductive season from April 2003 - May 2004; n2 = number of colonies sampled in the second reproductive season from September 2004 - May 2005. Colours: w = white, o = orange, p = pink, c = cerise.

Species	**n1**	**n2**	**# Oocytes**		**Oocyte size**			**Spermary size**		**Colour**
			mean	**sd**	**mean**	**max**	**sd**	**mean**	**sd**	
A. cytherea	3	3	6.9	1.6	557.5	667.0	56.7	445.0	126.9	w
A. nasuta	4	6	11.0	3.8	523.1	933.3	148.2	881.5	353.9	o, w
A. mossambica	12	23	19.3	5.7	522.8	800.4	68.3	1354.8	443.0	o, p, w
A. subulata	5	12	9.8	2.1	509.7	750.0	68.4	743.9	247.3	o, p, c, w
A. gemmifera	3	5	14.3	7.6	506.7	850.0	120.0	844.4	373.7	p
A. secale	9	9	15.1	5.1	498.9	733.7	95.3	1312.1	586.9	o, p, w
A. nana	0	3	10.6	1.6	493.1	655.9	57.7	816.6	249.2	p
A. lutkeni	1	2	19.2	2.2	491.7	606.7	58.9	1507.2	579.0	o, p
Acropora sp.1	30	17	17.8	5.8	479.5	833.3	76.1	1467.5	621.8	o, p, w
A. digitifera	3	3	8.7	3.1	474.6	716.7	84.1	584.1	253.0	o
A. kosurini	2	1	8.3	2.4	471.7	600.0	72.0	676.3	338.4	o, p
A. valida	24	25	16.7	5.6	468.3	733.3	87.4	1352.1	582.5	o, p, w
A. humilis	9	17	19.7	6.6	451.0	650.3	70.1	1202.1	538.7	o, p, w
A. tenuis	22	20	17.9	5.1	448.3	766.7	81.2	910.6	382.7	p, c
A. samoensis	8	6	16.0	6.0	434.4	667.0	95.6	1023.0	433.8	o, p, w
A. sordiensis	19	20	21.5	6.2	427.8	700.0	70.0	1368.1	500.8	o, p, w
A. glauca	1	0	14.4	0.9	417.1	516.7	36.5	933.3	326.4	p
A. divaricata	29	33	18.9	7.3	407.4	700.0	80.7	1013.7	396.1	o, p, w
A. branchi	6	0	12.0	8.2	404.4	516.7	89.7	1400.0	587.5	o, w
Total	**190**	**205**								

In species represented by greater than five colonies, spawning was split over 2-5 months. Partial spawning in individual colonies was less common in *Acropora* compared to faviid species (see Chapter 5), and was recorded in one *A. tenuis, A. mossambica* and *A. glauca* in 2004 (Fig. 6.13), and in two *A. tenuis*, one *A. humilis* and one *A. valida* colonies in 2005 (Fig. 6.14).

The length of the spawning period varied between species, with spawning occurring for shorter periods of 2 months in *A. sordiensis* and *A. samoensis* in 2003 - 2004, and in *A. subulata, A. divaricata* and *A. humilis* in 2004 - 2005. In contrast, *A. valida* had

the longest spawning period occurring over 5 months in 2003 - 2004, while in 2004 - 2005 *A. valida, A. sordiensis* and *A. mossambica* had the longest spawning periods, occurring over 4 months. The main (or peak) spawning months for individual species have been highlighted in grey in Table 6.3, and were found to differ between species. In some species, for example, *A. gemmifera* and *A. digitifera*, spawning occurred in October/November in both study years and did not overlap with the majority of the other species. *Acropora nasuta* and *A. subulata* spawned both early in the reproductive season in October/November as well as towards the end of the season in February/March in 2004 - 2005, with a 3-month period in between when no colonies released gametes. However, sample sizes were small for *A. nasuta* in both years, and further work is required to substantiate this pattern of reproduction.

In species represented by a minimum of ten colonies, the main spawning period was in January, February or March, when 30-80% (mean = 52.7%, sd = 14.1%) of the population of each species released gametes. No species had their main spawning period in the inter-monsoonal month of April, prior to the onset of the southeast monsoon season. In some species, the timing of spawning varied between consecutive years, while others were more consistent. For example, *A. sordiensis* spawned over 2 months from December - January in the first year, but spawned over 4 months from December - March in the second year. *Acropora valida* and *Acropora* sp.1 spawned over 3-4 months from December – March, with the main spawning period for the two species occurring in different months in 2004 (February and March), and in the same month in 2005 (February). The timing of spawning in *Acropora* sp.1 overlapped with *A. valida*, and hence this putative species cannot be separated by reproductive data alone.

Figure 6.13 (overleaf): Reproductive periods for marked colonies of *Acropora* species at Nyali Reef from 2003 - 2004. Each line represents a spawning record for a single colony. ●—○ = the period between the last sample date when gametes were present (closed circle) and the subsequent sample date when gametes were absent (open circle), ●—●—○ = the closed circles in the middle represent the date when some of the gametes had disappeared, indicating partial spawning occurred. ○= full moon, ●= new moon.

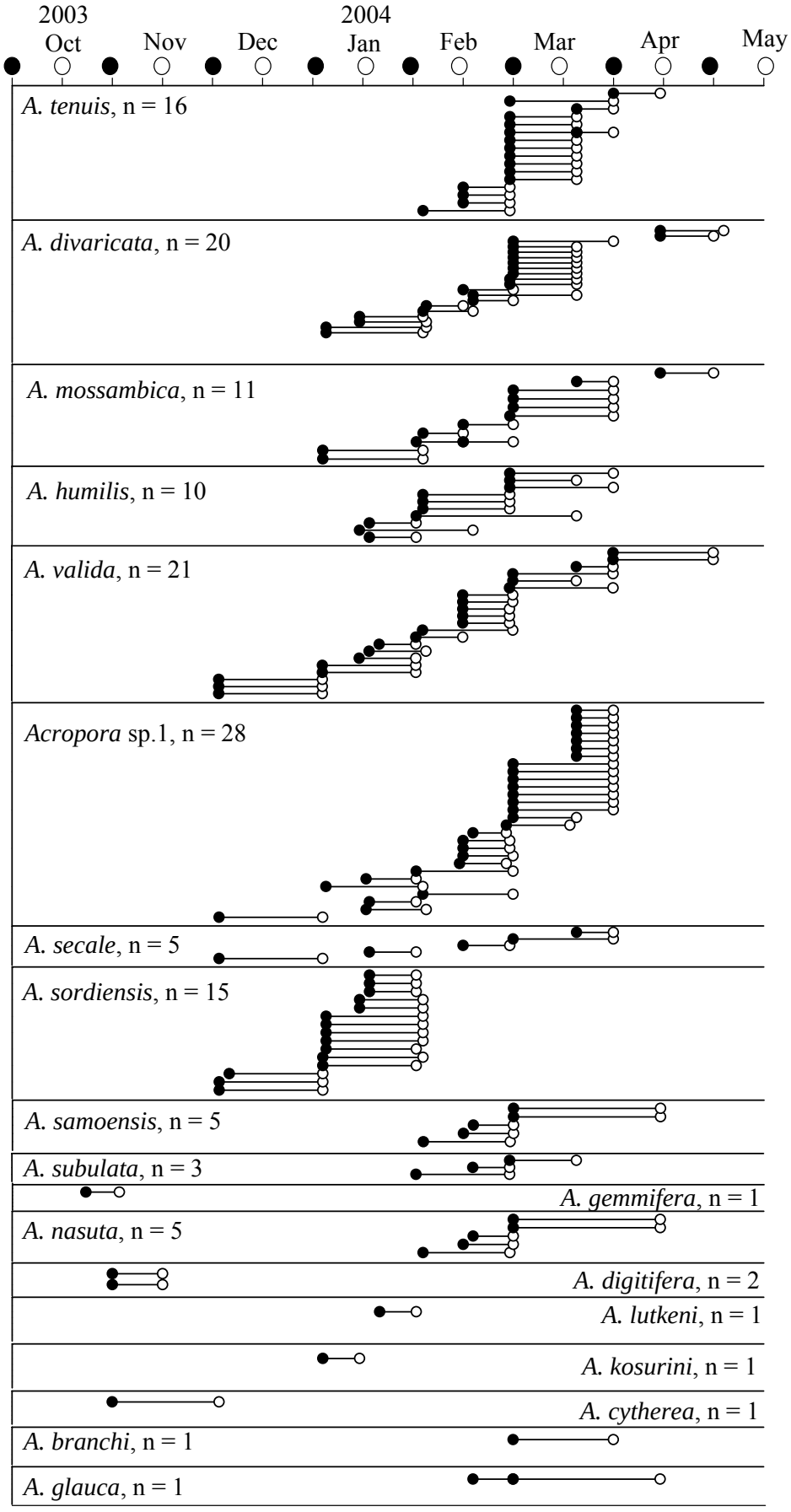

2003
Oct
Nov
Dec
2004
Jan
Feb
Mar
Apr
May
A. tenuis, n = 16
A. divaricata, n = 20
A. mossambica, n = 11
A. humilis, n = 10
A. valida, n = 21
Acropora sp.1, n = 28
A. secale, n = 5
A. sordiensis, n = 15
A. samoensis, n = 5
A. subulata, n = 3
A. gemmifera, n = 1
A. nasuta, n = 5
A. digitifera, n = 2
A. lutkeni, n = 1
A. kosurini, n = 1
A. cytherea, n = 1
A. branchi, n = 1
A. glauca, n = 1

Figure 6.14 (overleaf): Reproductive periods for marked colonies of *Acropora* species at Kijembe and Mamba Reefs from 2004 - 2005. Each line represents a spawning record for a single colony. ●—○ = the period between the last sample date when gametes were present (closed circle) and the subsequent sample date when gametes were absent (open circle), ●—●—○ = the closed circles in the middle represent the date when some of the gametes had disappeared, indicating partial spawning occurred.

○= full moon, ●= new moon.

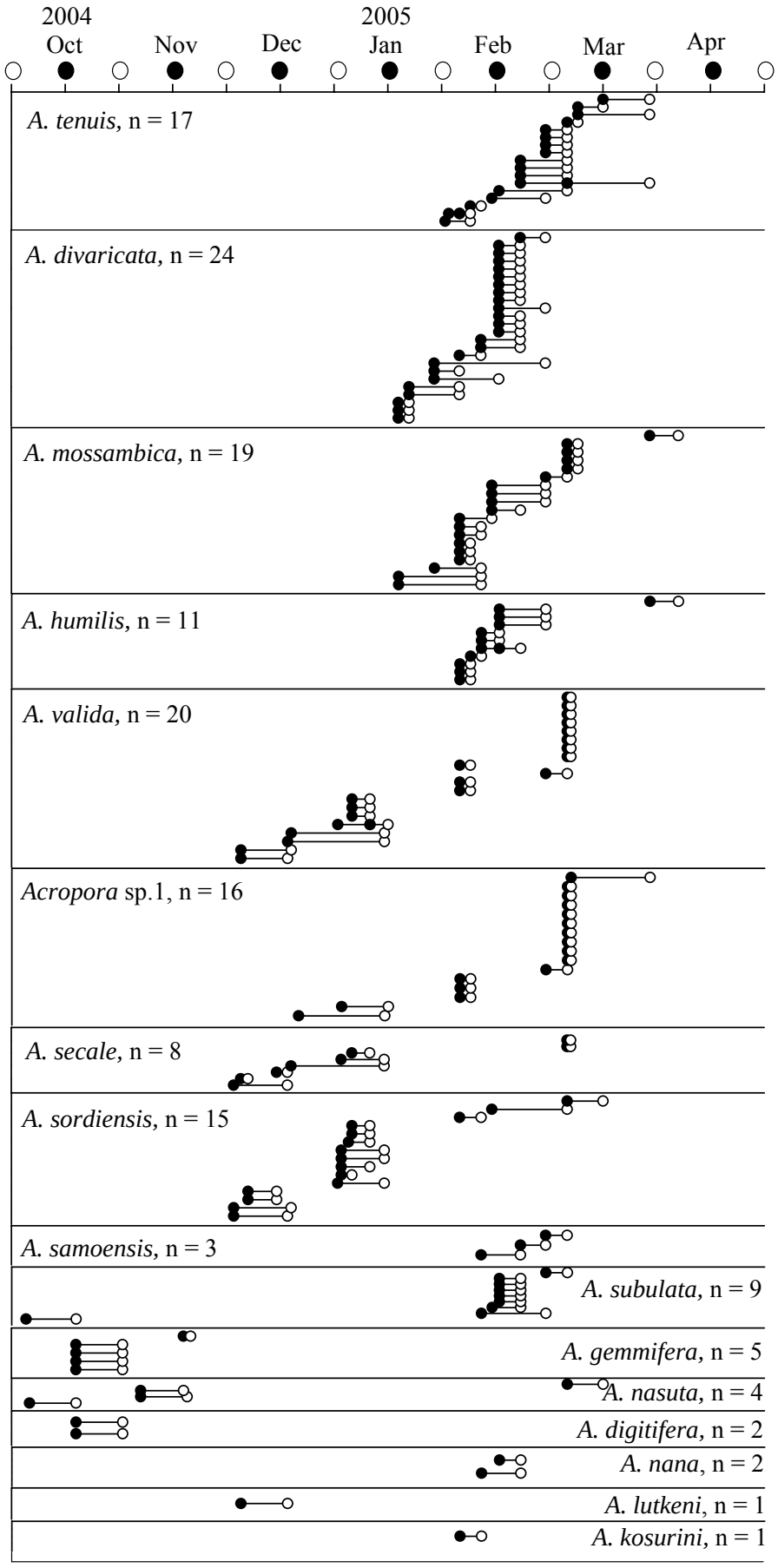

2004
Oct
Nov
Dec
2005
Jan
Feb
Mar
Apr
A. tenuis, n = 17
A. divaricata, n = 24
A. mossambica, n = 19
A. humilis, n = 11
A. valida, n = 20
Acropora sp.1, n = 16
A. secale, n = 8
A. sordiensis, n = 15
A. samoensis, n = 3
A. subulata, n = 9
A. gemmifera, n = 5
A. nasuta, n = 4
A. digitifera, n = 2
A. nana, n = 2
A. lutkeni, n = 1
A. kosurini, n = 1

Table 6.3: The proportion of the population (%) that spawned in each lunar month in April 2003 – May 2004 at Nyali Reef and in September 2004 – May 2005 at Kijembe and Mamba Reefs. Only the months where spawning was recorded are shown. Absent = colonies where no mature or maturing gametes was observed. Colonies that died or where collections were stopped before spawning occurred, have been excluded. The peak spawning month for individual species and for all colonies within each reproductive season has been highlighted in grey.

Species	**n**	**Oct 2003**	**Nov**	**Dec**	**Jan 2004**	**Feb**	**Mar**	**Apr**	**Absent**	**n**	**Oct 2004**	**Nov**	**Dec**	**Jan 2005**	**Feb**	**Mar**	**Apr**	**Absent**
A. gemmifera	1	100								5	80	20						
A. cytherea	2		50						50	1								100
A. digitifera	2		100							3	67							33
A. nasuta	4	25				25	50			5	20	40				20		20
A. sordiensis	17			18	71				12	16			31	44	13	6		6
Acropora sp.1	29			3	14	24	55		3	16				13	25	63		
A. secale	6			17	17	17	33		17	8			38	38		25		
A. valida	23			13	22	30	17	9	9	21			10	29	14	43		5
A. lutkeni	1				100					1			100					
A. kosurini	1				100					1					100			
A. humilis	10				30	30	40			14					71		7	21
A. divaricata	21				19	19	48	10	5	26				23	69			8
A. mossambica	11				18	27	45	9		21				14	52	19	5	10
A. tenuis	19					21	58	5	16	19				11	58	21		11
A. branchi	4					25			75	0								
A. glauca	1					100				0								
A. samoensis	6					50	33		17	5					60			40
A. subulata	3					67	33			10	10				80			10
A. microphthalma	1								100	0								
A. nana	0									2					100			
Total (colonies)	**162**	**1**	**2**	**5**	**20**	**23**	**35**	**4**	**10**	**169**	**5**	**2**	**6**	**17**	**42**	**18**	**1**	**10**
Total (# species)	**19**	**2**	**2**	**4**	**9**	**12**	**10**	**4**	**10**	**17**	**4**	**2**	**4**	**7**	**11**	**7**	**2**	**11**

6.3.4.3 Timing of spawning – lunar phase

Data showing the lunar phases over which coral spawning occurred, for those colonies with spawning periods inferred from samples taken over 14 days or less, are shown in Table 6.4, and colonies with spawning periods inferred from samples taken over 3 days or less, are shown in Table 6.5. Spawning in *Acropora* species in Kenya occurred over a range of lunar phases, with ten species spawning in the 3rd lunar quarter (after full moon), eight in the 4th quarter, five in the 1st quarter (after new moon), and two species in the 2nd quarter (Table 6.4). Species represented by more than two colonies, spawned in more than one lunar phase. For example, *A. mossambica* spawned predominantly in the 4th lunar quarter, between lunar day 21-24, but one colony spawned in the 1st quarter, and two colonies in the 3rd quarter (Table 6.4-6.5).

By contrast, *A. tenuis* spawned in the 1st/2nd, 3rd and 4th lunar quarters (Table 6.4), and it is likely that this species spawns on a number of consecutive nights or alternatively on different nights in different months (Table 6.5). *Acropora divaricata* and *A. subulata* spawn predominantly in the 1st lunar quarter (Table 6.4), and in three colonies of *A. divaricata* the timing of spawning was narrowed to the period 4-7 nights after new moon (Table 6.5). A number of the colonies identified as *A. divaricata* may be *A. solitaryensis* (see Chapter 3), and given that the majority of sampled colonies spawned in the 1st lunar quarter, it is highly likely that there is an overlap in the timing of spawning between the two species. The five species belonging to the *Acropora nasuta* group spawned in the 3rd and 4th lunar quarters, with *A. valida, A. secale* and *Acropora* sp.1 spawning on the same night on 2 March 2005, on the 6th night AFM (lunar day 21).

Coral spawning was observed in six of the nine *Acropora* species held in aquaria (Fig. 6.15). Of the branches from 16 colonies held in aquaria, three released gametes on the same night as the colonies in the field from which they were removed, and seven released gametes in aquaria 1-2 weeks earlier than their corresponding colonies in the field (Table 6.6). In most branches, the setting of egg-sperm bundles under the oral cavity commenced between 19:10-19:45 hours, with spawning commencing between 21:13-21:56 hours. *Acropora tenuis* commenced setting around sunset, and spawned

between 19:02-19:17 hours. In *Acropora* sp.1 and *A. valida* setting commenced at 19:10 hours, and spawning occurred between 20:55-21:00 hours. Compact positively buoyant egg-sperm bundles were extruded slowly through the mouth (Type I spawning behaviour, Babcock et al. 1986), and floated immediately to the water surface where water movement generated by the airstone caused the bundles to slowly break apart, separating individual oocytes and sperm clouds. All egg-sperm bundles were released rapidly from the branches, within 15-19 minutes of the commencement of spawning. Similar patterns of gamete released were recorded in *A. sordiensis, A. divaricata, A. tenuis* and *A. humilis*.

Table 6.4: The lunar phase when spawning occurred, as inferred from the absence of gametes between sequential sample taken less than 14 days apart, in September 2004 – May 2005. Lunar days are divided into four lunar quarters: 1st = 0-7, 2nd = 8-14; 3rd = 15-21, 4th = 22-29, where lunar day 0 = new moon and lunar day 15 = full moon.

Species	**n**	**1st**	**1st/2nd**	**2nd**	**2nd/3rd**	**3rd**	**3rd/4th**	**4th**	**4th/1st**
A. mossambica	17	1	3			2	1	10	
A. gemmifera	5	1	4						
A. nana	2	1							1
A. subulata	6	5				1			
A. divaricata	22	14	1	1	2	1		1	2
A. digitifera	2		2						
A. tenuis	15		2		4	5	1	2	1
A. humilis	11		3			1		4	3
A. samoensis	3			1		1			1
A. nasuta	1								1
A. secale	6					3	2		1
A. lutkeni	1						1		
Acropora sp.1	14					10	1	3	
A. kosurini	1							1	
A. valida	15					9	4	2	
A. sordiensis	12					1	7	3	1
Total (colonies)	**133**	**22**		**2**		**34**		**26**	
Total (# species)	**16**	**5**		**2**		**10**		**8**	

Table 6.5 The lunar phase when the last sample was observed (Moon-mat) and the subsequent sample when gametes were absent (Moon-abs) from coral colonies containing mature gametes. Data are shown for colonies with spawning periods inferred from samples taken over 3 days or less, in September 2004 – May 2005. Days: number of days between samples. Lunar quarter is defined in Table 6.4. Full moons were on 27 November, 27 December in 2004, and 25 January, 24 February, 26 March in 2005.

Species	**n**	**Mature**	**Absent**	**Days**	**Moon-mat**	**Moon-abs**	**Lunar quarter**
A. tenuis	1	28-Jan-05	31-Jan-05	3	18	21	3rd
	1	3-Feb-05	6-Feb-05	3	24	27	4th
	1	2-Mar-05	5-Mar-05	3	21	24	4th
A. valida	8	2-Mar-05	3-Mar-05	1	21	22	3rd
	2	31-Jan-05	3-Feb-05	3	21	24	4th
Acropora sp.1	9	2-Mar-05	3-Mar-05	1	21	22	3rd
	3	31-Jan-05	3-Feb-05	3	21	24	4th
A. secale	1	1-Dec-04	3-Dec-04	2	19	21	3rd
	2	2-Mar-05	3-Mar-05	1	21	22	3rd
	1	11-Dec-04	14-Dec-04	3	29	2	4th/1st
A. sordiensis	1	29-Dec-04	1-Jan-05	3	17	20	3rd
A. mossambica	6	31-Jan-05	3-Feb-05	3	21	24	4th
	4	2-Mar-05	5-Mar-05	3	21	24	4th
A. divaricata	3	14-Jan-05	17-Jan-05	3	4	7	1st
A. humilis	3	31-Jan-05	3-Feb-05	3	21	24	4th
	1	3-Feb-05	6-Feb-05	3	24	27	4th
A. gemmifera	1	15-Nov-04	17-Nov-04	2	3	5	1st

Figure 6.15: Photographs showing 'setting' and spawning of mature gametes in *Acropora* species held in aquaria. Species shown are *A. tenuis* (a-b), *A. valida* (b-c), *A. divaricata* (d) and *A. humilis* (e).

Table 6.6: The timing of setting and spawning in branches collected from marked colonies and held in aquaria between January – March 2005. Type: natural = spawning confirmed for the same night in colonies in the field; premature = branches in aquaria released gametes, but colonies in the field still had mature gametes; '–': no samples were taken in the field to confirm spawning.

Species	Date	Lunar	Type	Start setting	End setting	Start spawn	End spawn
A. sordiensis	5-Jan-05	24	-	19:30	20:54	21:13	21:27
A. divaricata	6-Jan-05	25	premature	19:36	21:09	21:25	21:35
	6-Jan-05	25	premature	19:37	21:09	21:25	21:35
	7-Jan-05	26	-	19:30	21:16	21:22	21:40
	10-Jan-05	0	premature	19:35	20:43	21:24	21:33
	11-Jan-05	1	premature	17:47	21:08	21:35	21:38
	12-Jan-05	2	premature	19:20	21:00	21:28	21:35
	17-Jan-05	7	-				21:30
	18-Jan-05	8	-		20:30	21:20	21:30
	19-Jan-05	9	-	19:39	21:19	21:30	21:30
A. tenuis	21-Jan-05	11	premature	17:45	18:50	19:02	19:17
A. humilis	27-Jan-05	17	premature	19:45	22:00	20:04	20:14
	29-Jan-05	19	-	20:17	21:27	21:56	22:03
Acropora sp.1	2-Mar-05	21	natural	19:10	20:38	20:55	21:05
	2-Mar-05	21	natural	19:10	20:38	21:00	21:19
A. valida	2-Mar-05	21	natural	19:10	20:38	20:55	21:05

6.3.4.4 Environmental parameters

Sea surface temperature patterns at the study sites are described in Chapter 5, and are therefore not repeated in this section. *Acropora* species spawned over the NE monsoon season and the inter-monsoonal months, from October - April, with spawning peaking in the months January – March when sea surface temperatures were at their annual summer maximum averaging 28.3 ºC (Fig. 6.16). Spawning occurred over the temperature range 26-29 ºC, and occurred just prior to and throughout the short rains in November, but finished prior to peak rainfall in May on the Kenya coast (see Fig. 2.4, Chapter 2), and when solar radiation was generally highest and above 20 mJ m^{-2} (Fig. 2.3, Chapter 2).

In Kenya, spring tides occur one or two days after the full and new moon, and neap tides just after the second and last lunar quarter. Spawning in *Acropora* species occurred over a range of lunar phases, and hence over both spring and neap tides (Fig. 6.17). In *A. valida, A. secale* and *Acropora* sp.1, spawning occurred on 2 March 2005, the 6^{th} night AFM, as inferred by the disappearance of gametes from sequential samples taken from 19 colonies in the field, and observations of spawning in three colonies kept in the aquaria at around 21:00 hours (Table 6.6). This spawning coincided with the tide dropping to the second low tide of the day, when tidal mixing was likely to be minimal (Fig. 6.18). The difference in tidal height between 19:59 and 02:18 hours on that night was 2.3 m.

As described in section 5.3.4.4, there is little seasonal variation in daylength in Kenya, with the greatest range being 10 minutes (Fig. 6.19). Spawning in *Acropora* species occurred when daylength was 12:05-12:12 hours, with peak spawning occurring just after the longest daylength in the year.

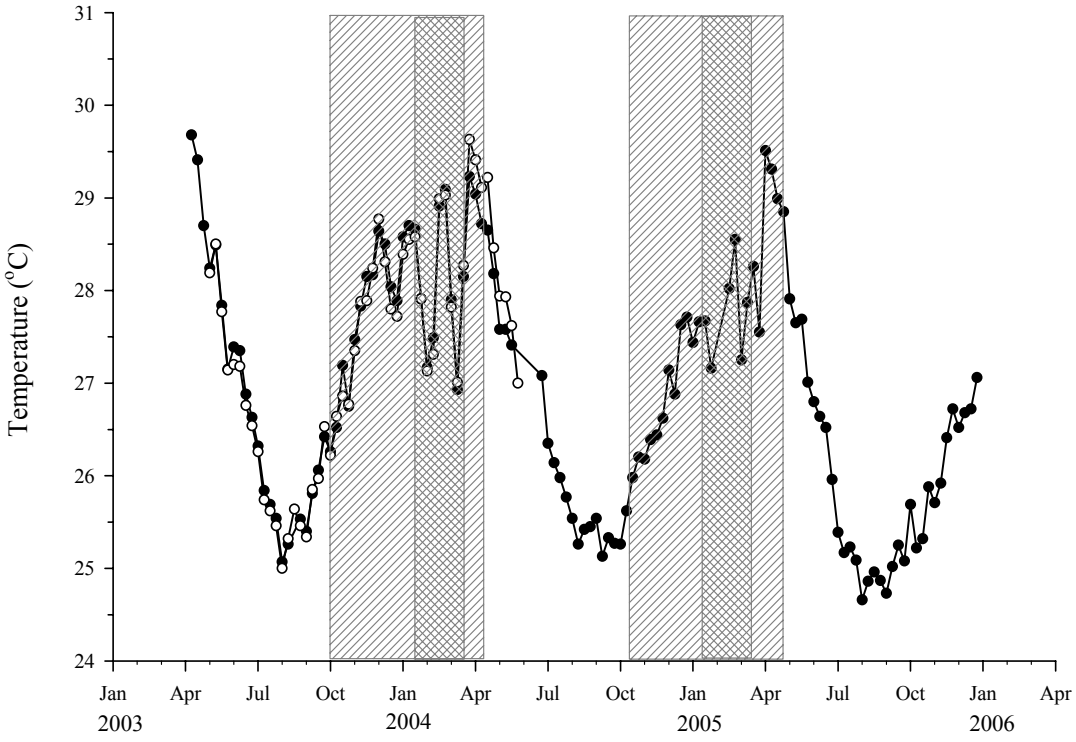


Figure 6.16: Mean weekly sea surface temperatures at Coral Gardens (white circle) and Nyali Reef (black circle) from April 2003 – December 2005. The larger shaded box indicates months when spawning was recorded in *Acropora* species. The smaller and darker shaded box indicates the peak period of spawning when the greatest number of species and colonies released gametes.

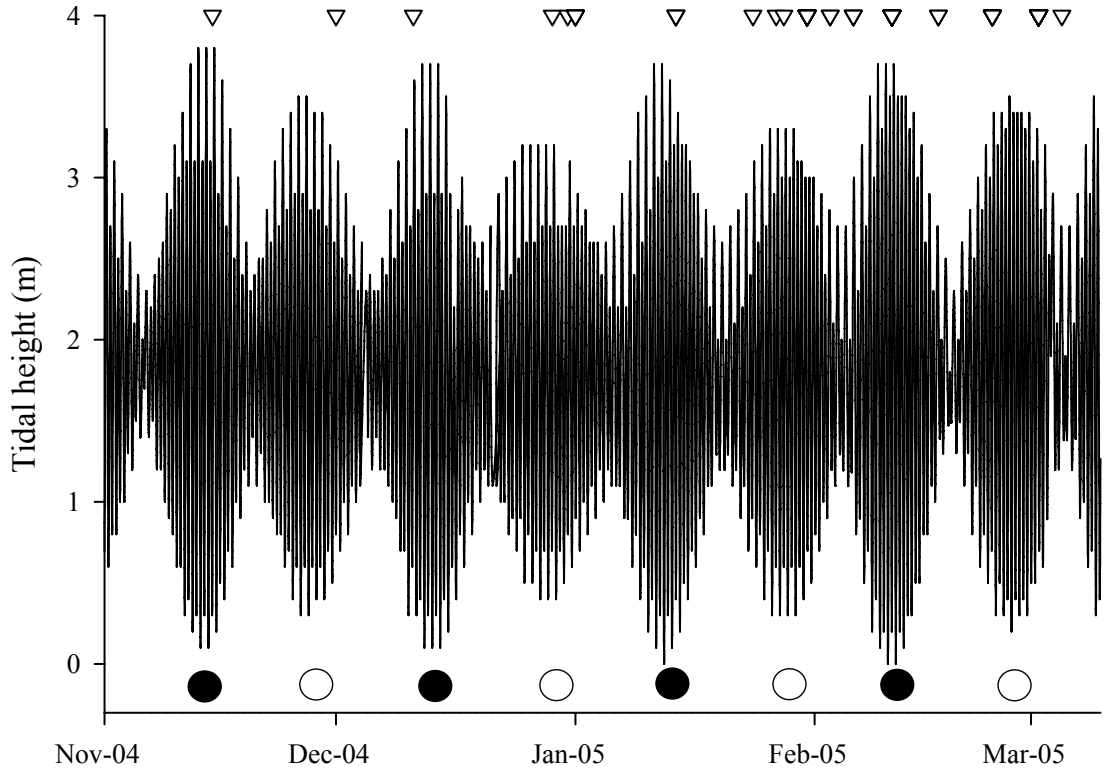


Figure 6.17: Tidal and lunar rhythms in Kenya during the northeast monsoon in 2004-2005. Triangles indicate when the last mature sample was recorded in *Acropora* species (within 7 days of spawning). ○: full moon, ●: new moon.

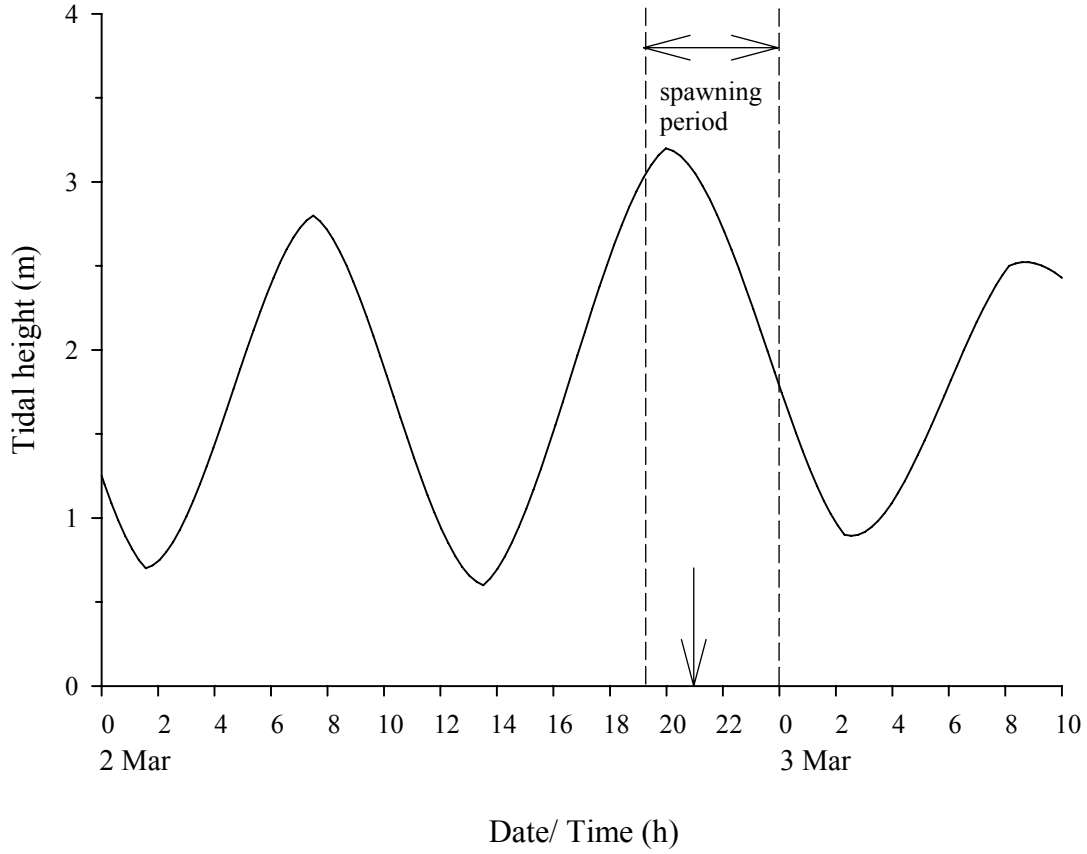


Figure 6.18: Tidal phase at Kijembe and Mamba Reefs on 2 March 2005, the 6th night after full moon. 'Spawning period' marks the hours between sunset and midnight, and the arrow on the x-axis indicates the timing of spawning in two *Acropora* sp.1 and one *A. valida* held in aquaria.

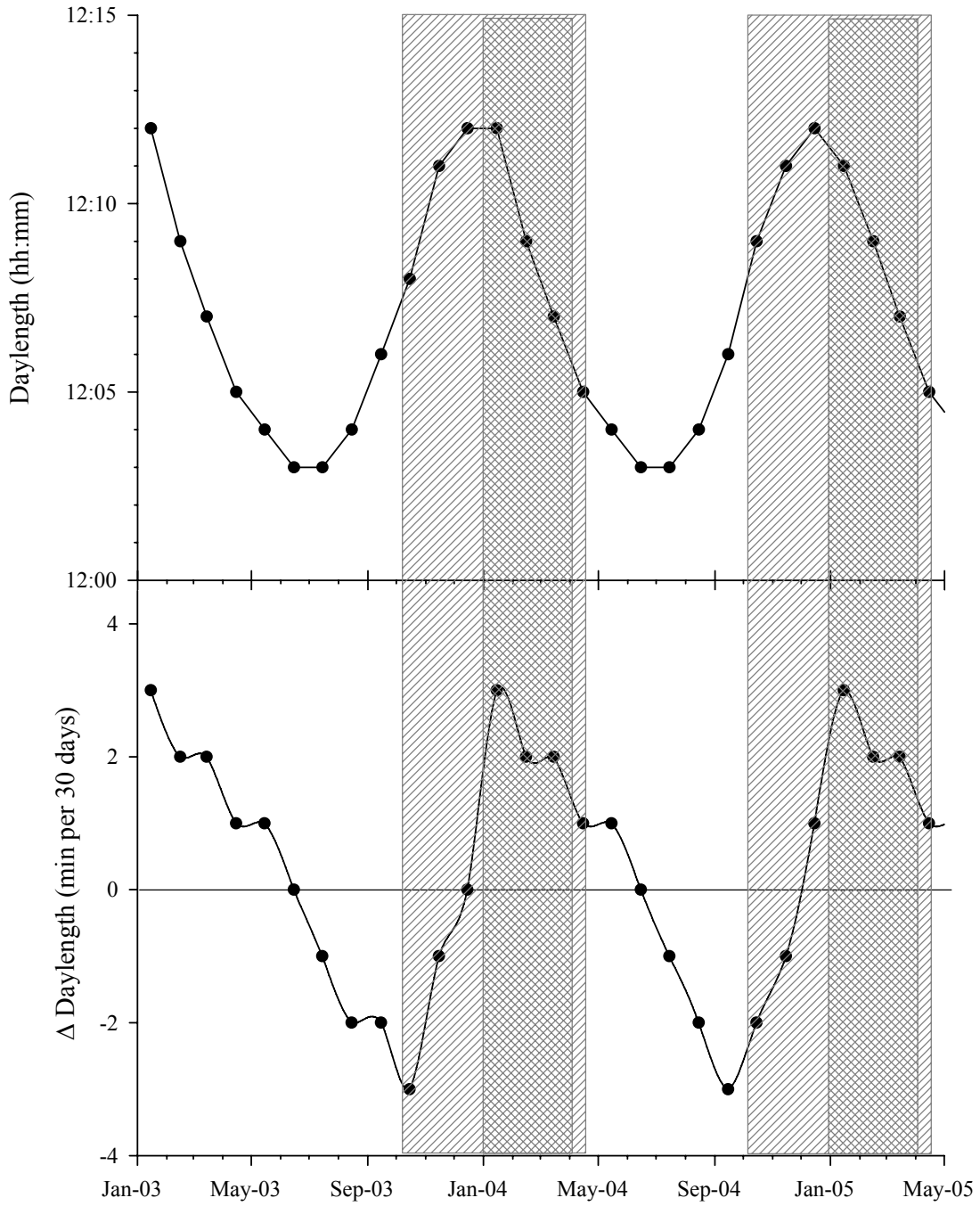


Figure 6.19: Seasonal variation in daylength in Kenya. The larger shaded box indicates the months when spawning was recorded in *Acropora* species. The smaller and darker shaded box indicates when peak spawning occurs in this genus. Daylength calculated from sunrise and sunset times from the internet (www.timeanddate.com/worldclock/astronomy.html) for Nairobi, Kenya.

6.4 Discussion

6.4.1 Reproductive patterns

The 23 *Acropora* species studied in the Mombasa Marine National Reserve in Kenya were simultaneous hermaphrodites, with protogynous gamete development with oocytes and spermaries on separate mesenteries. All *Acropora* species were broadcast spawners as evidenced by spawning observed in six species held in aquaria and inferred in a further 98 colonies sampled 1-8 days apart, and the lack of planulae in 1959 samples, including samples taken 1-2 weeks following spawning. This sexual pattern and mode of reproduction and development predominate in *Acropora* (subgenus *Acropora*), and are consistent with studies from other regions (reviewed by Harrison and Wallace 1990; Richmond and Hunter 1990; see also Wallace 1985a; Babcock et al. 1986, 1994; Kenyon 1992; Hayashibara et al. 1993; Shlesinger et al. 1998; Guest et al. 2005a; Carroll et al. 2006 among others).

6.4.2 Gametogenesis

Despite the abundance and diversity of *Acropora* species on tropical reefs and the ease of studying them without the need for complex histological processing, there have been very few studies that have described gametogenic cycles in this genus. In Kenya, single annual cycles of gametogenesis were recorded in *A. tenuis* and the majority of colonies of *A. valida* and *Acropora* sp.1. In *A. tenuis,* the onset of gametogenesis varied between individual colonies by up to a few weeks, but as gametogenesis progressed the population became more synchronised, with rapid gamete maturation occurring in the 1-2 months prior to spawning. This pattern of gamete maturation is consistent with descriptions of gametogenesis in 6 *Acropora* species (Wallace 1985a) and unpublished data on 12 *Acropora* species (P. Harrison, pers. comm.) from the central GBR, and with most broadcast spawners exhibiting a single annual reproductive cycle (Harrison and Wallace 1990).

In contrast, the onset and development of gametes within populations of *A. valida* and *Acropora* sp.1 were less synchronous, with gametes in the different colonies reaching maturity at different times (Fig. 6.10-6.11). Asynchronous maturation of colonies

within a species is less common in broadcast spawners compared with brooders, but has been recorded in *A. sarmentosa* on the GBR (Wallace 1985a), and in congenera on subtropical reefs in the Solitary Islands, eastern Australia (Wilson 1998). *Acropora* species are generally less synchronous in their spawning times compared to faviids and other massive species (Oliver et al. 1988; Baird et al. 2002; Hayashibara et al. 1993; Wilson and Harrison 2003), and some degree of 'staggered' maturation of colonies may occur within some *Acropora* species at other locations, including on the GBR (Wolstenholme 2004).

In *A. tenuis,* the length of oogenesis and spermatogenesis was 8-11 months and 3-4 months, respectively, while in *A. valida* and *Acropora* sp.1 oogenesis occurred over 11-12 months and spermatogenesis occurred over 7-8 months. The length of oogenesis and spermatogenesis in *A. valida* and *Acropora* sp.1 contrasts with congenera (including *A. valida)* on the GBR where oogenesis occurred for 8-10 months and spermatogenesis for 2-3 months (Wallace 1985a). *Acropora* species in the Red Sea also have shorter cycles of oogenesis (4-7 months) and spermatogenesis (2-4 months) (Shlesinger and Loya 1985; Shlesinger et al. 1998) compared to Kenya. Quiescent non-reproductive periods between reproductive cycles are longer in *Acropora* species on the GBR (3-4 months) and in the Red Sea (5-8 months) compared to Kenya, where quiescent periods were short (0-2 months) in the three species studied. Overlapping oogenic cycles occurred in *A. valida* and *Acropora* sp.1, but were not recorded in congenera on the GBR (Wallace 1985a; P. Harrison, unpubl. data), but were recorded in six colonies of *Acropora* (2 species) in the Solitary Islands (Wilson 1998), and in three biannually spawning *Acropora* species in Western Samoa (Mildner 1991). Overlapping oogenic cycles were also recorded in biannually spawning colonies of *Platygyra daedalea* and some annually spawning colonies of *Leptoria phrygia* in Kenya (see Chapter 5).

The length of spermatogenesis in the three Kenyan *Acropora* species (3-8 months) is similar to *Acropora* species in the Solitary Islands (29-30ºS), where spermary development occurred over 2-7 months (Wilson 1998). Wilson (1998) suggested that spermaries in *Acropora* species may require more time to develop in the subtropics compared to the tropics, because of the cooler sea surface temperatures. However, similarities in the length of spermatogenesis between Kenya and the Solitary Islands

may instead simply reflect the asynchronous pattern of reproduction found at both locations (see section 6.4.3).

Compared to *P. daedalea,* where biannual gametogenic cycles were recorded in up to 20% of the sampled population (see Chapter 5), only one colony of *A. valida* and one colony of *Acropora* sp.1 (3.8% of permanently marked colonies) underwent biannual cycles during the two year study. This suggests that biannual cycles of gametogenesis may not be a major reproductive characteristic of these two species, or the genus *Acropora* in Kenya. These findings are similar to Guest et al. (2005a) who recorded biannual cycles of gametogenesis in only two colonies of *A. humilis* on equatorial reefs in Singapore (1ºN) during a 15 month study, but contrast with a study by Mildner (1991), who recorded biannual cycles of gametogenesis in populations of *A. hyacinthus, A. gemmifera* and a branching morphotype of *A. humilis* on reefs in Western Samoa (15ºS). Biannual cycles were also recorded in populations of *A. hyacinthus* and *A. formosa* on reefs in Madang, PNG (5ºS) (Oliver et al. 1988), and three *Montipora* species (Family Acroporidae) on reefs at Magnetic Island, central GBR (19ºS) (Stobart et al. 1992).

It is not known why some colonies of *Acropora* species complete two cycles of gametogenesis in some locations, while the majority of colonies and species complete only one cycle each year. The occurrence of biannual cycles of gametogenesis in *Acropora* species, however, do not appear to be related to latitude, as they occur on both equatorial and non-equatorial tropical reefs (see examples above). In addition, the occurrence of biannual cycles does not appear to be related to temperature range, with low annual variation recorded in PNG (3 ºC, Oliver et al. 1988), Western Samoa (2.5 ºC, Mildner 1991), Singapore (3-4 ºC, Guest et al. 2004a) and Kenya (5 ºC, this study), and higher ranges recorded at Magnetic Island on the GBR (12 ºC). Further gametogenic work is required to quantify the extent to which other broadcast spawning reef coral species undergo biannual cycles among a wider range of species and geographic locations, and to determine what ecological advantage(s) may be gained by broadcast spawners having multiple cycles.

6.4.3 Gamete size and fecundity

With the exception of *A. cytherea*, *Acropora* species in Kenya generally have small oocytes and high polyp fecundity compared to species from other geographic locations (Table 6.7). This is consistent with the general trend in broadcast spawners of a 'trade-off' between the size and number of oocytes produced, which is thought to be related to resource allocation and life-history characteristics (Harrison and Wallace 1990).

Mean *Acropora* oocyte diameter ranged from 404-558 μm in Kenya, which is similar to mean oocyte sizes recorded in Taiwan (389-661 μm) (Dai et al. 1992), but is smaller than sizes recorded on the GBR (534-652 μm), Hawaii (605-669 μm) and in the Solitary Islands (615-712 μm) (Wallace 1985a; Kenyon 1992; Wilson 1998), and is larger than sizes recorded in the Red Sea (375-420 μm) (Shlesinger et al. 1985). Mean polyp fecundity was more variable and was high in Kenya ranging from 6.9-21.1 oocytes polyp^{-1} in different species, compared to ranges recorded in species on the GBR (5.6-12.8), Hawaii (2.3-7.6), Okinawa (7.8-9.5) and in the Solitary Islands (8.4-13.0) (Wallace 1985a; Kenyon 1992; Shimoike et al. 1992; Wilson 1998).

Wallace (1985a) and Wilson (1998) noted an inverse relationship between oocyte size and polyp fecundity in *Acropora* species on the GBR and in the Solitary Islands, respectively, but no such relationship occurred in the 19 *Acropora* species studied in Kenya. Differences between Kenya and the east coast of Australia may reflect geographic differences, or the lower number of species examined in the GBR (8 species, Wallace 1985a) and in the Solitary Islands (4 species, Wilson 1998) studies. There was, however, a significant positive relationship between polyp fecundity and mean spermary diameter in Kenyan *Acropora* species. This suggests that resources are allocated proportionally between oocytes and spermaries within individual species, presumably to maximise fertilisation and outcrossing. The importance of sperm to egg ratios was demonstrated experimentally by Benzie and Dixon (1994) who found fertilisation rates in crown-of-thorns starfish were reduced at lower ratios, and particularly at low sperm concentrations, and Oliver and Babcock (1992) showed experimentally that fertilisation in coral gametes was maximised at sperm concentrations of 10^5-10^6 ml^{-1}.

Table 6.7: Comparisons of mean oocyte size and fecundity (oocytes polyp^{-1}) recorded in *Acropora* species at different geographic locations, for which data are available for Kenya (bold). For each species, the data are ordered in decreasing mean oocyte size. Except where indicated (#), oocyte sizes were calculated by dissecting tissue samples under a stereomicroscope. Where data are available for more than one location within a country, the location name is given. '*': maximum diameter measured. '-': no data are available.

Species	Location	Oocyte size (µm)	Fecundity	Reference
A. cytherea	Kenya	**558**	**6.9**	This study
	Taiwan	486	-	Dai et al. 1992
	W. Australia	440	10.0	Rosser 2005
A. digitifera	W. Australia	585	11.6	Rosser 2005
	Kenya	**475**	**8.7**	This study
	Japan	-	7.8	Shimoike et al. 1992
A. divaricata	Taiwan	622	-	Dai et al. 1992
	Kenya	**407**	**18.9**	This study
A. glauca	Solitary Is. (Aus)	703	10.6	Wilson 1998
	Kenya	**417**	**14.4**	This study
A. humilis	Hawaii	714	7.3	Kenyon 1992
	W. Samoa	583	7.7	Mildner 1991
	Taiwan	507	-	Dai et al. 1992
	Kenya	**451**	**19.7**	This study
	Red Sea[#] *	395	-	Shlesinger et al. 1985
A. lutkeni	Solitary Is. (Aus)	627	9.9	Wilson 1998
	Kenya	**492**	**19.2**	This study
A. nana	Taiwan	568	-	Dai et al. 1992
	Kenya	**493**	**10.6**	This study
A. nasuta	Taiwan	646	-	Dai et al. 1992
	Kenya	**523**	**11.0**	This study
	Japan	-	9.4	Shimoike et al. 1992
A. samoensis	W. Australia	520	10.7	Rosser 2005
	Kenya	**434**	**16.0**	This study
A. secale	Palau	674	-	Kenyon 1995
	Kenya	**499**	**15.1**	This study
A. tenuis	W. Australia	605	10.5	Rosser 2005
	Kenya	**448**	**17.9**	This study
A. valida	Solitary Is. (Aus)	697	10.0	Wilson 1998
	Hawaii	644	7.3	Kenyon 1992
	GBR	633	5.6	Wallace 1985a
	Kenya	**468**	**16.7**	This study
	Taiwan	390	-	Dai et al. 1992

[#] histological samples used to measure oocyte size

6.4.4 Seasonality and spawning patterns

Mature gametes were seen on average 2-3 weeks prior to spawning, which is consistent with *Acropora* species on the GBR (Harrison et al. 1984; Babcock et al. 1986), though longer periods of 4-6 weeks were recorded in some colonies in Kenya. Mature white or pale oocytes were recorded in 14% of colonies and in 63% of species studied. These findings have important implications for researchers currently using rapid assessment techniques where maturity is assessed only on the presence or absence of pigmentation in large oocytes (e.g. Baird et al. 2001, 2002; Wolstenholme 2004; Guest et al. 2005a). An error of up to 14% may occur using such techniques, which limits the validity of their findings relating to the degree of synchrony or asynchrony of spawning between geographic locations. Furthermore, a study in the Red Sea showed oocytes in some *Acropora* species lost their pigmentation and became white during the final stages of maturation (Shlesinger et al. 1998). The repeated sampling of tagged or mapped colonies provides the best option for minimising the probability of mature eggs being misdiagnosed as immature oocytes in future studies, and provides a more complete picture of spawning patterns in a location. A longer sampling strategy is particularly important for describing reproduction in populations with an extended spawning period.

In Kenya, *Acropora* species spawned over a 7-month period between October – May in both study years. As discussed earlier (see Chapter 5), interspecific spawning synchrony was less synchronous in *Acropora* species compared to faviids, a pattern which is found on both equatorial (Oliver et al. 1988; Guest 2004) and higher-latitude reefs (Hayashibara et al. 1993) in some locations.

Spawning patterns in *Acropora* species in Kenya are complex, and are summarised as follows. The timing of reproduction in *Acropora* varied both within and among species, with the main release of gametes occurring from January - March, when ~78% of marked colonies released gametes. The greatest overlap in spawning among *Acropora* species occurred in February (11-12 species), which coincides with the spawning months of *P. daedalea* and *E. gemmacea* (see Chapter 5). Within the main spawning period (January – March), individual species had their main spawning in different lunar months (Table 6.3). The proportion of the population (within a species)

releasing gametes during their main spawning month ranged from 30-80% (mean = 53%). Within each lunar month, *Acropora* species generally released gametes in all lunar quarters, with the highest number of colonies and species spawning in the 3rd lunar quarter (i.e. during the period from full moon to 7 nights AFM).

The spawning pattern emerging for *Acropora* species in lagoonal reefs in Kenya is one of asynchrony, and contrasts markedly with the central GBR and western Australia where high intra- and inter-specific spawning synchronously results in an annual mass spawning event where individual species spawn over one or a few nights after full moon periods in the October/November (late spring/early summer) and March (summer), respectively (Harrison et al. 1984; Willis et al. 1985; Babcock et al. 1986, 1994; Simpson 1985, 1991). The results from this study also contrast with studies from Japan, Taiwan, Palau and Singapore, which display more synchronised multispecific spawning of *Acropora* assemblages (Dai et al. 1992; Hayashibara et al. 1993; Penland et al. 2004; Guest et al. 2005a). *Acropora* assemblages in Japan are characterised by high intraspecific spawning synchrony (i.e. 1-2 nights over 1-2 months), but are less synchronous among species, with spawning occurring over 4 months and over 10 nights (i.e. two lunar quarters). *Acropora* species in Singapore spawn biannually, with minor spawning occurring in October/November and major spawning in March/April (Guest et al. 2005a), while species in Taiwan and Palau spawn in May/June and August, respectively (Dai et al. 1992; Penland et al. 2004).

The spawning patterns recorded in Kenya share similarities with *Acropora* species on subtropical reefs in the Solitary Islands, where spawning was staggered among species and among colonies within some species, with reproduction occurring over 2-5 months from December to April, and over a range of lunar phases (Wilson and Harrison 1997, 2003). It was suggested that highly variable sea surface temperatures in the Solitary Islands, particularly during gamete maturation, may explain the extended and asynchronous spawning pattern observed in this location (Wilson and Harrison 2003). Sea surface temperatures in Kenya are generally less variable during maturation, but are more variable during the peak spawning period from January – April, with differences of 2.5 ºC recorded. The variability in sea surface temperatures is likely to be a result of the shallow depth of the lagoon, which makes it susceptible to temperature fluctuations associated with cloud cover and prevailing wind

conditions. However, temperature variability in Kenya during peak spawning periods are still less than those at the Solitary Islands where 6-8.5 ºC differences can occur during the peak spawning period from December – March (Wilson 1998; A. Scott, pers. comm.).

The spawning patterns recorded in Kenya also share some similarities with scleractinian corals in the northern Gulf of Eilat in the Red Sea, which exhibit 'temporal reproductive isolation', where spawning is separated in time (seasons, months and lunar phases) for different species (Shlesinger and Loya 1985; Shlesinger et al. 1998). There are, however, a number of notable differences between the two regions. Firstly, in Kenya a smaller percentage of corals (30-80%) participate in the main spawning month compared to the Red Sea (90-100%, Shlesinger et al. 1998), which means that intraspecific spawning is more asynchronous in Kenya. Secondly, *Acropora* species in Kenya may spawn in the month(s) immediately preceding and/or following the main spawning event, so that gamete release can occur over 2-5 consecutive lunar months in individual species. Broadcast spawning species in the Red Sea release gametes over 1 or 2 consecutive months (Shlesinger and Loya 1985; Shlesinger et al. 1998). Thirdly, in the Red Sea, species that spawn in the same lunar month will spawn in different lunar quarters from each other, which reduces the overlap between spawning species (see Table 1 and Fig. 1, in Shlesinger and Loya 1985). In Kenya, there is overlap between species during all lunar quarters, and colonies within most species generally spawn over >1 lunar quarter (Table 6.4). However, it is important to note that spawning times have only been described in six (Shlesinger and Loya 1985; Shlesinger et al. 1998) of the approximately 42 known species of *Acropora* in the Red Sea (Wallace 1999), and therefore there is a high probability that there would be overlap in spawning between some species in different lunar quarters.

It has been suggested that 'temporal reproductive isolation' is a mechanism by which corals can minimise hybridisation or mismatching, and therefore maintain individual species group abundances (Shlesinger and Loya 1985). However, the extended and overlapping reproductive periods exhibited by Kenyan *Acropora* species may facilitate some degree of hybridisation, and if so, may explain the high level of diversity often observed in the tropics (Willis et al. 1997). Through manipulative

breeding experiments, Willis et al. (1997) showed hybridisation occurred readily in more than 33% of species pairs from the genera *Acropora, Platygyra* and *Montipora*, particularly between morphologically similar species. Studies have shown that some *Acropora* species groups have a greater tendency to form natural hybrids, or display greater phenotypic plasticity and form distinct morphotypes within species (Wallace 1974, 1978, 1999; Wallace and Willis 1994; Wolstenholme et al. 2003). While hybridisation rates have not been quantified on Kenyan reefs, there is the potential for the putative species *Acropora* sp.1 to be a hybrid (see Chapter 3), as it shares characteristics with *A. valida, A. secale* and *A. lutkeni*, which are all within the *Acropora nasuta* group (*sensu* Wallace 1999). The timing of spawning in *A. valida*, *Acropora* sp.1 and *A. secale* in relation to lunar month(s), lunar quarter(s) and night, means there is a high probability of gametes from the three species mixing together at the seawater surface. *Acropora* sp.1 and *A. valida* also have very similar lengths and patterns of gametogenesis (Fig. 6.7), and spawned at the same time as each other, on the 6th night AFM.

Acropora sp.1 is a common species at Nyali, Kijembe and Mamba Reefs (pers. obs.) and further work is required to clarify its taxonomic status. The validity of *Acropora* sp.1 as a species or as a hybrid cannot be determined by the reproductive data presented in this thesis. Therefore, it is recommended that genetic and additional (more quantitative) morphometric studies be done to elucidate the taxonomic status of *Acropora* sp.1, in combination with controlled breeding experiments, to determine if there are fertilisation barriers between species belonging to the *A. nasuta* group in Kenya.

6.4.5 Environmental parameters

A detailed discussion of the relationships between spawning patterns and environmental variables in Kenya was provided in Chapter 5 (see Discussion section 5.4.4), as pertaining to spawning patterns in the three faviid species studied. Therefore, this section will focus on the key differences between *Acropora* and faviid species, in relation to the environmental parameters of temperature, solar radiation (light), lunar phase, tides, photoperiod and rainfall.

Acropora species spawned throughout the NE monsoon season and during the inter-monsoonal months when mean sea surface temperatures generally range from 26-29 ºC, and wind conditions are slow and steady, and seas are calm. No *Acropora* colonies (including the two that underwent biannual reproduction), spawned during the SE monsoon season, which suggests that the two seasons experienced by the East African coast strongly influences the reproductive patterns of corals. There was no relationship between spawning period and the timing of solar radiation maxima in Kenya. However, *Acropora* species spawned during the months when solar radiation was high, generally when it was above 20 mJ m^{-2} (Fig. 2.3, Chapter 2). Spawning commenced when sea surface temperatures were rising but peaked when temperatures were at their annual summer maximum (averaging 28.3 ºC). These patterns contrast with spawning patterns for *Acropora* in other regions where spawning occurs either as temperatures are rising (Harrison et al. 1984; Willis et al. 1985; Babcock et al. 1986; Wilson and Harrison 2003; Carroll et al. 2006) or are at their summer maximum (Babcock et al. 1994), and generally not during both.

Acropora species spawned over a range of tidal phases from springs through to neaps, which is similar to spawning patterns reported in Taiwan and Japan (Dai et al. 1992; Hayashibara et al. 1993). Spawning records for corals kept in aquaria suggested that spawning occurred mainly between 21:00 to 22:00 hours which coincided with ebb tide, three hours prior to low tide. The timing of spawning in five *Acropora* species were similar to *L. phrygia* which released gametes at 21:30 hours, which suggests that the timing of ebb and flood tides plays a greater role in determining the timing of gamete release on a spawning night, than the occurrence of neap or spring tides. As discussed earlier (see Chapter 5), tidal mixing in the Mombasa lagoon either side of low tide is usually minimal and this may decrease gamete dilution and enhance fertilisation during this period. Thus, there is potentially a 12-hour window for fertilisation and early embryo development before gametes and embryos are swept out to sea during the following daylight ebb tide.

The three faviid species studied spawned before both the short and long rain periods on the Kenya coast. By contrast, *Acropora* species spawned during the short rain period in November, but before the long rain period in May. While reduced salinity may be harmful to gametes (Richmond 1993; Harrison 1995), average rainfall is

generally low during the short rains, averaging <4 mm (Fig. 2.4, Chapter 2), and there are no large rivers along the coast. Therefore, the short rains in Kenya are unlikely to reduce seawater salinities to such low levels that would impact on the reproduction of *Acropora* species.

Seasonal variation in daylength is less pronounced at the equator, but the peak period of spawning in *Acropora* species occurred close to the March equinox, when changes in daylength are largest. However, there does not appear to be a strong relationship between spawning patterns in *Acropora* species and changes in photoperiod, with species spawning when daylength is longest through to when daylength is shortest (Fig. 6.19). These findings suggest that photoperiod may play a stronger role in some coral groups like faviids, and less so in others such as acroporids. However, this argument is based on correlative data, therefore further experimental research is required to examine the role of photoperiod in fine-tuning gamete maturation and the timing of spawning and how these might differ in their effect between coral groups within and between locations.

It is evident that the reproductive patterns in Kenyan *Acropora* species are variable, with species and colonies spawning over a wide range of environmental conditions. Short-term studies that focus on the collection of reproductive data only during the main spawning events, are likely to miss or oversimplify the diversity and complexity of reproductive patterns displayed by *Acropora* species. The level of reproductive plasticity recorded in this genus (cf. faviids), such as that recorded by this study, may explain the highly polymorphic nature of *Acropora* species, with high rates of hybridisation recorded between both similar and in some cases dissimilar morphological forms (Willis et al. 1997), their success in colonising reefs, and their dominance in most tropical reef habitats (Wallace and Willis 1994; Wallace 1999).

CHAPTER 7: PATTERNS OF SETTLEMENT, RECRUITMENT AND ABUNDANCE OF JUVENILE CORALS

7.1 Introduction

Knowledge of the spatial and temporal patterns of coral reproduction, settlement and recruitment are essential for understanding ecological and evolutionary processes on coral reefs (Harrison and Wallace 1990), and how well corals respond to natural and anthropogenic changes in their environment (Richmond 1997). Seasonal patterns of coral settlement and recruitment appear to be linked to the timing of spawning and planulation events and the mode of reproduction of corals. On the Great Barrier Reef (GBR) spat settlement and recruitment has been recorded in the months following mass spawning in the austral spring or summer (Harrison et al. 1984; Willis et al. 1985; Babcock et al. 1986), with broadcast spawners such as acroporids having a more pronounced settlement period, and brooders such as pocilloporids and poritids having a more extended period (Wallace 1985b; Harriott 1985; Harriott and Fisk 1988; Fisk and Harriott 1990).

Coral bleaching events are becoming more intense and frequent and are causing significant changes to some coral reef communities over relatively short time-scales (Hoegh-Guldberg 1999). If coral mortality is severe, there is an increased likelihood of a shift in the structure and composition of the coral community away from its pre-disturbance state (Done 1992; Connell 1997). Kenya's reefs changed dramatically in 1997-98 following the convergence of the El Niño Southern Oscillation and Indian Ocean Dipole (Saji et al. 1999), which resulted in widespread bleaching of 50-90% of corals along the entire coast (Wilkinson et al. 1999). Mortality was particularly high along the southern fringing reef complex with losses of live coral in the order of 66-80%, particularly of branching genera such as *Acropora, Pocillopora, Stylophora, Seriatopora* and *Millepora* (Obura et al. 2000b; McClanahan et al. 2001). Mean coral cover ranged from 30-50% on fore-reef slopes and lagoon patch reefs before the 1997-98 bleaching event, and was reduced to 5-11% after bleaching, with increases in fleshy, turf, calcareous and coralline algae on dead coral surfaces (Obura et al. 2000b; McClanahan et al. 2001). Coral recruitment was initially low in 1999, with few to no

recruits recorded in surveys (Obura et al. 2000b), but by 2001 recruit density had returned to pre-bleaching levels, although the taxonomic diversity of recruits was lower (Tamelander 2002).

The movement of the Inter-Tropical Convergence Zone, a zone of low pressure that migrates north and south of the equator results in two distinct monsoon seasons on the East African coast (Chapter 2), which have a marked influence on the timing of coral reproduction in Kenya (Chapter 5 and 6; see also Mangubhai and Harrison 2006), and are likely to influence settlement and recruitment patterns. To date, there has been no detailed analysis of spatial and temporal patterns in settlement and recruitment on equatorial reefs in Kenya. Therefore, the main aims of this chapter are to:

(1) quantify spatial and temporal patterns of settlement and recruitment at two sites within the Mombasa Marine National Park and Reserve, 5-7 years after the 1997-98 bleaching;
(2) examine relationships between larval settlement, early recruit and juvenile coral populations; and
(3) examine relationships between settlement and recruitment and the timing and extended duration of coral spawning on equatorial reefs in Kenya, and its implications for the long-term recovery of these reefs.

7.2 Methods

7.2.1 Benthic composition

Line intercept transect surveys were done in December 2003 to quantify benthic cover at Coral Gardens and Nyali Reef. Ten 10 m length transects were haphazardly placed parallel to each other on small patch reefs at each site. Cover was recorded for 11 benthic categories — corals (hard, soft), algae (coralline, *Halimeda* spp., fleshy), substrata (rock/turf, sand/rubble, rubble, sand, seagrass) and 'other'. Hard corals were further divided into five categories – massive, submassive, encrusting, branching and solitary.

7.2.2 Spat settlement on tiles

CORDIO East Africa has monitored coral settlement onto ceramic tiles at Coral Gardens since 1999 (D. Obura, unpubl. data.). For consistency with this long term dataset, the same type and number of tiles were placed at Coral Gardens and Nyali Reef from May 2003 - August 2005. Two mesh-covered metal frames (0.6 x 0.3 m), similar to those deployed in Tanzania (Franklin et al. 1998; Nzali et al. 1998), were anchored to substrata at 0.5-1 m depth (maximum low tide), and separated by a distance of <5 m (Fig. 7.1). Ten unconditioned tiles (0.15 x 0.15 m) were placed on each frame at 45 degrees with the rough surface facing down and smooth (glazed) surface up, because coral larvae preferentially settle on irregular surfaces (Carleton and Sammarco 1987) and on the underside of tiles in shallow environments (Birkeland et al. 1981; Wallace 1985b; Carleton and Sammarco 1987). Given that very few 'spat' settled on upper tile surfaces or edges (<8%), only those on lower surfaces are analysed in this chapter. To avoid confusion between larval settlement on tiles versus natural substrata recruits, the term 'spat' is used when discussing settlement onto tiles.

Settlement tiles were replaced in the field every 3 months in February, May, August and November each year, and removed tiles (Fig. 7.2) were placed in household bleach for 2-3 days to remove organic matter, then dried and labelled. For consistency with the CORDIO dataset, tiles collected from each site were placed together, and

were not separated according to which rack they were collected from. In May 2004, the majority of tiles were lost at Nyali Reef due to storm breakage and therefore, have been excluded from analyses. In May 2003 a settlement tile was damaged at Nyali Reef, and in May 2005 an extra tile was placed at Coral Gardens.

All coral spat were circled, numbered and the following information was recorded for each spat under a stereomicroscope: (1) identity to the family level, in accordance with Babcock et al. (2003), (2) maximum diameter to the nearest 0.1 mm, (3) number of polyps present, and (4) health status (i.e. undamaged, damaged, overgrown by other organisms). In addition, the number of oysters, serpulids, barnacles and bryozoans on each tile were recorded. Spat were listed as 'unknown' if the identity of the coral could not be determined due to damage, and listed as 'other' if the family could not be determined with sufficient confidence. Photographs were taken of representative members of each family under a scanning electron microscope. Tile data were available for Coral Gardens from August 2002 - May 2003, and these are also included in this chapter.

Figure 7.1: Photograph showing the mesh-covered metal frames and settlement tiles deployed in the Mombasa Marine National Park and Reserve.

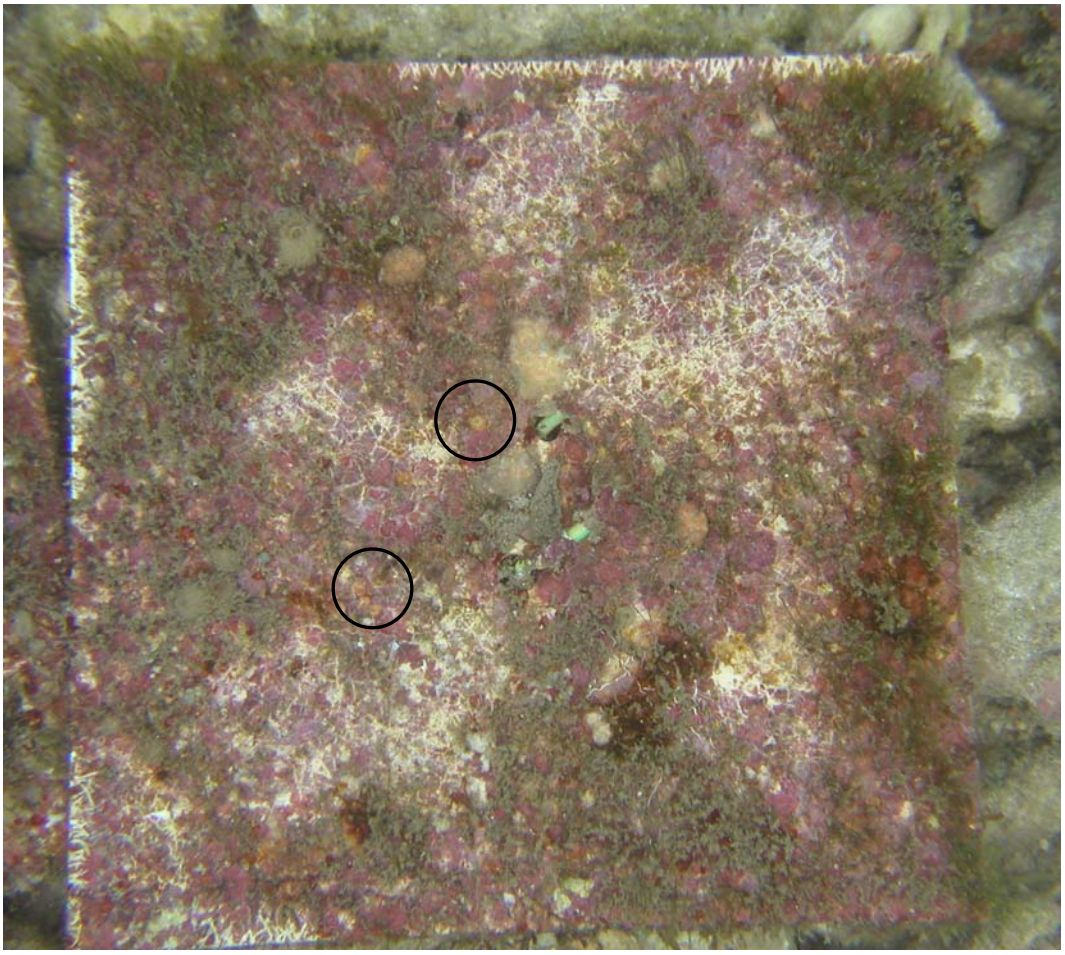


Figure 7.2: Photograph showing a settlement tile removed after 3 months immersion. Spat settled on the lower surface of the tile are circled.

7.2.3 Recruitment on natural reef substrata

Coral recruitment patterns onto natural substrata were examined at Coral Gardens and Nyali Reef from May 2003 - November 2005. Surveys were conducted in February, May, August and November each year, within seven days of the immersion of settlement tiles in the field. At each site, 20-35 quadrats were haphazardly selected by throwing a weight from above the water surface, and detailed searches were conducted in 1 m^2 circular quadrats (0.56 m radius) to find corals ≤10 cm maximum diameter. With the exception of the Family Fungiidae, most corals were identified to genus (Veron 2000), and their maximum diameter and perpendicular width were measured with a flexible tape to the nearest 1 mm. Other coral genera that could not be identified were listed as 'other'. On natural substrata, 'recruits' were defined as corals with a maximum diameter of ≤5 cm (Fig. 7.3), and 'juvenile' corals were

defined as those with a maximum diameter of 5.1-10 cm. The smallest coral recorded was 3 mm, and the majority of recruits (91.8%) had an area of ≤25 cm^2. Corals fitting into the recruit size category were not measured if they appeared to be fragmented adults, and quadrats that landed on 'unsuitable' substrata for recruitment (such as sand, seagrass or rubble areas) were not sampled.

7.2.4 Statistical analyses

Data were analysed using SPSS for Windows (version 11, 2001). Statistical analyses were done on the abundance of spat on settlement tiles from May 2003 - August 2005, which is the sampling period when data were available for both sites, and on natural recruit and juvenile coral data from May 2003 - November 2005. Levene's test was used to test for homogeneity of variance in coral spat, recruits and juvenile corals and was found to be significant ($p < 0.001$). Although the log-transformation of the data did not fully normalise the data, the residuals had a normal distribution, and hence a general linear model (GLM) univariate procedure was chosen because it is fairly robust to small deviations from normality (Zar 1999). Given that settlement tile data were not available for May 2004 at Nyali Reef, a Type IV sum of squares model was used because it is designed for situations where there are missing data. A Type III sum of squares model was used for natural recruit and juvenile coral data. Where significant differences occurred, pairwise multiple comparisons were done using the Bonferroni honestly significant difference (HSD) test to determine which means differed significantly.

The effects of covariate variables and covariate interactions with individual factors can be tested in a GLM, and parameter estimates can be generated with t-statistics to help determine the relative importance of each variable in the model. It is important to note that use of the term 'effect' in a GLM does not imply causality, only that variables are responding in some manner to each other. The effects of non-coral fauna on coral spat settlement were tested by including barnacle, serpulid, oyster and bryozoan densities as covariate variables in the GLM. Negative t-statistics may suggest that competition between faunal groups is occurring, while positive t-statistics may suggest that (a) the abundance of one faunal group is causing a corresponding increase in abundance in another, or that (b) both faunal groups are co-

exiting and independently responding to some other variable(s), such as the same environmental cues governing the timing of reproductive events.

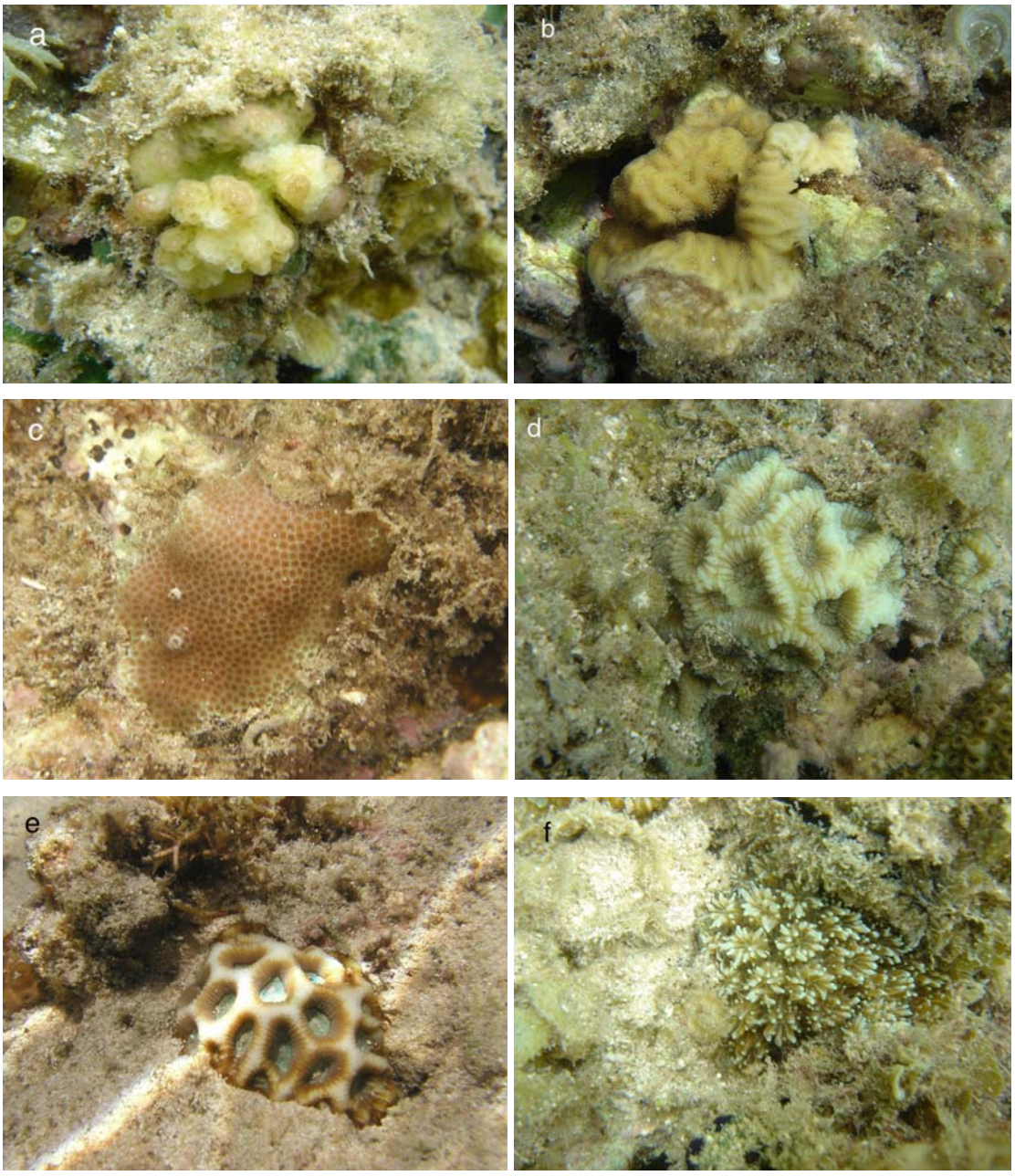


Figure 7.3: Photographs showing the most common coral recruits recorded in natural substrata surveys in the Mombasa Marine National Park and Reserve. All recruits are <5 cm maximum diameter, and the genera shown are (a) *Pocillopora*, (b) *Pavona*, (c) *Porites*, (d) *Favia*, (e) *Favites* and (f) *Galaxea*.

7.3 Results

7.3.1 Benthic community composition at study sites

Coral Gardens and Nyali Reef had similar benthic substrata and community composition with rock/turf areas dominating (~38% mean cover) followed by hard corals (~25% mean cover) (Fig. 7.4a). With the exception of rubble and seagrass, there were no significant differences in the mean percentage cover of major benthic categories between the sites (t-test, $p > 0.05$). The reef coral community was dominated by massive and submassive corals comprising 17-21% mean cover (Fig. 7.4b). Mean cover of branching corals at Coral Gardens was very low, comprising 0.6% benthic cover compared to 5.2% at Nyali Reef, which was about nine times greater cover and was significantly higher ($p < 0.05$).

7.3.2 Spat settlement on tiles

7.3.2.1 Total settlement

A total of 4294 coral spat were recorded on 400 tiles during the study, with representatives mainly from four families (Table 7.1, Fig. 7.5). The Family Pocilloporidae dominated comprising 93.7% of all spat, while Poritidae, Acroporidae and Faviidae comprised 3.2, 1.4 and 0.1%, respectively. Fifty-six tiles immersed at Coral Gardens (23.2%) had no spat, compared to two tiles at Nyali Reef (1.3%). Coral Gardens had an annual mean density of 2.3 spat tile^{-1} (101 spat m^{-2}) and a maximum of 10 spat tile^{-1} (444 spat m^{-2}), while Nyali Reef had an annual mean density of 20.4 spat tile^{-1} (908 spat m^{-2}) and a maximum of 73 spat tile^{-1} (3244 spat m^{-2}), for the period May 2003 - February 2005. It is important to note that while data were missing for May 2004 from Nyali Reef, the mean density of spat for this period was estimated by averaging the mean spat recorded on tiles immersed at the site in May 2003 and 2005. Overall, there was a nine-fold difference in the mean spat densities between the two sites.

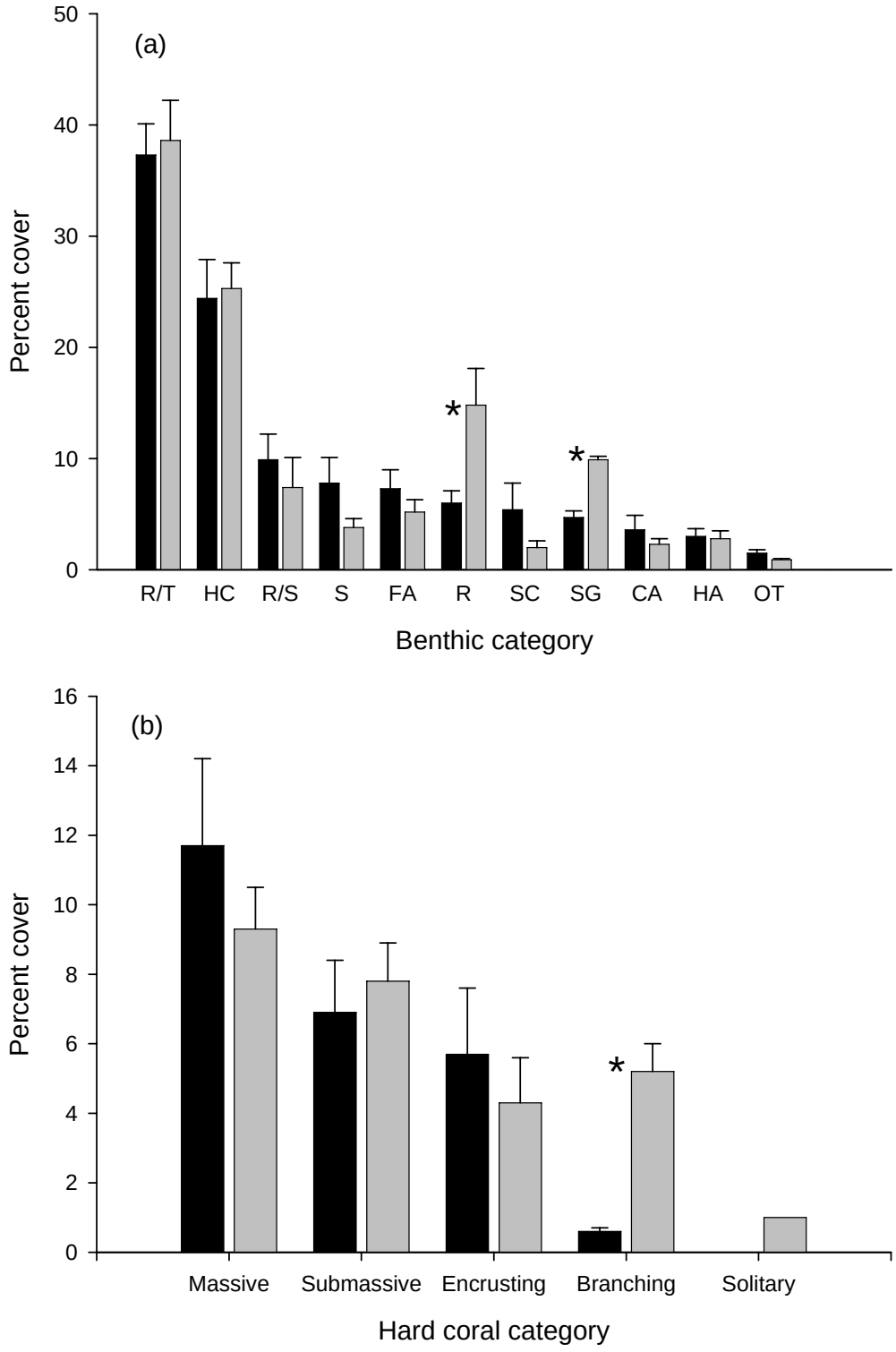


Figure 7.4: Mean percent cover of (a) benthic and (b) hard coral categories at Coral Gardens (black bars) and Nyali reef (grey bars). Error bars are standard error. Asterisks indicate significant differences between sites (t-test, $p < 0.05$). R/T: rock/turf, HC: hard coral, R/S: rubble/sand, S: sand, FA: fleshy algae, R: rock, SC: soft coral, SG: seagrass, CA: coralline algae, HA: *Halimeda* algae, OT: other.

Table 7.1: Number, percent composition and mean density (tile^{-1}) of coral spat for each taxon from August 2002 - August 2005. Period: number of times settlement tiles were placed in the field for a period of 3 months.

Taxa	**Coral Gardens**			**Nyali Reef**			**All sites**		
	N	**%**	**mean**	**N**	**%**	**mean**	**N**	**%**	**mean**
Pocilloporidae	920	88.6	3.82	3104	95.3	19.52	4024	93.7	10.06
Poritidae	87	8.4	0.36	52	1.6	0.33	139	3.2	0.35
Acroporidae	2	0.2	0.01	56	1.7	0.35	58	1.4	0.15
Faviidae	4	0.4	0.02	1	0.0	0.01	5	0.1	0.01
Other	9	0.9		5	0.2		14	0.3	
Unknown	16	1.5		38	1.2		54	1.3	
Total	1038			3256			4294		
No. tiles	241			159			400		
Period	12			8			20		

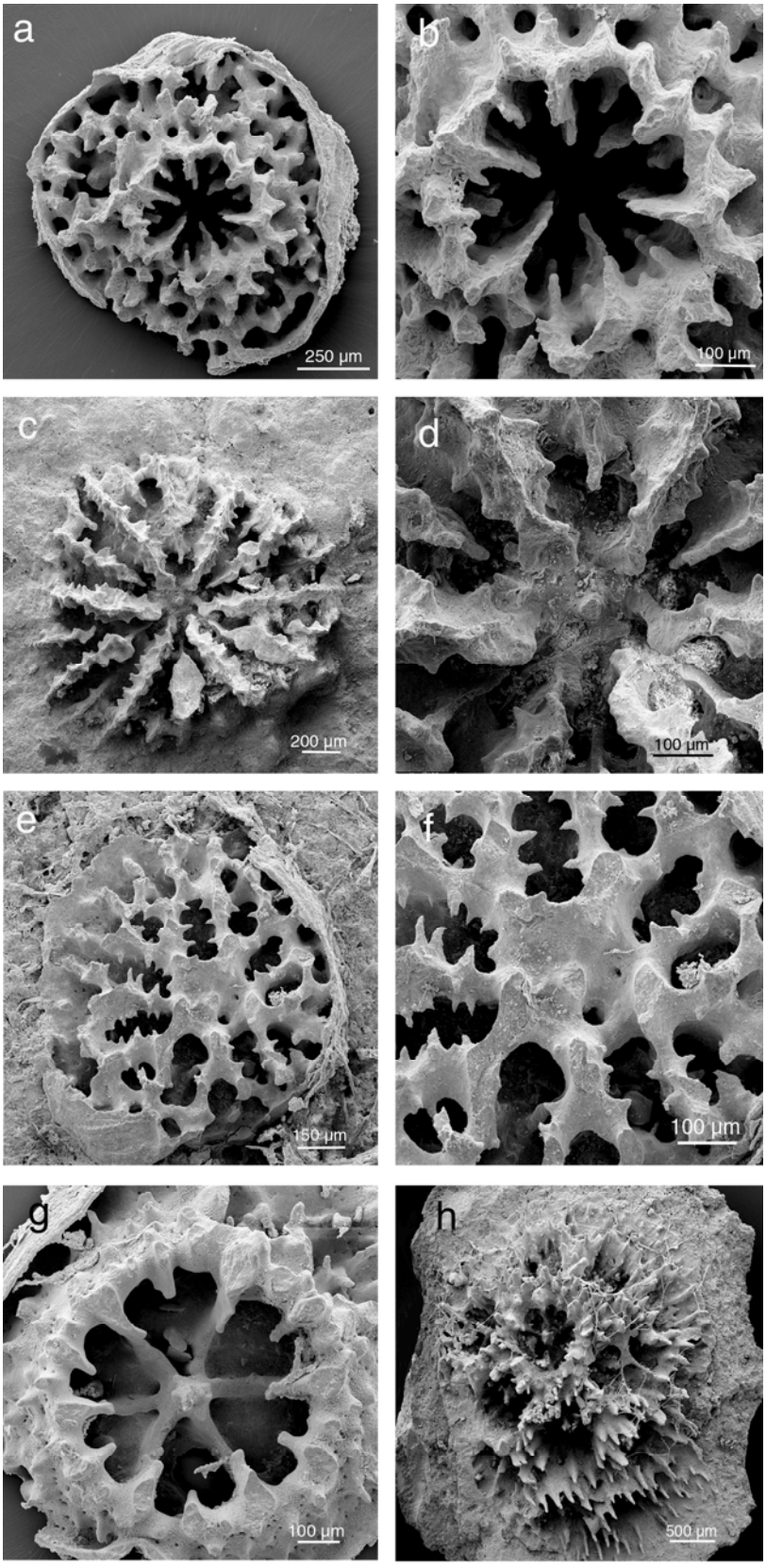


Figure 7.5: Scanning electron microscope images of coral spat (maximum age 3 months) belonging to the families Acroporidae (a-b), Faviidae (c-d), Poritidae (e-f), and Pocilloporidae (g-h) recorded on settlement tiles in Kenya.

7.3.2.2 Spatial and temporal spat settlement patterns

Coral settlement onto tiles varied significantly spatially and temporally. There were highly significant differences in settlement between sites, years and periods when tiles were immersed in the field ($p < 0.001$), but there were interactions between site*year and site*period (Table 7.2). These results show that temporal patterns were variable and not consistent from year to year or from one period to the next, and their effect was dependent on site (Table 7.2). Inter-annual and inter-period changes in the mean density of spat at sites are shown in Fig. 7.6. Mean spat density was consistently higher at Nyali Reef than at Coral Gardens, and was statistically significant for all periods (Bonferroni HSD, $p < 0.001$), except for May 2003 ($p = 0.406$).

Overall settlement onto tiles was approximately three times higher during the northeast (NE) monsoon period compared to the southeast (SE) monsoon period. It is important to note that while data were missing for May 2004 from Nyali Reef, the mean density of spat recorded on tiles immersed at that site in May 2003 and 2005 was low (≤4.4 spat tile^{-1}) (Fig. 7.6). Hence, proportional differences between monsoon seasons are not likely to be greatly affected by these missing data.

Peak settlement occurred in November - February (spring/summer) at Coral Gardens and in February - May (summer/autumn) at Nyali Reef, while the lowest settlement occurred in May - August (autumn/winter) at both sites (Fig. 7.6). The settlement patterns are dominated by Pocilloporidae spat. During peak periods, mean density of Pocilloporidae was 3.5 spat tile^{-1} (153 spat m^{-2}) at Coral Gardens and 37.5 spat tile^{-1} (1167 spat m^{-2}) at Nyali Reef. At Nyali Reef inter-annual differences occurred only for the period August - November (Bonferroni HSD, $p < 0.05$), while at Coral Gardens inter-annual differences occurred during all periods ($p < 0.05$) except for February - May ($p = 0.227$). Settlement was much higher in 2002 at Coral Gardens compared to the subsequent two years, with a mean of 15.8 spat tile^{-1} (702 spat m^{-2}) recorded in November that year. The inclusion of the 2002 data doubles the mean number of spat recorded at Coral Gardens to 4.3 spat tile^{-1} (191 spat m^{-2}), which is still lower than at Nyali Reef.

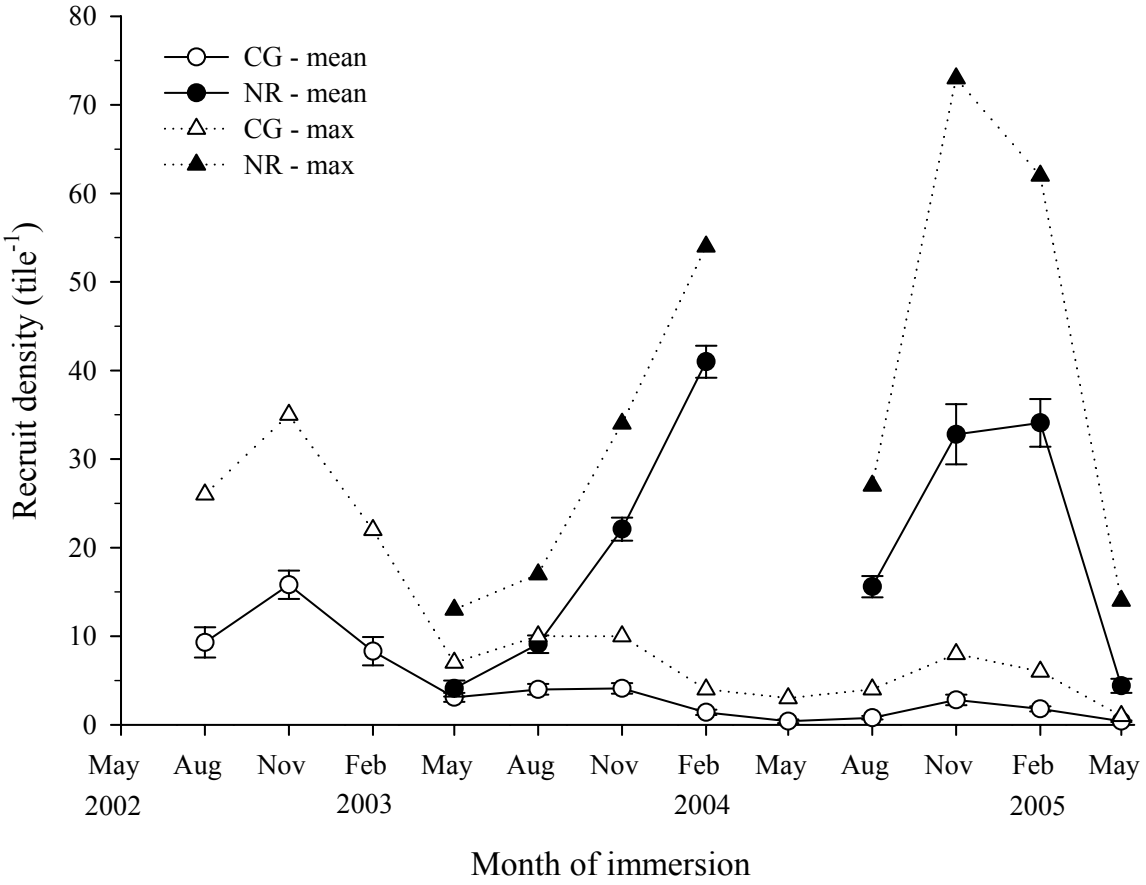


Figure 7.6: Abundance of spat tile^{-1} at Coral Gardens (CG) and Nyali Reef (NR) from August 2002 - May 2005. Mean, standard error and maximum values are shown.

Table 7.2: Analysis of spatial and temporal variance in coral spat on settlement tiles immersed for 3-month periods between May 2004 - August 2005 at Coral Gardens and Nyali Reef. GLM of log (x+0.5) transformed data with Type IV Sum of Squares. $r^2 = 0.81$

Source	df	MS	F	p
Site	1	313.63	754.80	< 0.001
Year	2	3.77	9.06	< 0.001
Period	3	9.95	23.95	< 0.001
Site*Year	2	5.16	12.41	< 0.001
Site*Period	3	5.50	13.23	< 0.001
Year*Period	3	1.07	2.56	0.055
Site*Year*Period	2	2.39	5.75	0.004
Error	323	0.42		

Coral settlement on tiles was highest in the NE monsoon for all taxonomic groups, and no family was found exclusively in one season (Fig. 7.7). Pocilloporidae dominated the spat in all seasons and occurred throughout the year at both sites. Peak settlement in Pocilloporidae occurred in November - February at Coral Gardens in all years. In contrast, peak settlement occurred in February - May in 2004 and over an extended period from November - May in 2005 at Nyali Reef (Fig. 7.7). The Family Poritidae also showed year-round settlement at Nyali Reef in both years, and at Coral Gardens in 2002 - 2003. Acroporidae spat were almost exclusively found at Nyali Reef and in all seasons during the study, with settlement peaking in February - May in both years (Fig. 7.7). Seasonal patterns of settlement in Faviidae cannot be determined because only five spat were recorded.

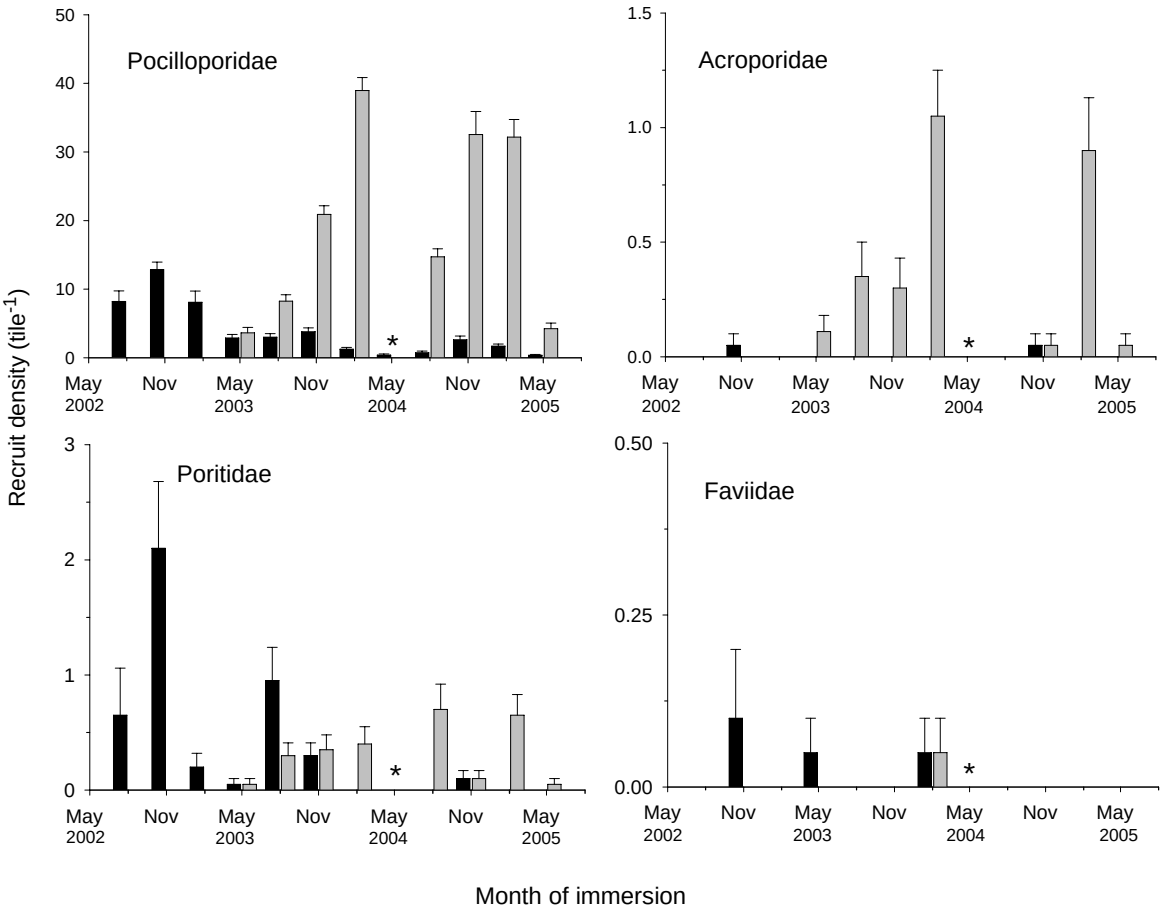


Figure 7.7: Relative abundances of spat tile^{-1} from four families at Coral Gardens (black) and Nyali Reef (grey) from August 2002 - May 2005. Error bars are standard error. Note that the y-axis scale differs in each graph. Asterisks indicate tiles were lost for Nyali Reef during this period.

7.3.2.3 Growth and health of coral spat

Growth was measured using the parameters spat diameter and number of polyps spat^{-1} for the 3 months of tile immersion. The maximum spat diameter recorded was 7.4 mm and the average was 1.9 mm, while the maximum number of polyps recorded was 23 polyps spat^{-1} and the average was 3.6 polyps spat^{-1} (Table 7.3). Pocilloporidae spat had the highest rate of addition of new polyps, while Poritidae and Faviidae had the lowest. All spat of Faviidae and 95.6% of Poritidae had one polyp present. Spat with 1-5 polyps dominated in Acroporidae (96%) and Pocilloporidae (74.3%). Spat with 6-10 polyps were found in the remaining Acroporidae (3.4%) and some Pocilloporidae (22.8%), and spat with >10 polyps were only found in Pocilloporidae (2.9%).

GLM analyses were done on the growth parameter measurements of Pocilloporidae spat. There was a positive linear relationship between Pocilloporidae spat diameter and number of polyps spat^{-1} ($p < 0.001$, $r^2 = 0.82$). While there were no significant differences between tile immersion periods, there was a significant interaction between site*year for both growth parameters ($p < 0.001$, Table 7.4). Multiple pairwise comparisons found significant differences in both growth parameters between sites in 2003 and 2005 ($p < 0.05$). Testing for the effect of year, there were significant differences in both growth parameters between years at Coral Gardens ($p < 0.001$) but not at Nyali Reef ($p > 0.05$).

Greater than 95% of coral spat were undamaged on tiles at both sites. Spat that were damaged or were overgrown by coralline algae and non-coral fauna comprised 2.5% and 1.7% of spat, respectively. While 56 (79.7%) coral spat in the 'overgrown' category were being impacted by coralline algae, it is not possible to determine if this interaction occurred while spat were alive, after they had died, or whether the interaction resulted in mortality. Ten spat (0.2%) were observed fused to an adjacent spat and all belonged to the Family Pocilloporidae.

Table 7.3: Spat size (mm) and number of polyps spat^{-1} on settlement tiles (pooled for sites).

Taxa	Maximum diameter			Number of polyps		
	mean	sd	range	mean	sd	range
Pocilloporidae	2.0	0.7	0.2-7.4	3.9	3.0	1-23
Faviidae	1.7	1.2	0.5-3.2	1.0	-	1
Acroporidae	1.2	0.5	0.3-3.5	1.4	1.3	1-8
Poritidae	1.0	0.5	0.4-2.8	1.1	0.3	1-3
Overall	1.9	0.7	0.2-7.4	3.6	3.0	1-3

Table 7.4: Analysis of variance of spat size ($r^2 = 0.173$) and number of polyps ($r^2 = 0.117$) in Pocilloporidae on settlement tiles immersed for 3-month periods between May 2003 - August 2005 at Coral Gardens and Nyali Reef. GLM of log (x+1) transformed data with Type IV Sum of Squares.

Source	Maximum diameter				Number of polyps			
	df	MS	F	p	df	MS	F	p
Site	1	0.02	0.44	0.508	1	0.12	0.43	0.510
Year	2	0.26	5.66	0.004	2	1.61	5.71	0.004
Period	3	0.10	2.21	0.087	3	0.01	0.05	0.984
Site*Year	2	0.62	13.43	< 0.001	2	3.06	10.86	< 0.001
Error	274	0.05			274	0.28		

7.3.2.4 Competition with non-coral fauna

A total of 17 980 non-coral fauna were recorded on tiles during the study, comprising 9457 barnacles (52.6%), 4953 serpulids (27.6%), 2400 oysters (13.3%) and 1170 bryozoans (6.5%). This equates to approximately four times as many non-coral fauna compared to coral spat. Coral Gardens consistently had a greater density of non-coral fauna averaging 60.2 animals $tile^{-1}$ (2676 animals m^{-2}) compared to 21.8 animals $tile^{-1}$ (969 animals m^{-2}) at Nyali Reef. While all four categories of non-coral fauna showed year-round settlement, the timing of peak periods of settlement varied between the groups (Fig. 7.8). Barnacle density peaked in August - November (2528 barnacles m^{-2}) at Nyali Reef in 2003 and 2004 and at Coral Gardens in 2004, while bryozoan density peaked in November - February at both sites (236 bryozoans m^{-2}). There was no statistically significant interaction effect of barnacle or bryozoan density on coral settlement (GLM, $p > 0.05$, Table 7.5). Serpulid density also peaked in November - February (946 serpulids m^{-2}), and had a positive interaction effect with coral settlement when adjusted for the factors site, year and period in the GLM ($p < 0.01$, Table 7.5).

In contrast, oyster density peaked in February - May (474 oysters m^{-2}) at both sites (Fig. 7.8), and had a more complex interaction with coral spat, with a significant interaction between oyster density*year ($p < 0.05$, Table 7.5). Parameter estimates for individual years showed that in 2003 there was a positive effect of oyster density on coral settlement when adjusted for the factors site and period in the GLM ($p < 0.05$), which may reflect that both spat groups are responding to the same environmental variables. In 2004 there was a small non-significant negative effect recorded between coral and oyster spat ($p = 0.623$).

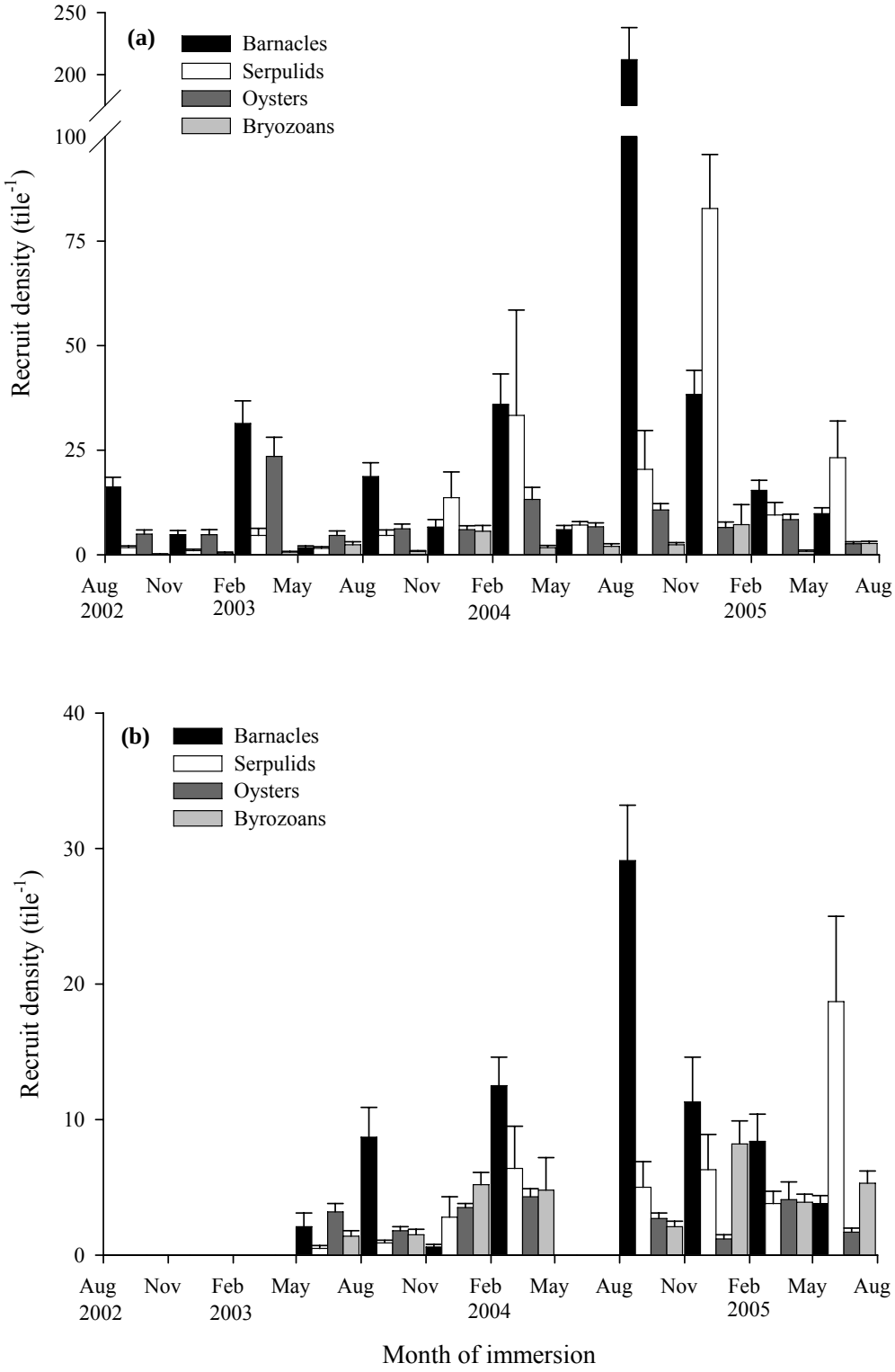


Figure 7.8: Abundance of non-coral fauna tile^{-1} at (a) Coral Gardens and (b) Nyali Reef from August 2002 - May 2005.

Table 7.5: Analysis of spatial and temporal variance in coral spat settlement with non-coral fauna (barnacles, bryozoans, serpulids, oysters) included in the GLM as covariates. GLM of log (x+0.5) transformed data with Type IV Sum of Squares.

Source	df	MS	F	p-value
Barnacles ($r^2 = 0.81$)				
Site	1	234.40	564.55	< 0.001
Year	2	3.02	7.28	0.001
Period	3	9.42	22.70	< 0.001
Barnacles	1	0.52	1.25	**0.264**
Site * Year	2	4.95	11.93	< 0.001
Site * Period	3	5.56	13.39	< 0.001
Year * Period	3	0.80	1.92	0.127
Site * Year * Period	2	2.36	5.68	0.004
Error	322	0.42		
Bryozoans ($r^2 = 0.81$)				
Site	1	299.61	719.42	< 0.001
Year	2	3.81	9.15	< 0.001
Period	3	9.84	23.63	< 0.001
Bryozoans	1	0.11	0.26	**0.609**
Site * Year	2	5.01	12.03	< 0.001
Site * Period	3	5.42	13.01	< 0.001
Year * Period	3	1.06	2.54	0.057
Site * Year * Period	2	2.41	5.78	0.003
Error	322	0.42		
Serpulids ($r^2 = 0.82$)				
Site	1	292.99	723.16	< 0.001
Year	2	5.36	13.23	< 0.001
Period	3	9.85	24.30	< 0.001
Serpulids	1	3.75	9.26	**0.003**
Site * Year	2	4.81	11.87	< 0.001
Site * Period	3	5.18	12.77	< 0.001
Year * Period	3	1.74	4.30	0.005
Site * Year * Period	2	3.03	7.48	0.001
Error	322	0.41		
Oysters ($r^2 = 0.82$)				
Site	1	260.42	638.16	< 0.001
Year	2	1.04	2.54	0.080
Period	3	9.93	24.32	< 0.001
Oysters	1	0.99	2.43	**0.120**
Site * Year	2	4.69	11.49	< 0.001
Site * Period	3	5.70	13.97	< 0.001
Year * Period	3	1.07	2.61	0.051
Year * Oysters	2	1.40	3.35	**0.036**
Site * Year * Period	2	2.16	5.29	0.006
Error	320	0.41		

7.3.3 Recruitment on natural reef substrata

A total of 1977 recruits and 1173 juvenile corals from 25 scleractinian genera representing 11 families were recorded during the study (Fig. 7.9). Mean recruit density was 3.4 recruits m^{-2} (sd = 2.9, max = 24) and 3.0 recruits m^{-2} (sd = 2.6, max = 12) at Coral Gardens and Nyali Reef, respectively, and site differences were not significant (t-test, $p > 0.05$). In comparison, mean juvenile coral density was lower and differed significantly between sites (t-test, $p < 0.001$), with 2.2 corals m^{-2} (sd = 2.1, max = 12) recorded at Coral Gardens, and 1.6 corals m^{-2} (sd = 1.5, max = 8) at Nyali Reef.

Four coral families dominated the recruit population at Coral Gardens and Nyali Reef, although their relative abundance differed between the two sites (Fig. 7.9). Faviidae dominated at Coral Gardens and comprised 35.3% of recruits, while Poritidae, Agariciidae and Pocilloporidae comprised 26.4, 17.4 and 10.4%, respectively. By contrast, Pocilloporidae dominated at Nyali Reef and comprised 43.4% of recruits, while Agariciidae, Poritidae and Faviidae comprised 29.4, 10.9 and 5.8%, respectively. The remaining seven families contributed less than 11% of the recruits at both sites. The same four families dominated juvenile corals, although their relative abundances differed from that of the recruit population (Fig. 7.9). Faviidae increased in dominance in the juvenile category at both sites to comprise 54.5 and 21.4% of the population at Coral Gardens and Nyali Reef, respectively, while Pocilloporidae and Poritidae decreased in relative abundance compared with smaller recruits. The response of Agariciidae differed between the two sites, decreasing in relative abundance at Coral Gardens to 10.0%, and remaining almost the same at 29.6% at Nyali Reef.

To determine whether overall changes in the relative abundance of coral recruits and juvenile corals were related to mortality (measured as a decrease in density), multiple t-tests were done comparing the mean densities of recruit and juvenile coral populations (years pooled) for the four dominant families, as well as for Acroporidae. The mean densities of Pocilloporidae, Poritidae and Agariciidae differed significantly between recruits and juvenile populations at both sites ($p < 0.001$), with mortality resulting in lower densities in juvenile coral populations (Table 7.6). Mean densities

of Faviidae recruits and juvenile corals were not significantly different at Coral Gardens ($p = 0.97$), despite a 19% increase in relative abundance (Fig. 7.9), suggesting that mortality was either low or negligible between the two categories. Similarly, Acroporidae density did not differ significantly between recruits and juvenile populations at either site ($p > 0.05$), also suggesting that mortality was either low or negligible in this Family. In contrast, the mean density of Faviidae juvenile corals at Nyali Reef was significantly higher than for recruits ($p < 0.01$). Mean densities for all five families were generally low and with the exception of Faviidae, were less <1 coral m^{-2} (Table 7.6).

Proportional differences in the densities of coral recruits and juveniles between sites are shown in Table 7.7. Differences in Pocilloporidae density between sites were five-fold for spat, three-fold for recruits and four-fold for juveniles. Poritidae densities were similar at sites for spat, but higher densities were recorded for coral recruits and juveniles at Coral Gardens. Acroporidae spat were almost exclusively found at Nyali Reef but mean recruit densities at the two sites were the same (Table 7.6). Differences in Faviidae density between sites were forty-fold for spat, six-fold for recruits and four-fold for juvenile corals.

Table 7.6: The mean density (m^{-2}) of recruits and juvenile corals at Coral Gardens (CG) and Nyali Reef (NR) on natural substrata from May 2003 - November 2005. (In almost all cases the standard deviations are higher than the means.)

Family	**Recruits**						**Juveniles**					
	CG		**NR**		**All sites**		**CG**		**NR**		**All sites**	
	mean	**sd**	**mean**	**sd**	**mean**	**sd**	**mean**	**sd**	**mean**	**sd**	**mean**	**sd**
Faviidae	1.2	1.5	0.2	0.4	0.7	1.2	1.2	1.6	0.3	0.7	0.8	1.3
Poritidae	0.9	1.2	0.3	1.0	0.6	1.1	0.4	0.7	0.1	0.5	0.3	0.6
Agariciidae	0.6	1.2	0.9	1.3	0.7	1.3	0.2	0.5	0.5	0.8	0.4	0.7
Pocilloporidae	0.4	0.7	1.3	1.8	0.9	1.4	0.1	0.4	0.4	0.7	0.3	0.6
Acroporidae	0.1	0.3	0.1	0.3	0.1	0.3	0.04	0.2	0.1	0.3	0.1	0.2

Table 7.7: Proportional differences between Coral Gardens (CG) and Nyali Reef (NR), calculated from the mean spat, recruit and juvenile coral densities presented in Table 7.1 and 7.6. The site with the higher density is shown in parentheses.

Family	Spat	Recruit	Juvenile
Pocilloporidae	5 (NR)	3 (NR)	4 (NR)
Poritidae	1	3 (CG)	4 (CG)
Acroporidae	35 (NR)	1	2.5 (NR)
Faviidae	40 (CG)	6 (CG)	4 (CG)

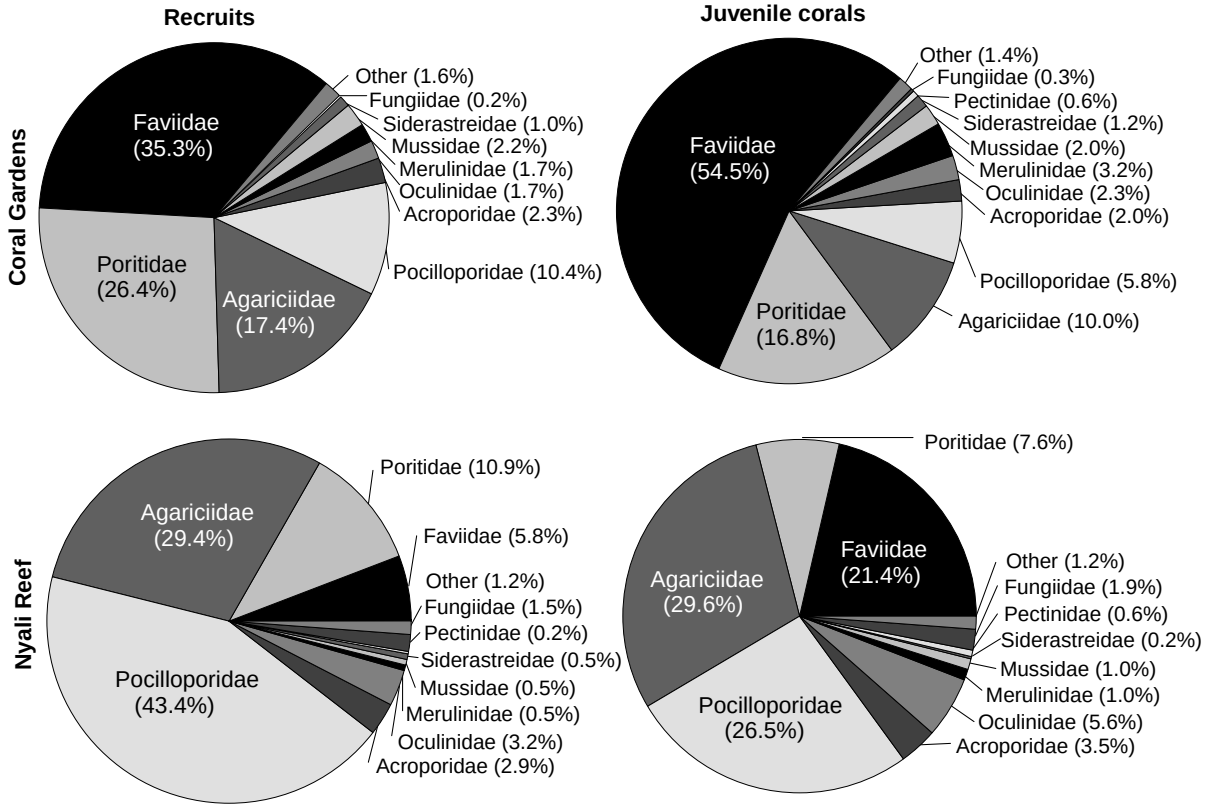


Figure 7.9: Relative abundance of coral recruits and post-recruits recorded in each family at Coral Gardens and Nyali Reef from May 2003 - November 2005.

Twenty-six genera of coral recruits and juveniles were recorded at Coral Gardens compared to 23 at Nyali Reef (Table 7.8). The Family Faviidae had the greatest number of genera represented (9), and the families Pocilloporidae, Agariciidae, Oculinidae, Merulinidae, Pectiniidae were represented by only 1 genus, namely *Pocillopora, Pavona, Galaxea, Hydnophora* and *Echinophyllia,* respectively. *Porites, Favia* and *Pavona* were the most abundant genera at Coral Gardens (in decreasing order), collectively comprising 65.9% of recruits at the site, while *Pocillopora, Pavona* and *Porites* (in decreasing order) were abundant at Nyali Reef comprising 83.2% of recruits (Table 7.8). The relative dominance of genera at individual sites changed in the juvenile size category, with *Favia*, *Porites* and *Favites* dominating at Coral Gardens to comprise 65.1% of juvenile corals. In contrast, *Pavona, Pocillopora* and *Favia* became more dominant at Nyali Reef comprising 67.8% of juvenile corals. The recruit abundances for Agariciidae (all *Pavona* species), should be interpreted with caution, as most corals were *Pavona varians* which is generally small in size in Kenya, and therefore it is highly likely that many adult colonies fell within the size range used to define recruits. Overall, *Acropora* species contributed less than 2% of recruits or juvenile corals, and 13 genera contributed <1% to recruit and/or juvenile coral populations (sites pooled) (Table 7.8).

The densities of recruits and juvenile corals for the five main families are shown in Fig. 7.10 from 2003 - 2005. The scale on the y-axis is the same for all graphs to enable comparisons between recruits and juvenile corals, as well as between sites. Recruit densities at Coral Gardens decreased slightly for all taxa from 2003 - 2005, but was more variable between taxa at Nyali Reef. In the juvenile coral category, mean densities remained fairly constant at the two sites (<1 coral m^{-2}) with the exception of juveniles of Faviidae which remained high and similar to recruit densities.

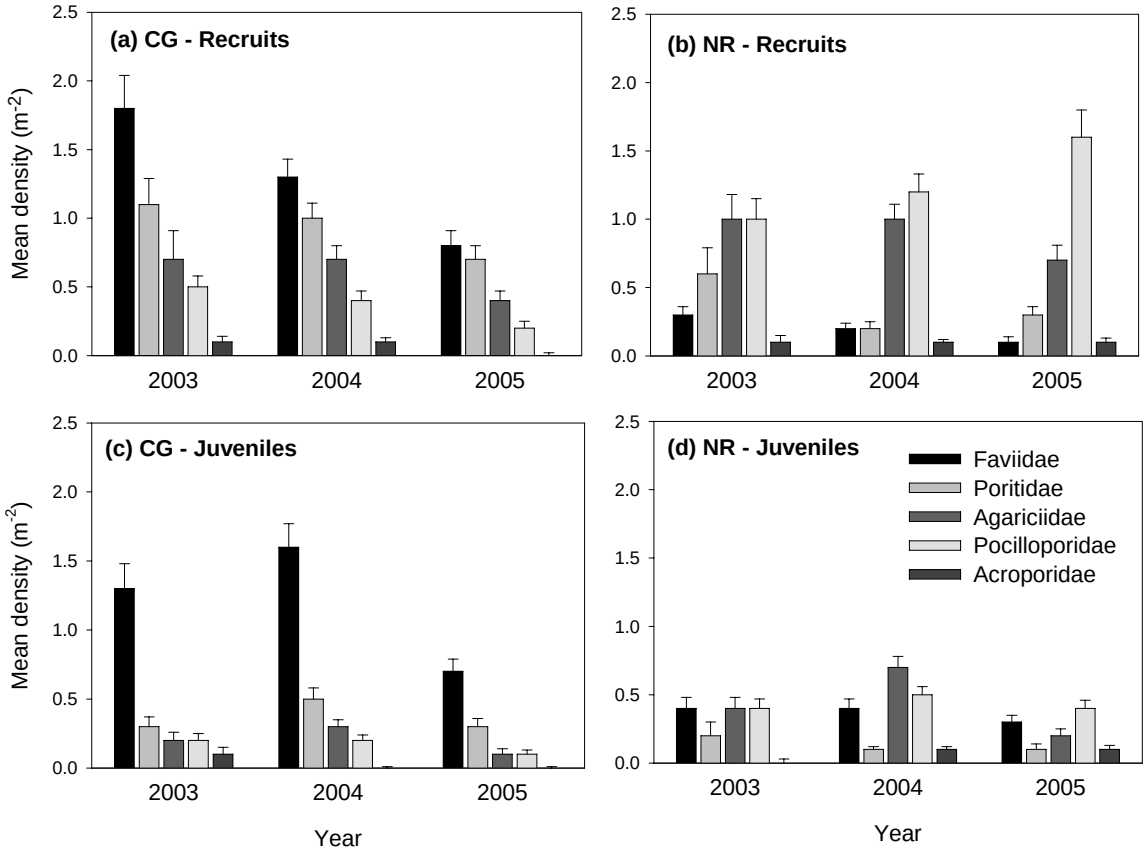


Figure 7.10. Mean density of recruits and juvenile corals (m^{-2}) at Coral Gardens (CG) and Nyali Reef (NR) from May 2003 - November 2005 for five families. The figure legend is shown in (d).

Table 7.8. Coral genera abundance and percent composition of recruits and juvenile corals recorded at Coral Gardens, Nyali Reef and for sites pooled ('All sites') from May 2003-November 2005. *: belong to the Family Faviidae. '–': no corals recorded in surveys.

Genus	**Recruits**						**Juveniles**					
	CG		**NR**		**All sites**		**CG**		**NR**		**All sites**	
	N	**%**	**N**	**%**	**N**	**%**	**N**	**%**	**N**	**%**	**N**	**%**
Porites	264	26.1	100	10.4	364	18.4	111	16.8	39	7.6	150	12.8
*Favia**	227	22.4	29	3.0	256	12.9	232	35.2	60	11.7	292	24.9
Pavona	176	17.4	283	29.4	459	23.2	66	10.0	152	29.6	218	18.6
Pocillopora	105	10.4	418	43.4	523	26.5	38	5.8	136	26.5	174	14.8
*Favites**	70	6.9	18	1.9	88	4.5	86	13.1	38	7.4	124	10.6
*Cyphastrea**	20	2.0	3	0.3	23	1.2	7	1.1	3	0.6	10	0.9
Acanthastrea	19	1.9	4	0.4	23	1.2	13	2.0	4	0.8	17	1.4
*Platygyra**	17	1.7	2	0.2	19	1.0	26	3.9	5	1.0	31	2.6
Galaxea	17	1.7	31	3.2	48	2.4	15	2.3	29	5.6	44	3.8
Hydnophora	17	1.7	5	0.5	22	1.1	21	3.2	5	1.0	26	2.2
*Echinopora**	16	1.6	3	0.3	19	1.0	3	0.5	3	0.6	6	0.5
Other	16	1.6	12	1.2	28	1.4	9	1.4	6	1.2	15	1.3
Acropora	10	1.0	20	2.1	30	1.5	7	1.1	14	2.7	21	1.8
Astreopora	9	0.9	5	0.5	14	0.7	5	0.8	-	-	5	0.4
Coscinaraea	6	0.6	4	0.4	10	0.5	8	1.2	1	0.2	9	0.8
*Goniastrea**	4	0.4	-	-	4	0.2	1	0.2	1	0.2	2	0.2
Montipora	4	0.4	3	0.3	7	0.4	1	0.2	4	0.8	5	0.4
Psammocora	4	0.4	1	0.1	5	0.3	-	-	-	-	-	-
*Leptastrea**	2	0.2	1	0.1	3	0.2	3	0.5	-	-	3	0.3
*Montastrea**	2	0.2	-	-	2	0.1	-	-	-	-	-	-
Alveopora	2	0.2	5	0.5	7	0.4	-	-	-	-	-	-
Scolymia	2	0.2	1	0.1	3	0.2	-	-	-	-	-	-
Fungiidae	2	0.2	14	1.5	16	0.8	2	0.3	10	1.9	12	1.0
Goniopora	1	0.1	-	-	1	0.1	-	-	-	-	-	-
Lobophyllia	1	0.1	-	-	1	0.1	-	-	1	0.2	1	0.1
*Plesiastrea**	-	-	-	-	-	-	1	0.2	-	-	1	0.1
Echinophyllia	-	-	2	0.2	2	0.1	4	0.6	3	0.6	7	0.6
N (total)	1013		964		1977		659		514		1173	

7.4 Discussion

7.4.1 Patterns of spat settlement

The Family Pocilloporidae dominated settlement on tiles at Coral Gardens and Nyali Reef throughout the study, comprising 93.7% of spat. These results contrast markedly with studies on the GBR where Acroporidae dominate artificial settlement substrata (e.g. Wallace 1985b; Harriott and Fisk 1988; Fisk and Harriott 1990; Hughes et al. 2002), but are similar to high-latitude reefs in eastern Australia (Harriott 1992; Harriott and Banks 1995), the northern Red Sea (Glassom et al. 2004) and South Africa (Glassom et al. 2006), and tropical reefs in French Polynesia (Adjeroud et al. 2006). Acroporidae spat comprised 1.4% of spat in Kenya, compared to a study in South Africa which recorded 9% in the first year, and 35.1% in the subsequent 2 years (Glassom et al. 2006). The dominance of Pocilloporidae on settlement tiles on equatorial reefs in Kenya (4ºS) and subtropical reefs in South Africa (27-28ºS), suggests the transition in dominance from broadcast spawning corals to brooders on settlement tiles observed along the east Australia coast (Harriott 1992; Harriott and Banks 1995; Hughes et al. 2002) is not apparent in East Africa. However, these patterns may also reflect the loss of *Acropora* species on Kenyan reefs following the 1997-98 coral bleaching event (Obura et al. 2000b; McClanahan et al. 2001) and the slow rate of recovery occurring in this genus.

Spat density was greater at Nyali Reef than at Coral Gardens, and this pattern was consistent for all settlement tiles from 2003 - 2005. Direct comparisons of settlement patterns between different reefs, locations or studies must be done cautiously because: studies vary considerably in their choice of substrata material, method of tile immersion, the length and timing of immersion relative to coral reproduction, and spatial variables such as depth, habitat and reef zone. However, the magnitude of the settlement at Nyali Reef (908 spat m^{-2} $year^{-1}$) fits within the ranges recorded on the GBR, while settlement at Coral Gardens (101 spat m^{-2} $year^{-1}$) is comparable with subtropical eastern Australia, the Caribbean and the Red Sea (see Table 6 in Glassom et al. 2004). On equatorial reefs in northern Tanzania (5-6ºS), the annual mean spat density on settlement tiles was estimated to be 500-600 spat m^{-2} (Nzali et al. 1998; Franklin et al. 1998), which is similar to tropical reefs in other parts of the world.

However, the density and composition of spat on settlement tiles in Kenya cannot be directly compared to the two Tanzanian studies (Nzali et al. 1998, Franklin et al. 1998), as these were done in the mid-1990s prior to the 1997-98 coral bleaching event and results from Kenya may be confounded by the impacts of bleaching.

In a recent subtropical South African study, mean spat density was 976 spat m^{-2} during peak settlement in March for tiles immersed for three months or longer (Glassom et al. 2006), which is similar to the 1167 spat m^{-2} recorded at Nyali Reef during peak settlement in February - May. While insufficient studies have been done along the East African coast to examine latitudinal gradients in spat density, the results from this study in Kenya suggest that differences in mean density between the tropics and subtropics observed along the eastern and western coasts of Australia (Harriott 1992; Harriott and Banks 1995; Harriott and Simpson 1997), do not occur in East Africa. Regional differences may be attributable the position of Kenya's reefs and the GBR in relation to the oceanographic systems operating in both regions. The South Equatorial Current in the Pacific splits between 14-18º latitude with southern flowing East Australian Current dominating along eastern Australia (Wolanski 1994; Veron 1995). The reefs of Western Australia are bathed by the southern-flowing unidirectional Leeuwin Current. In East Africa there are two opposite flowing current systems operating north and south of latitude 10˚S. These two current systems result from the South Equatorial Current flowing across the Indian Ocean and splitting near the border of Tanzania and Mozambique into the northerly East African Coastal Current (EACC) and the southerly Mozambique Current, that run parallel to the coast. It is possible that the similarities between Kenya and South Africa may reflect a linear dispersal pattern occurring along the coast and the relative positions of the two countries towards the extreme ends of the northward flowing EACC and the southward flowing Mozambique Current, respectively. It is hypothesised that the direction and strength of the EACC and Mozambique Current are likely to play an important role in the large-scale dispersal and recruitment of marine organisms, including corals, along the East African coast.

Coral settlement onto tiles varied significantly in space and time, with complex space-time interactions occurring (Table 7.2). Differences in spat density between the two sites were large despite their similarity in benthic cover, and may be attributable to

differences in hard coral cover composition, if reefs are largely self-seeding. Nyali Reef had a significantly higher mean percent cover of branching corals than Coral Gardens (Fig. 7.4b), mainly comprising *Pocillopora* and to a lesser extent *Acropora* species (pers. obs.). Given that *Stylophora* and *Seriatopora* were absent at the two sites, and are now extremely rare in Kenya (McClanahan et al. 2001), most spat identified as Pocilloporidae on settlement tiles are likely to be *Pocillopora* species. Site differences in branching coral cover and the overall densities of spat settling on tiles were both nine-fold, which suggests that *Pocillopora* spat availability may be a function of the relative abundance of adult colonies, and therefore these populations may be largely self-seeding.

Three species dominated the *Pocillopora* population at the study sites, *P. damicornis, P. eydouxi* and *P. verrucosa* (D. Obura, unpubl. data), and it is possible that these species may have been present on settlement tiles at both study sites. While its mode of reproduction is currently not known in the WIO, *P. damicornis* is hermaphroditic and broods sexually or asexually derived planulae in many parts of the world, and is capable of undergoing multiple cycles of gametogenesis and planulation, with brooded larvae competent to settle within hours following release (reviewed by Harrison and Wallace 1990). *Pocillopora damicornis* spat have been shown to aggregate around adult colonies in some locations (Tioho et al. 2001), but in other areas some larvae are long-lived and have the potential for long distance dispersal (Richmond 1987). A recent genetic study by Souter et al. (in prep.) found that this species has a clear population structure along southern reefs from Diani to Malindi in Kenya, with low levels of migration between reefs. Hence, there is a high likelihood that a large portion of the reproductive output of this species is retained within or near its natal reef, and this is likely to be reflected in the settlement patterns presented in this chapter. Souter et al. (in prep.) noted that sexual reproduction is the dominant mode of reproduction in *P. damicornis* at Coral Gardens and Nyali Reef.

In contrast, *P. verrucosa* is a broadcast spawner in most parts of the world (Harrison and Wallace 1990) and spawns gametes annually in South Africa (27ºS) and the Maldives (1ºN) in January and March, respectively (Sier and Olive 1994; Kruger and Schleyer 1998). Large oocytes were observed in tissue samples of *P. verrucosa* collected from Nyali Reef in December 2004 (unpubl. data), therefore, it is highly

likely that this species releases gametes early in the year in Kenya. Given its mode of reproduction and genetic evidence that populations of *P. verrucosa* in South Africa are panmictic (Ridgway et al. 2001), this species may recruit onto natal reefs as well as be dispersed to other reefs. However, population genetic studies are required to confirm this hypothesis. The mode of reproduction is not known in *P. eydouxi*.

Settlement of spat varied temporally between immersion periods of tiles, monsoon seasons and years, and similar temporal variability has been observed in other studies of coral settlement (Wallace 1985b; Hughes et al. 1999, 2002; Glassom et al. 2004). Settlement occurred predominantly during the northeast monsoon, which is consistent with the timing of gamete release in species of *Acropora* and faviids recorded at the two sites (Chapter 5 and 6; see also Mangubhai and Harrison 2006). No information is available on the timing of reproduction in the families Pocilloporidae or Poritidae in Kenya, although data from this study suggest that reproduction in Pocilloporidae occurs throughout the year, but predominantly from November - May. It is not known why there were site differences in the timing of peak settlement, occurring from November - May at Coral Gardens and from February - May at Nyali Reef. Similar site differences were also found in South Africa, where peak settlement occurred in March and May, at southern and northern reefs, respectively (Glassom et al. 2006). In both studies, reefs were separated by a distance of 10-15 km. High settlement rates were observed on tiles immersed in November and in February at Nyali Reef in 2005, suggesting that spawning may have occurred over a longer period in this year, perhaps in response to the shift in lunar month. In 2005, 23 species of *Acropora* and 2 faviid species commenced spawning earlier than in the previous year (Chapter 5 and 6).

While spat densities for Acroporidae were low (0.15 spat m^{-2}), settlement patterns generally coincided with the timing of broadcast spawning in *Acropora* species. In Kenya, *Acropora* species reproduce throughout the northeast monsoon from October to April with reproduction peaking in February and March (Chapter 6; see also Mangubhai and Harrison 2006). Settlement of Acroporidae spat occurred almost year-round at Nyali Reef, and peaked in February - May each year. The presence of Acroporidae spat on tiles in the winter months of August - October in 2003 was unexpected. Three potential explanations are: (1) winter spawning occurred in some *Acropora* species in 2003, (2) *Montipora* and *Astreopora* species present at the sites

(pers. obs.) may have spawned in winter, or (3) spat were dispersed from other reefs during this period. Biannual spawning in autumn/winter months has been recorded in *Platygyra daedalea* in Kenya (see Chapter 5), three *Montipora* species on the GBR (Stobart et al. 1992) and *Acropora* species in Western Australia (Rosser 2005), and *Acropora (Isopora) cuneata* planulates in winter on the GBR (Kojis 1986a), which provides some support for (1) and (2). Furthermore, *Acropora palifera* has been recorded south of the study sites between Kisite (near the border with Tanzania) to Diani (south of Mombasa town) (D. Obura, unpubl. data), and if this species planulates year-round as it does on equatorial reefs in Papua New Guinea (Kojis 1986b), it may explain the presence of Acroporidae on settlement tiles immersed from August - October.

While there is no published information on the timing of spawning from other locations to support (3), tile settlement studies from Tanzania (Franklin et al. 1998; Nzali et al. 1998) suggest that spawning in *Acropora* occurs predominantly during the northeast monsoon and peaks in April, with very few spat recorded in autumn/winter. This is similar to the settlement patterns recorded in Kenya. Given the SE monsoon winds would act in opposition to the northerly flowing East African Coastal Current, long-distance dispersal from Tanzanian to Kenyan reefs, particularly during May – August, is less likely to explain the patterns of spat settlement recorded in Acroporidae in this study.

Massive and submassive colonies of Faviidae and Poritidae are abundant at both Coral Gardens and Nyali Reef (unpubl. data) and both families were dominant in natural recruitment substrata surveys (Fig. 7.9), but were poorly represented on settlement tiles. Faviidae had the greatest number of genera represented in natural substrata surveys, which is consistent with the findings of Obura (1995) and Tamelander (2002). The low densities of Faviidae and Poritidae and the absence of other coral groups on tiles, may be caused by the absence of appropriate cues for metamorphosis and settlement on these tiles, which has been demonstrated for some corals and other marine invertebrates (reviewed by Pawlik 1992; see also Morse et al. 1988, 1996; Morse and Morse 1991; Baird and Morse 2004). Similar biases for and against different families have been observed on settlement tiles on the GBR (Harriott and Fisk 1988; Fisk and Harriott 1990; Dunstan and Johnson 1998), the Red Sea

(Glassom et al. 2004) and South Africa (Glassom et al. 2006). Poritidae showed year-round settlement with no distinct peaks, which suggests that spawning in this Family occurs over an extended period.

Competition may also influence the settlement of coral spat (Dunstan and Johnson 1998). Non-coral fauna were four times as abundant as corals on settlement tiles, but there was no evidence of significant competition between these two spat groups. Only 1.7% of coral spat were observed being overgrown by oysters, serpulids or bryozoans during the entire study. These results contrast markedly with Dunstan and Johnson (1998) who found a significant negative correlation between coral spat density and total cover of bryozoans and oysters, and observed non-coral organisms frequently overgrowing coral spat. However, Dunstan and Johnson (1998) noted that standard correlation analysis was not suited to 'triangular distributions' and their results must be interpreted with caution. In addition, a more asynchronous and extended breeding season such as that occurring in Kenya, may result (as suggested by Shlesinger and Loya 1985), in reduced competition during settlement.

7.4.2 Recruitment on natural reef substrata

The composition of genera of recruits and juvenile corals on natural substrata are similar to those recorded by Obura (1995) and Tamelander (2002) for the numerically abundant genera. Seven genera not recorded by Tamelander (2002) were recorded in this study, including *Cyphastrea* and *Acanthastrea* which comprised 2.4% of recruits, but eight genera recorded by Tamelander (2002) present as adults at the study sites (pers. obs.) were not recorded as recruits or juvenile corals. While no recruitment data are available for the Mombasa Marine National Park and Reserve prior to 1998, the number of genera recorded in this study (3.0-3.4 recruits m^{-2}) was similar to the densities recorded by Obura (1995) in Watamu and Malindi (approximately 100 km north of the study sites) from 1992 – 1994 (1-4 recruits m^{-2}), which suggests that recruit taxonomic diversity is currently at pre-bleaching levels.

The results from this study differed markedly from those of McClanahan et al. (2005) who recorded densities of 40-60 recruits m^{-2} in 1999 - 2001 along the Kenya coast. Differences between the two studies may be attributable to site differences or the

inclusion of fragmented adults by McClanahan et al. (2005) within their definition of recruits. Partial mortality was common on severely bleached reefs in Kenya (Obura 2001b) and the inclusion of fragmented adults would lead to an overly optimistic view of recruitment. By contrast, Tamelander (2002) defined recruits as <10 cm diameter and recorded densities of 4-21 recruits m^{-2} at different sites along the Kenyan coast. Pooling the two size categories in this study gave mean densities of 5.7 corals m^{-2} (sd = 4.0, max = 26) at Coral Gardens and 4.0 corals m^{-2} (sd = 3.2, max = 20) at Nyali Reef. The higher densities recorded by Tamelander (2002) at Coral Gardens (15-21 recruits m^{-2}) may reflect the inclusion of *Pocillopora* and *Acropora* colonies >10 cm to examine survivorship post-bleaching. Also, the use of permanent quadrats may over-estimate recruitment, as the observer is likely to select sites with a higher presence of recruits at the commencement of the study. It is also possible that recruitment may have initially been high in the Mombasa lagoon three years after bleaching (Tamelander 2002), perhaps in response to increased space availability, but has subsequently stabilised at a lower rate, or that variability is naturally high on Kenya's reefs. Similar findings have been reported in the Maldives, where an initial pulse of coral recruitment was reported in 1999 following the 1997-98 bleaching event (Schuhmacher et al. 2006), but in the subsequent years (2000-2002) recruitment decreased dramatically and stabilised at a lower rate (Bianchi et al. 2006).

If post-settlement processes were uniform on patch reefs in the Mombasa lagoon, proportional differences between sites for spat, recruit and juvenile coral density would be expected to remain constant as corals grow. However, this was not the case, and the results of this study suggest that recruitment success on lagoonal reefs is influenced by the supply and availability of coral larvae, as well as post-settlement processes and survival to adulthood, and that these differ between taxonomic groups and between sites. Similar conclusions were made by Sammarco (1991) who noted that coral recruitment and mortality varied on the GBR between inshore, mid- and outer-shelf reefs, with different genera dominating and taxonomic gradients occurring across the shelf.

The extent to which recruit and juvenile coral densities are influenced by larval supply and availability versus post-settlement processes is not known. Survivorship was higher at Coral Gardens for Poritidae and Faviidae, and this is consistent with findings

by Tamelander (2002) who noted survivorship differed between some sites in the Mombasa Marine National Park and Reserve. Acroporidae spat were almost exclusively found at Nyali Reef but *Acropora* recruit densities were identical at the two sites (Table 7.7). This suggests that Coral Gardens, which has very few adult *Acropora* colonies at the site (pers. obs.), may be receiving *Acropora* spat from other adjacent or more distant reefs. Planulae of broadcast spawning corals develop externally and require at least 2-6 days before they are competent to settle, which would promote wider dispersal in this group (Harrison and Wallace 1990; Nishikawa et al. 2003; Harrison 2006). Juvenile corals of *Acropora* had a higher survivorship at Nyali Reef (Table 7.7), which may explain why *Acropora* species are more abundant at this site than at Coral Gardens (D. Obura, unpubl. data). Densities of *Pocillopora* spat differed five-fold, recruits three-fold and juvenile four-fold, suggesting that populations may be in a more dynamic state of flux, reflecting pulses in recruitment throughout the year and high rates of mortality and turnover (this study; Tamelander 2002).

Previous studies in Kenya on the coral community structure 6 months after the 1997-98 bleaching event, showed a shift towards a dominance by *Porites, Pavona, Montipora, Galaxea* and a number of faviid corals (McClanahan et al. 2001). This pattern of dominance has generally persisted with recruits and juvenile corals primarily comprising *Favia, Favites, Porites, Pavona* and *Pocillopora* (Table 7.8). While losses of 86-100% were recorded for *Pocillopora* in 1998 (McClanahan et al. 2001), spat from this genus dominated on settlement tiles and are successfully recruiting onto reefs. By contrast, other branching genera have not recovered in abundance to their pre-bleaching levels. *Stylophora* was locally abundant prior to 1998, but was not recorded during this study or other recent studies (McClanahan et al. 2001; Tamelander 2002), and this genus has become highly patchily distributed and is now rare along the Kenya coast (D. Obura, unpubl. data). It is speculated that shorter-term recovery of this species to pre-bleaching levels is highly unlikely.

7.4.3 Post-bleaching recovery

The density and diversity of recruits and juvenile corals in Kenya (<4 corals m^{-2}) are similar to those recorded in the Maldives (<5 recruits m^{-2}), which is surprising since

the Maldives reef are considered to have suffered the highest coral mortality in the WIO, with coral cover reduced from 30-95% pre-beaching to 2-8% post-bleaching (Loch et al. 2002, Bianchi et al. 2006, Schuhmacher et al. 2006). *Acropora* has low spat, recruit and juvenile densities in Kenya (each ≤0.1 m^{-2}), and its recovery contrasts markedly with the Maldives where *Acropora* is recruiting at 1 recruit/juvenile m^{-2}, which is a ten-fold difference (Bianchi et al. 2006). It has been suggested that coral spawning in May 1998 may have contributed to the initial pulse in recruits recorded on Maldives reefs (Loch et al. 2002). However, the recent documentation of healthy *Acropora* stands (coral cover of 5-95%) on atoll reefs in the Maldives (Wallace and Zahir 2006) suggests that there are assemblages that survived the coral bleaching and these may a source of recruits for adjacent recovering reefs (Bianchi et al. 2006; Schuhmacher et al. 2006). In contrast, the slow recovery of *Acropora* in Kenya is likely to reflect the low abundance of this genus in lagoonal reefs prior to 1998 (6.5 cm m^{-2}), which was further reduced by bleaching (0.45 cm m^{-2}) (McClanahan et al. 2001), with recovery reliant on sexual rather than asexual reproduction. It is speculated that asexual reproduction through fragmentation is unlikely to contribute to the recovery of this genus because severe storms are rare and *Acropora* species in Kenya tend to have sturdier skeletons than their conspecifics on the GBR (C. Wallace and P. Harrison, pers. comm.; pers. obs.).

Seven years after the 1997-98 bleaching, some reef recovery is occurring in Kenya, with mean coral cover at the study sites currently at ~25% compared to 11% post-bleaching (Obura et al. 2000b), and macroalgae and coralline algae cover at 8-11% compared to 6-7% pre-bleaching (McClanahan et al. 2001). This rate of recovery of benthic cover is similar to Alphonse Atoll, Seychelles, which suffered similar coral losses to Kenya (Hagan and Spencer 2006). Unlike some of the reefs in the Chagos Archipelago and the Maldives, the structure of Kenya's reef has not collapsed or eroded, therefore much of the reef substratum is available for recolonisation (Sheppard et al. 2002; Loch et al. 2002). There is no evidence to suggest that Kenya's reefs have undergone or are in the process of a phase-shift towards dominance by fleshy algae or sponges. Similarly, no phase-shifts in community composition have been recorded in the Maldives or Seychelles (Schuhmacher et al. 2006; Hagan and Spencer 2006).

At the current rate of recovery, hard coral cover at the study sites may return to pre-bleaching levels in another 7-10 years, barring another bleaching event or major disturbance. However, the final community composition is likely to differ as families are recovering at different rates. The slow rate of recovery of Kenya's reefs is likely to reflect the scale of the mortality, source and availability of coral larval, the impact of other stressors (e.g. overfishing) as well as post-settlement processes operating at individual reefs. Efficient tidal flushing of the lagoon (Kirugara et al. 1998) may mean that gametes and larvae are retained in the lagoon for relatively short periods of time before they are swept out to sea. Tidal flushing and prevailing winds have a strong influence on the flow and movement of inshore, lagoonal and fore-reef waters (Obura et al. 2000a). Therefore, local hydrodynamics and oceanic processes are likely to limit dispersal to a single direction (northerly) along the northern part of the East African coast and in the short- to medium-term, recovery may be more strongly dependent on local reefs. However, with the recurrence of bleaching such as the minor event in March – May 2003 (unpubl. data), full recovery may not be realistic, especially with the current global predictions on climate change and increased rates and severity of mass bleaching events predicted (Hoegh-Guldberg 1999). The results of this study provide a 'baseline' for future recruitment studies, and will be important for looking at future disturbances and the long term recovery and management of Kenya's coral reefs.

CHAPTER 8: GENERAL DISCUSSION AND CONCLUSIONS

8.1 Seasonality and patterns of coral reproduction

Mass or multispecific spawning of coral communities is one of the most remarkable and spectacular phenomena on coral reefs, and yet the causal factors driving coral reproduction cycles and spawning events are still not understood. No single environmental variable or combination of variables appears to fully explain the complete range and complexity of coral spawning patterns that have been documented in different geographic regions. An earlier theory that sexual reproduction would not occur on subtropical reefs where sea surface temperatures of less than 18 ºC occurred (Wells 1957), has been disproved with the documentation of single species and multispecific spawning on high-latitude reefs in eastern and western Australia, Japan, the Arabian Gulf and South Africa (Babcock et al. 1994; Harrison 1995; van Woesik 1995; Fadlallah 1996; Schleyer et al. 1997; Wilson and Harrison 1997, 2003; Nozawa et al. 2006).

In contrast, very little detailed research has been done on spawning patterns of scleractinian corals in equatorial regions, where it has been hypothesised that seasonality and synchrony of reproduction may break down due to a narrow range in variation in environmental parameters such as temperature and tidal amplitude that are thought to influence the onset and timing of reproduction (Oliver et al. 1988). It has also been hypothesised that in equatorial environments where conditions are suitable for reproduction for longer periods in a year, marine invertebrates may (a) have a more protracted reproductive season, and (b) be capable of breeding year-round (Orton 1920; Pearse 1974).

Kenya, located in the tropics between the latitudes 1ºS and 5ºS, is ideally situated for determining the degree of spawning synchrony at the equator, and whether the East African monsoon seasons have a dominant influence on reproduction and recruitment patterns. This study found that coral reproduction occurred predominantly in the northeast monsoon (NE), from December to March each year, when prevailing wind and sea conditions are calm, which suggests that there is a correlation between

seasons and reproduction in Kenya. Spawning in the southeast (SE) monsoon season occurred only in a small number of biannually spawning colonies of *Platygyra daedalea* (representing <20% of the population), which released gametes mainly in August and September each year. While the exact night of spawning was recorded in only a small number of *Acropora* and faviid species, the narrowing of spawning times to lunar months and lunar quarters, and the overlap between reproducing species during these periods, suggests that some degree of multispecific spawning is a characteristic of Kenyan reefs. In addition, the presence of pigmented oocytes in colonies of *Hydnophora exesa, Turbinaria mesenterina, Favites pentagona* and *Astreopora listeri* sampled in December 2004, provides further evidence that other species, genera and families are reproductively mature at a similar period to *Acropora* and faviid species.

The extended seasonal pattern of spawning recorded in Kenya supports Guest et al. (2005b) who argued that no coastal environment was truly aseasonal, and therefore reproductive seasonality and some degree of multispecific spawning may occur on equatorial reefs. However, the suggestion that mass spawning is a characteristic of equatorial reefs (Guest et al. 2005b), is not supported by the coral reproductive data from this study. In contrast to other tropical reefs (reviewed by Harrison and Wallace 1990; Richmond and Hunter 1990), reproductive patterns in broadcast spawning corals are asynchronous in Kenya, with spawning occurring over an extended period of 9 months from August – April (when *Acropora* and faviid data are combined). Corals displayed some degree of 'temporal reproductive isolation' (*sensu* Shlesinger and Loya 1985) between species, in relation to the main lunar month and lunar quarter when spawning occurs. In the northern Red Sea and Caribbean, where corals studied to date display a higher level of asynchrony, spawning occurs over 6 months (April – September) (Shlesinger and Loya 1985; Shlesinger et al. 1998) and 4 months (July - October) (Szmant 1986; Van Veghel 1994), respectively. On subtropical reefs in the Solitary Islands, eastern Australia 13 *Acropora* species also showed an asynchronous pattern of reproduction with individual species spawning over 2-5 consecutive months (Wilson and Harrison 1997, 2003). Therefore, Kenyan coral reefs have the longest reproductive season recorded thus far for broadcast spawning corals, and the findings of this study support the hypotheses that reproductive seasons may be more protracted towards lower latitudes (Orton 1920; Pearse 1974), and that mass spawning does not

occur in equatorial regions due to a breakdown in spawning synchrony (Oliver et al. 1988).

The three faviid species studied split-spawned over 2-3 consecutive months with *Leptoria phrygia* spawning 1-2 months earlier than *Echinopora gemmacea* and *P. daedalea*. *Acropora* species showed both intra- and inter-specific spawning asynchrony, with spawning occurring over 7 months (October – April), and individual species releasing gametes over 2-5 months. On the Great Barrier Reef (GBR), the extent to which split-spawning occurs within and between populations is thought to be determined by the timing of the full moon and the rise in sea surface temperatures (Willis et al. 1985). In Kenya there was no clear relationship between coral spawning intensity and the timing of the full moon (i.e. earlier or later in the month), which suggests that split-spawning is a phenomenon that results in a protracted breeding season, and is not just a response to a shift in the lunar phase. Similarly, Van Veghel (1994) argued that in Curaçao split-spawning was a phenomenon that was not driven by the relative timing of lunar phases in the main spawning months.

Although reproduction occurred during 9 months of the year, there was no evidence from this study to suggest that individual broadcast-spawning *Acropora* or faviid species were capable of reproducing year-round, as suggested for other invertebrate groups by Orton (1920) and Pearse (1974). However, some colonies in Kenya underwent biannual cycles of gametogenesis, while conspecifics at higher latitudes undergo single annual cycles. Biannual cycles of gametogenesis occurred in both morphotypes of *P. daedalea* and one colony each of *A. valida* and *Acropora* sp.1, and two slightly overlapping cycles of oogenesis were recorded in *L. phrygia*. In contrast, single cycles of gametogenesis occur in *A. valida* and *L. phrygia* on the GBR (18-23ºS, Kojis and Quinn 1982; Wallace 1985a) and in *L. phrygia* in Western Samoa (15ºS, Mildner 1991).

Biannual reproduction was also recorded in broadcast spawning corals on equatorial reefs in northern PNG (5ºS, Oliver et al. 1988) and Singapore (1ºN, Guest 2004). In PNG, individual colonies of *P. daedalea, Turbinaria reniformis* and *Lobophyllia hemprichii* underwent biannual cycles of gametogenesis, with mature gametes recorded in September - November and January - March (Oliver et al. 1988). In

Singapore, biannual spawning was recorded in *Platygyra* sp. in September - October and March - April (Guest 2004), but it is not known whether individual colonies have biannual gametogenic cycles, or whether the population split-spawns, because a random sampling strategy was used to collect tissue samples. In addition, some repeatedly sampled colonies of *Porites lutea* had mature gametes in August - November and in March - April in Singapore (Guest 2004), indicating the presence of two gametogenic cycles, which have not previously been recorded for this species. *Porites lutea* has a single annual cycle of gametogenesis on the GBR (14-23ºS, Kojis and Quinn 1981b; Harriott 1983b) and in the northern Red Sea (29ºN, Shlesinger et al. 1998). Therefore, there is some evidence to suggest that biannual cycles of gametogenesis may occur in some broadcast spawning species in equatorial regions, and some species such as *P. daedalea* and possibly some congenera, may be capable of biannual spawning over an extended longitudinal range.

The occurrence of biannual cycles of gametogenesis in *Acropora* species, however, do not appear to be as strongly related to latitude, as they occur on both equatorial (e.g. Kenya, PNG, Singapore) (Oliver et al. 1988; Guest et al. 2005a), and on tropical reefs in Western Samoa (Mildner 1991), but have not been recorded in other locations. In addition, two *Acropora* species in the Dampier Archipelago, Western Australia (20ºS) underwent single annual cycles of gametogenesis but the population split-spawned, with individual colonies releasing gametes in either October (spring) or March (early autumn) (Rosser 2005). *Montipora digitata* (Family Acroporidae) underwent biannual gametogenic cycles and spawned in March and October on the GBR (19ºS, Stobbart et al. 1992), and biannual spawning was recorded in five *Montipora* species on equatorial reefs in Palau in February and September (7ºS, Penland et al. 2004), which is exactly one lunar month earlier than on the GBR.

The lack of year-round spawning in *Acropora* and faviid species is likely to reflect life-history patterns, energetic and physiological constraints within this sexual pattern and mode of reproduction or within the species studied. The studies summarised above suggest that broadcast spawning faviid and *Acropora* species may only be capable of up to two cycles of gametogenesis per year. Year-round spawning is more likely to occur in brooding species than broadcast spawners in equatorial regions, because brooders have a greater propensity for multiple cycles of gametogenesis

(reviewed by Fadlallah 1983; Harrison and Wallace 1990; Richmond and Hunter 1990). Settlement patterns of pocilloporids and poritids in Kenya suggest that year-round sexual reproduction may occur in these two taxonomic groups, as evidenced by the presence of settled spat on artificial settlement tiles in all 3-month immersion periods of the year (Chapter 7). Furthermore, the brooder *Acropora (Isopora) palifera* undergoes up to six cycles of gametogenesis and planulates year-round on equatorial reefs in PNG (7ºS), but has a single cycle of gametogenesis and planulates in summer at Heron Island reef (23ºS), southern GBR (Kojis 1986b). A number of pocilloporids planulate year-round on equatorial reefs in Palau (7ºS, Atoda 1947a, 1947b, 1951), but have a more seasonal pattern on the GBR (14ºS, Harriott 1983b; 23ºS, Tanner 1996) and in the Red Sea (Rinkevich and Loya 1979a; Shlesinger and Loya 1985; Zakai et al. 2006).

With the exception of the current study, only one other medium-term multi-species study has been undertaken to describe reproductive patterns in scleractinian corals on equatorial reefs, and this was done recently in Singapore (Guest et al. 2002, 2005a, 2005b; Guest 2004). It is, however, difficult to compare the asynchronous spawning patterns recorded in Kenya with patterns recorded in Singapore because different methods were used for examining reproduction in faviid and *Acropora* species and the data are not directly comparable. In Singapore, random colonies of *Platygyra* sp. and *Acropora* species were selected for sampling (see methods in Guest 2004), while in Kenya individually marked colonies were repeatedly sampled. The sampling strategy used in Kenya allowed patterns of gametogenesis and spawning to be interpreted at both the individual and population level, which is important for quantifying reproduction in populations with extended breeding periods. While the majority of spawning was concentrated in the March and April in Singapore, the presence of gametes in *Acropora* species over 10 months of the year (see Fig. 2 in Guest et al. 2005a), and the presence of gametes in October/November in *Platygyra* sp., *Porites* spp. and *Goniopora* spp. (Guest 2004), suggests that corals in Singapore may also spawn over an extended period, similar to that recorded in Kenya.

There is also some evidence to suggest that protracted breeding seasons occur on equatorial reefs in Palau with broadcast spawning occurring in the months April – September and February (Kenyon 1995; Penland et al. 2004), and year-round

planulation occurring in a number of pocilloporid species (Atoda 1947a, 1947b, 1951). Further studies in Palau documenting gametogenic cycles and the degree of intra- and inter-specific spawning synchrony would be useful to enable comparisons with scleractinian corals in Kenya, and to further test hypotheses relating to breeding patterns in equatorial regions. Other studies on equatorial reefs are either short (e.g. Kenyon 1995; Edinger et al. 1996; Baird et al. 2001, 2002) and/or involve single or too few species (e.g. Kojis 1986b; Sier and Olive 1994; Colley et al. 2002; Mangubhai et al. 2007), and therefore do not provide extensive information on reproductive patterns on low-latitude reefs with asynchronous spawning and protracted breeding seasons.

In Kenya, protracted breeding seasons are not limited to scleractinian corals and also occur in other marine invertebrates and fish on reefs, with most species showing distinct seasonal patterns (e.g. Nzioka 1979; Kulmiye et al. 2002; Muthiga and Jaccarini 2005; Muthiga 2006). The sea urchin *Echinometra mathaei* releases gametes over 6 month periods in Kenya, commencing spawning in December and peaking in the months February to May (Muthiga and Jaccarini 2005), while *Holothuria arenacava* (a new species of sea cucumber described by Samyn et al. 2001) spawns over 3 months between March and May (Muthiga 2006). *Echinometra mathaei* generally spawns over shorter periods of 2-3 months on higher latitude tropical reefs in Japan, the Gulf of Suez and the Red Sea, though year-round spawning has been recorded on Rottnest Island (32ºS) off Western Australia (see Table 2 in Muthiga and Jaccarini 2005). The thumbprint emperor fish *Lethrinus harak* has a prolonged spawning season in Kenya that extends over the same period as *Acropora* species, from October to April, with spawning peaks in the inter-monsoonal months of October and April (Kulmiye et al. 2002), and six *Lutjanus* species (snappers) spawn over a period of 2-6 months, with spawning peaking in October (Nzioka 1979). Furthermore, barnacles, bryozoans, serpulids and oysters settle on artificial substrata throughout the year, with peak settlement in the different groups occurring in different 3-month periods of the year (Fig. 7.8, Chapter 7).

There are also studies from other equatorial regions that support the hypothesis of protracted breeding seasons and a breakdown in spawning synchrony at the equator. Srinivasan and Jones (2006) found that in 40 of the most abundant fish species

(comprising 6 families) in Kimbe Bay, West New Britain, PNG (5ºS) recruitment occurred over 6-12 months of the year, with most wrasse species (Family Labridae) exhibiting year-round recruitment, with seasonal peaks in recruitment. The sea urchin *Diadema setosum* has continuous reproduction on equatorial reefs in Singapore (Hori et al. 1987) and Kenya (Muthiga 2003), but spawns in the summer months in tropical and higher latitude reefs in the Gulf of Suez, northern Red Sea, Japan and on the GBR (Pearse 1974). Extended aseasonal patterns of reproduction were recorded in the barnacles *Chthamalus malayensis* in Singapore (1ºN) and Malaysia (2ºN) (Koh et al. 2005) and *Marcia* species in Singapore (Tan 1994 cited in Koh et al. 2005).

Therefore, there is a growing body of evidence that indicates that there is a reduction in the degree of spawning synchrony on equatorial reefs, with breeding seasons becoming more protracted and that these patterns extend to a range of marine organisms, and include scleractinian corals.

8.2 Proximate cues and ultimate factors

The discovery of asynchronous spawning and protracted breeding seasons in *Acropora* and faviid species on equatorial reefs in Kenya, poses important theoretical questions on the evolutionary and ecological advantages ('ultimate factors') of asynchronous versus synchronous spawning and the role of different environmental variables ('proximate cues') in determining spawning patterns at different latitudes.

8.2.1 Proximate cues

Equatorial regions are not aseasonal, and many regions are influenced by monsoonal changes with associated variations in temperature, light, rainfall, and phytoplankton abundance, and these environmental variables may vary at different longitudes. The confounding effects of different non-independent environmental variables that may act as 'proximate cues' to regulate reproductive cycles makes it difficult to assess the role(s) individual variables have on reproductive processes in marine organisms, and the degree and extent to which they operate in synergy, or otherwise. In addition, the

interaction between endogenous rhythms and proximate cues is not well understood and may vary between different marine invertebrates (Olive and Garwood 1983).

Temperature is generally considered the most important environmental variable controlling reproduction in marine invertebrates (Orton 1920; Pearse 1974), with some studies suggesting that annual sea surface temperature range rather than absolute temperature, may determine the length of reproduction and degree of spawning synchrony (Shlesinger and Loya 1985; Babcock et al. 1986; Richmond and Hunter 1990). Annual sea surface temperature ranges are not uniform and can vary between different equatorial regions. For example, temperatures in the Mombasa lagoon had an annual range of 5 ºC, which is slightly higher than equatorial reefs in the Solomon Islands (2 ºC, Baird et al. 2002), PNG (3 ºC, Oliver et al. 1988) and Singapore (3-4 ºC, Guest et al. 2005a), and slightly lower than some areas of the central GBR (5-7 ºC, Oliver et al. 1988) and the central Red Seas (7 ºC, Fadlallah and Lindo 1988). The documentation of spawning asynchrony and a protracted breeding season in Kenyan corals suggests that temperature range or variability may not be the sole factors determining the length of breeding seasons or spawning synchrony in equatorial regions.

In Kenya, *Echinopora gemmacea, L. phrygia*, the majority of *P. daedalea* and many *Acropora* species spawned when sea surface temperatures were at their annual summer maximum during the NE monsoon season. However, 8 (out of 19) *Acropora* species spawned during rising sea surface temperatures, which suggests that for some coral groups, such as *Acropora*, there may be factors other than temperature that influence the timing of spawning, or alternatively, that there is a wider range in reproductively successful or optimal temperatures for spawning in this genus. Similar differences have been recorded between urchin species in Kenya. For example, *Diadema savignyi* and *E. mathaei* spawned when sea surface temperatures were at their maximum and when they were declining (Muthiga 2003; Muthiga and Jaccarini 2005), while *Tripneustes gratilla* spawned in the SE monsoon months of July and August when water temperatures were at their annual minimum (Muthiga 2005). In contrast, reproductive patterns in *D. setosum* were not strongly seasonal, with gonad indices remaining fairly constant throughout the year, increasing only slightly between October – December (Muthiga 2003).

Tidal ranges are also not consistent on equatorial reefs, with higher tidal amplitudes recorded in Kenya (4 m) and Singapore (2.4 m, Guest et al. 2005a), compared to PNG (0.5 m, Oliver et al. 1988) and the Solomon Islands (0.8 m, Baird et al. 2001, 2002). The three faviids studied spawned mainly on spring tides, while *Acropora* species spawned over a range of tides from springs through to neaps, which suggests that tidal phase may not play a strong role in determining the timing of spawning in corals in Kenya. While coral spawning recorded in aquaria coincided with the ebb tide dropping to low tide, this study was not able to confirm whether spawning always coincided with low tide because no *in situ* monitoring for coral spawning could be done. In addition, corals were only established in aquaria around the time of full moon, and therefore, there was a bias towards those species and individual corals that spawned in the 3rd lunar quarter and the associated tides during this period.

Spawning occurred only at night in aquaria, which suggests that the onset of darkness is an important cue for triggering spawning behaviour and is consistent with spawning patterns in scleractinian corals in general (Harrison et al. 1984; Babcock et al. 1986; Harrison and Wallace 1990). Night time spawning is thought to be advantageous for corals as they may avoid predators that are visual feeders and the damaging effects of ultraviolet light on gametes and developing embryos (Babcock et al. 1986; Wellington and Fitt 2003). Although there was a greater tendency for faviid and *Acropora* species to spawn in the 3rd lunar quarter (i.e. between full moon and lunar day 22), spawning was recorded in all lunar phases, mainly as a result of the asynchronous pattern recorded in *Acropora* species. Lunar cycles do not appear to fine-tune coral spawning in Kenya to the same degree and extent recorded in other locations (reviewed by Harrison and Wallace 1990). Instead, the timing of spawning in relation to lunar phases is more similar to species in the Red Sea and in the subtropical Solitary Islands, which spawn over a range of lunar phases (Shlesinger and Loya 1985; Shlesinger et al. 1998; Wilson and Harrison 1997, 2003). *In situ* monitoring of corals spawning, particularly during the main spawning months of January – March would further elucidate the role lunar phase and tidal amplitude have on the timing of spawning in Kenya.

While the proximate cues governing the timing of reproduction could not be clearly discerned in Kenya, it is clear that spawning patterns recorded during this study contrast markedly from mass spawning corals on the GBR, where temperature, monthly lunar (and associated tidal) cycles, and the onset of darkness are considered the three proximate cues that act to progressively, in that order, to fine tune and ultimately determine the month, day and hour of spawning (Babcock et al. 1986). Given that temperature and tidal amplitudes in the Kenya do not differ greatly from some areas of the GBR, it is possible that other proximate cues may have a greater role in controlling reproduction in Kenya, and cause a breakdown in spawning synchrony.

One environmental cue that has been largely over-looked or ignored is the role of photoperiod (i.e. light/dark cycles or daylength) in controlling reproduction and synchronising spawning in corals, though it has been shown to be important in some other marine invertebrates (e.g. Garwood 1980; Pearse and Eernisse 1982; Pearse and Walker 1986), and in plants in equatorial rainforests (Borchert et al. 2005). Photoperiod cycles are more consistent because of their independence from seasonal and inter-annual variation in climate, and therefore may provide a more reliable cue in synchronising gametogenic cycles in marine organisms. Pearse and Eernisse (1982) demonstrated that in laboratory-maintained starfish *Pisaster ochraceus,* a 6-month shift in photoperiod regime resulted in a 6-month shift in the timing of gametogenesis, gonadal growth and spawning, compared to individuals in the field or maintained in aquaria under ambient light conditions. A similar experiment with the North Atlantic starfish *Asterias vulgaris*, also resulted in a 6-month shift in gametogenic cycles in aquarium animals maintained under a photoperiod that was 6 months out of phase with ambient conditions (Pearse and Walker 1986). In the polychaete *Harmothoe imbricata* temperature and photoperiod appear to act synergistically with endogenous rhythms to synchronise individuals during gametogenesis (Garwood 1980).

In equatorial regions, daylength remains fairly constant with changes of ≤30 minutes $year^{-1}$, compared to other environmental variables such as temperature and tidal amplitude which may vary between locations. Therefore it is equally plausible to argue that under conditions of more constant daylength (i.e. low variation in photoperiod), spawning synchrony may break down and extended breeding seasons

may occur. This hypothesis does not imply that sensitivity to changes in photoperiod are lost in equatorial regions, nor does it exclude the role other variables such as temperature or solar radiation may have in fine-tuning reproductive cycles and the timing of spawning. For example, Kenyan corals spawn generally during periods when light intensity is above 20 mJ m^{-2}, which suggests that light may also play a role in the timing of spawning events. Muthiga (2006) found strong correlations between gonad maturation in *H. arenacava* and temperature and light intensity, and suggested that both these variables played a role in the control of reproduction in this species in Kenya.

With so few detailed studies done on reproduction in scleractinian corals in equatorial regions, it is not possible to determine whether the reproductive patterns recorded in Kenya are unique to Kenya, or reflect a general latitudinal trend that applies to corals on other equatorial reefs. However, there is growing evidence from other marine invertebrate groups such as sea urchins, sea cucumbers and barnacles as well as fish (see examples in section 8.1), to suggest that protracted breeding seasons and spawning asynchrony are features of equatorial reefs. It is clear that there is no simple relationship between latitude or the range and amplitude of environmental variables, which determines the degree of synchrony exhibited by corals. Further detailed medium to long-term studies in equatorial regions across a wider range in longitudes, will elucidate the extent to which spawning synchrony breaks down at lower latitudes, and the roles of different environmental variables on equatorial reefs.

8.2.2 Ultimate factors

The ultimate factors influencing spawning patterns are still poorly understood and remain largely theoretical (reviewed by Harrison and Wallace 1990). There are a number of possible advantages to coral populations dividing their reproductive effort over more than one lunar month. Split-spawning at the population level may be a strategy to reduce the probability of a single catastrophic event (e.g. unusually heavy rains) impacting on a population's entire reproductive outputs for any given year (Harrison et al. 1984; Richmond and Hunter 1990). Alternatively, it may provide an opportunity for colonies that were not fully reproductive or were stressed to participate in a spawning event (Rinkevich and Loya 1985; Shimoike et al. 1992; Van

Veghel 1994), or for reducing interspecific competition among corals during settlement (Shlesinger and Loya 1985). It has also been suggested that split-spawning may be a mechanism for adaptive drift in reproductive timing to enable corals to respond to a changing climate (Hagman et al. 1998).

However, there may be disadvantages to split-spawning such as gamete wastage, non-viable hybridisation, and low rates of fertilisation and outcrossing in self-fertile hermaphrodites (reviewed in Harrison and Wallace 1990; see also Oliver and Babcock 1992; Babcock and Mundy 1992; Babcock et al. 1992; Babcock 1995). Indeed much of the evidence presented to date suggests that high fertilisation success is achieved by marine invertebrate species (including both sessile and mobile forms) spawning in synchrony rather than asynchrony, and fertilisation success is considered an important factor controlling the overall reproductive success of marine invertebrate species (e.g. Oliver and Babcock 1992; Babcock and Mundy 1992; Babcock et al. 1992; Babcock 1995; Coma and Lasker 1997). Oliver and Babcock (1992) found fertilisation success was dependent on the proportion of the colonies spawning, with low fertilisation rates recorded in coral spawning slicks on the GBR during minor compared to major spawning nights. Babcock and Mundy (1992) found similar results when comparing fertilisation rates in crown-of-thorns starfish during minor and major spawning events, and Coma and Lasker (1997) showed that sperm limitation did not occur on nights when the population of the gorgonian *Pseudoplexaura porosa* spawned synchronously and when most of the eggs were released. Experimental manipulations have shown that there are optimum sperm concentrations for achieving high fertilisation rates, and this is thought to be maximised by species synchronising their spawning periods (e.g. Oliver and Babcock 1992; Babcock and Mundy 1992; Benzie and Dixon 1994; Babcock 1995; Willis et al. 1997).

The findings of these studies suggest that an asynchronous pattern of spawning in scleractinian corals is likely to result in low rates of fertilisation and hence would reduce recruitment and the rate of propagation of a species. However, this may not be the case in Kenya or on equatorial reefs in general, given that high biological diversity and flourishing reefs are found at low latitudes (Veron 1995, 2000). Coral fecundity in both faviid and *Acropora* species was higher in Kenya compared to other regions (Table 5.12 and 6.8), and it is proposed here that these high fecundities may allow

corals to stagger their reproduction over 2-5 months, without incurring a significant reduction in fertilisation rates. This argument is supported by models of egg size and sperm limitation proposed by Levitan (1993). Models of optimum egg size indicate that smaller egg sizes and greater sperm motility are selected when sperm availability is higher (Levitan and Petersen 1995). The reduction in fertilisation associated with smaller eggs sizes is compensated for by a higher fecundity, which increases the probability of zygote production (Levitan 1993, 1996; Podolsky and Strathmann 1996). In Kenya there was a significant positive relationship between number of eggs (polyp fecundity) and mean spermary sizes in *Acropora* species (section 6.4.3.1, Chapter 6), and therefore there may be a relationship between sperm concentration and fecundity that maximises zygote production. In addition, the presence of sperm-attractant molecules in eggs of some species (e.g. Coll et al. 1994, 1995) would increase the effective surface area of eggs, without increasing the amount of energy invested per egg. Field and laboratory studies, similar to those by Oliver and Babcock (1992) would be useful to repeat in Kenya, to quantify fertilisation rates across different lunar months or lunar quarters to understand how asynchronous spawning patterns maintain and propagate coral populations on equatorial reefs.

8.3 Settlement and recruitment patterns

A comprehensive discussion on the spatial and temporal patterns of settlement and recruitment within the Mombasa Marine National Park and Reserve, was provided in Chapter 7, hence only the main findings are summarised in this section. This study showed that spat from Family Pocilloporidae dominated settlement tiles at the two study sites comprising 93.7% of spat, which is similar to high-latitude reefs in South Africa, the northern Red Sea and eastern Australia (Harriott 1992; Harriott and Banks 1995; Glassom et al. 2004; 2006). Latitudinal gradients from the tropics to the subtropics in relation to density and composition of recruits along eastern Australia (Harriott and Banks 1995; Hughes et al. 2002), were not apparent in East Africa. However, the patterns recorded in Kenya may also reflect the loss of *Acropora* species on reefs following the 1997-98 coral bleaching event (Obura et al. 2000b; McClanahan et al. 2001) and the slow rate of recovery occurring in this species (Chapter 7).

Patterns of settlement of Acroporidae spat on tiles coincided with the timing and extended duration of broadcast spawning in *Acropora* species in Kenya. The presence of spat during the winter months of August – October suggested that winter spawning occurs in other genera or species not examined during this study, such as *Montipora* spp. or *A. palifera. Montipora* species spawn biannually on equatorial reefs in Palau (Penland et al. 2004) and the isoporan *A. palifera* planulates year-round in PNG (Kojis 1986b), and it is possible that similar reproductive patterns occur on other equatorial reefs such as in Kenya. The settlement patterns for Pocilloporidae and Poritidae suggest that reproduction may be more protracted in these two families and extend throughout the year in Kenya. In contrast, very few spat belonging to the Family Faviidae were recorded on settlement tiles, so the relationship between reproduction and settlement cannot be determined for this Family from the data in this study. The use of conditioned tiles in future studies may reduce the bias towards pocilloporids, which may respond to water-borne molecular cues and have a less stringent requirement for contact with crustose coralline algae, compared to, for example acroporids (Baird and Morse 2004).

There was no evidence of significant competition between coral spat and spat from non-coral fauna such as barnacles, bryozoans, serpulids, and oysters, which contrasts with a study on the GBR when fouling organisms were observed frequently overgrowing coral spat (Dunstan and Johnson 1998). Based on these findings, it is possible that a more extended breeding season with asynchronous spawning may result in reduced competition between different spat during settlement, similar to that described for the northern Red Sea (Shlesinger and Loya 1985).

The density and relative composition of coral recruits and juvenile corals on natural substrata were similar to those recorded before the 1997-98 bleaching event by Obura (1995). The degree to which recruit and juvenile coral densities are influenced by larval supply and availability versus post-settlement processes are not known, but survivorship was higher for the families Poritidae and Faviidae in the Mombasa Marine National Park (Coral Gardens), while Acroporidae had a higher survivorship in the National Reserve (Nyali Reef). Previous studies of the community structure 6 months after bleaching showed a shift towards dominance by *Porites, Pavona,*

Montipora, Galaxea and a number of faviid corals (McClanahan et al. 2001). This patterns of dominance has generally persisted, with recruits and juvenile corals mainly comprising of the four families Faviidae, Poritidae, Pocilloporidae and Agariciidae, and the genera *Favia, Favites, Porites, Pavona* and *Pocillopora*. There is no evidence to suggest that Kenya's reefs have undergone, or are in the process of, a phase-shift in community composition towards dominance by fleshy algae or sponges. Similarly, no shift in community composition has been recorded on other reefs in the WIO recovering from the 1997-98 coral bleaching event (e.g. Bianchi et al. 2006; Schuhmacher et al. 2006; Hagan and Spencer 2006).

The mean percent cover of hard corals has increased from 5-11% post-bleaching to current levels of 25%, which indicates that recovery is occurring. The slow rate of recovery is likely to reflect the scale of the mortality, source and availability of coral larvae as well as post-settlement processes operating at individual reefs. Given that spawning occurs predominantly in the NE monsoon season, when winds act against the northward moving East African Coastal Current, the results from this study suggest that in the short-medium term, recovery of Kenya's reefs may be more strongly dependent on larval supply from local reefs, rather than reefs situated further south in Tanzania and Mozambique.

8.4 Directions for future research

A number of suggestions for future research on coral reproduction and recruitment are provided to guide future research in Kenya and in a wider global context.

1) The findings of this study provide a strong foundation for further studies to narrow down the timing of spawning in faviid and *Acropora* species in Kenya to the exact night and hour. Given that most corals studied had a tendency to spawn in the summer months January – March, it is recommended that *in situ* monitoring be done during this period over a range of lunar phases (particularly the 3rd lunar quarter), and across a wider range of species, genera and families, in order to provide further clarity on the degree and extent to which multispecific spawning is a feature of Kenyan reefs.

2) The ultimate factors driving spawning patterns are still poorly understood, although there is a growing body of evidence to support the ecological advantages of synchronous spawning events, in relation to enhanced fertilisation rates. A new hypothesis is presented in this thesis, which concludes that high egg fecundities in Kenyan corals (compared to other higher latitude regions) may allow corals to stagger their reproduction over 2-5 months, without incurring a significant reduction in fertilisation rates. To test this hypothesis, a number of studies examining fertilisation rates both *in situ* and in the laboratory over a range of lunar months and lunar quarters and during major and minor spawning events, should be done to determine how populations that exhibit asynchronous spawning patterns maintain species populations, and the extent to which hybridisation occurs.

3) A greater focus on documenting reproductive patterns in scleractinian corals in East Africa, southeast Asia and in the Pacific Islands is required because much of our understanding of biogeographic and global patterns of coral reproduction will remain limited without data from these regions. The methods presented in this thesis are cost-effective and are applicable to other developing countries, and do not require a complex laboratory set-up or processing.

4) The role of photoperiod and its interaction with temperature has largely been neglected in studies of coral reproduction, particularly in relation to cycles of gametogenesis. Manipulative experiments adjusting photoperiod, temperature and both of these variables concurrently may elucidate the extent to which these variables act independently or concurrently in controlling and synchronising gametogenic cycles in reef corals.

5) More studies are required to quantify reproductive patterns of scleractinian corals in equatorial regions, with greater emphasis on multi-species medium- to long-term studies using repeated sampling of tagged or marked colonies, to determine if asynchronous spawning and protracted breeding seasons are characteristics of other equatorial regions, and the extent to which different environmental variables may be driving those patterns. Studies examining spawning patterns across latitudinal gradients and across a range of species, would also provide useful data needed to answer these questions. The fairly continuous reef along the East Africa coast makes it an ideal location for undertaking a latitudinal study examining reproductive patterns from subtropical reefs in South Africa to equatorial reefs in Kenya.

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APPENDICES: PAPERS PUBLISHED