

**SEXUAL REPRODUCTION OF *POCILLOPORA DAMICORNIS*  
(CNIDARIA: HEXACORALLIA) AT HIGH LATITUDE OFF  
DURBAN, SOUTH AFRICA**

by

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## ABSTRACT

*Pocillopora damicornis* is one of the best-studied and most widespread of corals. Previous studies on its sexual reproduction have yielded a diverse and contradictory view of its reproductive strategy. This coral has long been considered a typical hermaphroditic brooder. However, recent studies have demonstrated that its dispersal may also occur through broadcast spawning of gametes. Since both modes of reproduction have advantages for dispersal, *P. damicornis* reproductive traits are probably driven by environmental pressures. High-latitude habitats are considered marginal for corals since they fall beyond the “normal” limits of coral development. They provide, therefore, a good opportunity to study reproductive strategies that have evolved under different environmental pressures. The pattern and timing of reproduction were studied in *P. damicornis* on the high-latitude reefs of Durban, KwaZulu-Natal, South Africa (29°S). Branches were randomly selected from colonies on a monthly basis from October 2007 to April 2008. After fixation and decalcification, the coral tissues were processed for histology and cross-sectioned to reveal the presence and stages of gametes within the polyps. The number and size of gametes were estimated using image analysis. *P. damicornis* in Durban is hermaphroditic and all polyps contained oocytes and spermaries at the end of the breeding season. Since no brooding of embryos or planulae was found in the 175 polyps analysed during the seven-month study period, this coral is presumed to be a broadcast spawner in South African waters. *P. damicornis* invested seven to eight months in gametogenesis and oogenesis was initiated one month before spermatogenesis. Gametogenesis was confined to the warmer months of the year, commencing during the increase in seawater temperature at the onset of summer. Gamete development was poorly synchronised between colonies during the initial months of breeding, but mature oocyte stages were dominant in all polyps at the end of the breeding season. Spawning was inferred from the disappearance of gametes in April 2008, and may have occurred during full moon in March 2008. This happened before the drop in temperature at the end of summer. *P. damicornis* in KwaZulu-Natal exhibited a pattern and timing in its reproduction similar to that found in south Western Australia at 32°S.

**Keywords:** coral; Scleractinia; *Pocillopora damicornis*; high latitude; sexual reproduction; South Africa.

## **PREFACE**

The experimental work described in this dissertation was carried out at Treasure Beach, Durban, and histology was processed in the School of Biological and Conservation Sciences, University of KwaZulu-Natal (UKZN), Westville Campus from January 2007 to April 2009, under the supervision of Doctor A.J. Smit of the University of KwaZulu-Natal and co-supervision of Professor M. H. Schleyer and Ms A. Kruger of the Oceanographic Research Institute (ORI), Durban, South Africa.

This study represents original work by the author, and has not otherwise been submitted in any form for any degrees or diploma to any tertiary institution. Where use has been made of the work of others it is duly acknowledged in the text.

## DECLARATION - PLAGIARISM

I, ....., declare that

1. The research reported in this thesis, except where otherwise indicated, is my original research.
2. This thesis has not been submitted for any degree or examination at any other university.
3. This thesis does not contain other persons' data, pictures, graphs or other information, unless specifically acknowledged as being sourced from other persons.
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Signed

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## TABLE OF CONTENTS

ABSTRACT.....	i
PREFACE.....	iii
DECLARATION - PLAGIARISM.....	iv
ACKNOWLEDGEMENTS.....	v
BACKGROUND.....	1
INTRODUCTION.....	6
MATERIAL AND METHODS.....	9
1. Location.....	9
1.1 Physical conditions.....	9
1.2 Study site.....	9
2. Sampling procedure.....	11
3. Histology.....	12
4. Environmental factors and the timing of reproduction.....	14
5. Statistical analyses.....	15
RESULTS.....	17
1. Reproductive activity and polyp gender.....	17
2. Oocyte and spermary development.....	18
2.1. Histological examination of gonads.....	18
2.2 Gametogenesis.....	18
a. Oogenesis.....	18
b. Spermatogenesis.....	19
2.3 Duration and timing of gametogenesis.....	21
a. Timing of oogenesis.....	23
b. Timing of spermatogenesis.....	23
3. Synchronicity in gamete maturation.....	24
4. Environmental factors and the timing of reproduction.....	25
4.1 Lunar phase.....	25
4.2 Sea surface temperature (SST).....	25

DISCUSSION .....	29
1. Reproductive activity .....	29
2. Reproductive strategies .....	29
2.1 Asexual versus sexual reproduction.....	29
2.2 Broadcast spawning versus brooding.....	31
3. Oocyte and spermary development .....	32
3.1 Histological examination of the gonads .....	32
3.2 Gametogenesis .....	32
3.3 Duration and timing of gametogenesis.....	33
4. Synchronicity in gamete maturation .....	34
5. Environmental factors and the timing of reproduction .....	35
5.1 Lunar cycle .....	35
5.2 Seasonal variation in sea temperature .....	36
CONCLUSION .....	39
REFERENCES.....	40

## BACKGROUND

Reef-building corals are limited to a narrow range of environmental variables, being mostly dependent on light availability, seawater temperature, salinity, and aragonite saturation (Ladd 1977; Achituv and Dubinsky 1990; Veron 1995). Due to the presence of symbiotic algae in their tissues, corals require light for photosynthesis (Falkowski *et al.* 1984). They are therefore limited to shallow and clear water, and occur mainly above 30 m in depth (Achituv and Dubinsky 1990; Veron 1995, 2000). At a broader scale, seawater temperatures and currents are the main regulators of coral distribution (Veron 1995). Optimum temperatures for coral growth appear to be in the high twenties (25-29°C) (Vaughan and Wells 1943). It is generally accepted that reef corals are sensitive to temperatures below 18°C (Stoddart 1969), with the lower lethal limit for many corals being 14°C (Porter *et al.* 1982; reviewed in Veron 1995). Conversely, the sustained maxima of temperature tolerated by corals are estimated to be 30-34°C (Jokiel and Coles 1977; Glynn 1984; Hoegh-Guldberg and Smith 1989). Repetitive exposure to high temperature causes loss of symbiotic algae (coral bleaching), increased mortality, and reduced calcification (Jokiel and Coles 1977; Hoegh-Guldberg and Smith 1989; Brown 1997). In addition, corals require an optimum salinity of 35.5 PSU that may be disrupted by precipitation, river outflow or evaporation (Coles and Jokiel 1978; Muthiga and Szmant 1987). They occur, therefore, away from river mouths and estuaries, and in areas where the salinity is stable over long timescales (Hoegh-Guldberg and Smith 1989; Coles and Jokiel 1992). Finally, aragonite saturation controls reef distribution since declining levels of this parameter result in diminished reef accretion (Harriott and Banks 2002; Perry and Larcombe 2003). The degree of aragonite saturation varies with latitude (*ca.* 4.1 at the equator, and *ca.* 1.5 at the poles) and decreases with temperature (Mucci 1983; Kleypas *et al.* 1999a). It is also being affected by ocean acidification associated with climate change (Kleypas *et al.* 1999b; Hoegh-Guldberg *et al.* 2007). Consequently, reefs are mostly associated with warm and nutrient-poor shallow tropical water and largely confined between the 20° parallels.

Several studies have shown that corals are able to adapt to environmental conditions previously considered hostile for their development (reviewed in Kleypas *et al.* 1999a). In numerous locations, corals occur in marginal habitats that fall beyond their 'normal' limit of development, often at high latitude (Kleypas *et al.* 1999a). In such environments, corals do not necessarily form true accretive reefs (*i.e.* due to low aragonite saturation and temperature),



and are considered “coral communities”. Marginal reefs and coral communities are found on both the south-east and west coasts of Australia (Hatcher 1985; Spalding *et al.* 2001), in Japan (Kan *et al.* 1995; Yamano *et al.* 2001), in Florida and the Gulf of Mexico (Duane and Meisburger 1969; Goldberg 1973), in Bermuda (Laborel 1966; Thomas and Logan 1992), in the eastern Pacific and South America (Cortés 1997; Castro and Pirés 2001), and on the east coast of southern Africa (Riegl *et al.* 1995). Along the latter, they find their southernmost limit of distribution in KwaZulu-Natal, South Africa (Riegl *et al.* 1995; Schleyer 1999, 2000). Here they develop on a thin veneer of Pleistocene sandstone substrata which run parallel to the coast (Ramsay and Mason 1990; Ramsay 1996). Certain coral species (*i.e.* mainly pocilloporids) occur in the shallow bays associated with the rocky shores of this region to 30°S (Riegl 1993).

Wells (1957) and Veron *et al.* (1974) suggested that coral reproduction is inhibited in the cooler water temperature that occurs at high latitude. Therefore, it was hypothesised that the maintenance of marginal coral populations was mainly dependent on recruitment input from tropical reefs (Veron *et al.* 1974; Veron and Done 1979; Grigg 1983). High-latitude coral communities would then be considered pseudo-populations since they do not contribute to subsequent regeneration (*see* van Woesik 1995). However, several studies have shown that marginal reefs and coral communities are sexually reproductive and self-seed at high latitudes exposed to low temperature. These include coral populations in Tarut Bay (Fadlallah 1996) and Kuwait, the Arabian Gulf (Harrison 1995), Houtman Abrolhos Islands, Western Australia (Babcock *et al.* 1994), Shikoku Island (van Woesik 1995) and Tokyo Bay, Japan (Harii *et al.* 2001). Hence, most marginal coral communities represent true isolated populations.

Reef-building corals display various patterns of reproduction being able to reproduce both sexually and asexually. Asexual processes result in clonal propagules and involve the production of larvae (Stoddart 1983; Ayre and Reising 1986; Ward 1992), fragmentation of large colonies (Highsmith 1982), polyp bail-out (Sammarco 1982), and production of specialised buds (Rosen and Taylor 1969). In contrast, sexual reproduction occurs through gametogenesis and fertilisation and results in genetically diverse planula larvae which may settle, metamorphose and develop into primary polyps (Harrison and Wallace 1990; Richmond and Hunter 1990).

Corals exhibit four types of sexual reproduction which are: (1) hermaphroditic broadcast spawner; (2) gonochoric broadcast spawner; (3) hermaphroditic brooder; (4) gonochoric brooder (Fadlallah 1983; Harrison and Wallace 1990). Most coral species are hermaphroditic, having male and female gametes occurring in the same polyp; the remainder is gonochoric, having separate male and female colonies. Brooding of embryos has long been accepted as the dominant mode of reproduction in corals, yet recent studies have shown that the majority of corals are broadcast spawners (Harrison and Wallace 1990; Richmond and Hunter 1990). In brooding colonies, fertilisation and larval development occur in the polyps, and planulae are brooded internally until maturity and then released. Conversely, gametes from broadcast spawning colonies are shed into the surrounding waters, and fertilisation and larval development is external. Patterns of planula recruitment vary depending on the mode of reproduction (Harrison and Wallace 1990). Planula larvae of broadcast spawning corals are usually associated with high dispersal since they may remain for 4-6 days in seawater before becoming competent for settlement and metamorphosis (Babcock and Heyward 1986; Richmond 1987a; Harrison and Wallace 1990). Conversely, planulae of brooding species are released at an advanced developmental stage, and tend to settle near the parental colony (Stimson 1978; Fadlallah 1983; Harrison and Wallace 1990; Sakai 1997).

Similar species may exhibit different modes of reproduction depending on locality (Harrison and Wallace 1990). For instance, *Pocillopora damicornis* is a broadcaster at Rottnest Island, south Western Australia (Ward 1992), but broods planulae in Okinawa, Japan (Diah Permata *et al.* 2000). Another pocilloporid species, *P. verrucosa*, also manifests differing reproductive patterns depending on geography. It is a broadcast spawner in South Africa (Kruger and Schleyer 1998) and the Red Sea (Shlesinger and Loya 1985) but broods planulae at Enewetak Atoll (Stimson 1978). Similar variation in the reproductive pattern is also observed in other coral families such as the Acroporidae. For example, *Acropora humilis* broods planulae at Enewetak Atoll (Stimson 1978), but broadcasts gametes at Heron Island, Great Barrier Reef (Bothwell 1981).

Mass spawning occurs when colonies from different species release their gametes in synchrony (Willis *et al.* 1985). Although this event has been well-documented on the Great Barrier Reef (Harrison *et al.* 1984; Wallace 1985; Willis *et al.* 1985; Babcock *et al.* 1986), it does not occur elsewhere (*e.g.* Shlesinger and Loya 1985). Synchronised mass spawning has the advantage of increasing the chances of fertilisation and genetic mixing between colonies, and of reducing overall predation by predator satiation (Oliver *et al.* 1988). Hypotheses have

been formulated on the major cues that may influence synchronization in gametogenesis and spawning (Harrison *et al.* 1984; Jokiel *et al.* 1985; Schlesinger and Loya 1985; Wallace 1985; Willis *et al.* 1985; Babcock *et al.* 1986; Oliver *et al.* 1988; Mendes and Woodley 2002). Temperature, lunar cycle, tides and solar radiation are considered proximate cues, which operate at successively finer time scales (Harrison *et al.* 1984; Babcock *et al.* 1986; Oliver *et al.* 1988; Penland *et al.* 2004). On the Great Barrier Reef, Babcock *et al.* (1986) suggested that sea temperature controls the time of year, monthly lunar or tidal cycles control the time of month, and diurnal light cycles control the hour of spawning. Yet, the timing of synchronous spawning varies geographically (Harrison and Wallace 1990) and other environmental factors (or combination of factors) have to be considered (Harrison and Wallace 1990).

Mass spawning has also been reported to occur at high latitude despite regional variations in environmental cycles (Babcock *et al.* 1994). On the marginal reefs of the Houtman Albrosos Islands, Western Australia, annual synchronous spawning occurs in the same month as on the tropical Ningaloo Reef, Western Australia, although the timing of peak seasonal temperature in the two regions is substantially different (Babcock *et al.* 1994). Spawning in the Houtman Albrosos Islands occurs at temperature values that differ by 5-7°C from those on the tropical reefs and it does not seem to be synchronised with the tidal cycle (Babcock *et al.* 1994). In contrast, mass spawning on Ningaloo Reef is associated with the highest Sea Surface Temperature (SST), and occurs at neap tide as observed on the Great Barrier Reef (Harrison *et al.* 1984; Babcock *et al.* 1986). This suggests that corals may respond differently to environmental factors depending on local conditions. Therefore, comparisons between high latitude and tropical reefs may provide a means of isolating and identifying common factors which may synchronize spawning in coral (Babcock *et al.* 1994).

The coral *P. damicornis* extends in distribution from the Red Sea and eastern Africa to the Indo-West Pacific, and the central and eastern Pacific (Veron and Pichon 1976a; Veron 2000). It occurs in shallow reef environments from fringing to exposed offshore reefs (Veron 2000). It is generally hermaphroditic but exhibits variability in its reproductive mode, being either a brooder or broadcast spawner depending on locality (Harriott 1983a; Stoddart and Black 1985; Glynn *et al.* 1991; Ward 1992; Diah Permata *et al.* 2000). In addition, it may reproduce asexually through the production of brooded larvae (Stoddart and Black 1985; Ward 1992). Lunar cycle and temperature are known to influence the timing of planulation and/or spawning in *P. damicornis* (Harriott 1983a; Richmond and Jokiel 1984; Jokiel 1985;

Jokiel *et al.* 1985; Tanner 1996). Other factors have yet to be considered since the timing of reproduction varies between localities. The sexual reproduction of *P. damicornis* has been investigated in various localities (e.g. Harriott 1983a; Stoddart and Black 1985; Glynn *et al.* 1991; Ward 1992; Diah Permata *et al.* 2000). However, no study has focused on this aspect of its biology in South Africa where it occurs on the east coast, including the reefs along the shores of Durban in KwaZulu-Natal.

## INTRODUCTION

*Pocillopora damicornis* is one of the most widespread and best-studied scleractinian corals. It exhibits diversity in its life-history traits with major differences between widely separated populations (Richmond 1985). Studies on its sexual reproduction have yielded a diverse and contradictory view of its reproductive strategy (Stoddart 1983; Ward 1992; Miller and Ayre 2004). This coral has long been considered a typical hermaphroditic brooder (Marshall and Stephenson 1933; Atoda 1947; Harrigan 1972; Stimson 1978; Harriott 1983a) with peak planular production occurring during summer months (Richmond and Jokiel 1984; Tanner 1996). Yet, depending on locality *P. damicornis* can also be a broadcast spawner with an annual gametogenic cycle (Stoddart and Black 1985; Glynn *et al.* 1991; Ward 1992; Diah Permata *et al.* 2000). Furthermore, it can generate asexually-produced planulae (Stoddart 1983; Ward 1992) that are similar to sexually-produced planulae and that cannot be differentiated by direct observation (Stoddart 1983). Such variations in the mode of reproduction in a coral are unprecedented (Ayre and Miller 2004). Further histological studies are required to determine the origin of planulae and the dominant pattern of reproduction in *P. damicornis*.

Colonies of *P. damicornis* inhabit the shallow bays and coves associated with the rocky shores of KwaZulu-Natal (29°S), South Africa, close to their southernmost limit of distribution (Riegl 1993; Veron 2000). This environment is considered marginal since it falls beyond the “normal” limits of coral distribution (Kleypas *et al.* 1999a). In contrast with the tropics, high-latitude reefs exhibit elevated levels of natural induced stress due to lower temperature, higher seasonal variation, and increased competition with macro-algae (Glynn and Stewart 1973; Johannes *et al.* 1983; Kleypas *et al.* 1999a). Furthermore, these habitats are often associated with frequent and severe natural physical disturbances (*e.g.* storms) associated with cold fronts (Forristall and Ewans 1998; Rouault *et al.* 2002).

Under such conditions, *P. damicornis* reproductive success will be highly dependent on the mode of larval dispersal. Since this coral exhibits plasticity in its life-history traits, its reproductive strategy is likely to be driven by these environmental pressures (Williams 1975; Stearns 1989). Both conditions (asexual versus sexual) and modes (broadcast spawning versus brooding) of reproduction have advantages depending on environmental parameters.

Asexual reproduction may be favoured in stable habitats to multiply locally-adapted clones (Williams 1975; Glesener and Tilrnan 1978; Maynard Smith 1978; Bell *et al.* 1988; Stearns 1989; Carvalho 1994; Karlson *et al.* 1996) while sexual reproduction can produce genotypically diverse colonists that may adapt to changing environments (Williams 1975; Maynard Smith 1978; Carvalho 1994). Furthermore, brooding may favour local colonisation since planulae are released at an advanced developmental stage, and may settle soon close to the parental colonies (Stimson 1978; Fadlallah 1983; Harrison and Wallace 1990; Sakai 1997). Conversely, broadcast spawning of gametes is often associated with higher fecundity and wide planular dispersal and may be a means of “escaping” from unsuitable local habitats (Willis *et al.* 1985; Babcock *et al.* 1986; Babcock and Heyward 1986; Harrison and Wallace 1990). Therefore, a comparison of the reproductive strategy of *P. damicornis* at this high-latitude locality with those on tropical reefs may reveal specific adaptation of this coral to its environment.

Hostile environmental conditions at high latitude can affect coral metabolism, yielding a lower growth and halted or reduced sexual activity (Wells 1957; Glynn and Stewart 1973; Veron *et al.* 1974; Coles and Jokiel 1978; Harriott 1999). Corals are therefore expected to exhibit decreased reproductive activity at high latitude that may be estimated through failure to generate reproductive products or reduced gamete production, diminished fertilisation, and decreased amounts of lipid in the planulae (Ward 1995; Fabricius 2005). At present, few studies have focused on the effect of the environmental conditions associated with marginal habitats on the reproduction of corals (Babcock *et al.* 1994). Further studies are needed to compare the reproductive activities of similar species at different latitudes to reveal how corals maintain their populations in marginal environments.

Low seawater temperature is generally accepted to be the main factor affecting reproduction at high latitudes (Wells 1957; Veron *et al.* 1974; Jokiel and Guinther 1978). It is known to reduce coral fecundity and the duration of the breeding season in *P. damicornis* and *P. elegans* (Glynn *et al.* 1991). In addition, it can alter the quality of the reproductive products as reported for the soft coral *Heteroxenia fuscescens* in the northern Red Sea (Ben-David Zaslów and Benayahu 1996; Ben-David Zaslów *et al.* 1999). During winter, this coral produces a higher proportion of deformed planulae that are unable to settle (Ben-David Zaslów *et al.* 1999). Low temperature can also affect coral recruitment (Harriott and Banks 1995; Hanny *et al.* 2001). Jokiel and Guinther (1978) found that the number of new recruits decreases below 26°C in *P. damicornis* with the lowest recruitment rate occurring below

24°C. Therefore, the capacity of coral to reproduce and recruit at high latitudes is presumed to be diminished compared to the tropics.

The highest rate of fertilisation is ensured when gametogenesis and spawning are synchronised between similar species (Harrison *et al.* 1984; Willis *et al.* 1985; Babcock *et al.* 1986; Oliver *et al.* 1988). Environmental factors, such as lunar cycle, seasonal variation in sea temperature and solar insolation, are known to influence the timing and synchrony of reproduction in corals (Harrison *et al.* 1984; Jokiel *et al.* 1985; Schlesinger and Loya 1985; Wallace 1985; Willis *et al.* 1985; Babcock *et al.* 1986; Oliver *et al.* 1988; van Woesik *et al.* 2006). Yet similar species may respond differently to these factors depending on locality (Harrison and Wallace 1990). For instance, brooding colonies of *P. damicornis* planulate during new moon at Enewetak (Richmond and Jokiel 1984), and in Japan (Diah Permata *et al.* 2000), while larval release occurs at full moon in Hawaii (Harrigan 1972; Stimson 1978) and on the Great Barrier Reef (Harriott 1983a). Since the environmental factors vary geographically, corals should adapt to the local conditions to maximise their reproductive success (Babcock *et al.* 1986; Oliver *et al.* 1988). Therefore, different patterns of timing and synchrony are expected between widely separated species (Wilson and Harrison 2003).

This study aims to document the reproductive strategy of *P. damicornis* at high-latitude off Durban, South Africa and to compare it with those observed in the tropics. Its overall objective is therefore to determine how latitude and the associated environmental conditions may affect coral reproduction. In particular, this study addresses questions concerning (1) the fecundity of *P. damicornis* close to its southernmost limit of distribution in South Africa; (2) its reproductive strategy; (3) the environmental factors associated with its synchronicity and timing of reproduction at this high latitude.

## MATERIAL AND METHODS

### 1. Location

#### 1.1 Physical conditions

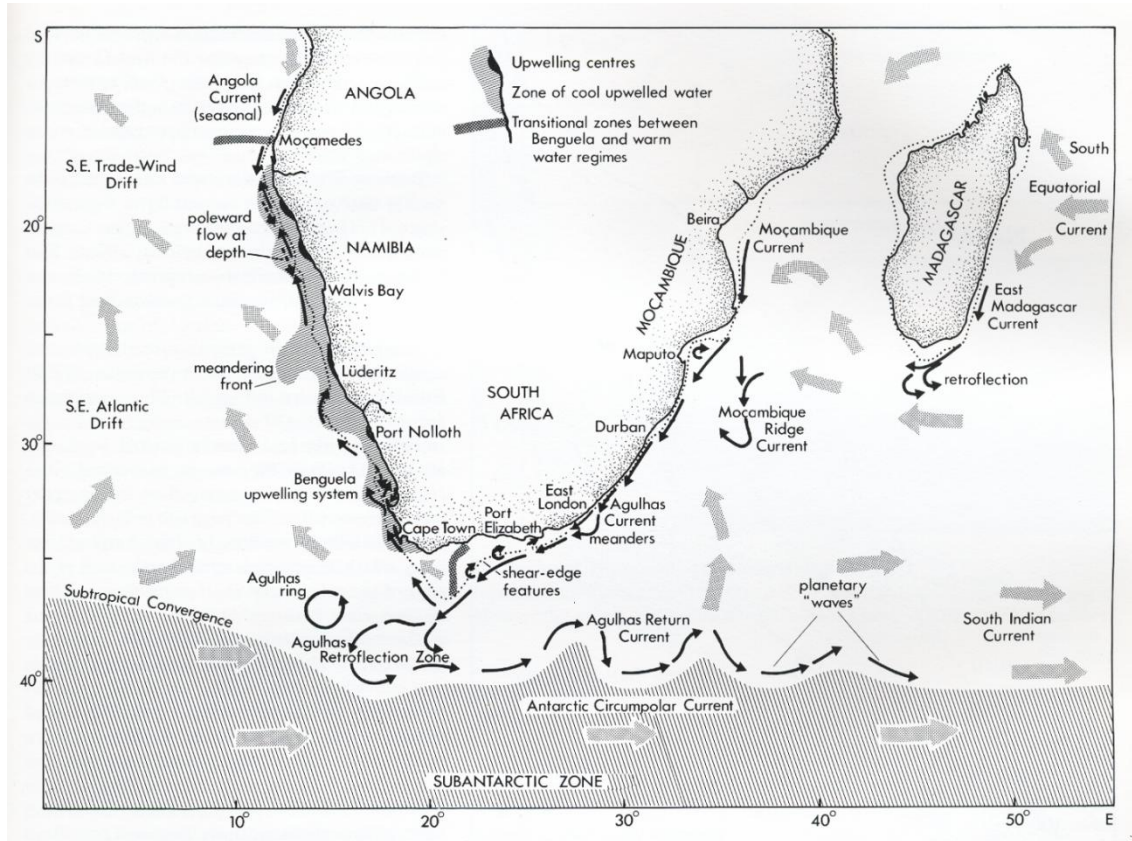
This study was conducted on the coast of KwaZulu-Natal, South Africa that is influenced by the warm, southward-flowing Agulhas Current (Fig. 1). This current is formed off southern Africa by the confluence of tropical water from the Mozambique Channel, of subtropical water derived from the East Madagascar Current flowing past the southern tip of Madagascar and the Agulhas retroflexion (Lutjeharms 2006). While the current flow is largely linear and follows the shelf break close inshore, it does generate cyclonic eddies on its western boundary (Lutjeharms 2006). The average surface speed of the Agulhas current is  $1.5 \text{ m}\cdot\text{s}^{-1}$  and it has a strength of 60 Sverdrup, a rate comparable with the flow of the Gulf Stream in the western tropical Atlantic (Lutjeharms 2006).

Since the current comprises a mixture of tropical and subtropical waters, the water that flows along the KwaZulu-Natal is warm and nutrient-deficient. The water temperature along the Durban coastline varies seasonally from a minimum of  $18.5^{\circ}\text{C}$  in winter to a maximum of  $26^{\circ}\text{C}$  in summer (1981-2008; KwaZulu-Natal Sharks Board *unpublished data*). The mean annual temperature is  $22.1^{\circ}\text{C}$  (1981-2008; KwaZulu-Natal Sharks Board, *unpublished data*), with August and March being respectively the coolest and warmest months of the year (KwaZulu-Natal Sharks Board *unpublished data*). Salinity in the current varies between 35.0 to 35.5 PSU. The tidal flux is *ca.* 2 m at spring tides and 1 m at neap tides (Schleyer 1995). In general, the coastline of KwaZulu-Natal is straight and exposed to wind that blows parallel to the coast giving rise to substantial swells and water movement (Schleyer 1995).

#### 1.2 Study site

*P. damicornis* colonies were collected in four rocky pools at Treasure Beach ( $29^{\circ}58'S$ ,  $30^{\circ}58'E$ ), 10 km south of Durban (Fig. 2A). Due to difficult access and isolation, these pools were not unduly affected by human activities such as fishing or bathing. They measured approximately 2-5 m across with a depth range from 0.7-1.8 m. A great diversity of organisms inhabited the pools, ranging from seaweed and zoanthids to juvenile fish and corals, attesting to the relative health of the pools.





**Figure 1:** Physical oceanography around southern Africa. General background drifts are shown by grey arrows, local currents by thin black arrows. From Payne and Crawford (1989).



**Figure 2:** **A,** View of the rocky shores at Treasure Beach, Durban, South Africa, where colonies of *Pocillopora damicornis* were collected. **B,** Typical colony of *P. damicornis* in the shallow bay (1m deep) off Treasure Beach. Both photos were taken on the 13/11/2007.

Twenty-four colonies of *P. damicornis* inhabited the four pools (Fig. 2B). Due to intense wave exposure, the pools were constantly flushed even at low tide. Therefore, their temperature and salinity was similar to those of the surrounding water.

## 2. Sampling procedure

Sampling was conducted on a monthly basis from October 2007 to April 2008 (Table 1). Each month, five branches were randomly selected from *P. damicornis* colonies and removed using garden shears. Since the size at first reproduction of *P. damicornis* colonies has been estimated at 4-7 cm (Harrigan 1972; Stimson 1978; Holloran *et al.* 1986), only colonies bigger than 10 cm in diameter were sampled to prevent collection of immature colonies with reduced fecundity. In an attempt to avoid selecting cloned colonies, the samples were collected at least two meters apart. The samples were fixed in 4% formal-saline immediately after collection.

**Table 1:** Dates and lunar cycle when samples of *Pocillopora damicornis* were collected at Treasure Beach, Durban, South Africa for studies on their reproductive potential. FM, full moon; NM, new moon; d, day.

<i>Sample no.</i>	<i>Date</i>	<i>Lunar phase</i>
<b>I</b>	18/10/07	NM + 7d
<b>II</b>	24/11/07	FM – 2d
<b>III</b>	28/12/07	FM + 4 d
<b>IV</b>	19/01/08	FM – 3 d
<b>V</b>	06/02/08	NM – 1 d
<b>VI</b>	03/03.08	NM – 4 d
<b>VII</b>	06/04/08	NM

After 10 to 15 days of fixation, coral nubbins were gradually decalcified in 1% to 3% hydrochloric acid (HCl) solution made up with distilled water according to the protocol described by Wallace (1985). This procedure is quicker than that used by Diah Permata *et al.* (2000) and therefore avoids the disintegration of the tissues. It is also cheaper and more convenient than those used by Kruger and Schleyer (1998) and Glynn *et al.* (1991) which involve decalcification in formal-nitric acid solution and in a mixture of HCl, EDTA, and sodium potassium tartrate respectively. After three to four days, the coral nubbins were completely decalcified. The remaining coral tissue was then rinsed and stored in 70% ethanol.

### 3. Histology

Gamete development was assessed in histological preparations of *P. damicornis*. Decalcified tissue was cut into 3 × 2 cm pieces comprising 30 to 60 polyps. Tips and bases of the branches were discarded because intermediate segments were reported to be the most fecund (Harrigan 1972; Stimson 1978). The tissues were then placed in histological cassettes, dehydrated in a series of alcohols, and cleared using xylene (Kruger *pers. comm.*; Table 2). Lastly, the tissues were embedded in histological paraffin wax (melting point 57-60°C) following the protocol described in Table 2 (Kruger *pers. comm.*).

**Table 2:** Manual embedding procedure for coral tissues employed in the preparation of the decalcified *Pocillopora damicornis* specimens (Kruger *pers. comm.*)

	<i>Chemical</i>	<i>Processing time in hours</i>
<b>Dehydration</b>	Ethanol 30%	2
	Ethanol 50%	2
	Ethanol 70%	2
	Ethanol 90%	2
	Ethanol 100% (1)	2
	Ethanol 100% (2)	1
	Xylene	3
<b>Embedding</b>	Paraffin wax (1)	3
	Paraffin wax (2)	3
	Paraffin wax (3)	1

**Table 3:** The composition of Erlich's haemalum stain (Drury and Wellington 1967)

<b>Chemical</b>	<b>Quantity</b>
<b>Haematoxylin</b>	2 g
<b>Absolute ethanol</b>	100 ml
<b>Glycerol</b>	100 ml
<b>Distilled water</b>	100 ml
<b>Glacial acetic acid</b>	10 ml
<b>Potassium aluminium sulphate</b>	10 g
<b>Sodium iodate</b>	0.3 g

Cross-sections of 7 µm were cut with a microtome (Microm HM310) and one section in every four (one section every 28 µm) was mounted on a glass slide. Twenty serial sections

were cut for each sample, corresponding to a total thickness of 560  $\mu\text{m}$ . The sections were then stained with Ehrlich's haemalum stain (Drury and Wellington 1967; Table 3) and aqueous eosin solution (Mahoney 1966; Table 6) following the staining procedure described by Kruger and Schleyer (1998; Table 5). The Ehrlich's haemalum stain was prepared 8 h in advance and sodium iodate was added 1 h before use. Permanent slides were made, using DPX microscopic mountant and cover slips.

**Table 4:** The composition of aqueous eosin solution (Mahoney 1966)

<i>Chemical</i>	<i>Quantity</i>
<b>Eosin (water soluble)</b>	1g
<b>Distilled water</b>	100 ml

To assess the reproductive stage of the corals, five polyps per colony were randomly selected from the serial sections. Histological sections were examined under a compound microscope (NIKON Eclipse 8i), and photographed using a NIKON DXM1200C digital camera. The size and number of oocytes and spermaries were measured using Image Pro Plus 6.0 analysis (Media Cybernetics Inc.) and the measurements were then exported to Excel 2007 (Microsoft©) for compilation. Because of deformation, the size of oocytes and spermaries was estimated by calculating the mean values of the maximum and minimum diameters at right angles.

The gametogenic stages were identified following the descriptions of Stoddart and Black (1985), Glynn *et al.* (1991) and Diah Permata *et al.* (2000). These descriptions are summarised in Tables 6 and 7. The different stages were classified in four categories defined by Stoddart and Black (1985) and their frequency was noted.

**Table 5:** Staining procedure adapted from Kruger and Schleyer (1998).

	<i>Chemical</i>	<i>Processing times</i>
<b>Hydration</b>	Xylene	10 min
	Ethanol 100% (1)	9 s
	Ethanol 100% (2)	9 s
	Ethanol 90%	9 s
	Ethanol 70%	9 s
	Ethanol 50%	9 s
	Tap water	9 s
<b>Staining</b>	Ehrlich's haemalum	20 min
	Tap water	9s
	Warm tap water (30°C)	Until tissue turned purple blue
	Aqueous eosin	70 s
	Tap water	9 s
<b>Dehydration</b>	Ethanol 30%	9 s
	Ethanol 50%	9 s
	Ethanol 70%	9 s
	Ethanol 90%	9 s
	Ethanol 100% (1)	9 s
	Ethanol 100% (2)	9 s
	Xylene (1)	5 min
	Xylene (2)	5 min

#### 4. Environmental factors and the timing of reproduction

The correlation of lunar phase with *P. damicornis* gametogenesis was recorded by noting the timing of gametogenesis with lunar phase obtained for Durban from the South African Astronomical Observatory ([www.saaao.ac.za](http://www.saaao.ac.za)). In addition, the correlation of gamete stages in the polyps was noted with the SSTs measured by the KwaZulu-Natal Sharks Board (*unpublished data*; accuracy 0.5°C) at the Durban shark nets (400 m offshore) from January 1981 to March 2009. Monthly SSTs were calculated for the study period and expressed as mean  $\pm$  SD.

**Table 6:** *Pocillopora damicornis*. Classification of the oogenic stages according to different studies.

Stage	Stoddart and Black (1985)	Glynn <i>et al.</i> (1991)	Permata <i>et al.</i> (2000)
<b>I</b>	Multiple oocytes per ovary; oocytes usually <50 µm (smallest oocyte: 10 µm in diameter).	Enlarged interstitial cell with large nucleus in the mesenteric mesoglea; 10 to 20 µm in diameter.	Oocyte with a germinal vesicle and a prominent nucleolus. Some contain a few yolk granules; less than 30 µm in size.
<b>II</b>	Single oocyte per ovary; oocytes <50 µm, although usually >30 µm diameter.	Enlarged interstitial cell with accumulation of cytoplasm; 20 to 40 µm in diameter.	Oocytes surrounded by a follicle layer with yolk granules arranged in a circle around the germinal vesicle; 30 to 50 µm in diameter.
<b>III</b>	Nucleolus usually well-developed and intensely stained, granular cytoplasm invested with numerous small vacuoles; 50 to 70 µm diameter.	Oocyte stained orange, sometimes a light blue, revealing a clear nucleus; undergoing vitellogenesis; 40 to 80 µm in diameter.	Large germinal vesicle located at the periphery of each oocyte. Yolk granules distributed throughout the cytoplasm. A vitelline membrane or cortical layer visible at the surface of the oocytes; 50 to 70 µm in diameter.
<b>IV</b>	Oocyte usually surrounded by a darker membrane and contracted slightly from the ovary wall; cytoplasmic vacuoles enlarged; nucleus and nucleolus less obvious than in the previous stage. No zooxanthellae evident in the oocytes. Oocytes >70 µm in diameter (up to 116 µm).	Oocytes often with an indented nucleus. Nucleus condensed, slightly detached from the vitellogenic material in some oocytes. Lipid vacuoles increased in number; often stained red to orange-brown; zooxanthellae present. About 100 µm in diameter.	Germinal vesicle no longer apparent and the follicular layer has zooxanthellae. Stage IV about 100 µm in diameter with thick vitelline membrane or cortical layer.

### 5. Statistical analyses

Fecundity was used to estimate reproductive effort (Harrison and Wallace 1990), expressed as the mean number of oocytes per polyp. Polyp fertility was based on the presence of one or more oocytes within the polyp section. Only fertile polyps were considered in determining fecundity to ascertain development during the gametogenic cycle. Data are reported as means ± standard error (SE). Statistical analyses were performed using Statistica 6.0 (Statsoft, Inc.). One-way ANOVA was carried out to determine differences in the proportion of female to male polyps.

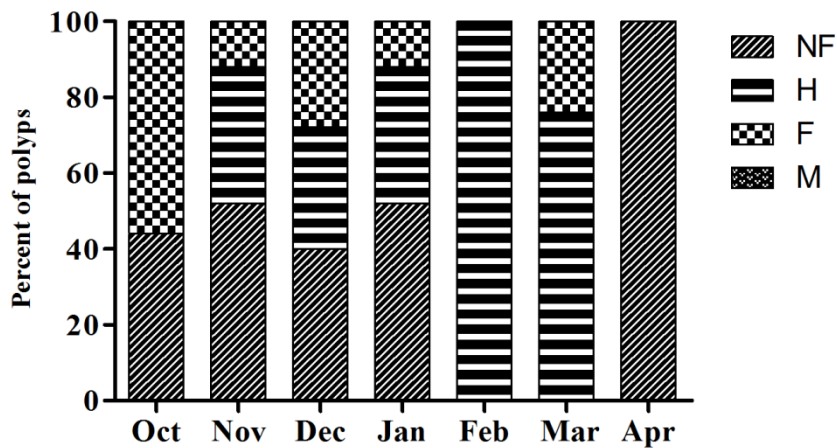
**Table 7:** *Pocillopora damicornis*. Classification of the spermatogenic stages according to different studies.

Stage	Stoddart and Black (1985)	Glynn <i>et al.</i> (1991)	Permata <i>et al.</i> (2000)
<b>I Primary spermatocyte</b>	Spermaries usually <30 µm in diameter; primary spermatocytes surrounded by a thickened spermatogonial wall.	Stage I spermaries characterised by small clusters of interstitial cells, rarely seen.	Not recognised in the material.
<b>II Secondary spermatocyte</b>	Testes of varying size; secondary spermatocytes with a characteristic 'hollow circle' appearance.	Stage II spermaries with clusters of spermatocytes; large nuclei and distinct spermary boundaries. Spermaries visible on stalk-like extensions of the mesoglea; stain orange-brown colour.	Stage II testes with thick spermatogonial wall, attached to the mesentery by a stalk.
<b>III Spermatid</b>	Large (usually >100 µm in diameter) testes; densely stained spermatids; testes not vacuolated.	Stage III spermatids more numerous than early stage spermatocytes but relatively small with small nuclei. Lumina present in some spermaries.	Stage III testes packed with spermatids, with thinner spermatogonial wall.
<b>IV Mature sperm</b>	Mature sperm with tails; the middle of the testes often vacuolated or the entire testis loosely packed with sperm.	Stage IV spermatozoa, approximately half the size of the Stage III spermatids; small and dense. Tails usually present and sperm bouquets frequently seen.	Not recognised in the material.

## RESULTS

### 1. Reproductive activity and polyp gender

The percent of non-fertile, male, female and hermaphroditic polyps of *P. damicornis* over the sampling period is shown in Figure 3. Of the 175 polyps analysed over the sampling period, 37.95% ( $n = 63$ ) showed no reproductive activity, 42.77% ( $n = 71$ ) had both oocytes and spermaries, and 19.28% ( $n = 32$ ) contained only oocytes. No colonies possessed only male gonads. In October 2007, no hermaphroditic polyp was observed within the colonies. A small percentage of female polyps was encountered throughout the breeding season, except in February and April 2008.



**Figure 3:** *Pocillopora damicornis*. Polyp gender and fertility from October 2007 to April 2008. *NF*, non-fertile; *F*, female; *M*, male; *H*, hermaphrodite.

No significant difference was found in the proportion of female to male polyps from November 2007 to January 2008 (one-way ANOVA,  $df = 1$ ,  $F = 1.49$ ,  $p > 0.05$ ). During the first months of gametogenesis, a high number of polyps were infertile. However, this trend was reversed in February and March 2008 when all the polyps contained gonads. As the breeding season progressed, the number of hermaphroditic polyps increased and reached the highest number in February and March 2008. In April 2008, no gonads were observed within the polyps.



## 2. Oocyte and spermary development

### 2.1. Histological examination of gonads

The oocyte and spermary development are illustrated respectively in Figures 4 and 5. Figure 4A shows a general view of a tissue section. Polyps appear as a circle delimited by a wall. Each *P. damicornis* polyp contained six pairs of male and female gonads arranged alternately in the gastro-vascular cavity (Fig. 4B). Gonads were attached to the edges of the basal mesentery by prominent stalks protruding into the coelenterons (Fig. 4B). Four oocytes and spermary stages were identified according to their morphology and size, and are described in §2.2 (Figs. 4C, D, E, and F and 5).

Ovaries containing early stage oocytes appeared as twisted seed pods (Fig. 4D); they became enlarged as the gametes grew until only a thin membrane persisted around the mature oocytes (Fig. 4F). Oocytes tended to develop in the upper (oral) part of the polyp cavity while spermaries developed basally. Spermaries were spherical in their early development stage (Fig. 5A) but became highly variable in shape as they developed (Figs. 5B, and C). Mature spermaries occupied a larger volume than ovaries *e.g.* up to 60-80% of the total polyp volume (Fig. 5D) and were long and folded into U-shapes in the polyp cavity (Fig. 6).

### 2.2 Gametogenesis

#### a. Oogenesis

The development of oogenesis was characterized by four oocyte stages.

Stage I oocytes were enlarged interstitial cells with little cytoplasm of uniform structure (Fig. 4C). Since early ovaries often contained 10-15 gametes in a small volume, the primary oocytes partly obscured each other. Their nucleoli were visible as dark spots, and these remained visible in the subsequent oogenic stages. The nucleus was not discernable at this stage. Stage I oocytes ranged between 5-20  $\mu\text{m}$  in diameter (mean diameter of  $17.05 \pm 2.00 \mu\text{m}$ ;  $n = 45$ ). The smallest oocyte measured was 5.84  $\mu\text{m}$  in diameter.

In Stage II oocytes, a narrow white nucleus was distinguishable around the nucleolus and the cytoplasm was increased in volume (Fig. 4D). A small number of small lipid droplets were present in the cytoplasm, indicating the initiation of vitellogenesis. Oocytes ranged between 20-40  $\mu\text{m}$  (mean diameter of  $30.31 \pm 1.39 \mu\text{m}$ ;  $n = 66$ ).

Stage III oocytes contained pronounced nuclei, often stained light pink with eosin (Fig. 4E), filling one third of the egg volume; cytoplasm occupied the remaining space. Lipid droplets were larger and more numerous than in Stage II, and were regularly distributed throughout the cytoplasm. The cytoplasmic membrane was clearly visible and stained dark purple. Stage III oocytes ranged between 40-70  $\mu\text{m}$  in size (mean diameter of  $54.22 \pm 1.05 \mu\text{m}$ ;  $n = 68$ ).

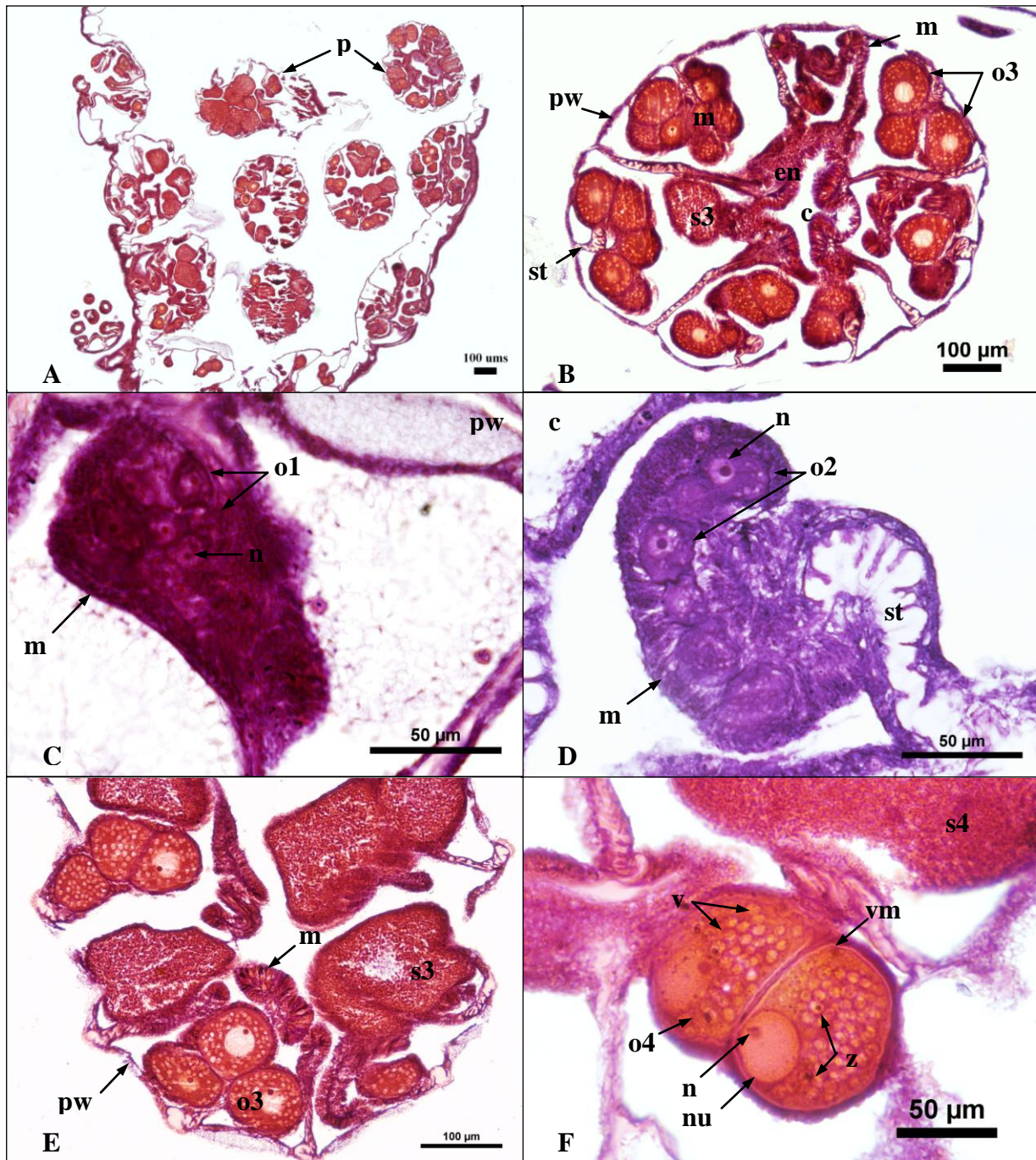
Stage IV oocytes were mature gametes about 80  $\mu\text{m}$  in diameter (mean diameter of  $83.27 \pm 1.29 \mu\text{m}$ ;  $n = 66$ ; Fig. 4F). The maximum size attained by the oocytes was 108.79  $\mu\text{m}$ . The nucleus and nucleolus had migrated to the periphery of the oocyte and the cytoplasm was occupied by enlarged, lipid-filled vacuoles. A vitelline membrane or cortical layer was visible at the surface of each oocyte that stained light pink. In a few cases, zooxanthellae were observed in the cytoplasm. Among the 175 polyps analysed, no further maturation or change in fecundity was observed and free, mature oocytes were never seen in the polyp cavity. In addition, no brooding of embryos or planulae was observed during the study period.

During oogenesis, the transition from Stage I to Stage IV was accompanied by a reduction in the number of oocytes. The average number of early oocytes in October 2007 ( $13.03 \pm 0.29$  Stage I oocytes per polyp) was more than 1.49 times (67%) greater than that of the mature oocytes in March 2008 ( $8.72 \pm 0.42$  Stage IV oocytes per polyp).

### *b. Spermatogenesis*

Four gametogenic stages were identified during spermatogenesis based on their morphology. Their size was highly variable, rendering this parameter useless in the differentiation of the different stages.

Stage I spermaries consisted of spermatogonia comprised of small clusters of numerous interstitial cells with large nuclei (Fig. 5A; Kruger and Schleyer 1998). They were surrounded by a thick spermatogonial wall and were identifiable by their circular shape. Their size ranged from 20-40  $\mu\text{m}$  (average size of  $27.62 \pm 0.32 \mu\text{m}$ ;  $n = 5$ ) and the smallest Stage I spermary was 16.86  $\mu\text{m}$ . Stage I testes were very difficult to distinguish within the polyp mesenteries and were rarely seen in the sections.



**Figure 4:** Oocyte maturation in *Pocillopora damicornis*. **A**, General view of a cross-section. **B**, Distribution of the six female mesenteries through the upper part of a polyp cross-section. **C**, Early ovary containing Stage I oocytes. **D**, Stage II oocytes in a “seed pod”-like ovary. **E**, Stage III oocytes undergoing vitellogenesis adjacent to Stage III spermaries. **F**, Mature Stage IV oocytes containing zooxanthellae. *c*, coelenteron; *en*, endoderm; *m*, mesentery; *mf*, mesenterial filament; *n*, nucleolus; *nu*, nucleus; *o1*, *o2*, *o3*, *o4*, oocytes Stage I, II, III, IV respectively; *p*, polyp; *pw*, polyp wall; *s3*, *s4*, spermaries Stage III and IV respectively; *st*, mesenterial stalk; *v*, vitellogenenic reserves; *vm*, vitellogenenic membrane; *z*, zooxanthellae.

Stage II spermaries consisted of clusters of spermatocytes with dark-stained nuclei (Fig. 5B). They were surrounded by a thicker spermatogonial wall than Stage I testes and were usually oval-shaped. Stage II spermaries usually ranged from 40-80  $\mu\text{m}$  (average size of  $54.50 \pm 0.19 \mu\text{m}$ ;  $n = 16$ ).

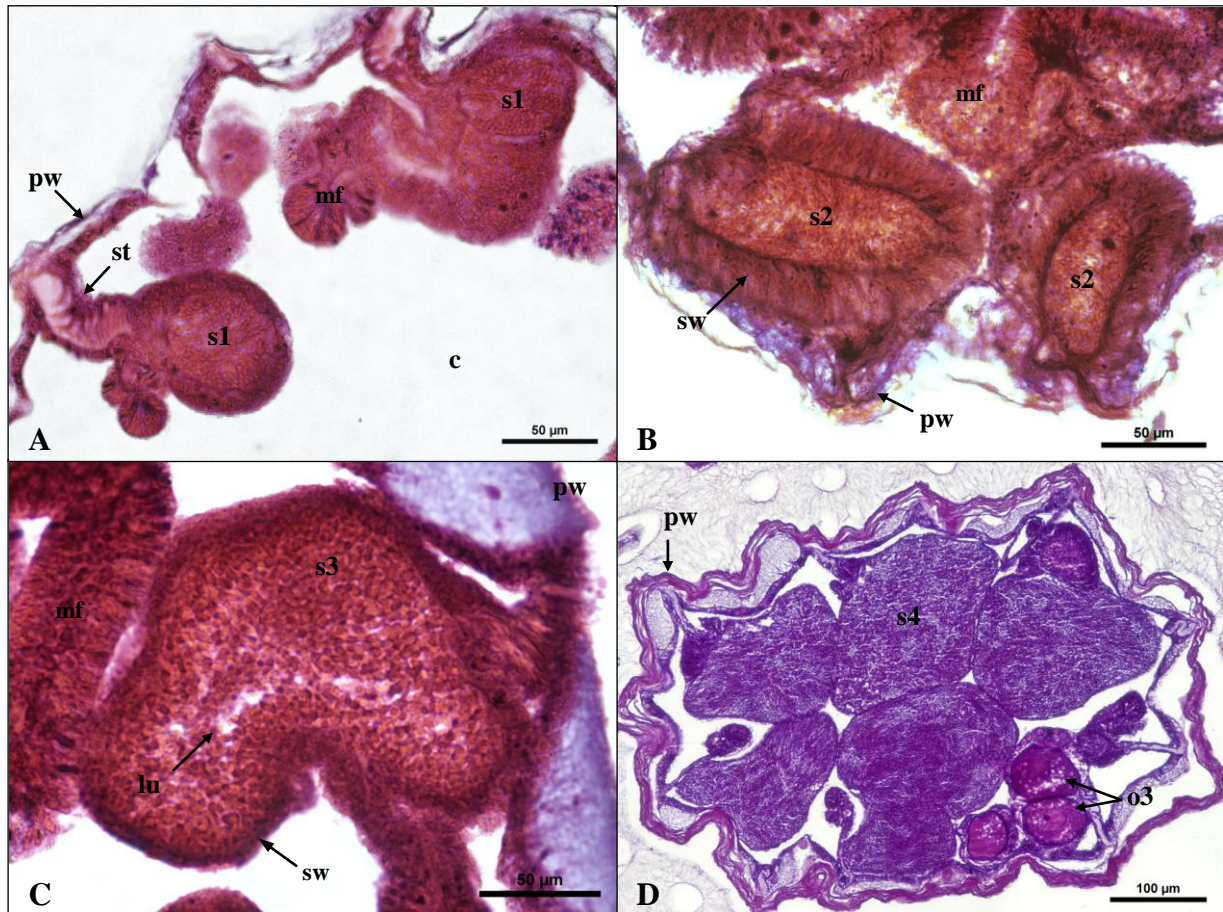
Stage III spermaries consisted of numerous spermatids, giving the gonad a granular appearance (Fig. 5C). Spermatids were mostly concentrated at the periphery of the spermary and arranged around a central lumen. The spermatogonial wall was drastically reduced compared to Stage II spermaries and its boundary was less obvious. Stage III spermaries ranged in size from 80-140  $\mu\text{m}$ , (average size of  $126.62 \pm 0.16 \mu\text{m}$ ;  $n = 15$ ).

Stage IV spermaries contained mature sperm and were large-bodied and intensively stained (Fig. 5D). The spermatogonial wall in the previous stages was reduced to a very thin membrane not often clearly visible. Since the spermaries were extremely dense, the distinctive characteristics of the spermatozoa were not visible. Stage IV spermaries ranged mainly from 140-200  $\mu\text{m}$  (average size of  $176.63 \pm 0.4 \mu\text{m}$ ;  $n = 19$ ). The maximum size attained by the spermaries was 274.05  $\mu\text{m}$ .

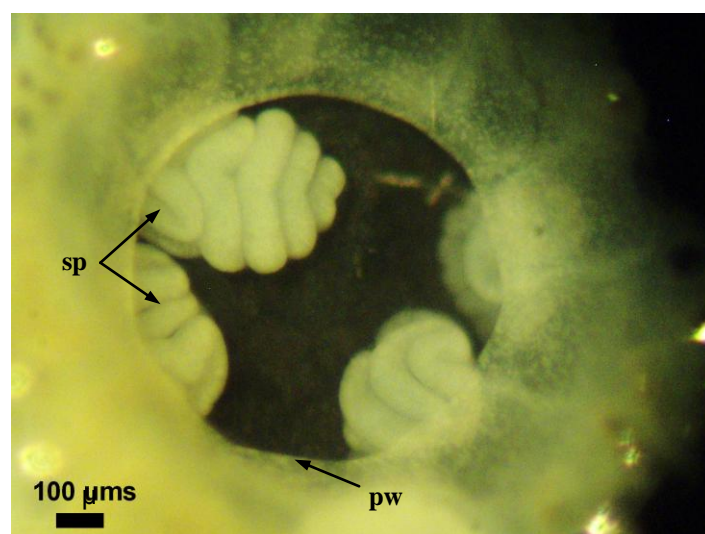
In contrast with oogenesis, the transition from Stage I to Stage IV during spermatogenesis reflected an increase in the average number of spermaries. Early spermaries were about 1.63 (61%) times less numerous in November 2007 ( $0.97 \pm 1.83$  Stage I and II spermaries combined) than the later spermary stages in March 2008 ( $1.58 \pm 1.64$  Stage III and IV spermaries combined).

### *2.3 Duration and timing of gametogenesis*

The development of gametogenesis in *P. damicornis* is shown in Fig. 7. Colonies of *P. damicornis* in KwaZulu-Natal exhibited a protracted breeding season, oocytes being found in the polyps throughout the study period from October 2007 to April 2008. By October 2007, Stages I and II oocytes were prolific in the polyps, and Stage III oocytes were developing. Therefore, oogenesis may have commenced before the study was initiated. No early spermary or oocyte was observed within the polyp sections obtained in April 2008, indicating that no further gametogenic cycle had commenced. Thus, this species appeared to have an annual gametogenic cycle that extended over seven to eight months (from September/October to April).



**Figure 5:** Spermary maturation in *Pocillopora damicornis*. **A**, Stage I spermaries. **B**, Stage II spermaries. **C**, Stage III spermary with lumen. **D**, Mature Stage IV spermaries. *c*, coelenteron; *lu*, lumen; *mf*, mesenterial filament; *o3*, oocytes Stage III; *pw*, polyp wall; *s1*, *s2*, *s3*, *s4*, spermaries Stages I, II, III and IV respectively; *st*, mesenterial stalk; *sw*, spermatogonial wall.



**Figure 6:** Dorsal view of a *Pocillopora damicornis* polyp with four folded, mature spermaries within the gastric cavity. The oral disk and tentacles have been removed from the polyp using dissecting forceps. *sp*, spermary; *pw*, polyp wall.

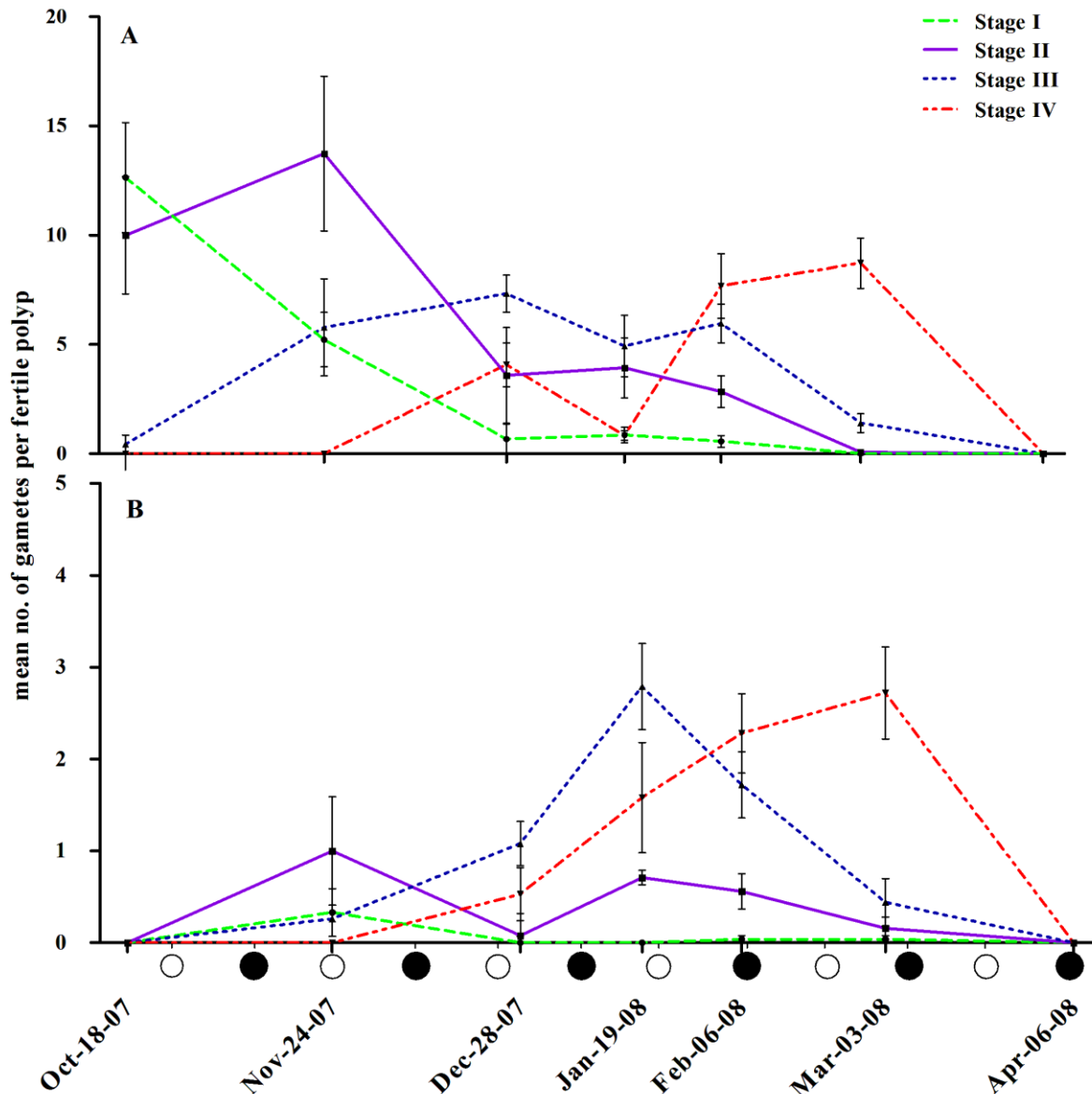
### *a. Timing of oogenesis*

All oogenic stages had distinct peaks, Stage I oocytes peaking in October, Stage II in November, Stage III in December and Stage IV in March. Early stages (Stage I and II) of oogenesis were dominant in the polyps at the beginning of the breeding season, until November 2007. As the reproductive season progressed, the mean number of Stage I and II oocytes declined drastically and remained low until March 2008. The decline in the mean number of early oocytes was accompanied by a rise in the number of mature oocytes (Stage III and IV). Stage III oocytes became dominant in the polyp sections obtained in December 2007. Their average number fell gradually from January to April 2008 as they matured to Stage IV. Stage IV oocytes were observed for the first time in November 2007 and peaked in December 2007. A first decline in the average oocyte number was observed in January 2008. Since no Stage IV oocyte was observed in April 2008, spawning may have occurred between March, the 3<sup>rd</sup> and April, the 6<sup>th</sup>.

### *b. Timing of spermatogenesis*

Spermatogenesis was initiated one month after oogenesis in November 2007 and continued until April 2008. A slight peak in the number of Stage I spermaries was observed in November 2007. Thereafter the mean number of Stage I spermaries remained close to zero. The remaining spermatogenic stages manifested sequential peaks every two months.

Stage II spermaries were dominant during the first month of spermatogenesis. From December 2007, the average number of Stage II declined and remained low until March 2008. As the breeding season progressed, the mean number of Stage III and IV spermaries increased. A few Stage III oocytes were observed during the first month of spermatogenesis in November 2008. Their numbers increased rapidly until January 2008 and then declined gradually until April 2008. Stage IV spermaries occurred one month after the appearance of the other gametogenic stages in December 2007. Their numbers increased rapidly until March 2008 and then declined drastically. In April 2008, no gonad was observed and sperm may have been shed in synchrony with oocytes after March the 3<sup>rd</sup>.



**Figure 7:** Lunar periodicity and monthly average number of the four gametogenic stages in *Pocillopora damicornis* fertile polyps. **A**, Oogenesis; **B**, Spermatogenesis. The open and dark circles indicate respectively the full and new moon phases.

### 3. Synchronicity in gamete maturation

Gamete production was poorly synchronised within colonies and polyps during the first months of gametogenesis (October 2007 to January 2008). Certain colonies manifested a high rate of gamete maturation and produced Stage III gametes from November 2007 whereas others still contained only Stage I and II gametes. In February and March 2008, most of the colonies were at the same stage of reproductive activity, with the last gametogenic stages (Stage III and IV) being dominant within the polyp sections. Peaks and lows in the different gametogenic stages were not synchronised between oogenesis and spermatogenesis, except for Stages II and IV (Fig. 7).

#### 4. Environmental factors and the timing of reproduction

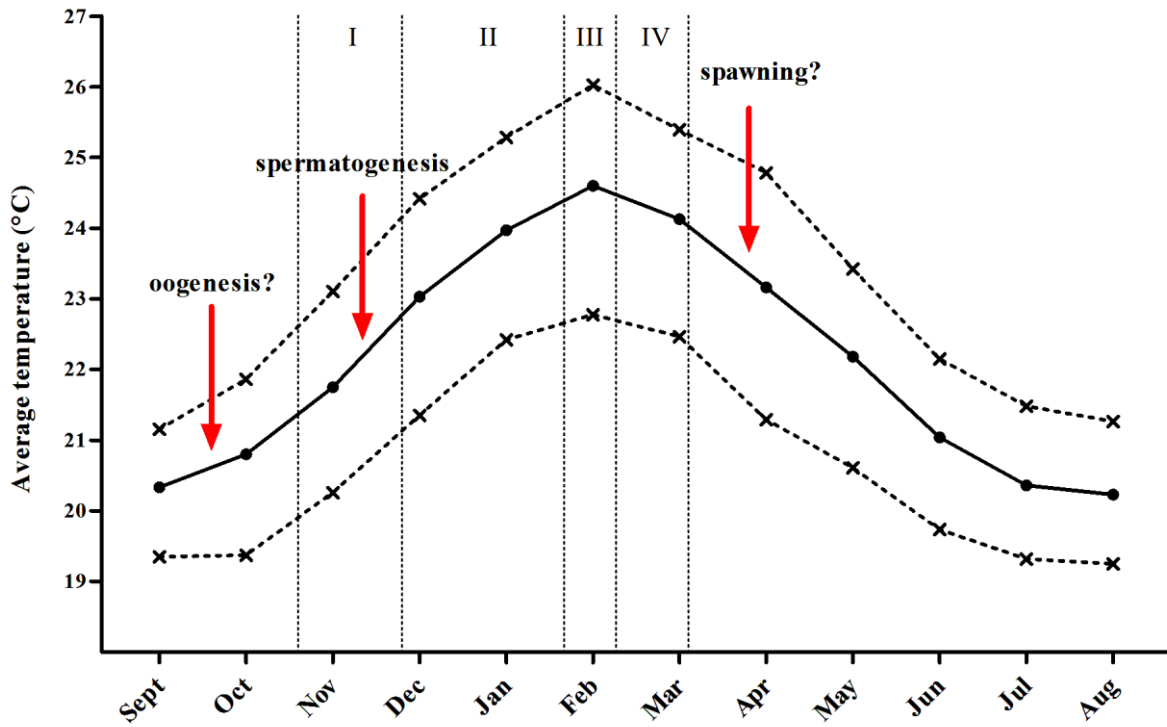
##### 4.1 Lunar phase

Timing of peaks in Stage II and III oocyte and spermary development coincided with full moon periods. Stage I spermary development also peaked during full moon; however, no information is available on Stage I oocytes since they may have peaked prior to commencement of sampling. In contrast, Stage IV oocytes and spermaries peaked during the new moon period (Fig. 7). The disappearance of gametes within the polyp sections occurred between the new moons of March (07/03/2008) and April (06/04/08, Fig. 7). Therefore, gametes may have been released during the full moon period in March.

##### 4.2 Sea surface temperature (SST)

Monthly SSTs measured off Durban (400m offshore) from January 1981 to March 2009 are presented in Fig. 8, relative to gametogenesis in *P. damicornis*. The presence of gametes within polyps was confined to the warm summer months. The onset of oogenesis and spermatogenesis was correlated with the rise in SST that occurs at the beginning of the summer. Oogenesis occurred when SST was  $20.8 \pm 0.5^{\circ}\text{C}$  (September 2007) while spermatogenesis occurred at  $21.8 \pm 0.5^{\circ}\text{C}$  (November 2007). Stage I and II oocytes were dominant during rising sea temperatures at the beginning of the summer and appeared to persist longer than late stage oocytes. Stage III oocytes prevailed whilst SST peaked at  $24.7 \pm 0.9^{\circ}\text{C}$  (February 2008). From the estimated date of spawning (see §3), this occurred before the drop in water temperature at the end of the summer. At this time, the SSTs ranged from  $24.0 \pm 0.6^{\circ}\text{C}$  (March 2008) to  $23.1 \pm 1.1$  (April 2008).





**Figure 8:** Timing of gametogenesis in *Pocillopora damicornis* colonies off Treasure Beach and seasonal variation in SSTs in Durban from January 1981 to March 2009 (KwaZulu-Natal Sharks Board, unpublished data). The unbroken line represents the average monthly temperatures while the curves above and below show respectively the maximum and the minimum monthly average temperatures. The dominant stages of oocytes within the polyps are indicating between the discontinuous vertical lines that represent the sampling dates. I, II, III, and IV, Stages I, II, III, and IV oocytes respectively.

**Table 8:** Mode and timing of reproduction in *Pocillopora damicornis* according to locality and lunar cycle. *B*, brooder; *FM*, full moon; *FQ*, first quarter; *LQ*, last quarter; *NM*, new moon; *oo*, oogenesis; *S*, broadcast spawner; *sp*, spermatogenesis. Dashes (–) indicate no data.

Reproduction		Location		Timing of reproduction			Authors (year)
Sexual	Asexual	Locality	Latitude	Breeding season	Planula/gamete release	Lunar cycle	
<b>Central Pacific (Marshall Island, Palau)</b>							
<b>B</b>	–	Palau	7°N	Year-round	Year-round	–	Kawaguti (1941)
<b>B</b>	–	Palau	7°N	Year-round	Year-round	NM–FQ	Atoda (1947)
<b>B</b>	–	Enewetak	11°N	Year-round	Year-round	NM–FQ	Richmond and Jokiel (1984)
<b>B</b>	–	Enewetak (shallow water)	11°N	–	Jun, Jul, Jan	LQ–FQ	Stimson (1978)
<b>B</b>	–	Enewetak (reef slope)	11°N	–	Oct, Dec, Feb	–	Richmond (1981)
<b>B</b>	–	Kanohe Bay (reef flat)	11°N	–	Oct, Dec, Feb	–	Richmond (1981)
<b>B</b>	–	Hawaii	20°N	Year-round	Year-round	–	Edmonson(1946)
<b>B</b>	–	Hawaii	20°N	–	Mostly Jun–Aug	NM	Reed (1971)
<b>B</b>	–	Hawaii	20°N	Year-round	Year-round	FM–NM	Harrigan (1972)
<b>B</b>	–	Hawaii (shallow water)	20°N	Year-round	Year-round	FM	Stimson (1978)
<b>B</b>	–	Hawaii	20°N	Year-round	Year-round	Type Y: NM Type B: FM	Richmond and Jokiel (1984)
<b>Japan</b>							
<b>B</b>	–	Amakasu	32°N	–	Jul	FM–LQ	Hanny <i>et al.</i> (2001)
<b>B</b>	–	Okinawa	26°N	–	Aug	NM	Diah Permata <i>et al.</i> (2000)

Table 8 (continued)

Reproduction		Location		Timing of reproduction			Authors (year)
Sexual	Asexual	Locality	Latitude	Breeding season	Planula/gamete release	Lunar cycle	
<b>South Western Australia</b>							
S	brooded planulae	Rottnest Island	32°S	Nov-Mar. Up to 3 cycles	Dec, Jan, Mar	LQ-NM	Stoddart and Black (1985)
S	brooded planulae	Rottnest Island	32°S	Oo: Sept-Apr Sp: year-round	Feb, Apr	NM	Ward (1992)
<b>Great Barrier Reef, Australia</b>							
B	–	Low Isles	16°S	Year-round	Year-round	NM: Dec–Apr FM: Jul–Sep	Marshall and Stephenson (1933)
B	–	Lizard Island	14°S	May–Jun	Peak in June	FM	Harriot (1983a)
<b>Eastern Pacific</b>							
S	–	Galapagos	0°N	Jan–Apr	–	No lunar synchronicity	Glynn <i>et al.</i> (1991)
S	–	Uva Island, Gulf of Chiriqui	8°N	Year-round	–	FM with minor spawning at NM	Glynn <i>et al.</i> (1991)
S	–	Gulf of Panama	8°N	Jun–Dec	Nov–Dec	No lunar synchronicity	Glynn <i>et al.</i> (1991)
S	–	Cano Island, Costa Rica	9°N	Year-round	–	FM with minor spawning at NM	Glynn <i>et al.</i> (1991)
<b>Caribbean</b>							
S	–	Gulf of Mexico	24.5°N	Year-round	–	–	Chavez Romo and Reyes Bonilla (2007)
<b>Southern Africa</b>							
S	–	Durban, South Africa	29°S	Oo; Sept-Mar Sp: Oct-Mar	Mar–Apr	FM?	Present study

## DISCUSSION

### *1. Reproductive activity*

When examined histologically, *Pocillopora damicornis* collected in KwaZulu-Natal, South Africa, proved to be reproductive, revealing that 73.4% of the colonies contained gametes during the study period. The fecundity of this coral was lower in brooding colonies collected at Lizard Island, Great Barrier Reef, with only 35.5% of the colonies containing reproductive material (Harriott 1983a). However, a fecundity ranging between these two values was found in broadcasting *P. damicornis* colonies collected in Costa Rica and the Gulf of Chiriqui (Glynn *et al.* 1991). Despite the lower seawater temperatures in KwaZulu-Natal compared to the tropics, the fecundity of *P. damicornis* colonies found here has not been impaired.

### *2. Reproductive strategies*

#### *2.1 Asexual versus sexual reproduction*

In the present study, no brooding of embryos or planula larvae were found in the 175 polyps analysed, although mature oocytes and spermatozoa (Stage IV) were detected within the polyps over a six-month period. Therefore, asexual reproduction through the production of brooded larvae did not appear to occur during the sampling period. Moreover, no evidence of asexual reproduction through fragmentation of colonies was observed at the study site, suggesting that *P. damicornis* in Durban might rely mainly on sexual reproduction for its regeneration.

However, life-history theory predicts that asexual reproduction would be favoured under the variable conditions on marginal reefs once colonised by successful genotypes (Bell *et al.* 1988; Stearns 1989). These would be adapted to the local conditions that typify high-latitude reefs. Conversely, the greater spatial and temporal variability on tropical reefs caused by intense competition within the coral community should favour genotypically diverse organisms resulting from sexual reproduction (Williams 1975; Bell *et al.* 1988). Again, it could be expected that asexual reproduction of clones should be favoured in marginal habitats due to low competition.

The relative contribution of asexual versus sexual reproduction in coral population may be estimated using genetic (*e.g. see* Stoddart 1983; Ayre *et al.* 1991; Ayre *et al.* 1997; Miller and Ayre 2004). Several genetic studies on the level of cloning in *P. damicornis* populations have been undertaken (Stoddart 1983, 1984a, b; Stoddart 1986; Miller and Ayre 2004). They showed that populations in south Western Australia (32°S) (Stoddart 1984a, b) and Hawaii (20°N) (Stoddart 1986) were highly clonal. In contrast, populations on the Great Barrier Reef (Benzie *et al.* 1995; Ayre *et al.* 1997) and Lord Howe Island, eastern Australia (31°S) (Miller and Ayre 2004) manifested no asexual recruitment. These results suggest that the reproductive condition in *P. damicornis* does not depend on latitude or competition with other coral species.

In habitat exposed to intense storms or wave action, asexual reproduction may occur through the fragmentation of large coral colonies (Highsmith 1982; Adjeroud and Tsuchiya 1999). Depending on the environmental conditions and type of substratum, some fragments may survive and develop into new colonies, which will contribute to the growth of the reef. In eastern Pacific, colonies of *P. damicornis* on exposed reef slopes were found to rely strongly on asexual fragmentation to colonise and dominate certain reef zones (*see* Highsmith 1982). Similarly, Adjeroud and Tsuchiya (1999) suggested that fragmentation was the key form of asexual propagation in populations of *P. damicornis* in the Ryuku Islands (24-26°N) exposed to high-frequency typhoons. This mode of reproduction has the advantage of avoiding the high mortality rates of larvae and juveniles, and allowing for rapid growth of reefs on which the corals are abundant (Highsmith 1982). One would expect that asexual fragmentation of large *P. damicornis* colonies would be favoured at high latitude, since this coral grows on rocky substrata exposed to highly hydrodynamic conditions.

However, in the present study, sampled colonies of *P. damicornis* had small branches that were densely crowded (Fig. 2B). This morph may have been favoured by such high hydrodynamic conditions but does not favour fragmentation. In addition, populations of *P. damicornis* colonies from sheltered and exposed reefs in Lord Howe Islands manifested no differences in their genotypic diversity, as predicted by the aforementioned hypothesis (Miller and Ayre 2004). Therefore, asexual reproduction through fragmentation in the coral *P. damicornis* does not necessarily occur in marginal and exposed habitats. Further research is needed to elucidate the variation in coral reproductive strategies relative to environmental pressures.

## 2.2 Broadcast spawning versus brooding

*P. damicornis* in KwaZulu-Natal is hermaphroditic and all the polyps contained oocytes and spermaries at the end of the breeding season. Spawning of gametes was not observed in the rocky pools. However, a significant decline in the number of gametes was noted between March and April 2008, indicating that the gametes may have been shed or resorbed. Since mature oocytes and spermaries did not exhibit damage and/or significant change in shape and structure over the sampling period, it is unlikely that they were resorbed. Therefore, the gametes were probably released in the surrounding water for external fertilisation. Since no brooding of larvae was observed at the end of the breeding season, it is likely that *P. damicornis* in KwaZulu-Natal is a broadcast spawner.

A similar reproductive pattern was observed in colonies of *P. damicornis* at Rottneest Island (Richmond 1985; Stoddart and Black 1985; Ward 1992), in Costa Rica, Panama, the Galapagos Islands (Glynn *et al.* 1991) and in the Gulf of California (Chavez-Romo and Reyes-Bonilla 2007; Table 8). However, this species was found to brood sexually-produced planulae at Enewetak Atoll and Hawaii (Richmond and Jokiel 1984), Lizard Island (Harriott 1983a) and Okinawa (Diah Permata *et al.* 2000; Table 8). Therefore, the variability in the reproductive mode in *P. damicornis* does not appear to be related to latitude; other environmental factors have to be considered.

None of the hypotheses discussed thus far regarding the mode of reproduction relative to coral morphology or habitat justify the reproductive variability in *P. damicornis*. Early studies suggested that the reproductive mode in corals is related to polyp size (Rinkevich and Loya 1979; Fadlallah and Pearse 1982a). Yet, *P. damicornis* displays different reproductive patterns depending on location but retains a uniform branching morphology (Veron 2000) and relatively small polyps throughout (0.75-1.5 mm diameter; Marshall and Stephenson 1933). Moreover, the reproductive mode in this species seems not to be driven by depth constraints as proposed by Stimson (1978), since both modes of reproduction are found in shallow water colonies (Harriott 1983a; Glynn *et al.* 1991). Indeed, *P. damicornis* colonies sampled at the same depth (3-8 m) in Australia (Harriott 1983a) and in the eastern Pacific (Glynn *et al.* 1991) were respectively brooders and broadcast spawners (Table 8).

High-latitude habitats are considered hostile for coral development due to the limited tolerance of corals to certain environmental parameters such as temperature (Kleypas *et al.* 1999a). In the Durban region, the average seawater temperature is slightly under the optimum

temperature for corals (Glynn and Stewart 1973; Clausen and Roth 1975; Jokiel and Guinther 1978). Few coral species occur on the rocky reefs in Durban Bay and, therefore, the inter-specific competition between the corals is low. However, strong competition occurs between corals and an abundance of locally well-adapted sessile organisms such as macro-algae and ascidians (Johannes *et al.* 1983; *pers. obs.*). In such a habitat, broadcast spawning may allow coral larvae to escape a crowded environment and colonise reefs more suitable for their development some distance away (Glesener and Tirlnan 1978; Johannes *et al.* 1983; Karlson *et al.* 1996). Yet, this mode of reproduction may be expensive for the corals since planular survival in marginal environments may be low. Conversely, water movement on the rocky shores of KwaZulu-Natal is turbulent and highly dynamic (Branch and Branch 1981; Bell *et al.* 1988; Bustamante and Branch 1996). Brooding of planulae would enable more rapid settlement of coral larvae and their subsequent metamorphosis (Stimson 1978; Fadlallah 1983; Richmond 1985, 1987b) since planulae are released at an advanced development stage. The relative benefits of one mode of reproduction compared to the other in marginal habitats are thus not immediately evident and the success of *P. damicornis* at all latitudes may be attributable merely to its adaptable, “tramp”-like nature.

### 3. Oocyte and spermary development

#### 3.1 Histological examination of the gonads

In the present study, gonads of *P. damicornis* were connected to the mesenteries by short stalks (Figs. 5B, D and 6A) as reported by Harriott (1983a) and Stoddart and Black (1985), and in another pocilloporid coral, *Stylophora pistillata* (Rinkevich and Loya 1979). However, gonads were embedded in the mesenteries of *P. damicornis* collected in the eastern Pacific and Japan (Glynn *et al.* 1991; Diah Permata *et al.* 2000). The pattern of gonad attachment does not seem to be related to the mode of reproduction as previously thought (see Harriott 1983a), since *P. damicornis* in the Eastern Pacific and KwaZulu-Natal were both broadcast spawners and exhibited both forms of gonad attachment (Glynn *et al.* 1991; present study) .

#### 3.2 Gametogenesis

The description of the gametogenic stages and the size range of gametes in the present study were similar to those reported in Stoddart and Black (1985), Glynn *et al.* (1991), and Diah Permata (2000), as described in Tables 6 and 7. Stoddart and Black (1985) found that the smallest oocytes were approximately 10  $\mu\text{m}$  in diameter (5.84  $\mu\text{m}$  in this study). This

difference may be attributable to variability in the precision of the methods used to measure gamete size, *e.g.* use of a stage micrometer (Glynn *et al.* 1991) versus image analysis (*present study*). In addition, it may be due to differences in the fixing and histological preparation. The best approach to measure gonad and gamete size would therefore be to dissect live coral fragments and obtain true measurements (Harrison and Wallace 1990). Unfortunately, this was not possible in *P. damicornis* due to the small size of its polyps.

During gametogenesis, a reduction in the early stages and simultaneous increase in late stage gametogenesis implied the progressive development of the early stages into later stages (Ward 1992). The transition from Stage I to Stage IV oocytes was accompanied by a 67% reduction in the average number of oocytes. Reduction in the number of oocytes in gonads during gametogenesis was also reported for *P. damicornis* on the Great Barrier Reef (Harriot 1983) and in south Western Australia (Stoddart and Black 1985), in *P. verrucosa* from southern Africa, and in *S. pistillata* from the Red Sea (Rinkevich & Loya 1979a). This reduction is, however, not confined to pocilloporid corals as it also occurs in *Acropora* spp. (Kojis 1986), *Astrangia danae* (Szmant-Froelich *et al.* 1980) and *Porites porites* (Tomascik and Sander 1987). To date, no clear explanation has been formulated for this phenomenon. Possibly, the reduction in oocyte number during oogenesis may be due to resorption of some early stage oocytes to provide nutrition for the later stages (Harrison and Wallace 1990). It may also be attributable to the fusion of several oocytes into one (Tardent 1974; Rinkevich and Loya 1979). No resorption or fusion of oocytes was observed in this study. However, the occurrence of these events might be rapid (Kruger 1995). Conversely, the transition of *P. damicornis* spermaries from Stage I to Stage IV resulted in their increase in average number by 61% in KwaZulu-Natal. This increase in the number of spermaries during spermatogenesis has not been documented in the literature. In the present instance, it may be attributable to the difficulty in identifying early stage spermaries and/or to their rapid transition from early to late stages during spermatogenesis.

### *3.3 Duration and timing of gametogenesis*

In the majority of corals, the duration of gametogenesis varies depending on the mode of reproduction and latitude (Harrison and Wallace 1990). Broadcast spawners tend to have a shorter and discrete period of breeding, while brooding corals may planulate over extended periods or do so year-round (Fadlallah 1983; Harrison and Wallace 1990). Gametogenesis in hermaphroditic broadcast spawners usually takes less than 12 months (Harrison and Wallace 1990) except in the solitary coral *Paracyathus stearnsii* in which oogenesis is extended over



14 months (Fadlallah and Pearse 1982b). The duration of gametogenesis (eight months) in *P. damicornis* colonies in KwaZulu-Natal is slightly longer than that encountered in other broadcast spawning pocilloporids. In comparison, *P. verrucosa* in South Africa and Red Sea was found to have a short breeding season of four months (Fadlallah 1985; Kruger and Schleyer 1998). However, the duration needed to complete oogenesis in *P. damicornis* at Rottneest Island, south Western Australia (Ward 1992) was the same as in Durban (*present study*). Conversely, spermatogenesis occurs throughout the year in this coral at Rottneest Island, south Western Australia (Ward 1992) while it was confined to the summer months off Durban (*present study*). It clearly undergoes several spermatogenic cycles per year in south Western Australia, while this was documented once per annum in the present study.

#### 4. Synchronicity in gamete maturation

Examination of the gametogenic stages in colonies of *P. damicornis* in KwaZulu-Natal revealed that gametogenesis was usually synchronised within polyps and colonies, although gamete development was variable during the early months of gametogenesis. It became more synchronised towards the end of the breeding season in February 2008, when the mature gametes were being dominant within the polyp sections. Consistent patterns in the synchronicity of gamete maturation have been observed in *P. damicornis* from south Western Australia (Stoddart and Black 1985) and in many other scleractinian corals (Kojis and Quinn 1981, 1982; Harriott 1983a; Szmant 1986). Differences in the onset of oogenesis and spermatogenesis were also observed in this study at the beginning of the reproductive season with oogenesis being initiated one to two months prior to spermatogenesis. This phenomenon occurs in several hermaphroditic species (Szmant-Froelich *et al.* 1980; Fadlallah and Pearse 1982b; Harriott 1983b; Szmant 1986; Harrison and Wallace 1990), and is called annual protogynous hermaphroditism. However, the time lapse in the initiation of oogenesis and spermatogenesis has not been found in other histological studies on *P. damicornis* (Stoddart and Black 1985; Glynn *et al.* 1991; Ward 1992). Yet, it occurs in another pocilloporid, *S. pistillata*, in which spermary development commenced three months after that of the oocytes (Rinkevich and Loya 1979). In contrast, Harriot (1983a) found that spermaries appeared to develop and mature before oocytes in *P. damicornis* on the Great Barrier Reef.

Multiple (or epidemic) spawning events within similar species have been observed in numerous scleractinian corals in both low and high latitude regions (*e.g.* Shlesinger and Loya 1985; Kenyon 1992; Wilson and Harrison 2003). Several broadcast-spawning species may release their gametes twice or more during their breeding season, within a few days or a

month interval (Harriott 1983b; Shlesinger and Loya 1985; Babcock *et al.* 1986; Wilson and Harrison 2003). Although there is no clear explanation for this reproductive pattern, multiple spawning may be due to the overlapping of several gametogenic cycles (*e.g.* Stoddart and Black 1985), asynchronous gamete maturation between colonies (*e.g.* Harriott 1983b; Kenyon 1992), or varying responses of colonies to environmental factors (*e.g.* Harriott 1983b; Kenyon 1992; Wilson and Harrison 2003).

In *P. damicornis* from south Western Australia, Stoddart and Black (1985) found that individual heads of corals matured up to three cycles of gametes and planulae per season (November to March). Successive declines in the number of gametes were observed in mid-December, mid-January and mid-February, suggesting that this species may have spawn repetitively during the reproductive season. Similarly, in *P. damicornis* colonies from the eastern Pacific, Glynn *et al.* (1991) observed significant declines in the number of mature gametes several times during the breeding season, although the precise date of spawning was not determined. In this study, monthly histological analyses revealed the occurrence of one cycle of gametogenesis and a synchronous decline in the number of gametes in mid-February. An earlier decline in the number of mature oocytes (Stage IV) was observed in January 2008. However, it was not accompanied with a decline in the number of mature spermaries, suggesting that spawning did not take place at this stage. No early stage gametes were observed within the polyps in April 2008, indicating that no further gametogenic cycle had commenced. Since spawning was not observed directly, the successive release of gametes may have occurred over a few days in March 2008. However, spawning would have to be confined to this month since no gametes were observed in the polyp mesenteries in April 2008. Compared to synchronous spawning, multiple spawning events are less likely to ensure high rates of fertilisation and genetic mixing (Harriott 1983b; Oliver *et al.* 1988; Harrison and Wallace 1990; Glynn *et al.* 1991). Further investigation is required to understand the ecological benefit of this reproductive pattern that occurs in numerous coral species.

## 5. Environmental factors and the timing of reproduction

### 5.1 Lunar cycle

Lunar periodicity is known to influence the time of spawning in *P. damicornis* and numerous studies have investigated the influence of moon phase on its spawning or release of planula (*e.g.* Harriott 1983a; Stoddart 1983; Richmond and Jokiel 1984; Jokiel 1985; Jokiel *et al.* 1985; Glynn *et al.* 1991). Yet, it is a geographically variable phenomenon that seems not to be linked with latitude, seawater temperature or other environmental factors (*e.g.* Harriott

1983a; Glynn *et al.* 1991; Diah Permata *et al.* 2000; Hanny *et al.* 2001). Furthermore, different lunar periodicities have been reported between brooding *P. damicornis* colonies occurring at similar localities *e.g.* in Hawaii (Harrigan 1972; Stimson 1978; Richmond and Jokiel 1984) and Japan (Diah Permata *et al.* 2000; Hanny *et al.* 2001). Similar variability has been found in broadcasting colonies of *P. damicornis* that release their gametes during either new or full moon (Stoddart and Black 1985; Glynn *et al.* 1991; Ward 1992), or show no lunar periodicity (Glynn *et al.* 1991). This variability implies a great plasticity in the reproductive ecology of this species that may be advantageous for the colonization of widely dispersed and differing habitats (Harriott 1983a). Lunar periodicity *per se* thus does not explain the timing of spawning in *P. damicornis*. Other factors or combinations of factors have to be considered to explain its spawning activity.

In the present study, peaks in Stage II and III oocytes and spermaries as well as in Stage I spermaries occurred during full moon phases. Conversely, the peak in Stage IV oocyte and spermary production was correlated with new moon. Synchronization between lunar cycles and peaks in gametogenesis was also observed in *P. damicornis* on the high-latitude reefs of south Western Australia (Stoddart and Black 1985). Stoddart and Black (1985) found that a peak in Stage III oocytes occurred on lunar day 26 (*i.e.* between last quarter and new moon), while Stage III and IV spermaries peaked during lunar days 18-25 (*i.e.* between full moon and last quarter) and 26-27 (*i.e.* between last quarter and new moon) respectively. There appeared to be no particular trend in the lunar control of gametogenesis in the present study and that of Stoddart and Black (1985). The influence of lunar cycle on the development of gametogenesis has been poorly investigated in other coral species (*e.g.* Wallace 1985; Babcock *et al.* 1986; Szmant 1991). This is almost certainly attributable to the regular and intensive sampling needed to document the state of gamete maturation at each moon phase. Nevertheless, lunar phase may be a factor that influences the gamete development.

### 5.2 Seasonal variation in sea temperature

It is generally thought that the timing of spawning is regulated by seasonal variation in sea temperature that controls gamete development (Harrison *et al.* 1984; Willis *et al.* 1985; Babcock *et al.* 1986; Harrison and Wallace 1990). On the Great Barrier Reef, maturation of gametes coincides with rapidly rising sea temperatures in spring (Harrison *et al.* 1984; Willis *et al.* 1985; Babcock *et al.* 1986; Harrison and Wallace 1990). Furthermore, mass coral spawning takes place a few months before the peak in sea temperature in summer (Harrison *et*

*al.* 1984; Babcock *et al.* 1986). However, synchronous spawning events have also been observed in Singapore (1°N) where seasonal variation in seawater temperature is negligible (Guest *et al.* 2002). Therefore, coral spawning and gametogenesis may not require temperature as a cue for spawning but rather some optimal range within which these events will occur (Babcock *et al.* 1986; Mendes and Woodley 2002).

In the present study, *P. damicornis* gametogenesis was confined to the warmer months of the year. The onset of gametogenesis was initiated during the rise in sea temperatures in spring as observed on the Great Barrier Reef, yet spawning occurred at the end of the summer, several months after the peak in sea temperatures. Similar timing of gametogenesis was observed in *P. damicornis* of Rottneest Island, south Western Australia (Ward 1992) that is exposed to cooler seawater temperature compared to the tropics (Hodgkin and Phillips 1969). In the eastern Pacific, *P. damicornis* broadcast spawning colonies reproduce year-round on the warmer reefs of the Gulf of Chiriqui and Costa Rica (Glynn *et al.* 1991). In contrast, gametogenesis is confined to the summer months on reefs where sea water temperatures are lower *e.g.* in the Galapagos Islands and Gulf of Panama (Glynn *et al.* 1991). These suggest that the number and timing of gametogenic cycles in *P. damicornis* are controlled by seawater temperature.

In the present study, early gametogenic stages (Stage I and II) persisted longer within the polyp mesenteries than late stages (Stage III and IV). This difference in the timing of maturation between early and late gametogenic stages was also observed in *P. damicornis* from south Western Australia (Ward 1992). In South Africa, the slower maturation of early-stage gametes was associated with lower seawater temperature at the beginning of the summer. In contrast, rapid maturation of late-stage gametes coincided with the temperature peak in mid-summer (Fig. 8). Therefore, low temperatures may have slowed down the development of gametogenesis in *P. damicornis*, and this may explain why this species exhibits a protracted breeding season of 7-8 months.

However, other environmental factors such as day-length may also have contributed to this outcome. Day-length is directly related to the amount of light that reaches the coral and allows its photosynthetic activity. Shorter day-length at the beginning of the summer may have reduced the photosynthesis activity, and, therefore decreased the energy available for skeletal growth and reproduction (Falkowski *et al.* 1990; Muscatine 1990). In return, gamete maturation may have been slowed down by limited energy availability in the coral. Since light intensity is lower at high latitude (Kleypas *et al.* 1999b), one would expect that variation in

day-length would strongly influence coral photosynthesis in South Africa. Therefore, further investigations are required to determine the influence of both day-length and seawater temperature on *P. damicornis* gametogenesis.

## CONCLUSION

In South African *P. damicornis* colonies, latitude and its associated environmental factors do not seem to influence its fecundity or its reproductive strategy. However, lower seawater temperatures may have regulated the length and timing of its gametogenic cycle and account for its slower gamete maturation. A comparison of gametogenesis in colonies of *P. damicornis* exposed to a similar temperature regime in south Western Australia (Ward 1992) and the eastern Pacific (Glynn *et al.* 1991) corroborates this tendency.

Overall, *P. damicornis* exhibits a wide pattern of reproductive strategies that does not seem to be related to locality, or other environmental factors. This species appear to have a remarkable capacity to adapt to local environment (Harriott 1983a; Richmond 1985). This may explain its widespread distribution from the western Indian Ocean to the eastern Pacific and the Caribbean on both calm and shallow reefs as well as those that are exposed and deeper (Veron and Pichon 1976b; Veron 2000).

Yet, the variability in its life-history traits is so remarkable that this may be attributable to not only different selective pressures, but also different gene pools or species (Richmond 1985; Knowlton and Jackson 1994; Ayre *et al.* 1997). Richmond and Jokiel (1984) identified two types of *P. damicornis* colonies (type Y and type B) that co-exist on Hawaiian reefs. Each type exhibits differing reproductive timing and lunar synchronicity (Richmond and Jokiel 1984) and responds differently to a number of environmental variables including sea temperature, salinity and night irradiance (Jokiel 1985; Jokiel *et al.* 1985). Furthermore, the types exhibit dissimilar colouration and morphs (Richmond and Jokiel 1984). These differences may be the result of differentiation of one parental species into two different types that have developed their own biological traits.

Differences in biological traits in *P. damicornis* on other reefs support this idea. These include differences in reproductive pattern, gonad arrangement, the acquisition of zooxanthellae by mature oocytes and varying responses to environmental factors (e.g. Harrigan 1972; Harriott 1983a; Glynn *et al.* 1991; Ward 1995; Diah Permata *et al.* 2000). Genetic studies on *P. damicornis* are needed to determine whether the variability in its life-history traits is due to its highly adaptive capacity or the occurrence of several sub-species.

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