Reproductive seasonality and biannual spawning of Acropora on two
north-west Australian reefs

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ABSTRACT

Studies of coral spawning are necessary for the adequate management of coral reef ecosystems due to the environmentally sensitive nature of the coral spawning period, when millions of coral eggs are released and float to the surface of the ocean. Biannual spawning refers to the incidence of broadcast spawning corals that spawn twice annually, instead of once that is typical of most broadcast spawning species in Australia. Two species of *Acropora* that had been observed by the Australian Institute of Marine Science to have mature gametes in both October 2002 and February 2003 in the Dampier Archipelago, *Acropora samoensis* and *Acropora cytherea*, were examined to determine whether individual colonies had mature gametes twice, in both March and October, or whether individual colonies within the population were spawning at two different times. This study showed that each individual colony produced mature gametes only once, in either October or February. In *A. samoensis* 55% of colonies had ripe gametes in October, the other 45% had ripe gametes in February (n=11) while in *A. cytherea* 80% of colonies had ripe gametes in October, and 20% in February (n=5). The number of eggs per polyp was measured in both October and February in *A. samoensis*, with averages of 10.56 eggs per polyp and 10.24 respectively, indicating that there was no difference in reproductive output between the October and March spawners.

Seasonality of spawning was investigated further south at Ningaloo Reef (Coral Bay region) to determine if spawning occurred in October there also. Thirty-one species across five families were examined in October and there was no sign of mature gametes in any. The two species with mature gametes in October that were
found in Dampier could not be located in Coral Bay, so it is still not known whether they are spawning twice at Ningaloo Reef also.

Egg development was monitored from October to March in six sympatric species of *Acropora* at Coral Bay. Five species were found to have mature gametes in March, and participated in the mass spawning event 7-8 days after the full moon in March. Mass spawning was monitored and the proportion of colonies that participated in the event ranged from 83-100% among the five species. Coral spawning occurred in the last quarter lunar phase, after dark, on an ebbing tide as tides were approaching neap.

One species, *Acropora papillare*, did not spawn in the mass spawning event, but was found with mature gametes in October and January. Spawning is assumed to have taken place in December and January in this species.

Fecundity and oocyte size were measured in October, January and March in all six species and oocyte degeneration was observed between January and March in three species. Reproductive output (number of eggs per polyp and oocyte diameter) recorded in this study was compared with the figures in the World-wide *Acropora* database, which showed that reproductive output was greater at Ningaloo than elsewhere, in all four species in which comparisons could be made.
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CHAPTER 1.

INTRODUCTION
1.1 Introduction

Mass spawning events are one of the most spectacular natural phenomena observed on coral reefs, yet they are still poorly understood. The mass coral spawning phenomenon that occurs on both the east and west coasts of Australia has been of interest to scientists for decades yet relatively little is known about the complex factors that act as cues for multi-specific mass spawning in corals. Numerous theories have been proposed to explain the factors controlling mass spawning but as yet there are no definitive answers. Further experimental studies are required among different locations, physical conditions and species to gain insight into the ultimate and proximate factors that determine the timing of coral spawning (Oliver et al, 1988; Hayashibara et al, 1993).

Furthermore, not only are the cues for mass spawning shrouded in uncertainty, but in some circles the very idea of a single mass spawning event occurring off both east and west coasts of Australia, is also being challenged (AIMS Media release 2003; AIMS unpublished data, 2004). While corals on many Australian reefs do display a notable degree of synchrony, there are also exceptions. Some corals spawn many months later than the majority on the Great Barrier Reef (Willis et al., 1985; Wallace, 1985; Wolstenholme, 2004), while others have been found to spawn bi-annually on both the Great Barrier Reef, (Stobart et al., 1992) and recently at Scott reef in Western Australia (AIMS unpublished data, 2004).

An investigation into species that appear to reproduce in a manner contrary to the single annual mass spawning event that traditionally typified east and west coasts of
Australia, may provide possible clues to the ultimate factors controlling mass spawning.

1.2 Reproduction in corals

Reproduction in Scleractinian corals consists of both sexual and asexual reproduction. Asexual reproduction is employed by corals for colony growth through budding, as well as for the formation of new colonies (or clones) through processes such as fragmentation.* Sexual reproduction is the process of egg and sperm development and genetic exchange through fertilisation. Sexual reproduction is the most important part of the reproductive process because it allows genetic exchange to occur and therefore aids populations in coping with changing environmental conditions, such as El Niño events, disease and immigration of new predators.

1.2.1 Modes of sexual reproduction

Scleractinian corals display two modes of sexual reproduction: broadcast spawning and planular brooding, of which broadcast spawning is by far the dominant mode of reproduction. Broadcast spawning is a process where gametes (eggs and sperm) are released into the water column for external fertilisation and development. Planula brooding is a contrasting process where eggs are retained inside the polyp and fertilisation and development of larvae take place internally (Harrison and Wallace, 1990). Harrison and Wallace (1990) reported that a total of 157 species are

* a process in which coral fragments become detached from the parent skeleton and subsequently fuse to the substrate and continue growing
known to spawn gametes in comparison to only 50 species which are known to brood planulae.

Scleractinian corals have two distinguishable types of sexuality which are *hermaphroditism* and *gonochorism* (meaning separate sexes). Hermaphroditic coral species produce both male and female gametes within the same colony, while gonochoric species typically produce only male or female gametes in each colony (Harrison and Wallace, 1990). It was initially thought that most corals were gonochoric, however research over the past 20 years established that in fact most scleractinian species are hermaphroditic (Harrison and Wallace, 1990). Within each polyp of hermaphroditic corals, ovaries and testes can be intermingled on the same mesentery, they can develop separately but are adjacent on the same mesentery, or ovaries and testes can develop on separate pairs of mesenteries within the polyp.

1.2.2 Gametogenesis

Gametogenesis is defined as the development of eggs and sperm and can be further defined as oogenesis: the development of eggs, and spermatogenesis: the development of testes. In most species oogenesis is initiated prior to spermatogenesis, as oogenesis takes around nine months in comparison to spermatogenesis which takes only ten weeks, with both sexes maturing together in the final stages of maturation.

*Oogenesis*

In the earliest stage of oogenesis stem cells in the polyp’s gastrodermis migrate into the mesogloea where they continue to develop for nine months. There are twelve
mesenteries arranged in six bilateral pairs in the polyp, two pairs of which are incomplete and don’t usually contain gonads, and oocytes develop on mesentery pairs 1 and 2 (Wallace, 1999). In the final stages of maturation oocytes become pigmented prior to spawning (Harrison and Wallace, 1990). Mature eggs are commonly pink or red but can also be yellow, grey, green or purple (Harrison and Wallace, 1990).

A feature of oogenesis in corals is that in some species oocytes are degenerated and reabsorbed prior to spawning which may be used to provide nutrients for the remaining oocytes (Harrison and Wallace, 1990). Wyers (1985) documented 30% of advanced oocytes in each colony of Diploria strigosa (Scleractinia, Favidae) were degenerated and rapidly reabsorbed just prior to maturation. However reabsorption is still poorly understood and it is not yet known whether environmental, nutritional or physiological limitations induce oocyte degeneration during development (Harrison and Wallace, 1990).

**Spermatogenesis**

As with oogenesis, the first stage of spermatogenesis is the accumulation of cells in the polyp’s gastrodermis, which migrate into the mesogloea and develop into testes containing sperm. Testes appear initially as thin opaque sac-like structures which enlarge during spermatogenesis and are separated from one another by a layer of mesogloea (Wallace, 1999). In mature testes, sperm are arranged in a fan shape with the sperm heads arranged peripherally and the tails positioned inwards (Harrison and Wallace, 1990). In the final stages of maturation, approximately a week prior to
spawning, sperm heads condense, which often provides an index of gonad maturity and proximity to spawning.

1.2.3 **Gamete release and fertilisation**

Broadcast spawning corals usually engage in relatively short period of gamete release during an annual mass spawning period. In most hermaphroditic broadcast spawning species gametes are released from the gonads into the gastric cavity prior to spawning, and eggs and sperm are bundled together in preparation for release. These bundles become visible in the mouth of the polyp in what is known as a “setting” stage just prior to spawning (Wallace, 1985b). When the corals begin to spawn the egg-sperm bundles are squeezed slowly through the polyp mouth and upon release they float to the surface where they break apart releasing individual eggs and sperm, allowing fertilisation to take place. Gametes remain viable for fertilisation 6-8 hours after spawning after which time the unfertilised eggs begin to lyse (Harrison and Wallace, 1990; Willis *et al.*, 1997).

When corals release gametes synchronously, gametes aggregate and mix at the water surface providing the potential for fertilisation between different species thus there are mechanisms in corals that serve to reduce the incidence of hybridisation. The most commonly cited one is that corals engage in temporal reproductive isolation, which occurs on the scale of hours, where different species spawn up to 1-3 hours apart within the mass spawning period (Babcock *et al.*, 1986; Szmant *et al.*, 1997; Wallace, 1999; Fukami *et al.*, 2003), and on the scale of weeks, where species spawn weeks or months out of phase with mass spawning (Shlesinger and Loya, 1985; Babcock *et al.*, 1986; Hayashibara *et al.*, 1993; Wolstenholme, 2004).
Wolstenholme (2004) also found a substantial variation in the time taken for egg-sperm bundles to break apart, ranging from instantaneously to 4 hours, providing another source of temporal reproductive isolation between species. Babcock and Heyward (1986b) also suggested that cross-fertilisation of gametes is enhanced by a delayed ability to self-fertilise (through a self-fertilisation barrier) which exists in the gametes of some corals for several hours after spawning, and chemotactic studies have also found that some scleractinian coral release chemotactic molecules to attract conspecific sperm to reduce interspecific fertilisation (Coll et al., 1994).

1.3 Mass spawning in Scleractinian corals

Willis et al. (1985) defined mass spawning as “the synchronous release of gametes by many species of corals, in one evening between dusk and midnight” and that a mass spawning period refers to the discrete phase following a full moon during which mass spawning is observed. Oliver et al. (1988) further refined the definition of mass spawning to emphasize that mass spawning is multi-specific in nature, including species from different families and genera.

Mass coral spawning occurs on most tropical reefs around the world in regions, including Australia, Japan, the Red Sea, the Caribbean, South East Asia and the South Pacific; however the timing and synchrony of spawning varies considerably among different geographic locations, regions and latitudinal gradients. In most locations synchronous multi-specific spawning occurs periodically after the full moon over a period of several months (Shlesinger and Loya, 1985; Heyward et al., 1987; Wyers et al., 1991; Hayashibara et al., 1993; Van Veghel, 1993; Szmant et
1.3.1 Mass spawning in Australia

Coral spawning in Australia occurs over a shorter, more discrete period than in many other regions, as the major mass spawning event tends to occur largely during one month on both the east and west coasts, compared to the Red Sea for example, where coral spawning occurs over four months (Shlesinger et al., 1998). Mass spawning in Australia takes place during spring on the east coast and autumn on the west coast (Simpson, 1991). One of the theories to explain this difference in timing is Simpson’s (1985) genetic legacy hypothesis, which suggests that the breeding season of corals in Australia is an inherited legacy from ancestral corals further north. The southward-flowing currents in Australia: the Leeuwin Current on the west coast and the East Australian Current (EAC) on the east coast ‘sorters’ for exporting coral larvae down the Australian coasts, depositing larvae on the west coast in autumn when the Leeuwin Current flows strongly, and on the east coast in spring when the EAC flows strongly (made possible by the extended breeding season in the equatorial region which spans several months).

One criticism of this theory is that present day currents may not be the same as the currents that were operating thousands of years ago, therefore an explanation of evolutionary patterns that are based on today’s currents may not be correct (L. Smith pers. comment). As there is little in the literature about the evolution and past history of the currents operating at Ningaloo, it is difficult to make a decision on the
role that these currents might have as an ultimate cue for the timing of coral spawning.

### 1.3.2 Hypotheses on the ultimate causal factors of mass spawning

There are two hypotheses that seek to explain the ultimate reasons for the development and persistence of mass spawning. The first hypothesis proposes that many coral species spawn together to ‘swamp’ predators, thereby gaining the advantage of satiating predators, such as fish and filter feeders, and increasing the chance of fertilisation (Harrison *et al.*, 1984; Babcock *et al.*, 1986), however there are some objections to this hypothesis. In some regions where mass spawning occurs spawning is highly synchronous *within* species but much less synchronous *between* species, such as in Japan and the Red Sea (Hayashibara *et al.*, 1993; Shlesinger *et al.*, 1998); yet if predator satiation were the reason for synchronous spawning, high levels of synchrony between species would be expected (Oliver *et al.*, 1988; Richmond and Hunter, 1990). Furthermore Oliver *et al.* (1988) pointed out that if this were the prime factor underlying causality of mass spawning, it would suggest that seasonality plays no part in determining the timing of mass spawning and therefore mass spawning would occur at varying times between different locations of a reef region; however this does not occur (Oliver *et al.*, 1988).

The most likely hypothesis suggests that multi-specific spawning has evolved as a result of ecological and physiological parameters that constrain the optimal time of spawning to the same discrete annual periods in various locations (Oliver *et al.*, 1988; Harrison and Wallace, 1990; Babcock *et al.*, 1994). Mass spawning at a
particular time of year in various locations may have evolved to utilize a
combination of optimal environmental conditions during that season (e.g. temperature, currents, wind conditions) that serve to maximize reproductive success.

1.3.3 Advantages and disadvantages of mass spawning

The advantages of synchronisation of spawning and a discrete breeding period within a population are clear: this mode of reproduction is advantageous to each coral species by increasing the chance of fertilization and allowing for genetic exchange through cross fertilization (Harrison et al., 1984; Willis et al., 1985). The advantages of synchronous spawning between species are less clear, but are generally considered to be predator satiation and optimal environmental conditions.

One of the disadvantages of multi-specific mass spawning is the potential for large numbers of non-viable hybrids and gamete wastage (Harrison, 1985; Babcock et al., 1986; Szmant, 1986; Harrison and Wallace, 1990; Willis et al., 1997), as synchronous gamete release between species provides a potential for hybridisation which has been demonstrated to occur under laboratory conditions (Szmant et al., 1997; Willis et al., 1997; Fukami et al., 2003). However corals employ several mechanisms to reduce the incidence of hybridisation as discussed previously.

Another disadvantage of mass spawning is the risk of engaging in a single annual spawning event. This was illustrated at Magnetic Island in 1981 when a heavy rain storm coincided with spawning, resulting in the destruction of propagules on the sea surface, thereby negating the reproductive effort of those corals for the year
(Harrison *et al.*, 1984). It was again illustrated in Western Australia in 1993 when atypical environmental conditions resulted in coral spawning slicks becoming trapped in Coral Bay on Ningaloo Reef, causing hypoxia and the mass death of newly fertilised coral larvae, as well as the mature corals themselves (Simpson *et al.*, 1993).

### 1.3.4 Environmental factors co-related to the time of spawning

In any discussion about the factors that influence the timing of coral spawning, a distinction must be made between ultimate cues and proximate cues. Ultimate cues are the evolutionary reasons that coral spawning occurs when it does – factors that guide spawning to occur at certain times of the year, such as seasonal temperature or current patterns (Campbell, 1974; Oliver *et al.*, 1988).

Proximate cues on the other hand are fine scale environmental signals, such as lunar cycles, or tidal regimes that synchronise spawning to occur on the same night (Oliver *et al.*, 1988). A number of environmental factors have been suggested to have an influence on both the season (ultimate cues) and synchronisation (proximate cues) of mass spawning which are discussed below, however the evidence surrounding many of these factors is still inconclusive, despite 25 years of investigation.

*Temperature*

Temperature has been attributed to playing both a proximate and an ultimate role in defining the timing of coral spawning, as well as synchronising it. Seasonal variation in sea temperature is frequently cited as the most significant ultimate cue
influencing the season of coral spawning in scleractinian corals (Kojis and Quinn, 1981; Van Moorsel, 1983; Harrison *et al.*, 1984; Willis *et al.*, 1985; Babcock *et al.*, 1986; Babcock and Heyward, 1986) as corals would be more likely to spawn when the water is warm to increase the rate of larval development and survival (Oliver *et al.*, 1988; Mendes and Woodley, 2002).

Some scientists have suggested that an increase in the water temperature prior to mass spawning also acts as a proximate cue synchronising the timing of coral spawning (Kojis and Quinn, 1981; Babcock *et al.*, 1986; Hayashibara *et al.*, 1993) such as Hayashibara *et al.* (1993) who postulated that corals may become sensitive to temperature when their gametes reach maturity and that an increase in temperature acts as a proximate cue to induce spawning.

On the other hand, Simpson (1991) proposed that temperature is *not* a universal proximate cue, due to the evidence from Western Australia, where sea temperatures along the Western Australian coastline are highly variable (due to the varying influence of the Leeuwin current) yet mass spawning occurs synchronously between regionally separate reefs from Scott Reef to the Abrolhos Islands despite more than two months difference in the timing of seasonal temperature minima between the two regions (Babcock *et al.*, 1994).

*Tides*

Coral spawning has been observed to consistently occur during the same tidal phase year after year in areas where mass spawning has been observed, and thus tides
have also been credited with synchronising coral spawning and providing a cue for gamete release (Simpson, 1985; Babcock et al., 1986; Hayashibara et al., 1993).

Marchant (1987) postulated that temperature, seasonal currents and winds are all subject to inter-annual variation and therefore have a negligible effect on the timing of spawning, and that the highly regular, highly synchronous mass spawning period is related to tides because they are highly regular and predictable themselves. Babcock et al. (1986) suggested that spawning during periods of low neap tides coincides with periods of low water volume and low water motion, which have the advantage of reduced dispersal of gametes thereby increasing the chance of fertilisation. Hayashibara et al. (1993) suggested on the other hand, that the dispersal of gametes might be a more important factor than fertilization, because corals in Japan spawn on a high tide. Simpson (1988) suggested that spawning on an ebbing tide would facilitate the flushing of propagules to deeper offshore waters and may also be required to escape the many predators found in shallow water reef communities.

**Lunar period**

For many years authors have documented a correlation between the mass spawning period and lunar phase, with most mass spawning events reported to take place after the full moon (Babcock, 1984; Harrison et al., 1984; Simpson, 1985; Wallace, 1985b; Babcock et al., 1986; Richmond and Hunter, 1990; Hayashibara et al., 1993; Baird et al., 2000; Guest et al., 2002). Lunar period has often been suspected of acting as a proximate signal cuing gamete release and synchronising spawning, however while spawning is highly correlated with lunar phase in Australia, it is less
so in Japan (Hayashibara et al., 1993), and much less so in the Red Sea, where there is little correlation between spawning and lunar phase (Shlesinger and Loya, 1985).

As lunar cycles and tidal cycles are linked, it is difficult to evaluate which of these is essentially responsible for synchronising coral spawning. Babcock et al. (1986) proposed that the lunar cycle may act as a calendar for corals, to impel spawning to occur during a particular tidal rhythm, i.e. the tidal rhythms are of ultimate importance in determining the timing of coral spawning and corals use moonlight simply as the proximate signal to predict the tidal regime.

**Onset of darkness**

Most corals spawn at night between dusk and midnight and it usually occurs at a specific time in each population, which is generally consistent from year to year (reviewed in Harrison and Wallace, 1990). Laboratory experiments manipulating light and dark cycles of broadcast spawning corals have illustrated a clear effect on the time that colonies release gametes (Babcock, 1984; Hunter, 1988), thus the onset of darkness has been attributed to being one of the proximate cues synchronising spawning.

Hayashibara et al. (1993) suggested that spawning is induced by a dark period; Oliver et al. (1988) suggested that coral spawning takes place at night to reduce the exposure of the gametes to predators; Babcock (1980) suggested that spawning at night minimises exposure of gametes and newly fertilised larvae to the sun. However some species have been recorded spawning during the afternoon or before sunset (Kojis and Quinn, 1981; Tranter et al., 1982; Babcock et al., 1986; Krupp et
There are no conclusions yet about the role darkness plays on the timing of spawning. Seemingly it provides an advantage to corals to spawn in the darkness, as most corals choose to do this, nevertheless it is not understood why some corals spawn during daylight and what advantages this might provide for certain species.

**Currents**

There are some hypotheses on the role that currents might play on influencing the timing of mass spawning in Australia, but there is relatively little information from the rest of the world. Simpson (1988) observed that mass spawning on the GBR and in WA coincides with periods of wind changes and thus changes in large scale water circulation patterns, and suggested that this might be significant in the evolution of mass spawning in Australia. Similarly, Taylor and Pearce (1999) suggested that the interaction of currents at Ningaloo Reef during March/April could act as an ultimate cue for dictating the spawning period, because the hydrodynamics during the mass spawning period are responsible for maintaining a large proportion of the coral spawn within the Ningaloo reef system, providing an evolutionary reason for spawning in March at Ningaloo Reef.

**Rainfall**

Mendes and Woodley (2002) suggested that coral spawning is timed to avoid months of high rainfall, which have the potential to damage gametes and suggested that in each region where coral spawning occurs, it never occurs during months of high rainfall. However the weather patterns in Dampier do not concur with this theory as coral spawning takes places in March, which is the month with the second highest annual rainfall (Bureau of Meteorology, 2005).
Solar insolation

Penland *et al.* (2004) proposed that timing of coral reproduction is related to solar insolation, which is the electromagnetic energy incident on the surface of the Earth. They suggested that the onset of gametogenesis and synchronous spawning is related to solar insolation, therefore acting as an ultimate cue for the timing of spawning. They reported that solar insolation cycles coincide with coral reproductive cycles for the entire Western Pacific Rim, therefore suggesting that solar insolation should be considered as one of the major variables driving coral reproductive cycles.

1.3.5 The incidence of biannual spawning

Colonies of broadcast spawning species usually have an annual gamete cycle and spawn once a year (reviewed in Richmond and Hunter, 1990 and Harrison and Wallace, 1990). However some studies have found broadcast spawning species with colonies that have two gamete cycles per year culminating in spawning twice a year, which is known as biannual spawning.

Szmant-Froelich *et al.* (1980) showed that colonies of a broadcast spawning species that spawn once a year in their natural environment, are capable of spawning year round if kept under a constant temperature and feeding regime in the laboratory (Harrison and Wallace, 1990). Several scientists subsequently documented examples of biannual spawning in the field. Oliver *at al.* (1988) and found evidence of two gamete cycles in some colonies for several broadcast spawning species in Madang, Papua New Guinea. They reported that in 16 colonies of five different
species ripe gonads were present during September to November and again in the same individuals in January and March. Stobbart et al. (1992) found that tagged colonies of three species of *Montipora* were observed to spawn twice a year at Magnetic Island in Queensland and all colonies that spawned in March also did so in October. The Australian Institute of Marine Science (AIMS) reported the occurrence of two mass spawning events each year at Scott Reef in Western Australia: a primary spawning occurring during March at the same time as other corals in WA, and a secondary spawning event occurring in October, at the same time as on the Great Barrier Reef (AIMS unpublished data, 2004). However it was not reported whether individual colonies were spawning twice, or whether different individuals were spawning in March to October.

It is not clear why some broadcasting species of coral are able to sustain two gamete cycles per year. These differences may be related to the way in which different species allocate their resources for reproduction and growth. Biannual spawning increases the likelihood of genetic recombination and facilitates speciation within sympatric environments, promoting high coral diversity (Penland, *et al.* 2004). The capacity to spawn twice, and at a second time when other species are not spawning, poses an obvious advantage for the species concerned – if availability of substrate is a limiting factor, competition for space between species will be reduced (Stobbart *et al.*, 1992). Spawning twice a year also reduces the risk of catastrophic events destroying a species’ annual reproductive output effort (Stobbart *et al.*, 1992).

Evidence of biannual spawning is important to studies on the allocation of resources to growth and reproduction, as well as larval recruitment to coral reefs (Stobbart *et al.*...
al., 1992). However more importantly, studies of biannual spawning may provide vital clues to understanding and identifying proximate and ultimate cues controlling the mass spawning phenomenon; therefore further research should be encouraged into species that appear to be spawning twice.

1.4 Fecundity

Measures of fecundity such as the number of eggs per polyp can provide a useful index of reproductive effort and are therefore a useful indicator of the health of a coral (Kojis and Quinn, 1984; Harrison and Wallace, 1990). Reproductive effort is the most commonly used estimate of fecundity and is usually expressed as the number of eggs per polyp, while size of oocytes is measured to identify the stage of maturity (Wallace, 1985b; Harrison and Wallace, 1990).

1.4.1 Temporal and spatial variation in fecundity

Fecundity varies over the lifetime of a coral. Reproduction is delayed in corals, which is thought to promote greater reproductive success over the life time of the coral by providing an initial allocation to growth thereby decreasing infant mortality (Harrison and Wallace, 1990). Polyp fecundity normally increases with age through an increase in the number of egg bearing mesenteries or the number of eggs per mesentery, or both. Several studies have demonstrated that smaller colonies produce fewer eggs per polyp than larger members of the population (Harrison and Wallace, 1990; Sakai, 1998)

Fecundity also varies spatially within the colony and polyps in growing branch tips are often sterile (known as the sterile zone). Fecundity has also been observed to be
reduced in peripheral tissues, and marginal polyps have been shown to be smaller in volume and have a lower number of eggs than non-marginal ones, probably acting as a buffer against competition and grazing which are likely to be heavier at the colony edge (Sakai, 1998).

Hall and Hughes (1996) also found that the morphology of a species plays a crucial role in determining reproductive output. This is due to some morphologies being more susceptible to physical damage than others, hence the morphology of a coral dictates the trade-off between fecundity and mortality.

1.4.2 Factors affecting fecundity

Allocation of resources
The allocation of resources is an important factor affecting fecundity, as resources must be shared between a variety of life functions such as growth, reproduction and repair. For example, *Acropora palifera* (a brooding scleractinian coral) was studied on Heron and Lizard Islands in Queensland and in Papua New Guinea (PNG), and it was found that colonies of *A. palifera* reproduced once in spring on Heron Island, compared with year round in PNG and Lizard Island (Kojis, 1986). It was suggested that the reason for this was because Heron Island is exposed to lower temperatures than PNG or Lizard Island, therefore colonies on Heron Island had evolved a life history strategy that allocates more energy to growth in a less optimal environment, and less energy to reproduction.

Coral symbionts
As most of the energy in corals is derived from the products of photosynthesis from their algal endosymbionts (zooxanthellae) (Sorokin, 1995), any factors that affect
the ability of the zooxanthellae to photosynthesise, will affect the energy output
received by the coral and thus fecundity. Studies in which fecundity has been
monitored over several years have shown that fecundity can vary considerably from
year to year depending upon environmental conditions (Wallace, 1985b; Stobart et
al., 1992). Additionally different clades of zooxanthellae among corals have been
shown to provide varying levels of nutrients to their hosts which may also have the
potential to affect fecundity (Little et al., 2004).

**Stress**

A variety of natural and human disturbances can cause stress to corals and result in
diminished fecundity. Sediment resuspension is an important factor affecting
fecundity as it increases turbidity thus decreasing the overall energy available for
photosynthesis (Jokiel, 1985; Tomascik and Sander, 1987). Sedimentation results in
an energetic cost to the corals in that it must cleanse its surface, resulting in a
diversion of resources into maintenance and less energy available for reproduction
(Kojis and Quinn, 1984).

Several studies have demonstrated that oil and other petroleum products in the
water can cause significant reduction in the size of gonads and the number of
ovaries per polyp (Loya, 1976; Rinkevich, 1979; Guzman and Holst, 1993), and can
also inhibit fertilisation (Negri and Heyward, 2000). Nutrient enrichment also
effects fecundity as not only can eutrophication cause reduced light levels for
photosynthesis, increased nutrient levels can also give fast growing organisms such
as algae, tunicates, bryozoans and sponges a competitive advantage over slower
growing corals and can dominate available substrata, preventing coral larvae from settling (Richmond, 1987; Birkeland, 1997).

A number of environmental disturbances including lowered water salinity, unusually low tides, high sea temperature and low irradiance can cause a reduction in egg volume (Kojis and Quinn, 1981). Of these, the effects of high water temperature have been most extensively studied due to the incidence of coral bleaching worldwide, and this has shown that high temperatures significantly reduces the numbers of eggs per polyp (Kojis and Quinn, 1981; Hoegh-Guldberg, 1999).

Damage and fragmentation affect reduce fecundity because these processes shift energy allocation from reproduction to regeneration (Lirman, 2000). Szmant-Froelich et al. (1985) also showed that colony size affects the ability of some corals to reproduce and frequent fragmentation can severely reduce the reproductive output of coral populations.

1.5 North-west Australian coral reefs

The customary eastern boundary current off the west coast of continents throughout the world is a northward flowing cold current, often accompanied by upwelling at coastal edges, due to the Coriolis force and the trade winds (Hatcher, 1991). On the west coast of Australia however, the prevailing current is a warm southward flowing current known as the Leeuwin current, which is a stream of warm, low salinity, low nutrient tropical water flowing southwards at a relatively high velocity
(0.1-0.4 ms⁻¹) along the continental shelf of Australia (Hatcher, 1991). The source of the Leeuwin current is broad (400 km) and shallow (50 m); its origin is in the area to the north-west of North West Cape and it flows along the coastline past Cape Leeuwin and into the Great Australian Bight (Cresswell, 1991; Holloway, 1995). Its waters are sourced from the Pacific-Indian Throughflow (PIT) to the north and Eastern Gyral Current (EGC) to the west. The PIT carries Pacific Ocean water to the region through the Indonesian Archipelago, while the EGC Indian Ocean water into the region eastward off the North West Cape (CALM, 2004). It is due to the presence of the Leeuwin current that coral reefs are found off the west coast, as it is responsible for the transport of northern tropical waters which modify the water temperature such that the conditions are suitable for coral growth in what would otherwise be temperate conditions (LeProvost et al., 2000).

Well developed, extensive coral reefs occur at a number of locations along the continental shelf of WA, from as far north as Scott Reef to as far south as the Houtman Abrolhos (Hatcher, 1991).

1.6 The Dampier Archipelago

1.6.1 Physical and Biological Structure

The Dampier Archipelago lies off the Pilbara coast of north west Western Australia (20°40’ S; 116-117° E) and is comprised of over 40 islands. It lies in the biogeographical overlap between the Tropical Indo-Pacific and Warm Temperate Oceanic Zones (Pearce et al., 2003), though the marine biota is overwhelmingly tropical (Wells and Walker, 2003). The coral reefs on the islands in the Archipelago
are a relatively young 6-8,000 years old; the outer islands are remnants of limestone
ridges while the rest of the Archipelago is on a gently rising subtidal plain with a
depth of 5-20 m. The major river in the region is the Fortescue River, which flows
most strongly during summer/autumn due to cyclone-related rainfall, which can
often result in large volumes of sediment-laden water entering the Archipelago
(Pearce et al., 2003).

1.6.2 Climate
Dampier lies in the arid tropics, where average rainfall is 250mm but erratic, with
most rain falling between January and May as a result of depressions or tropical
cyclones, of which there are an average of 1.4 per year (Wells and Walker, 2003).
Sea surface temperatures range from 22° C in winter to 30° C in summer, while
wind patterns are at their weakest and most variable around April and August
(Osborne et al., 2000).

1.6.3 Hydrodynamics
The tides are semi-diurnal (two highs and two lows each day) with one tide being
slightly larger than the other, with maximum speeds occurring at mid-tide and slack
water coinciding with high and low tides. There is a well-defined spring-neap lunar
cycle and the largest tides of the year occur in April (Pearce et al., 2003). The
Leeuwin Current flows along the outer shelf of the Archipelago and is strongest
from February to July, although periods of strong south-westerly winds in summer
can cause short term reversals of the current, generating eddies and weak upwelling
on the outer shelf (Pearce et al., 2003). The major forces driving water circulation
in the Dampier Archipelago are large scale ocean circulation (from the Leeuwin Current), tides, local winds and continental shelf waves.

Water quality is highly variable in the Archipelago; levels of sedimentation are periodically high after storm activity, and relatively restricted flushing in the Archipelago can lead to variations outside normal oceanic ranges in water quality (Pearce et al., 2003).

1.6.4 Mass spawning in Dampier

Multi-specific mass spawning takes place in the Dampier Archipelago after the full moon in March in most years (Simpson, 1985; 1988). Mass spawning occurs mainly around the third quarter of the moon on neap, nocturnal, ebb tides, with Simpson (1991) documenting 102 species spawning during the discrete mass spawning period.

1.7 Ningaloo Reef

1.7.1 Physical and Biological Structure

The Ningaloo Reef Tract is a fringing barrier reef that extends some 280km parallel to the Western Australian coastline from 21°30’ to 24°S and along 113°30’ E (Simpson et al, 1993; Sanderson, 1997; D’Adamo & Simpson, 2001). It is the largest fringing coral reef in Australia and the only extensive coral reef in the world fringing the west coast of a continent (Taylor and Pearce, 1999). The reef forms a discontinuous barrier enclosing a lagoon which varies in width from 200 m to 7 km, with its maximum width near Coral Bay (Hearn et al, 1986; Hearn and Parker,
1988; CALM, 2004). Gaps regularly intercept the main reef line resulting in elongated reef segments backed by a shallow sedimentary lagoon, which has a mean depth at AHD of approximately 2 m, interspersed with patch reefs and nearshore platform reefs (D'Adamo and Simpson, 2001; CALM, 2004).

Seismic profiling and a coring and dating program indicate that the reef ages 115-120,000 years, and suggests two major periods of growth: during the last interglacial (120,000 years ago) followed by growth during the Holocene (10,000 years ago) (Sanderson, 1997; Collins et al., 2000).

Ningaloo is a complex and unique ecosystem with high species diversity. It is at the southern edge of the tropical belt of the Indo-Pacific faunal region and in the Western Australian Overlap zone where there is a biogeographic transitional zone between the tropical fauna and the temperate fauna of the Southern Australian Faunal Region (CALM 2004). Many of the tropical species are at the southern limit of their geographical range while some temperate species, such as the Western Rock Lobster, are at the northern limit of their range (CALM, 2004).

The physical structure of Ningaloo Reef is characterised by cross shelf range of habitats from intertidal reef environments, lagoonal and fringing reef communities to offshore oceanic environments which support 200 species of coral, 600 species of mollusc and 500 species of fish (CALM 2004).
1.7.2 Climate

The climate of the area is arid with an annual rainfall of 200-300 mm and an annual evaporation of 2700 mm, and experiences a considerable annual variation in climate (CALM, 2004). During most of the year the prevailing winds are from the south-east during the night, and are replaced by stronger south-southwesterly sea-breezes in the afternoon. During April the prevailing winds swing to the east delaying the onset of the south-westerly sea breeze and giving calm conditions during most of the day (Taylor and Pearce, 1999; D'Adamo and Simpson, 2001).

Ningaloo reef is located just north of the transitional zone from the South Western Australian tidal zone (diurnal and micro-tidal) and the North Western tidal zone (semi-diurnal and macro-tidal) (CALM 2001, 2004). Tides at Ningaloo are semi diurnal with spring and neap tides occurring 2-4 days and 8-10 days respectively, after a full or new moon (Simpson and Masini, 1986).

1.7.3 Hydrodynamics

Ningaloo reef is a classic fringing reef where surf coming over the reef brings an inundation of richly oxygenated water into the lagoon which returns to the open ocean via gaps in the reef (Taylor and Pearce, 1999). The Leeuwin current places warm tropical water onto the reef shelf where it enters the lagoon via ocean/lagoon exchange processes. In addition to the Leeuwin current is another current known as the Ningaloo current, which is a cool northward counter-current which predominates on the reef front from September to mid-April, driven largely by the south east trade winds (Taylor and Pearce, 1999). During spring/summer the Ningaloo current flows close to the coast forcing the Leeuwin current to flow
further offshore than it normally does, and these opposing currents generate a recirculation of water in the region.

Numerical modelling of broad scale circulation patterns by CSIRO marine research suggest that on a regional scale, shelf currents connect Ningaloo Reef with Dampier Archipelago and Montebello/Barrow Islands, and that Ningaloo Reef may act as a source for recruitment to the northern reefs during summer and as a sink for recruitment from the northern reefs during autumn (D’Adamo and Simpson, 2001). Travelling times between these reefs are predicted to be in the order of tens of days (D’Adamo and Simpson, 2001).

1.7.4 Mass spawning at Ningaloo

Mass spawning at Ningaloo Reef generally takes place 7-9 nights after the full moon in March, on neap, nocturnal ebb tides (Simpson et al., 1993; Smith, 1993; Stewart, 1993). In most years minor spawnings also occur after the February and April full moons, and some authors have also observed a small percentage of colonies spawning after the new moons from March-May (Stewart, 1993).

1.8 The genus Acropora

The family Acroporidae is comprised of four genera, of which Acropora and Montipora are the two largest genera of the Scleractinia order. Acropora is the most important genus of the Scleractinia, having the greatest number of species and the greatest abundance on most Indo-Pacific reefs, with 364 known species (Veron and Wallace, 1984). Many studies of coral spawning events have focused on the genus
Acropora because it is a large genus exhibiting a diverse array of morphologies and distributions and large numbers of Acropora live sympatrically in many localities. Acropora is considered a very old genus and a good evolutionary model (Frank and Mokady, 2002).

1.8.1 Characteristics of Acropora

Assemblages of Acropora are characteristic of mid to outer-continental shelf reefs in shallow reef localities with high energy levels (Wallace, 1985b; Wallace, 1999). Their location relative to other coral assemblages is correlated with strong water movement, good light penetration and clear water (Wallace, 1985, 1999). All Acropora species are hermaphroditic with male and female gonads developing within the same polyp but on separate and specific mesenteries.

In recent years, studies of the timing of mass spawning in many species of Acropora have revealed evidence that indicate that there is much variability within the genus on spawning behavior. Studies from the Great Barrier Reef, Papua New Guinea and the Solomon Islands showed a great deal of plasticity in spawning synchrony within this genera; while many species in these three locations did release gametes during the mass spawning periods, others did not, instead spawning several months outside the mass spawning period (Wolstenholme et al., 2003) indicating that some asynchrony in the release of gametes between colonies may be a feature of the reproductive biology of Acropora (Wallace, 1985b; Oliver et al., 1988; Baird et al., 2000).
1.9 The aims of this project

Samples of four Acropora species: Acropora millepora, A. hyacinthus, A. samoensis and A. cytherea, were collected from the Dampier Archipelago by the Australian Institute of Marine Science (AIMS) during October 2002, February 2003 and October 2003. It was observed that during October 2002 and 2003 many of the samples collected contained pink eggs, an obvious sign that they were about to undergo gamete release. When each colony was sampled in February 2003, many of the colonies contained large white eggs, indicating that, again, they contained mature gametes.

The first element of this study was to examine the samples collected from the Dampier Archipelago by AIMS, and investigate the nature of the observed biannual spawning. The aims were two-fold: firstly to establish whether each colony was spawning twice a year or whether different colonies were spawning at different times of the year, and secondly, to determine whether or not there was any difference in the reproductive output between the colonies spawning in October and March.

The second element of this study was to investigate seasonality of spawning further south at Ningaloo reef. The first aim was to determine whether the two species found to be spawning twice in the Dampier Archipelago (A. samoensis and A. cytherea) were also spawning twice at Ningaloo, and also to investigate whether there were any other species potentially spawning during October at Ningaloo. The second aim was to monitor the mass spawning event at Ningaloo and the conditions under which it occurred, and the third aim of the investigation at Ningaloo was to
monitor egg development and production in each of the selected species to
determine whether or not oocytes were being absorbed and to measure fecundity at
Ningaloo Reef in order to compare results from elsewhere.
CHAPTER 2.

MATERIALS AND METHODS
2.1 Introduction

The data presented in this thesis involved the collection and examination of coral samples from two locations, and at various times throughout the year. The samples were decalcified and dissected to examine the gonads in individual polyps in order to gauge the size and number of developing gametes. This work provides a means of estimating stage of development and proximity to spawning, and provides a basis for comparisons between sites, and some understanding of the factors determining spawning.

2.2 Dampier field methods

2.2.1 Study site
The samples analysed in this study were collected from the Dampier Archipelago by the Australian Institute of Marine Science (AIMS) during 2002-2003. The study site was located at Elphinks Knob, (20°28’S, 116°37’E) in the outer region of the Archipelago, approximately 18 km off shore, in a lagoon on the north-east end of Rosemary Island (Figure 1).

2.2.2 Sampling regime
Colonies were initially tagged in October 2002. A 30 m transect was laid out, colonies of Acropora samoensis, Acropora millepora, Acropora hyacinthus and Acropora cytherea were tagged along this transect and samples taken from each tagged colony. The site was revisited and the tagged colonies sampled again in February 2003, and once again in October 2003. Once collected the samples were preserved in 10 % formalin/seawater where they remained until analysis during this
study. All samples were decalcified and dissected (see laboratory methods) and examined for the presence of eggs.

Figure 1. The location of the AIMS study site in the Dampier Archipelago (taken from Pearce et al. 2003)
2.3 Ningaloo field methods

2.3.1 Study site
This study was conducted in the southern region of Ningaloo Reef, near Coral Bay, which is located approximately 1200km north of Perth (Figure 2).

The study site was located south of Lottie’s Lagoon (S23°10’348, E113°45’406) on the reef flat of a large barrier reef (Figure 3). The outer reef front was approximately 300m from the study site; the site was exposed and there was a strong tidal current across the reef flat. The substratum on the reef flat was solid and comprised of limestone skeleton from old reef (with new colonies of live coral growing on top), and species of Acropora dominate the reef flat.

The search for a study site was conducted south of Monck’s Head for one week, during which time manta tows were conducted all around the lagoon, searching for Acropora samoensis and Acropora cytherea, the two species found to be spawning in Dampier during October. This site was finally chosen for the study because it was located outside the CALM sanctuary zone and there was suitable diversity and replication of Acropora species. It was also thought that one of the species at this site was A. samoensis, however this was later ruled out when the species were formally identified.
Figure 2. Ningaloo Reef locality showing the Ningaloo Marine Park boundaries and the relative location of Coral Bay within the Marine Park (taken from Commonwealth of Australia, 2002)
2.3.2 Sampling regime

Two transects were set up on the reef flat, labeled shallow and deep. The shallow transect was situated on the edge of the reef flat (just before it dropped off into the sandy lagoon on the eastern side) in very shallow water: 30cm to 1m, and parts of it were often exposed at very low tide (Figure 4). The deep transect was located subtidally in 1.5-2.5m of water in the lagoon approximately 10m east of the blue-green transect. It was in a sand patch and was more protected than the shallow transect (Figure 5).

Figure 3. The location of the study site relative to Coral Bay
Figure 4. The study site at low tide showing part of the reef exposed. The shallow transect was located on the reef flat, while the deep transect was located on the lagoon floor (photo N. Rosser).

Figure 5. The deep transect on the lagoon floor, showing tagged colonies (photo N. Rosser)
Along each transect, ten replicate colonies of each *Acropora* species on the transect were marked with small plastic tags (Figure 5). Each tag was labeled with a number written in permanent ink and was attached with a cable tie that was looped over a branch of the colony and tightened (Figure 6). All colonies of the same species were separated by at least 3 m to minimize the likelihood of sampling clonemates.

![Figure 6. Acropora millepora. Plastic tags were attached to all colonies with cable ties (photo N. Rosser)](image)

Each colony along the two transects was sampled in October 2004, January 2005 and March 2005. Tagged colonies were 30 cm or more in diameter to ensure not only that the colony was of reproductive age (Wallace, 1985b) but also that it was large enough to be able to withstand repeated sampling. Samples were removed using a small chisel; the chisel was inserted between the branches of the colony and a small piece approximately 4 cm long (long enough to avoid the sterile zone at the tip of the branch). Samples were taken from the inner region of each colony to avoid the peripheral non-reproductive zone at the perimeter of the colony, described by Heyward and Collins (1985). On the second and third field trips in January and
October, some colonies had died, or tags had come off in which case the colony was classed as ‘missing’.

The surface area of each colony was also measured in order to compare the size of colonies. The length and breadth of the crown of the colony was measured with a steel rule and recorded. As the species in this study all have a corymbose growth form, length and breadth of the crown could be measured easily. The area of an oval was used to calculate area:

\[
\text{Area (cm}^2\text{)} = \pi(\frac{1}{2}L) \times (\frac{1}{2}B)
\]

Equation 1

where \(L\) = length and \(B\) = breadth of the crown of the colony

2.3.3 Monitoring of mass spawning

It was predicted that spawning would occur 7-9 days following the full moon in March, from previous studies conducted on coral spawning at Ningaloo Reef (Marchant, 1987; Simpson et al., 1993; Smith, 1993; Stewart, 1993).

The technique for predicting spawning date described by many authors was used, whereby oocyte colour change is used as an indicator for proximity to spawning (Babcock, 1984; Harrison et al., 1984; Wallace, 1985b; Harrison and Wallace, 1990; Baird et al., 2001).

Tagged colonies were broken open on the 29th March, three days after the full moon to check for the presence of pigmented eggs. Pink eggs were seen on this date.
(Figure 7) and as such, trips were made to the study site each evening thereafter to monitor spawning in the field.

Each night snorkellers entered the water just after sunset and swam up and down the two transects looking for signs of setting (the appearance of pink bundles in the polyp mouth) at intervals of approximately 20 minutes, until 11 pm. During the nights of mass spawning, once the colonies were observed setting snorkellers and divers remained in the water monitoring the tagged colonies and recording which of the colonies released gametes and the time of gamete release.

![Broken branch of *Acropora digitifera* on the 29th March, showing pink and white eggs (photo N. Rosser)](image)

Figure 7. Broken branch of *Acropora digitifera* on the 29th March, showing pink and white eggs (photo N. Rosser)

Following mass spawning, on the tenth day after the full moon all tagged colonies were broken open to check for the presence of eggs. Samples were also collected from each colony and fixed in 10% formalin, decalcified, dissected, and examined.

* On the fifth and sixth nights after the full moon the wind and rain were too strong to take the boat to the study site
under the stereo microscope, as it was difficult to differentiate between white eggs and mesenteries in the field.

2.3.4 Physical measurements recorded during the coral spawning period

*Tides*
The tidal measurements that were used in these results were the actual readings from Carnarvon, provided by the Department for Planning and Infrastructure (DPI, 2005). Simpson and Masini (1986) stated that the tidal regime at Coral Bay is close to the tidal regime at Carnarvon and therefore the use of the data from Carnarvon is valid. The reason that the actual values from Carnarvon were used and not the predicted tidal measurements from Coral Bay, which are also available, is because there was a tsunami in Indonesia on the 28th March 2005, the effects of which were felt in Coral Bay. This therefore had the capacity to effect the predicted tidal measurements, so the actual tidal measurements from Carnarvon were likely to be a more accurate measure.

*Temperature*
A temperature logger was situated in the lagoon approximately 1.5 km north of the study site and recorded temperature every two hours throughout the coral spawning period. Tennille Irvine (PhD student, Murdoch University) provided this data.

2.3.5 Random Sampling
Random sampling of species from a variety of families was conducted on the reef flat near the study site during October, (Figure 8) to determine whether any different species from the ones that were tagged had mature/ripe gametes during October to gauge whether spawning was imminent. Most of the species growing in
the vicinity of the transect were sampled: colonies were broken open and examined in the field for the presence of eggs and recorded accordingly. Colonies were identified to genus level where possible, though in some cases only family level.

During the March field trip, random sampling was conducted only on colonies of the six *Acropora* species in this study, to ensure that the tagged colonies on the transects were spawning at the same time as other colonies of the same species within the region. Numerous colonies of the *Acropora* species were broken open and examined for the presence of mature pigmented eggs on the days prior to the observed mass spawning event, up to one square kilometre from the study site (Figure 8).

**Figure 8.** The area to the north and largely to the south of the study site in which the random sampling was conducted. The area of the rectangle is approximately 1200m by 600m.
2.4 Fecundity sampling regime

2.4.1 Dampier
Colonies of *Acropora samoensis* and *Acropora cytherea* were sampled in October 2002, February 2003 and October 2003. The fecundity of each of these colonies was compared to determine whether there was a difference in the reproductive output between the March spawning and October spawning colonies. Due to the small sample size in October 2003 (as many colonies had died) only the data from October 2002 was used for comparison with March.

While colonies of *Acropora cytherea* were also found to have ripe gametes in both October and March, there were only five colonies sampled, four of which had ripe gametes in October and the other had ripe gametes in March. With such a small data set a comparison of fecundity between October and March was not feasible so this data was not used.

2.4.2 Coral Bay
Each colony along the two transects were sampled in October 2004, January 2005 and March 2005. Fecundity and oocyte diameter were measured in each sampling period, and in this way a record of the gametogenic cycle and fecundity was obtained for each individual colony. During the March sampling regime, all colonies were sampled four days prior to the mass spawning event to obtain the maximum oocyte diameter for each species.
While monthly sampling of the colonies may have provided a more comprehensive record of increasing oocyte diameter and would have provided more specific information on the timing of gamete release in some species, sampling every month ran the risk of annihilating the colony, or stressing it so much that its reproduction may have been affected. Funding was also insufficient to take monthly samples, and it was decided that two-month intervals were adequate to obtain the desired information.

2.4.3 Dampier and Coral Bay comparison
The Australian Institute of Marine Science (AIMS) collected samples of *Acropora millepora* from Ningaloo Reef and the Dampier Archipelago a few days apart in February 2003. As these samples were collected at the same time in the same year a comparison could be made between the fecundity of this species at two different locations. Samples from 11 colonies from each location were examined, and the number of eggs per polyp and the size of the eggs were compared between the colonies at Ningaloo and Dampier.

The samples of *A. millepora* from Ningaloo were collected from the large bommie at the Lotties Lagoon dive site (near the present study site). The samples from Dampier were collected from Elphinks Knob at the north-eastern end of Rosemary Island.
2.5 Laboratory methods

2.5.1 Decalcification and dissection of coral polyps
Samples were fixed in 10% formalin/seawater for a minimum of one week. They were then transferred to an acid solution for decalcification. An acid solution of 5% Formic acid was used to decalcify the samples initially and the solution changed every 24 hours, following standard methods described by Wallace (1985b). Using these methods the decalcification took approximately 4-5 days for the skeleton to dissolve, although different species decalcified at different rates. During the course of decalcification a solution of 5% HCL was also used dependent upon which acid was available, with no noticeable change in the result on the decalcified tissue, or on the length of time taken to decalcify the samples. Formalin was not added to either acid solution (Formic or HCL) despite its common use by others during decalcification, as Drury and Wallington (1967) state that the use of formalin during decalcification with acid is not necessary. The samples in this study did not appear to be harmed in any way through the absence of formalin in the decalcification process.

After decalcification, samples were transferred to 70% ethanol where they remained for the duration of this project. Samples were dissected under a stereo microscope lit by a fibre optic light source. The methods for dissection were followed directly from Wallace (1985b) as follows. The decalcified sample was placed on a wax dissecting dish (Figure 9a) and the stomodeum was severed down the vertical axis of the central branch/branches using a steel pin, and then gently teased apart.
The opened stomodeum was then pinned to the wax with steel pins, displaying each polyp’s internal structure (Figure 9b). The dissected sample was then examined under the stereo-microscope so that the oocytes could be counted (Figure 10). Often the mesenteries were encased in a cone-shaped sac and the sac was gently teased apart to reveal the egg-bearing mesenteries within (Figure 11) so that an accurate count of the number of eggs per polyp could be made (Figure 12).

**Figure 9.** (a) Decalcified sampled of *Acropora* (b) dissected sample of *Acropora* displaying the internal structure
A sample of 5 polyps per colony were counted, and the number of oocytes per polyp recorded. Polyps in the post sterile zone (Heyward and Collins, 1985; Wallace, 1985a) were avoided and polyps located at the base of the branch (closest to the inner region of the colony) were chosen, as marginal polyps have been shown to be smaller in volume and have a lower number of eggs than non-marginal ones (Sakai, 1988). A sample size of 5 polyps was chosen as this number has been found to give statistically valid comparisons in Acropora (Wallace, 1985b). The oocytes were then removed from the mesentery, placed on a graticule slide and measured under the stereo microscope. The length and breadth of the largest oocyte on the mesentery, from each of the five polyps, was recorded.

Figure 10. *A. cerealis* as viewed under the stereo microscope showing many polyps with eggs. Each egg is approximately 300µm in diameter (photo N. Rosser).
Figure 11. A dissected polyp viewed under the stereo microscope showing three mesenteries with eggs. Egg diameter approximately 300µm (photo N. Rosser)

Figure 12. The dissected polyp opened up to reveal all four egg bearing mesenteries in order to accurately count the number of eggs per polyp. Egg diameter approximately 300µm (photo N. Rosser)
2.5.2 Measurement and counting of oocytes

Size of oocytes is the most commonly used measurement to identify stages of maturity. Some authors measure maximum and minimum diameter of the oocytes and then average the two measurements (Kojis, 1986; Stobart et al., 1992). Others simply measure the maximum and the median diameter of the oocytes (Wallace, 1985b), while others again use the maximum and minimum radius of each oocyte to calculate the volume of each oocyte according to the formula for the volume of a spheroid (Stewart, 1993; Crane, 1999; Wallace, 1999; Heltzel and Babcock, 2002). This latter method was chosen to enable ease of direct comparison of oocyte volume between replicate colonies of a species.

Due to the shape of the eggs in *Acropora* species, the volume of each oocyte was determined using the following equation for a prolate spheroid:

\[
\text{volume} = \frac{4}{3} \pi a b^2
\]

*Equation 2*

where \(a\) = maximum radius and \(b\) = minimum radius

Harrison and Wallace (1990) state that fecundity and size are best measured from live samples or dissected polyps as this allows entire gonads to be viewed and measured. Harriott (1983) also found that histological sections underestimate the size of eggs because tissue shrinkage that accompanies histological processing can be up to as much as 30%. For these reasons it was decided that decalcified samples were to be used to measure fecundity rather than histological sectioning. Hayward and Collins (1985) cautioned that while dissection of live material revealed regular spheroid eggs, fixation caused eggs to become irregular in shape and therefore
preserved egg length should be considered cautiously as a guide to egg dimensions. However Stobart et al. (1992) subsequently pointed out that variation caused by skeletal morphology during preservation will be similar from month to month, therefore within morph comparisons would be valid.

2.6 Species Identification

A small sample of the skeleton from each species was bleached in freshwater with swimming pool chlorine added, so that the skeleton could be examined for identification. Accompanied by a photo of the colony from which it was collected, these were then sent to the Museum of Tropical Queensland in Townsville for identification by Dr Carden Wallace.

2.7 Statistical analysis

All statistics used in this study, ANOVA, t-test and correlation co-efficient, were analysed at a significance level of 0.05 (all the assumptions of ANOVA were met) and statistics were run on SPSS 12.0.1.
CHAPTER 3.

RESULTS
3.1 Biannual spawning in Dampier

3.1.1 Presence of eggs
Examination of the four species *Acropora samoensis*, *Acropora cytherea*, *Acropora millepora* and *Acropora hyacinthus* collected from Dampier by the Australian Institute of Marine Science (AIMS) in October 2002, revealed that both *Acropora samoensis* and *Acropora cytherea* contained large eggs in October (440-580µm) and testes were present, suggesting that these colonies were in a late stage of maturity. Seven colonies of *A. samoensis* (n=11) and four colonies of *A. cytherea* (n=5) contained eggs in October 2002 (Table 1). By October 2003 many colonies of *A. samoensis* had died and there were only three remaining with eggs in October (n=6). In *A. cytherea* all colonies that had eggs in October 2002 also had eggs in October 2003 (Table 1). Field notes recorded by AIMS in both stated that when the colonies were broken open in both October 2002 and 2003 the eggs were pink, indicating that they were preparing to spawn. When colonies were broken open in February 2003, the eggs were still white indicating that they were still a few weeks away from spawning, which would explain the difference between the size of the eggs in the October and February samples.

Both *A. samoensis* and *A. cytherea* contained mature eggs in either October or February, but not both (Table 1). Therefore in these species, each colony is undergoing only one gamete cycle per year, but there is a split in the population into two groups that are spawning in different seasons (October and March). These results were consistent over both Oct 2002 and October 2003, whereby those colonies with mature eggs in October 2002 also contained mature eggs in October
2003. There was no incidence of colonies containing mature eggs in 2002 and not in 2003.

Table 1. Presence, absence and size (µm) of eggs in *Acropora samoensis* and *Acropora cytherea* over the three sampling periods. ◆ indicates the absence of eggs and □ indicates the absence of a sample due to colony death

<table>
<thead>
<tr>
<th></th>
<th>Oct-02</th>
<th>Feb-03</th>
<th>Oct-03</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Acropora samoensis</em></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>500</td>
<td>◆</td>
<td></td>
<td>540</td>
</tr>
<tr>
<td>500</td>
<td>◆</td>
<td></td>
<td>540</td>
</tr>
<tr>
<td>580</td>
<td>◆</td>
<td>450</td>
<td>◆</td>
</tr>
<tr>
<td>420</td>
<td>◆</td>
<td></td>
<td></td>
</tr>
<tr>
<td>560</td>
<td>◆</td>
<td></td>
<td>□</td>
</tr>
<tr>
<td>440</td>
<td>◆</td>
<td></td>
<td>□</td>
</tr>
<tr>
<td>460</td>
<td></td>
<td>□</td>
<td></td>
</tr>
<tr>
<td>580</td>
<td></td>
<td>□</td>
<td>□</td>
</tr>
<tr>
<td>540</td>
<td></td>
<td>□</td>
<td>□</td>
</tr>
<tr>
<td>□</td>
<td></td>
<td>425</td>
<td>□</td>
</tr>
<tr>
<td><em>Acropora cytherea</em></td>
<td>◆</td>
<td>510</td>
<td>◆</td>
</tr>
<tr>
<td>580</td>
<td>◆</td>
<td>400</td>
<td>400</td>
</tr>
<tr>
<td>470</td>
<td>◆</td>
<td></td>
<td>420</td>
</tr>
<tr>
<td>440</td>
<td>◆</td>
<td></td>
<td>340</td>
</tr>
<tr>
<td>440</td>
<td>◆</td>
<td></td>
<td>360</td>
</tr>
</tbody>
</table>

The examination of the samples from *Acropora millepora* and *Acropora hyacinthus*, revealed that both of these species contained mature eggs in February alone; they did not contain mature eggs in October, indicating that these two species release gametes only once during the year – in the March/April mass spawning event.

The distribution of the *A. samoensis* colonies along the transect they were collected from was mapped diagrammatically to visualize whether there was any segregation.
between the location of the October and March spawners (Figure 13). No segregation was apparent, and October and March spawners were often located side by side on the transect. As there were only five colonies of _A. cytherea_ sampled, little analysis could be made on this data.

![Diagrammatical map of the AIMS transect at the Dampier study site showing the distribution of the March and October spawners](image)

**Figure 13.** Diagrammatical map of the AIMS transect at the Dampier study site showing the distribution of the March and October spawners

### 3.1.2 Environmental parameters in Dampier

Sea temperatures in 2002-2003 were compared against those for a twenty-year average (data courtesy of A. Pearce, CSIRO Marine Research, from the Reynolds
2002 ranged from 0.5° below average to 0.5°C above average (Figure 14) while 2003 ranged from 0.5°C above average to 0.75°C below average (Figure 14).

3.2 Seasonality of spawning at Ningaloo Reef

3.2.1 Species distribution at the study site
Six of the most common Acropora species found on the reef flat were included in this study (Table 2). Of these species, Acropora digitifera, Acropora spicifera, and Acropora millepora were the most common on the reef flat. All species in this study were identified by Paul Muir and Carden Wallace from the Museum of Tropical Queensland.

A. digitifera and A. millepora were found on both the shallow transect (0.5m) and the deeper transect (1.5m). A spicifera and A. papillare were found only on the shallow transect in water less than 1m, while A. tenuis and A. cerealis were found only on the deeper transect in 1.5-2m of water.
<table>
<thead>
<tr>
<th>Species included in this study</th>
<th>Transect location</th>
</tr>
</thead>
<tbody>
<tr>
<td>Acropora spicifera</td>
<td>Shallow transect</td>
</tr>
<tr>
<td>Acropora papillare</td>
<td>Shallow transect</td>
</tr>
<tr>
<td>Acropora digitifera</td>
<td>Shallow and deep transects</td>
</tr>
<tr>
<td>Acropora millepora</td>
<td>Deep transect</td>
</tr>
<tr>
<td>Acropora cerealis</td>
<td>Deep transect</td>
</tr>
<tr>
<td>Acropora tenuis</td>
<td>Deep transect</td>
</tr>
</tbody>
</table>

Snorkelling and diving surveys of the lagoon from Point Maud to South Passage were conducted over several weeks, and it was observed that this distribution pattern was repeated throughout the region. *A. spicifera* and *A. papillare* were only ever observed growing in very shallow water less than 1m at high tide, and at low tide *A. papillare* was often exposed, illustrating a preference by these species for such an environment. *A. digitifera, A. millepora, A. tenuis* and *A. cerealis* were found in shallow water on the reef flat, and also in deeper areas of the lagoon up to 3m at high tide, indicating a more diverse occupation of habitats than the other two species.

The two species that were found to be mature in Dampier in October, *Acropora samonensis* and *Acropora cytherea*, were searched for via manta tows in Coral Bay in order to be included in the sampling regime, but they could not be located.

### 3.2.2 Percentage of colonies containing eggs

All colonies of each species were sampled in October, January and March for the presence of eggs. Different species appeared to develop at different rates; in most species less than 50% of colonies contained visible oocystes in October (Figure 15)
however *Acropora millepora* had a much higher number with 88% of colonies containing visible oocytes in October. In *Acropora papillare* all colonies contained mature eggs during October (this species will be discussed at the end of the results section).

Random sampling of numerous different families and genera conducted on 31st October near the study site, showed that no species that was sampled contained mature oocytes and spawning was not imminent (Table 3).

**Table 3. Results of random the sampling conducted near the study site on the 31st October**

<table>
<thead>
<tr>
<th>Family</th>
<th>Genus</th>
<th>No. species examined (no. of colonies of each species)</th>
<th>No. colonies with eggs in each species</th>
<th>No. colonies with pigmented eggs</th>
</tr>
</thead>
<tbody>
<tr>
<td>Acroporidae</td>
<td><em>Montipora spp</em></td>
<td>7 (2)</td>
<td>1</td>
<td>0</td>
</tr>
<tr>
<td>Poritidae</td>
<td><em>Poritites spp</em></td>
<td>6(2)</td>
<td>3</td>
<td>0</td>
</tr>
<tr>
<td>Pocilloporidae</td>
<td><em>Pocillopora spp</em></td>
<td>4 (2)</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Fungidae</td>
<td></td>
<td>2 (1)</td>
<td>2</td>
<td>0</td>
</tr>
<tr>
<td>Favidae</td>
<td><em>Favities spp</em></td>
<td>5 (1-2)</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Favidae</td>
<td><em>Platygyra spp</em></td>
<td>2 (2)</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Favidae</td>
<td><em>Goniastrea spp</em></td>
<td>2 (2)</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Favidae</td>
<td></td>
<td>3 (1)</td>
<td>0</td>
<td>0</td>
</tr>
</tbody>
</table>

In January, oocytes were present in over 75% of colonies of all species except *A. spicifera*, which still had less than 50% of colonies containing oocytes. It’s likely that this figure is an underestimate however, as some of these samples were probably collected from the sterile zone (given the difficulty of sampling this species, due to the tabular morphology and size of the sterile zone).
By March, 80% of colonies contained oocytes in all species except *A. tenuis*. *A. tenuis* showed a decrease in the percentage of colonies with oocytes from 80% in January down to 50% in March. This will be discussed in more detail at the end of the results section.

### 3.2.3 Mass spawning in Coral Bay

Each species included in this study was identified as a broadcast spawning coral, which releases egg and sperm bundles during an annual spawning period. During the five months that these corals were monitored there was no evidence that any
species had more than one gamete cycle. Most species in this study, with the exception of *Acropora papillare*, spawned over two nights in April. Some of the tagged colonies in this study first released gametes on the 2nd April, seven nights after the full moon in March, and spawning continued over the following night but had finished by the third night (5th April) when no gametes were released. The first night that the tagged colonies of *Acropora* in this study spawned, three out of the six tagged species spawned—*A. digitifera*, *A. cerealis* and *A. millepora* (Table 4) and of these species the percentage of colonies that spawned was 17, 43 and 50 % respectively. In comparison, on the second night all species spawned (except *A. papillare*) and the percentage of colonies that spawned was much higher ranging from 83 % to 100 % (Table 4).

While none of the tagged colonies, or any of the other colonies at the study site released eggs outside these two evenings, large pink slicks were observed on the surface of the water on the 30th March, 4 nights after the full moon, in the sheltered area of Bills Bay on the north side of Moncks Head. It is not known where the slick originated from, whether it was from corals spawning in Bills Bay, or on the outer reef. Every night thereafter until the 5th April, pink gametes were sighted throughout the water column in Bills Bay. The 30th March and the 3rd April were the only two nights on which a large pink slick formed, presumably because these were the only two nights on which it was not extremely windy, therefore allowing a slick to form that was otherwise blown away. The night of the 3rd April (the last night of the coral spawning period) was the main spawning night where the magnitude of spawning in Coral Bay was far greater than any other night, which was also mirrored in the tagged colonies. Bills Bay was covered in a large pink
slicks the following morning that stained the shoreline, and which remained in the bay for two days.

Table 4. Species and colonies that spawned during the mass spawning period

<table>
<thead>
<tr>
<th>Spawning date</th>
<th>Species</th>
<th>Percentage of colonies that spawned</th>
<th>No. nights after full moon</th>
<th>Time spawning occurred</th>
</tr>
</thead>
<tbody>
<tr>
<td>1-Apr-05</td>
<td>None</td>
<td>0</td>
<td>6</td>
<td></td>
</tr>
<tr>
<td>2-Apr-05</td>
<td>A. millepora</td>
<td>50 (n=9)</td>
<td>7</td>
<td>2100</td>
</tr>
<tr>
<td>2-Apr-05</td>
<td>A. digitifera</td>
<td>17 (n=29)</td>
<td>7</td>
<td>2115</td>
</tr>
<tr>
<td>2-Apr-05</td>
<td>A. cerealis</td>
<td>43 (n=7)</td>
<td>7</td>
<td>2100</td>
</tr>
<tr>
<td>3-Apr-05</td>
<td>A. millepora</td>
<td>100 (n=9)</td>
<td>8</td>
<td>2045</td>
</tr>
<tr>
<td>3-Apr-05</td>
<td>A. digitifera</td>
<td>100 (n=29)</td>
<td>8</td>
<td>2100</td>
</tr>
<tr>
<td>3-Apr-05</td>
<td>A. cerealis</td>
<td>100 (n=7)</td>
<td>8</td>
<td>2045</td>
</tr>
<tr>
<td>3-Apr-05</td>
<td>A. spicifera</td>
<td>89 (n=18)</td>
<td>8</td>
<td>2015</td>
</tr>
<tr>
<td>3-Apr-05</td>
<td>A. tenuis</td>
<td>83 (n=6)</td>
<td>8</td>
<td>1930</td>
</tr>
<tr>
<td>4-Apr-05</td>
<td>None</td>
<td>0</td>
<td>9</td>
<td></td>
</tr>
</tbody>
</table>

A. papillare was the only species in this study that spawned outside of the spawning period, most likely during December and January. This species will be discussed in detail at the end of this section.

The actual release of eggs and sperm took place after dark. The coral polyps released their gametes as an egg-sperm bundle, a small pink sac containing the eggs and sperm (Figure 16). Prior to spawning the polyps were observed “setting” for around 30 minutes to an hour, during which time the pink egg-sperm bundle was held in the polyp cavity, ready to be ejected (Figure 17). The polyps were not feeding and did not have their tentacles extended in the feeding position, but rather had them retracted around the polyp cavity, which was distended (Figure 16 and
Axial polyps were frequently observed setting (and releasing egg-sperm bundles) in most species (Figure 17).

When the polyps started “spawning” the egg-sperm bundles were released (Figures 18, 19 and 20) and floated to the surface where they remained in bunches. After several hours (presumably when the bunches had broken apart) the water then became extremely cloudy and visibility was less than 50cm. By this time thousands of gametes were on the surface and had formed a large thick slick (Figure 21).

On the first night the corals were observed spawning, eggs and sperm were released at around 9pm (Table 4) and each colony spawned for about 30 minutes, so that by 10pm everything had finished spawning. On the following night the corals commenced spawning earlier at 7.30pm (Table 4). On the third night after the tagged corals began spawning, no gametes were released by either the tagged colonies or any other colonies in Bills Bay.
Figure 16. Egg and sperm bundle being held in the polyp cavity prior to release (photo: P. Buzzacott)

Figure 17. Polyps “setting” prior to coral spawning (photo P. Buzzacott)
Figure 18. Polyp releasing egg and sperm bundle (photo P. Buzzacott)

Figure 19. Polyps spawning (photo P. Buzzacott)
Figure 20. Colony of *Acropora* spawning (photo N. Thake)

Figure 21. Coral spawn slick on the surface at approximately 10.30pm on the 3rd April 2005 (photo N. Rosser)
Following the spawning period, the tagged colonies were examined for the presence of gametes on the 5th April. One colony of *A. digitifera* and one colony of *A. tenuis* were found to contain a small number of polyps with eggs (Table 5). Within these two colonies, the percentage of polyps containing eggs in each one of these colonies was very low (less than 5 %), therefore the potential for colonies to spawn again the following month was minimal. 1-2 residual eggs that had not been spawned were present in occasional polyp in some colonies, but in the majority of colonies no eggs were found at all.

**Table 5.** The proportion of colonies containing eggs on the 5th April

<table>
<thead>
<tr>
<th>Species</th>
<th>% of colonies with a polyp containing a full compliment of eggs</th>
<th>% colonies with a polyp containing residual eggs</th>
<th>% colonies with no eggs</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>A. millepora</em></td>
<td>0</td>
<td>22</td>
<td>78</td>
</tr>
<tr>
<td><em>A. digitifera</em></td>
<td>3</td>
<td>10</td>
<td>87</td>
</tr>
<tr>
<td><em>A. cerealis</em></td>
<td>0</td>
<td>0</td>
<td>100</td>
</tr>
<tr>
<td><em>A. spicifera</em></td>
<td>0</td>
<td>6</td>
<td>94</td>
</tr>
<tr>
<td><em>A. tenuis</em></td>
<td>17</td>
<td>0</td>
<td>83</td>
</tr>
</tbody>
</table>

Random sampling of untagged colonies of the six *Acropora* species in this study was conducted on the 31st March and the 1st April (prior to the observed spawning of these species) for two square kilometers around the study site. This sampling revealed that all colonies still contained pink or red eggs indicating that they had not yet spawned, therefore confirming that the patterns observed along the transects at the study site were a true reflection of the reef flat in the region.
3.2.4 Physical conditions during the coral spawning period

Lunar and tidal phase
The coral spawning period took place around the third quarter moon, from the 4th night after the full moon to the 8th night after the full moon (Figure 22). During this period the weather was overcast, windy and it frequently rained.

An examination of the tidal regime shows that the coral spawning period occurred as neap tides were being approached, and the main night of coral spawning coincided approximately with a neap tide (Figure 22). The neap tides around the coral spawning period were also larger than the previous neap tides around the 20th March, or the following neap tides, around the 20th April (Figure 22). At the end of the coral spawning period the semi-diurnal tidal pattern of four tides per day had largely become diurnal, with only two tides per day (Figure 22).

Temperature
Temperature was recorded by a temperature logger situated near Lotties lagoon at three hourly intervals, which was then averaged to provide one figure for each 24 hour period (Figure 23) (Data courtesy of T. Irvine, Murdoch University). Diel variation was apparent in the raw data, the temperature consistently dropping by 1 degree at night, however because the diel variation was so consistent these averages present an accurate representation of the variation in temperature on a daily basis.

The results show that there can often be a considerable change in temperature over a short period within the lagoon, such as between 12-16 March where the temperature rose from 26°C to 29°C over a period of 4 days and then dropped back down again to 26°C by the 21st March (Figure 23). During the coral spawning period temperature dropped from 26.5 °C to 24.8 °C over the five days (Figure 23).
3.2.5 Species spawning outside the mass spawning period

*Acropora tenuis*

*Acropora tenuis* showed a decrease in the percentage of colonies containing eggs from 80% in January to 50% in March. At least two colonies that contained eggs in January, did not contain eggs when sampled at the end of March, indicating that some colonies of *A. tenuis* released gametes prior to the mass spawning period.

Anecdotal records from Coral Bay observed a coral spawning slick on the 6th March, 10 days after the February full moon (F. McGregor, pers. comm.) so it is possible that *A. tenuis* participated in this event.
Figure 22. Observed tidal measurements in Carnarvon from Midnight on the 20th March 2005 to Midnight on the 20th April 2005. Tidal measurements were taken every 5 minutes and this was averaged and given a value for each three hour period. Data courtesy of DPI.
Figure 23. Temperature recorded in Coral Bay from a temperature logger located near Lotties Lagoon. Data courtesy of T. Irvine, PhD student, Murdoch University
**Acropora papillare**

Unlike other species in this study, all colonies of *A. papillare* contained large eggs in October (range 400-600µm). The size of the eggs in October indicated that they were close to maturity, however testes were not present indicating that they were still at least 8 weeks away from spawning. When the colonies were re-sampled again on 18\textsuperscript{th} January, 80 % of colonies had no eggs remaining.

Two of the *A. papillare* colonies were sampled in December (by F. Webster, PhD student, Murdoch University) and when I examined them under the dissecting microscope eggs were present. The eggs by this stage had testes, indicating they were close to maturity, but it is not known whether or not the eggs were pigmented (which would provide a closer indicator to maturity) as once the samples are put in formalin any pigmentation becomes white. As most broadcasting corals spawn after the full moon and on neap tides, it is assumed that *A. papillare* spawned sometime after the December full moon (which occurred on the 24\textsuperscript{th} December), though it could also have occurred on the neap tides after the January new moon (Figure 24). When the colonies were sampled on the 18\textsuperscript{th} January, polyps sometimes contained one or two residual eggs that were presumably left over from spawning and had not yet deteriorated. 20 % of the colonies still contained large white eggs on the 18\textsuperscript{th} January (range 500-600µm); testes were present in January but the eggs were not pigmented, indicating that they were still a few weeks away from spawning. No colonies contained any eggs when sampled again in March, so presumably these colonies released their gametes after the January full moon, which occurred on the 25\textsuperscript{th} January (Figure 24).
All colonies with eggs

December '2004

20 % colonies with eggs

January '2004

February '2004

Assumed spawning period

Assumed spawning period

Figure 24. Timeline showing New and Full Moons December 2004-February 2005 and periods during which spawning of *Acropora papillare* is assumed to have taken place
3.3 Oocyte development and fecundity

3.3.1 Dampier

_Fecundity comparison between March and October spawners_

The average number of eggs per polyp in each colony of _Acropora samoensis_ was measured in October 2002, February 2003 and October 2003 (Table 6). The average number of eggs per polyp per colony was compared for October 2002 (n= 8) and February 2003 (n=5) in a t-test to determine whether there was a difference in reproductive fecundity between the March spawners and the October spawners. The result showed that there was no difference between the mean number of eggs in October and February (mean October = 10.56, mean for February =10.24, df= 11, p=0.8) indicating that there is no difference in fecundity between the colonies spawning in October and those spawning in March.

A repeated measures t-test was performed on the three colonies that contained eggs in both October 2002 and October 2003 to determine whether there was a difference in the number of eggs per polyp in the same colonies between the two years. The results showed that in each colony there was a significant increase in fecundity between October 2002 and October 2003 (mean Oct 2002 = 8.7, mean Oct 2003 = 11.3, p=0.001, df =14) indicating that a significant inter-annual variation in fecundity exists in this species, however with such a small sample size (3 colonies) this result is circumspect.
Table 6. The average number of eggs per polyp measured in *A. samoensis* and *A. cytherea* from each of the three sampling periods

<table>
<thead>
<tr>
<th></th>
<th>Oct-02</th>
<th>Feb-03</th>
<th>Oct-03</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Acropora samoensis</em></td>
<td>10.56 (n=8)</td>
<td>10.24 (n=5)</td>
<td>11.33 (n=3)</td>
</tr>
<tr>
<td><em>Acropora cytherea</em></td>
<td>9.35 (n=4)</td>
<td>5.2 (n=1)</td>
<td>10.56 (n=4)</td>
</tr>
</tbody>
</table>

3.3.2 Ningaloo Reef

*Oocyte development in Coral Bay*

All species had the same gonad arrangement in which oocytes and testes were located in the same polyp, on adjacent mesenteries. In mature polyps, the oocytes appeared in a string in the lateral pairs of mesenteries with the ventral pair (or inner pair) bearing more oocytes than the dorsal (or outer) pair of mesenteries. The testes appeared as elongate cones on the directive mesenteries, with the ventral (outer) mesenteries bearing long testes and the dorsal (inner) mesenteries bearing short testes.

Immature oocytes were visible in the polyp mesenteries in October, under the stereo-microscope (Figure 25). Oocytes were small (range 100-200µm) and translucent, and broke apart easily. *A. papillare* was the exception as it contained large eggs in October.

In most species, oocytes were much larger in January (range 200-500µm) and zooxanthellae could be seen in the mesenterial filaments surrounding the oocytes in some polyps, which was not visible in October (Figure 26). Testes were not present in the polyps in January, indicating that testes only developed during the last 10 weeks of development which is consistent with *Acropora* species (Wallace, 1985b).
Figure 25. Dissected polyp of *A. digitifera* in October 2004 showing the appearance of the oocytes. Oocyte diameter is approximately 100 µm (photo N. Rosser)

Figure 26. Dissected polyp from *A. digitifera* in January showing the zooxanthellae in the mesenterial filaments surrounding the oocytes. Oocyte diameter is approximately 400 µm (photo N. Rosser)
Figure 27. Dissected polyp of *A. digitifera* in March showing the presence of testes. This photo is also testament to the high numbers of eggs per polyp recorded in this study – 19 eggs can be seen in this polyp. Egg diameter is approximately 600 µm (maximum)

Figure 28. Broken branch of *A. digitifera* in the field, showing pigmented eggs four days prior to spawning
Figure 29. Mean egg volume in each species in each sampling season.

In March, testes were present and visible in all other species (Figure 27); ooctyes were large (range 500-700µm) and when branches were broken open in the field many were pink (Figure 28).

Growth of ooctyes was rapid prior to coral spawning. Growth rate in developing ooctyes was graphed (Figure 29) and illustrates that the growth rate is higher during the last two months of development from January to March, than it is for the previous two months from October to January.
**Fecundity in Coral Bay**

Fecundity (number of eggs per polyp) and size of oocytes were measured in each species, from samples collected on the 29th March, four days prior to spawning, to provide a measurement of the mature fecundity and egg size for each species (Table 7). Each species showed large variation in the average number of eggs per polyp (Table 7). Variation in the number of eggs per polyp within a colony was not considerable, however a one way ANOVA at a significance level of 0.05 showed that all species except *Acropora papillare* had significant variability in the number of eggs per polyp between colonies (Table 8).

**Table 7.** Polyp fecundity (no. eggs per polyp) mean oocyte diameter, and mean oocyte volume was recorded from colonies with mature testes. Mean of 5 counts per colony, and 10-20 colonies per species.

<table>
<thead>
<tr>
<th>Species</th>
<th>No. polyps counted</th>
<th>Mean polyp fecundity (range)</th>
<th>Mean mature oocyte diameter (µm)</th>
<th>Mean mature oocyte volume (mm³)</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>A. tenuis</em></td>
<td>N=15</td>
<td>10.53 (6-17)</td>
<td>605</td>
<td>0.08</td>
</tr>
<tr>
<td><em>A. spicifera</em></td>
<td>N=81</td>
<td>10.84 (6-18)</td>
<td>554</td>
<td>0.07</td>
</tr>
<tr>
<td><em>A. digitifera</em></td>
<td>N=157</td>
<td>11.63 (5-21)</td>
<td>585</td>
<td>0.07</td>
</tr>
<tr>
<td><em>A. millepora</em></td>
<td>N=49</td>
<td>11.73 (8-16)</td>
<td>596</td>
<td>0.07</td>
</tr>
<tr>
<td><em>A. cerealis</em></td>
<td>N=58</td>
<td>13.51 (8-20)</td>
<td>594</td>
<td>0.07</td>
</tr>
<tr>
<td><em>A. papillare</em></td>
<td>N=51</td>
<td>10.39 (7-15)</td>
<td>527</td>
<td>0.05</td>
</tr>
</tbody>
</table>
Table 8. Results from one way ANOVAs testing the variability in the number of eggs per polyp between colonies of the same species

<table>
<thead>
<tr>
<th>Species</th>
<th>df</th>
<th>p value</th>
</tr>
</thead>
<tbody>
<tr>
<td>A. digitifera</td>
<td>30</td>
<td>0.001</td>
</tr>
<tr>
<td>A. cerealis</td>
<td>9</td>
<td>0.001</td>
</tr>
<tr>
<td>A. millepora</td>
<td>8</td>
<td>0.01</td>
</tr>
<tr>
<td>A. tenuis</td>
<td>3</td>
<td>0.01</td>
</tr>
<tr>
<td>A. spicifera</td>
<td>15</td>
<td>0.001</td>
</tr>
<tr>
<td>A. papillare</td>
<td>8</td>
<td>0.293</td>
</tr>
</tbody>
</table>

Differences between the two transects

A. digitifera was the only species to occur on both the shallower and deeper transect, so colony size, fecundity and oocyte diameter was compared between the two transects by T-tests which were performed at a significance level of 0.05. This showed that A. digitifera colonies on the deeper transect were significantly smaller than those on the shallower transect (mean on deep = 628 cm², mean area on shallow = 1,157 cm², p=0.003, df=26). Prior to spawning in March, colonies on the deeper transect also had a significantly lower number of eggs per polyp than those on the shallower transect (mean No. eggs per polyp on deep = 9, mean No. on shallow = 13, p=0.004, df=26). Therefore a correlation co-efficient at a significance level of 0.05 was carried out to determine whether there was a relationship between the size of the colony and fecundity. A positive correlation was found between the number of eggs per polyp, and the size of the colony in this species (0.34, p=0.04) signifying that as the size of the colony increases, the number of eggs per polyp also increases. For example, one of the largest colony colonies of A. digitifera that had an area of 1,484 cm² had an average fecundity of 16 eggs per polyp, compared to one of the smallest colonies with an area of 393 cm², that had an average fecundity of 7 eggs per polyp. This correlation could account for the lower fecundity on the
deeper transect, as the colonies on the deeper transect are much smaller than those on the shallow transect.

**Change in fecundity over time**
The number of eggs per polyp in each tagged colony was measured in October, January and March to determine whether there was any change in fecundity over the six month period in any of the species being studied (Table 9). For *A. digitifera*, *A. spicifera*, *A. tenuis* and *A. cerealis*, the small number of polyps containing eggs in October (less than 50% in each species) prevented the October data from being suitable for analysis; for these species, analysis was limited to a nested ANOVA on repeat measures of January and March (conducted on a significance level of 0.05). These results showed that there was a significant decrease in fecundity in *A. tenuis* from a mean in January of 10.3 eggs per polyp to 3.8 in March. (Table 9). The colonies of *A. digitifera* located on the shallow transect also had a significant decrease in fecundity between January and March, but those on the deep transect did not (Table 9). *A. spicifera* and *A. cerealis* showed no significant decrease in fecundity between January and March (Table 9).
Table 9. Results from a nested ANOVA on repeat measures from January and March

<table>
<thead>
<tr>
<th>Species</th>
<th>N</th>
<th>Jan mean fecundity</th>
<th>March mean fecundity</th>
<th>P value</th>
<th>df</th>
<th>F value</th>
</tr>
</thead>
<tbody>
<tr>
<td>A. digitifera</td>
<td>79</td>
<td>12.86</td>
<td>12.77</td>
<td>0.82</td>
<td>1</td>
<td>0.48</td>
</tr>
<tr>
<td>(shallow T)</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>A. digitifera</td>
<td>55</td>
<td>10.24</td>
<td>9.29</td>
<td>0.002</td>
<td>1</td>
<td>11.12</td>
</tr>
<tr>
<td>(deep T)</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>A. cerealis</td>
<td>50</td>
<td>13.72</td>
<td>13.42</td>
<td>0.60</td>
<td>1</td>
<td>0.28</td>
</tr>
<tr>
<td>A. spicifera</td>
<td>40</td>
<td>12.55</td>
<td>12.25</td>
<td>0.52</td>
<td>1</td>
<td>0.41</td>
</tr>
<tr>
<td>A. tenuis</td>
<td>20</td>
<td>10.35</td>
<td>3.80</td>
<td>0.001</td>
<td>1</td>
<td>105.21</td>
</tr>
</tbody>
</table>

In *A. millepora* however, 88% of polyps had eggs in October, therefore for this species a repeated measures ANOVA with a significance level of 0.05 was run on those colonies that had values in all three seasons to determine whether there was a difference in the number of eggs per polyp between October, January and March. The results showed that there was a significant difference (f=6.3, df=1, p=0.01), and a Tukey test revealed that this difference was only significant between January and March (mean January = 12.18, mean March = 11.03 p=0.01). *A. millepora, A. tenuis* and some colonies of *A. digitifera* had a significant decrease in the number of eggs per polyp between January and March, indicating that in these species there was a degeneration of developing ooctyes in late oogenesis.

3.3 Fecundity in Dampier compared to Coral Bay

The average number of eggs per polyp in *Acropora millepora* was compared between samples from 11 colonies collected from Dampier in February 2002 and samples from 11 colonies collected from Coral Bay in February 2002, by a one-way ANOVA and this showed that mean fecundity was significantly higher in Coral Bay
than in Dampier (Coral Bay mean = 12.6 eggs per polyp, Dampier mean = 10.6; p=0.03, df=20). Mean fecundity per colony in Dampier and Coral Bay was graphed (Figure 30) to illustrate the difference.

There was no significant difference in the mean egg volume between Coral Bay and Dampier (Coral Bay mean = 0.25 mm$^3$, Dampier mean = 0.20 mm$^3$; p=0.5, df=20). A t-test comparing the size of colonies in Coral Bay and Dampier found no difference between the two locations, indicating that the size of the colonies is the same in both Coral Bay and Dampier and therefore colony size does not account for the difference in fecundity (mean CB = 1304 cm$^2$, mean Dampier = 1163 cm$^2$; df=20, p=0.23).
Figure 30. Average number of eggs per polyp, per colony, in 11 colonies of *A. millepora* collected from Dampier and Coral Bay in February 2003.

3.4 Fecundity in Coral Bay compared to elsewhere

The mean fecundity (number of eggs per polyp) recorded prior to spawning in each the species in this study was compared with the fecundity for the same species published in Wallace (1999) (Table 10). The figures in Wallace were compiled from the literature, from information from specimens in the World-wide *Acropora* database, and from material stored in the Museum of Tropical Queensland
collections. Where comparisons could be made, fecundity was higher at Ningaloo than in the figures for the same species in Wallace (1999).

**Table 10.** Egg size and fecundity of *Acropora* species measured in this study compared with figures compiled from the literature, information from specimens in the World-wide *Acropora* database, and material stored in the Museum of Tropical Queensland collections; published in Wallace (1999), Table 5 pg 38.

<table>
<thead>
<tr>
<th>Species</th>
<th>No. polyps counted in present study</th>
<th>Mean polyp fecundity in this study (range)</th>
<th>Mean polyp fecundity in database (range)</th>
<th>Mean mature oocyte diameter in this study (µm)</th>
<th>Mean mature oocyte volume in database</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>A. tenuis</em></td>
<td>N=15</td>
<td>10.53 (6-17)</td>
<td>10*</td>
<td>605</td>
<td>517</td>
</tr>
<tr>
<td><em>A. spicifera</em></td>
<td>N=81</td>
<td>10.84 (6-18)</td>
<td>-</td>
<td>554</td>
<td>446</td>
</tr>
<tr>
<td><em>A. digitifera</em></td>
<td>N=157</td>
<td>11.63 (5-21)</td>
<td>7.8 (6-10)</td>
<td>585</td>
<td>517</td>
</tr>
<tr>
<td><em>A. millepora</em></td>
<td>N=49</td>
<td>11.73 (8-16)</td>
<td>7.5(5-10)</td>
<td>596</td>
<td>561</td>
</tr>
<tr>
<td><em>A. cerealis</em></td>
<td>N=58</td>
<td>13.51 (8-20)</td>
<td>9.0</td>
<td>594</td>
<td>503</td>
</tr>
<tr>
<td><em>A. papillare</em></td>
<td>N=51</td>
<td>10.39 (7-15)</td>
<td>-</td>
<td>527</td>
<td>-</td>
</tr>
</tbody>
</table>

*= one colony only*
CHAPTER 4

DISCUSSION
4.1 Bi-annual spawning in Dampier

Studies of biannual spawning in broadcast spawning corals are important because they can provide important insights into coral physiology, reproductive cycles and cues influencing the timing of mass spawning. This is the first time that biannual spawning has been documented in the Dampier Archipelago, and the first time broadcast spawning has been witnessed in October.

Simpson (1985) did not find any evidence of spawning in spring in the Dampier Archipelago, after examining colonies of many species and failing to find eggs. However Simpson did not sample the two species examined in the present study, and if other species do participate in the October/November spawning they may have spawned before they were sampled. Simpson surveyed 1-5 colonies of 28 species (including 13 Acropora) on 12th-13th November 1984 and found that none contained eggs, but based on the results of the present study the spawning may have occurred after the October full moon, which fell on the 10th October in 1984. Furthermore 13 of the species that Simpson examined in March did not have eggs, which could be an indication that they spawned in October.

In both species, examined in the present study A. samoensis and A. cytherea, the population contained ripe gametes (spawning is assumed) in both March and October, but each individual colony spawned at only one of these two times and had only one gamete cycle. This is an unusual aspect of the bi-annual spawning occurring in Dampier because other cases of biannual spawning (where individuals have been sampled twice a year) have been found undergoing two gamete cycles per year, culminating in individuals spawning twice per year (Oliver et al., 1988;
Stobart et al., 1992; Guest et al., 2005). No other studies in which a split spawning occurring six months apart in the same population were found in the literature, most studies documented a protracted spawning period within a season.

It is known that environmental conditions affect fecundity, as fecundity varies significantly inter-annually due to differing conditions in temperature, nutrient availability, colony damage, pollution and other parameters each year (Wallace, 1985a; Stobart et al., 1992). Therefore, it was considered possible that these species were spawning in both March and October during these years, due to atypical environmental conditions. Most of these parameters could not be tested in the present study, however sea temperatures in 2002-2003 were compared against those for a twenty-year average to determine whether 2002-2003 were atypical years. The comparison showed that 2002 and 2003 were not atypical years; during these years the temperature ranged from half a degree below average to half a degree above average, and no extreme temperature occurred in any month (high or low). This would suggest that adverse sea temperatures played no role in causing bi-annual spawning to occur in Dampier in these years.

The results of this study provide an important exception to the paradigm of mass-spawning in March/April in lower latitude reefs in Western Australia, and which should be supplemented by more detailed surveys to determine the proportion of colonies and species participating the in October/November event.
4.1.1 Hypotheses on the reasons for biannual spawning in Dampier

There are three hypotheses to explain the observed pattern of biannual spawning in March and October in the Dampier Archipelago: (a) that there is a genetic difference between the March and October spawners, (b) that individuals are able to respond differently to environmental conditions, or (c) that there is a difference in the symbiotic algae (zooxanthellae) residing in the tissue of the corals that promotes differences in spawning periods.

Genetic difference

The first hypothesis is that there is a genetic difference between the March and October spawners and therefore they are acting like two different species. Because the two groups are spawning six months apart there would be no genetic exchange between them and thus the phenomenon would be maintained.

Simpson (1998) hypothesized that the breeding season on the west coast may have been inherited from ancestral corals further north; if this is true a genetic difference in the population in Dampier may have arisen from the source population in the north. A wide variation in spawning seasonality has been observed in the Indo-Pacific Archipelago above Australia, Oliver et al. (1988) found ripe colonies from September to March in Papua New Guinea, while Baird et al. (2001) found that only 30% of colonies spawned during mass spawning in March. Thus this temporal reproductive asynchrony could result in genetic differences and speciation in the source population, as temporal reproductive isolation has been shown to do (Wolstenholme et al., 2003; Wolstenholme, 2004). Simpson’s theory that spawning on the west coast is a legacy from further north, is based on the correlation between the mass spawning event and the strengthening of the Leeuwin Current, as larvae
from corals spawning in the Indo-Pacific during March are swept down the west coast of Australia by the strongly flowing Leeuwin Current. The Leeuwin Current flows most strongly between the months of March and September (Cresswell, 1991; Holloway, 1995; Taylor and Pearce, 1999), therefore a decrease in the velocity of the current in October could explain how coral larvae arrived on the west coast in that month. But it does not explain why corals are not spawning in the months between October and March, when the Leeuwin Current is weak, as corals further north have been found with ripe gametes in September, October, November, January and March (Oliver et al., 1988; Guest et al., 2005). While no samples were collected during November-January, during the months that the samples were collected there were no intermediate stages of development observed; in October and March gametes were either in a late stage of maturity or a very early stage of maturity, suggesting that spawning was limited to the months of October and March only. A wider examination of coral reproduction in the Dampier Archipelago is required to investigate whether any other species are spawning in October and any other month. Research into the spawning behavior of these species in the Indonesian Archipelago and genetic comparisons of the population may also help to determine whether the population in Dampier is emulating the spawning season in Indonesia and whether the populations are genetically related to substantiate Simpson’s hypothesis.

Environmental response
A second hypothesis is that if there is no genetic difference between the March and October spawners, then environmental conditions in Dampier allow corals to be able to spawn in either October or March. It is not known whether this pattern of spawning in both March and October is repeated every year or only in some years,
nor is it known whether they are capable of switching – whether those colonies found to be spawning in October during this study will in a few years be spawning in March. It is apparent that for the two years that these samples were collected in the present study, individuals spawned in the same period each year and switching did not occur. If it is an environmental component controlling the time of spawning, then switching might occur in response to stress. For example, if a colony was developing gametes and environmental conditions became stressful for the coral (e.g. increase in water temperature, or decrease in salinity due to a cyclone) maturation of gametes could be delayed over this period to be subsequently matured and released in October. Very small eggs were detected in colonies in March and October, so this is a possibility. The findings from the present study in Coral Bay found that maturation of oocytes occurred rapidly in the last two months of development, prior to which oocytes developed much more slowly, providing a possible mechanism for gamete maturity to be delayed (discussed in the fecundity section). Other studies have also shown that some colonies do not spawn every year suggesting that gamete cycles can be affected by environmental conditions (Stobart et al., 1992).

The problem with the suggestion that environmental conditions are responsible for the split spawning, is that the population is being subjected to the same environmental conditions (and there was no obvious difference in local conditions surrounding individual colonies, such as the presence of stresses or competitors) so it is puzzling why part of the population would delay gametogenesis in response to stress while the other half of the population spawned. Therefore while this
hypothesis is possible, it is more likely that variations in environmental conditions are not responsible.

\textit{Difference in zooxanthellae}

The third hypothesis is that rather than there being a difference between the corals themselves, there is a difference between the symbionts they harbor, which results in the ability to spawn at two different times of the year. Recent studies have shown that coral-zooxanthella associations are both dynamic and flexible, and the physiological properties of reef corals may vary according to the clades of zooxanthellae (\textit{Symbiodinium}) in the coral (Little \textit{et al.}, 2004). For example, \textit{Symbiodinium C} is known to be associated with faster growth of the host while \textit{Symbiodinium D} is associated with greater thermal tolerance (Baker, 2003).

Thus it is possible that the population in Dampier contains different symbionts with different life history consequences for the corals, such as the time of reproduction. For example it may be that the October spawners have a clade of zooxanthellae that promotes growth but has limited thermal tolerance, and therefore is more suited to reproduction in the cooler month of October than in March. Adults of some coral species can form associations with different \textit{Symbiodinium} strains according to different microhabitats within the coral colony (Little \textit{et al.}, 2004), indicating that selection of zooxanthellae can be dictated by very fine scale influences resulting in different patterns within the population. Research into the physiological effects zooxanthellae can have on their hosts is only just beginning. Further assessment of these ideas will have to await more detailed information on the impact of zooxanthellae on life history strategies and gametogenesis in corals.
4.2 Mass spawning of *Acropora* in Coral Bay

One of the reasons that seasonality of spawning was studied in Coral Bay, was because colonies of *Acropora samoensis* and *Acropora cytherea* were observed to have mature eggs in October in Dampier, and so we wished to know whether these species were mature in Coral Bay in October also. Unfortunately though, these species could not be found in Coral Bay. More extensive searches are required to ascertain whether they do occur at Ningaloo Reef, and to address the important question of whether the population at Ningaloo also participates in spawning during October.

4.2.1 Proximate cues influencing the time of spawning

Mass spawning took place following the full moon in March, as is consistent with previous studies at Ningaloo Reef (Marchant, 1987; Simpson, 1991; Smith, 1993; Stewart, 1993). Five out of the six *Acropora* species in the present study participated in the mass spawning event at this study site which took place from the 2\(^{nd}\)-3\(^{rd}\) April, 7-8 nights following the full moon in March. One of the aims of this project was to observe the physical conditions under which spawning took place so that these could be compared with other regions. Hayashibara *et al.* (1993) stated the importance of studying populations engaging in coral spawning at different locations to determine the physical conditions cuing gamete release and how populations at different locations react to them, in the hope of providing more clues to the mechanisms responsible for the timing and synchronization of coral spawning. Proximate cues are fine scale environmental conditions that provide a signal for gamete release and synchronise the time of spawning within a multi-
specific population, such as an increase in water temperature, the lunar phase or tidal phase; the season during which coral spawning occurs, for example, is not a proximate cue for gamete release.

A number of physical factors and how the population may be responding to them as proximate cues synchronizing the timing of coral spawning were considered in this study. It must be acknowledged however, that the results from this study are from one year only and the conclusions are based on observations from only one spawning period, therefore further research on the conditions cuing gamete release at Ningaloo Reef are required to substantiate these findings.

**Water temperature**

Babcock *et al.* (1986) suggested that an increase in the temperature prior to mass spawning on the Great Barrier Reef (GBR) acts as a proximate cue for coral spawning because the corals on the inshore reefs spawn one month earlier than corals on the offshore reefs due to an earlier rapid rise in sea temperatures at the inshore reefs. Hayashibara *et al.* (1993) also attributed temperature to paying a major role in cuing the time of spawning, as they found that water temperature rose rapidly at the same time that synchronous spawning occurred, and therefore suggested that an increase in temperature acts as a proximate cue inducing spawning.

In comparison to these suggestions, the evidence from the present study would suggest that temperature is not acting as a proximate cue for coral spawning at Ningaloo Reef. While the temperature did increase by one degree during the five days prior to spawning, it also decreased by two degrees during the five days over
which spawning occurred, indicating that temperature in the lagoon is highly variable. This has also been supported by other studies where Simpson and Masini (1986) found that a rapid decline in temperature over a short period was not infrequent, and Davidson and D'Adamo (2001) also recorded rapid changes in water temperature by up to 7°C over periods of as little as two days. While diel variation in temperature is apparent in the lagoon, with temperatures dropping by 1-2 degrees at night, this does not account for such dramatic changes in temperature such as a seven-degree decrease in two days. Hearn et al. (1986) postulated that the possible cause of these rapid changes in temperature was the swift advection of relatively cold oceanic water into the lagoon periodically, caused by upwelling on the shelf slope.

The high variability of seawater temperature within the shallow Ningaloo Reef lagoon makes the argument for temperature acting as a proximate cue inducing spawning at Ningaloo improbable, because with such variability it is hard to see how the corals could use temperature as a reliable time cue.

Tides
The coral spawning event observed in this study took place on an ebbing tide, which Simpson (1988) reasoned is to facilitate the flushing of propagules to deeper offshore waters, and to escape the many predators found in shallow water reef communities.

The two major nights on which coral spawning occurred coincided approximately with neap tides, which is consistent with the observations of other authors from Coral Bay (Simpson, 1991; Smith, 1993; Stewart, 1993). Marchant (1987)
postulated that spawning during March at Ningaloo is triggered by spring and neap tides of a much smaller amplitude than in any other month, thus the exposure of an intertidal reef during spawning is kept to a minimum. However the results from the present study do not concur with this theory, as the spring and neap tides during the coral spawning period were of a larger amplitude than the spring and neap tides before and after coral spawning.

Babcock et al. (19986) documented that mass spawning on the GBR takes place during a period of neap tides, and thus suggested that periods of low water motion have the advantage of reduced dispersal of gametes thereby increasing the chance of fertilisation. In addition to this suggestion, the observations from the present study propose another idea. Ningaloo Reef has a semi-diurnal tidal regime of two-high tides and two-low tides each day. Coral spawning occurred during a time when the second low tide had decreased to a point where the tides had become diurnal, with only one high and one low tide occurring each 24-hour period. Consequently instead of a change from high to low tide occurring over six hours, it was occurring over a period of 12 hours, thus the velocity of water motion over this period would be reduced. This may serve the same effect as Babcock et al. (1986) postulated, to spawn at a time of reduced water motion to increase the chance of fertilisation. This is supported by the author’s observations that during the period that the corals spawned at the study site water motion was greatly reduced; the normally strong tidal current that is experienced at this site was absent, and the site was unusually calm.
Over the five nights that mass spawning occurred during this study, the weather was windy, overcast and it rained during a few storms that occurred. These are not optimal conditions for coral spawning: windy conditions reduce the potential for gametes to aggregate at the surface for fertilization, and rain damages coral gametes on the surface as was illustrated at Magnetic Island in 1981 (Harrison et al., 1984). Yet the corals spawned anyway, despite these conditions, indicating that the timing of spawning had already been chosen, and the cues they were responding to were far more regular than the weather. Therefore it would appear that tidal influences play an important role in as a proximate factor signaling gamete release for the coral spawning period at Ningaloo Reef. Coral spawning occurs during this discrete period in the month to utilize tidal conditions that are most appropriate for fertilization and dispersal.

*Lunar phase*

The main nights that coral spawning occurred (and the nights which the five species in this study participated) took place on the 7th and 8th nights following the full moon in March. This is consistent with other reports from Ningaloo that have documented the main nights of coral spawning occurring 7-10 nights after the full moon (Marchant, 1987; Simpson, 1991; Stewart, 1993). Coral spawn slicks were also observed on the surface on the 4th night after the full moon, and gametes were sighted in the water column each night thereafter, indicating that corals spawned over a five day period.

The consistency of spawning at the same time in the lunar phase each year at Ningaloo Reef, and the numerous other studies that have found a correlation between lunar phase and spawning period (Babcock, 1984; Harrison et al., 1984;
Simpson, 1985; Wallace, 1985b; Babcock et al., 1986; Richmond and Hunter, 1990; Hayashibara et al., 1993; Baird et al., 2000; Guest et al., 2002) suggest that moonlight and lunar phase are an important proximate cue for coral spawning at Ningaloo. The precise role that the lunar phase plays in signalling gamete release is unclear. As lunar and tidal phases are so closely linked, the lunar cycle may act as a calendar for corals, to compel spawning to occur during a particular tidal rhythm (Babcock et al., 1986).

4.2.2 Evidence of protracted spawning at Ningaloo Reef
While a single, large mass spawning event is apparent during the months of March/April at Ningaloo Reef (and split spawning over both March and April occurs every three years due to a 13 month lapse between spawning – see Simpson (1985)) there have also been minor spawning events in the months either side of the mass spawning event documented by other scientists (Simpson et al., 1993; Stewart, 1993). Stewart (1993) observed coral spawning occurring after both the full and new moons from March to May – a protracted spawning period of three months. The results from the present study also found evidence of spawning before the mass spawning event as some colonies of Acropora tenuis released their gametes before the mass spawning period in April, which corresponds to anecdotal reports of a coral spawning slick on the 6th March, ten days after the full moon in February (F. McGregor, pers. comm.).

Stewart (1993) proposed that this extended breeding season could arise from disturbance to the gametogenic cycles of a proportion of the colonies, whereby the affect of stress on the coral colony may assist in accelerating or prolonging the
breeding cycle for these colonies. Brief annual spawning periods are potentially risky due to expelling the entire annual reproductive clutch at one time, which could be negated by the occurrence of natural disturbances, (Harrison et al., 1984; Simpson et al., 1993) therefore protracted spawning may be an attempt to reduce the exposure of the clutch all at one time.

4.2.3 Spawning outside the mass spawning period in Coral Bay
Evidence of spawning in December/January, 3 months before the mass spawning event, was evident in *Acropora papillare* which is the first documented case of a species spawning during December at Ningaloo Reef. Studies of broadcast spawning species that do not participate in mass spawning may provide important insight into the adaptations these corals have evolved which free them from the constraints which may force so many other corals to spawn together during a discrete period (Oliver et al., 1988).

There are a number of ideas that may explain the occurrence of spawning during December in Coral Bay. Firstly, as most other species spawn during the mass spawning period in March, it would seem that this species has different preferences to many other species on the reef flat. This species was only ever found growing in very shallow water on the reef flat (never in the lagoon) and was frequently the only species exposed at low tide, indicating that it lives in an extreme environment where temperatures could get very high. In such an environment thermal stress on the colony could prevent this species from spawning during a period when temperatures are at their peak (as they are in March) and it may be more preferable to spawn in the cooler months of December/January, before the temperature reaches its
maximum. It is unknown whether this species spawns every year in December/January or just in some years.

Secondly, while the Acropora genus is a genus with considerable synchrony in spawning times, the observations of spawning of different species of Acropora worldwide indicate that some species characteristically spawn outside of the mass spawning period. A number of Acropora species have been observed spawning outside the mass spawning period on the GBR (Wallace, 1985b; Wolstenholme, 2004) and it is possible that asynchrony in the release of gametes between colonies may well be a feature of the reproductive biology of Acropora (Baird et al., 2000).

Thirdly, there may be a significant advantage for a species to spawn at a different time to everything else. Space for settlement and development is one of the most important limiting factors of coral reef development, (Shlesinger and Loya, 1985; Hatcher, 1991; Lough, 1998) thus there may be a considerable advantage gained by spawning when there is less competition for available space for settlement by new coral polyps.

The spawning of A. papillare was not directly observed, therefore it is not known exactly when this species spawns, or if there are any other species that also participate in a December/January spawning. However anecdotal reports from two Coral Bay residents of over 12 years who have witnessed corals spawning during December in other years (M. Zerbe pers. comm.) indicate that other species may also participate in spawning over this period. More research is required to investigate the occurrence of a December/January spawning event.
4.3.4 The ultimate reasons for the season of spawning at Ningaloo Reef

The results from the present study together with the results from Smith (1993) and Stewart (1993) show that to date, no species has been found to have ripe gametes in October at Ningaloo Reef. The present study closely monitored six species of Acropora and examined colonies from another 31 species in October and none were found to contain mature oocytes. Smith (1993) and Stewart (1993) examined another eight species (four Acroporidae and four Faviidae) and found no evidence of an October spawning. Currently A. papillare is the only species to be found spawning in December. Therefore, the majority of species studied so far at Ningaloo spawn during the March/April mass-spawning event, and thus strong selection pressure remains for this period to be more suitable than the rest of the year. Taylor and Pearce (1999) believe that March/April is selected for because during this period the hydrodynamics of the currents at Ningaloo cause coral spawn to be retained within the region (rather than being carried progressively south by the Leeuwin Current) and therefore local settlement rates are high. Additionally, March/April is the calmest time of the year at Ningaloo – the normally persistent strong wind has abated, and the water is frequently glassy and smooth (F. McGregor, pers. comm.). Spawning at the calmest time of the year may serve to increase the chance of fertilization, because when gametes are aggregated on the surface they would have a better chance of coming into contact with each other if it was calm rather than windy when the wind will disperse the gametes. In 1993 coral spawn slicks became trapped in Bills Bay and caused hypoxia and the mass death of corals, fish and invertebrates in the bay (Simpson et al., 1993). The cause was attributed to several environmental conditions including low swell and light winds, and therefore it could be argued that spawning at a time of light winds is not an
evolutionary advantage. However this was an atypical event that does not happen the majority of the time when corals spawn in March. Furthermore, Simpson (1993) attributed the trapping of the coral spawn not necessarily to the calm conditions, but to the corals spawning on a flood tide rather than an ebb tide, thus bringing the spawn into Bills Bay (rather than flushing it offshore as normally occurs) and then the absence of any wind, together with low swell reduced flushing and trapped the coral spawn in the bay. Therefore the calm conditions were secondary to spawning on a flood tide, which had a greater impact on the cause of the hypoxic event.

These two factors: the hydrodynamics on Ningaloo Reef in March, together with the weather patterns, support the environmental constraints hypothesis (Oliver et al., 1988) that the season of coral spawning is dictated by local environmental conditions that constrain the time of spawning to an optimal period each year.

While *Acropora papillare* is spawning outside the ‘optimal’ spawning period, possibly because environmental conditions are better suited to this species to spawn in December, this still provides evidence that corals are responding to local environmental conditions because while *A. papillare* is spawning outside the mass spawning period at Ningaloo, it spawns during the mass spawning period on the Great Barrier Reef (van Oppen et al., 2002), similarly *Acropora digitifera* spawned during the mass spawning period at Ningaloo, but does not participate in the mass spawning period on the GBR (Wolstenholme, 2004). Thus this is two examples of completely different reproductive strategies on the east and west coasts of Australia in the same species, and suggests that local environmental influences are impacting upon their reproductive cycles.
If the majority of species spawn in March possibly due to optimal environmental conditions, why then does a minority of the population spawn in the months either side of the mass-spawning period? Perhaps some species have a more flexible response to the environmental conditions and are able to apportion their gametes and release them over several months, to utilize the advantages of spawning more than once. It is likely that the same proximate cues are responsible for synchronizing gamete release each month, and the environmental conditions in the months either side of mass spawning may be less optimal but still favorable enough for those species that have the ability to prolong gamete release, to spawn.

An alternative theory on the seasonality of spawning at Ningaloo Reef refers back to the hypothesis proposed by (Simpson 1988), that spawning occurs during this season as a result of a genetic predisposition inherited from corals at a lower latitude. One of the criticisms of this theory in explaining spawning in October in Dampier was that it did not explain why corals are not spawning in the months between October and March, as corals further north have been found with ripe gametes in November and January. The observations of *Acropora papillare* spawning in December at Ningaloo may be the evidence required, of a species spawning between the months of October and March from an inherited legacy from an ancestral population in the north, to substantiate this theory. More research is required including genetic analysis to confirm this theory.
4.3 Fecundity

Measures of fecundity such as the number of eggs per polyp can provide a useful index of reproductive effort and, as such, are a useful indicator of the health of a coral (Ward and Harrison, 2000). Consequently, changes in these measures can be used as a bio-indicator of stress levels in corals. This is the first examination of fecundity in these six dominant species of the reef flat to be undertaken at Ningaloo Reef, therefore these results provide important baseline information with which a comparison can be made in future years, as the inevitable development of Coral Bay and the Ningaloo Reef progresses.

4.3.1 Oocyte development and degeneration

Three species out of the six species in this study showed a decline in the number of eggs per polyp between January and March, indicating that in these species there was a degeneration of developing oocytes. There are other reports of the number of oocytes in each ovary being reduced during development in Acropora species however it is not well understood and it is not known whether environmental, nutritional or other physiological limitations induce oocyte degeneration in corals (Harrison and Wallace, 1990).

In the only species in which fecundity could be measured in all three months of October, January and March, Acropora millepora, the results showed that there was no decline in fecundity between October and January, only a decline between January and March, at the end of the reproductive cycle just prior to spawning. This means that at the same time that eggs are growing rapidly they are also being reabsorbed. This observation would suggest that there is strong link between
increased nutritional requirements for growth, and reabsorption of oocytes and provides a rational explanation for its occurrence.

Each species in which a decline in fecundity was recorded, was located on the deeper transect, none of the colonies on the shallower transect recorded a decline in fecundity. *Acropora digitifera* was the only species located on both transects; on the deep transect there was a decline in fecundity, but on the shallow transect there was not. This would suggest that under less optimal conditions eggs are reabsorbed to supply required energy for the development of the remainder – thus a strategy by which the maximum number of eggs can develop if conditions in the later stages of development are optimal. There are a number of conditions on the deep transect that may make environmental conditions less favorable, which include levels of light, water movement and sedimentation. Although the difference in depth between the two transect was < 2m, it may have been sufficient to reduce the rate of photosynthesis by zooxanthellae and the amount of energy available for egg development. Additionally the deeper transect is also located on the floor of the lagoon and is much more sheltered from water movement potentially proving poorer nutrition and increased levels of sedimentation, both of which could reduce energy available to egg development.

Higher fecundity in colonies of *A. digitifera* on the shallower transect was also accompanied by larger colony size. Thus a higher number of eggs per polyp in the colonies on the shallow transect may also be due to their larger size, in contrast to, or in addition to, better environmental conditions. Several studies have demonstrated that larger colonies produce more eggs per polyp than smaller
colonies that are reproductively mature (Sakai, 1998). However the fact that colonies were larger may also be related to more favourable environmental conditions, or simply reflect the modal age of the population.

### 4.3.2 Fecundity in Dampier compared to Coral Bay

Fecundity and egg size was greater in Coral Bay than in Dampier when compared in *Acropora millepora*. Other studies have shown that cooler temperatures depress growth rates in corals therefore in a cooler environment the amount of energy devoted to reproduction may be less, as more energy must be devoted to growth (Kojis 1986). As sea temperature is 5°C cooler in Coral Bay than in Dampier during summer (Bureau of Meteorology, 2005) it was expected that fecundity would be higher in Dampier due to the warmer water. These results illustrate that despite the warmer water in Dampier, conditions for reproduction may be better in Coral Bay than in Dampier.

The lower fecundity in *A. millepora* in Dampier than in Coral Bay may be due to less optimal conditions for reproduction due to more stresses or disturbances, such as cyclones or sedimentation. Dampier has a higher incidence of cyclones than Coral Bay (Pearce *et al.*, 2003; CALM, 2004) and cyclones are known to have damaging effect on fecundity because they cause high levels of sedimentation (Gilmour, 2004) as well as damage and fragmentation to colonies which has been shown to reduce fecundity (Lirman, 2000).

Sedimentation and water turbidity is another likely reason that fecundity is higher in Coral Bay than in Dampier. Sedimentation has been shown to affect reproduction because water clarity is decreased, reducing energy available for photosynthesis,
and resources are diverted away from sexual reproduction and into other functions such as cleaning and maintenance (Kojis and Quinn, 1984; Jokiel, 1985; Tomascik and Sander, 1987; Harrison and Wallace, 1990). Dampier has higher rates of sediment deposition than Coral Bay, one reason for this being the Fortesque River that enters the sea west of the archipelago and during floods causes large amounts of sediment to enter the archipelago (Pearce et al., 2003). In contrast Coral Bay has no river nearby and therefore lower levels of sedimentation. Dampier also has higher turbidity than Coral Bay because Dampier has a gently sloping sea bed composed of sand and rock which are inundated and exposed twice daily due to semi-diurnal tides, resulting in higher turbidity in Dampier compared to Ningaloo where the substrate is solid limestone.

In light of the differences between Dampier and Coral Bay it would seem that environmental conditions for corals in Dampier reduce energy availability for reproduction, compared with Coral Bay. Thus the impact of disturbances on the reproductive output of coral in the Dampier Archipelago, might have more of an impact than water temperature.

4.3.3 Fecundity at Ningaloo compared to elsewhere
Polyp fecundity and mature oocyte diameter measured in this study at Coral Bay are greater than that reported for the same species at other locations in the World-wide database of Acropora (Wallace, 1999) and this was consistent for four species.

One explanation to account for these findings is that environmental conditions at Ningaloo Reef result in high levels of fecundity. The interaction of the Leeuwin Current bringing warm water from the north onto the reef, and the Ningaloo current
bringing cooler water from the south, causes a recirculation of water in the region and generates eddies that result in a significant degree of upwelling in this region, providing a source of cold nutrient rich water onto the reef (Taylor and Pearce, 1999; D'Adamo and Simpson, 2001). This upwelling would provide a source of rich nutrients to the organisms on the reef and could substantially increase productivity (Sorokin, 1995) and thus fecundity, at Ningaloo Reef. Ningaloo is also a classic fringing reef where surf coming over the reef brings an inundation of richly oxygenated water into the lagoon, which has a rapid flushing time of less than 24 hours (Hearn and Parker, 1988).

As there are no major rivers near Ningaloo there is very little runoff entering the water. In comparison, on the east coast there are at least 6 major rivers that flow into the ocean on the Great Barrier Reef (Wolanski et al), which have the potential to increase levels of eutrophication relative to Ningaloo Reef. Waters discharged to reefs from rivers can contain nutrient fertilizers, pesticides, insecticides, herbicides and other various effluents (Sorokin, 1995) which accumulate in the tissues of corals and are toxic. Eutrophication also increases turbidity, which decreases light available for photosynthesis therefore having a direct impact upon fecundity.

Another explanation for the higher levels of fecundity observed at Ningaloo Reef, is that it could be associated with different symbionts residing in the tissues of the corals. As yet there have been no studies conducted comparing the zooxanthellae on the west coast with the east coast, so it is not known whether corals on the west coast harbour the same species of zooxanthellae to the east coast and what influence (if any) that may have on fecundity. Some studies have shown that the distribution of
of dinoflagellates is correlated with latitude (Rodriguez-Lanetty and Hoegh-Guldberg, 2003) and that different clades of zooxanthellae predominate in the Caribbean, the Red Sea and the GBR (Karako-Lampert et al., 2004). Currently there have been no studies on the link between different clades of zooxanthellae and fecundity, however Little et al. (2004) showed that different zooxanthellae provide different levels of nutrients and energy to the host, which would suggest that zooxanthellae have the ability to impact upon fecundity. More research is required to investigate the impact of different symbionts on fecundity and reproduction, and how this may vary geographically.

4.4 Conclusion

The aims of this project were ultimately to add to the knowledge base of mass coral spawning, a phenomenon of which a true understanding is still elusive. As we learn more about this remarkable event, the patterns that have been observed in the last 20 years begin to break down, as more exceptions to the paradigm that the mass spawning of corals in Australia occurs during one short, annual period, emerge. The patterns of coral spawning at two different locations on the north west coast of Western Australia that were observed in this study provide more evidence of such exceptions, where coral spawning has been shown to occur biannually in some species, and well outside the usual mass spawning period in others.

Some of the proximate cues for coral spawning that have been observed elsewhere could not be applied to the west coast (e.g. temperature), which adds to what we know about proximate cues on different reefs, and supports the notion that each
individual reef is unique and has its own distinctive relationship with the physical environment.

The results from this study of coral fecundity provide baseline data for Ningaloo Reef and again suggest that conditions on this reef may be unique. The observation that fecundity at Ningaloo is higher than elsewhere for the species studied reinforces Ningaloo’s high conservation status. It is also clear however that much further study is required to better understand the factors influencing coral fecundity and, ultimately, reproductive success.


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