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Sexual Reproduction in *Pocillopora damicornis* at High Latitude off South Africa

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Abstract—Sexual reproduction in *Pocillopora damicornis* was studied off Durban in South Africa (29°S), close to its southern most distribution in Africa. This was compared with *P. damicornis* reproduction on tropical reefs to ascertain how corals may adapt their reproduction on marginal reefs. Monthly gametogenesis was correlated with SST, light intensity, and day length. *P. damicornis* proved to be a hermaphroditic broadcast spawner in South Africa and had a higher fecundity than its tropical counterparts. However, its gamete development was slow (6-7 months) and confined to the warmer months of the year at this high latitude. Its reproductive pattern was similar to that found in this species in south Western Australia (32°S). Spawning in *P. damicornis* off South Africa occurred at the end of the summer and was inferred from the disappearance of mature gamete in April 2008. No correlation was found between monthly mean gamete diameter and light intensity or day length, but the increase in gamete size was correlated with a rise in SST, suggesting that this parameter regulates its spawning. The lower SST at high latitude may account for its extended gametogenesis and late spawning.

INTRODUCTION

Hostile environmental conditions at high latitude can affect coral metabolism, causing reduced growth and lower or suspended sexual activity (Veron *et al.* 1974; Veron & Done 1979; Johannes *et al.* 1983; Harriott *et al.* 1999). Corals were therefore expected to exhibit decreased reproductive activity in such environments, failing to produce gametes or manifesting reduced gamete production, diminished fertilisation, and decreased amounts of lipid in their planulae (Ward 1995; Fabricius 2005). Coral populations have proven, however, to be sexually reproductive at high latitudes with low temperatures (Babcock *et al.* 1994; van Woesik 1995; Fadlallah 1996; Harii *et al.* 2001; Wilson & Harrison 2003; De Putron & Smith 2011). Furthermore, they may participate in mass

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spawning events similar to those that occur on the Great Barrier Reef (GBR) e.g. in the Houtman Albrohos Islands at 28-29°S (Babcock *et al.* 1994). At present, few studies have focused on the effects of environmental conditions associated with high latitude on the reproduction of corals (Babcock *et al.* 1994). Research is thus needed on the fecundity, reproductive strategies and breeding season of species at different latitudes to reveal how corals maintain their populations in marginal environments.

Pocillopora damicornis is one of the most widespread and best-studied scleractinian coral, yet its mode of sexual reproduction remains unclear. Histology has shown that it may be a hermaphroditic brooder (e.g. Stimson 1978; Harriott 1983) or broadcast spawner (Stoddart & Black 1985; Glynn *et al.* 1991; Ward 1992; Diah Permata *et al.* 2000). It can further generate asexually-produced planulae (Stoddart 1983; Ayre & Miller 2004; Sherman *et al.* 2006; Yeoh & Dai 2010). Its plasticity in reproduction is unprecedented and it may constitute a species complex (Miller & Ayre 2004; Sherman *et al.* 2006) comprising several sympatric species with different reproductive strategies depending on locality.

Colonies of this species inhabit the rocky reefs off Durban (29°S), South Africa, close to their southernmost limit of distribution on the east African coast (Riegl 1993; Schleyer *et al.* 2006). This provided a good opportunity to investigate geographical variation in *P. damicornis* reproduction, addressing 1) the fecundity of *P. damicornis*, 2) its reproductive mode and 3) seasonality, and 4) the environmental factors associated with synchronicity and timing in its reproduction on the high-latitude rocky reefs of South Africa.

MATERIALS and METHODS

Sampling

The study was conducted on the east coast of Africa that is influenced by the warm, southward-flowing Agulhas Current (Lutjeharms 2006). The water temperature along the Durban coastline varies seasonally from a monthly average of 20.8°C in winter (May to October) to 23.4°C in summer (November to April), with a mean annual temperature of 22.1°C (1981-2008; KwaZulu-Natal Sharks Board, unpub. data). *P. damicornis* colonies were randomly collected on shallow reefs associated with the rocky shores, 10 km south of Durban (29°58'S, 30°58'E). Sampling was conducted on a monthly basis from October 2007 to April 2008. Each month, a large branch was collected from five *P. damicornis* colonies bigger than 10 cm in diameter and fixed in 4% formal-saline. The samples were collected at least two meters apart to reduce the likelihood of sampling cloned colonies. Special attention was also given to avoid repetitive sampling of the same colonies. After 2 to 4 days of fixation, coral nubbins were gradually decalcified in 1-3% hydrochloric acid and stored in 70% ethanol.

Histology

Decalcified tissue was cut into 2 × 3 cm pieces comprising 30 to 60 polyps. Tips and bases of the branches were discarded as intermediate segments are the most fecund (Stimson 1978). Samples were then prepared for histological examination according to the methods outlined by Kruger and Schleyer (1998). Cross-sections of 7 µm were cut and one section in every four was mounted on a glass slide. Twenty such serial sections from each sample were stained with Ehrlich's haemalum stain and aqueous eosin solution. Five polyps were randomly selected in the serial sections to assess the reproductive stage of the colonies. The size and number of spermaries and oocytes sectioned through the nucleus were subjected to image analysis (Image Pro Plus 6.0, Cybernetics Inc.). Gamete size was estimated by calculating the mean values of the maximum and minimum diameters measured at right angles to correct for deformation. The gametogenic stages were classified according to their morphology and size as per Stoddart and Black (1985). Their frequency was noted and polyp fertility was rated according to the presence of one or more gametes within the polyp section. Only fertile polyps were evaluated to ascertain reproductive development during the gametogenic cycle.

Environmental factors

Timing in *P. damicornis* reproduction was correlated with lunar phase (South African Astronomical Observatory, www.saao.ac.za) and daily Sea Surface Temperature (SST) recorded off Durban (KwaZulu-Natal Sharks Board, 1981-2009, unpublished data). In addition, monthly average satellite data on light intensity (kW m^{-2} day^{-1}) and day length (daylight hours) were obtained from the Surface Meteorology and Solar Energy (SSE) Release 6.0 project (http://eosweb.larc.nasa.gov/sse/). The SSE data set was formulated from NASA satellite- and reanalysis-derived insolation and meteorological data compiled for a 22-year period (July 1983 to June 2005), the results being provided in 1° x 1° grid. Correlations between the increase in mean monthly gamete diameter and these environmental parameters were tested using Spearman product moment correlation.

RESULTS

Fecundity and reproductive mode

Colonies of *P. damicornis* collected off Durban were sexually active and 74% of the colonies sampled contained gametes during the study period. The proportion of hermaphroditic, non-fertile and female colonies varied over the sampling period with non-fertile and female colonies found mostly during the first months of gametogenesis from October to January. By the end of gametogenesis in February and March, 100% of the colonies had both male and female gametes. No brooding of embryos or planulae was found in the 175 polyps analysed, although mature oocytes and spermatozoa (Stage IV) were detected within the polyps over a three-month period. In April 2008, no gametes were found within the polyp mesenteries, suggesting that they had been released through spawning. It is unlikely that gametes were resorbed since no mature oocytes and spermaries exhibited significant change in shape and structure and/or degradation over the sampling period. These observations suggest that *P. damicornis* is a hermaphroditic broadcast spawner off Durban.

Gametogenesis

Each fertile *P. damicornis* polyp contained six pairs of male and female gonads. Gonads were attached to the edges of the basal mesentery by prominent stalks protruding into the coelenteron as described by Harriott (1983) and Stoddart and Black (1985). Ovaries containing early stage oocytes appeared as twisted seedpods (Figs 1A, B); they became enlarged as the gametes grew until only a thin membrane persisted around the mature oocytes (Figs 1C, D). Oocytes tended to develop in the upper (oral) part of the polyp cavity while spermaries developed basally. Several zooxanthellae were observed in the cytoplasm of mature oocytes (Fig. 1D). Spermaries were spherical in early development (Figs 2A, B) but became highly variable in shape as they matured (Figs 2C, D). Mature spermaries occupied a larger volume than ovaries e.g. up to 60-80% of the total polyp cavity; they were long and folded into U-shapes in the polyp cavity. The mean number and diameter of each gametogenic stage are presented in Table 1

P. damicornis off Durban exhibited a protracted breeding season, oocytes being found in the polyps for 6-7 months throughout the study period (Fig. 3). By October 2007, Stages I and II oocytes were prolific in the colonies, and a few Stage III oocytes were observed (Fig. 3A). Therefore, oogenesis may have commenced before the study was initiated, probably in September 2007. In contrast, spermatogenesis was initiated in November 2007, one to two months after oogenesis (Fig. 3B). Gamete production was poorly synchronised within both colonies and polyps during the first four months of gametogenesis. This trend was, however, reversed toward the end of the breeding season, when the mature gametes were prevalent within the polyp sections. Early stages (Stage I and II) of oogenesis peaked in October and November and their decline was accompanied by a rise in the number of late-stage gametes (Stage III and IV, Fig. 3). Overall, the average number of oocytes per polyp declined by 67%

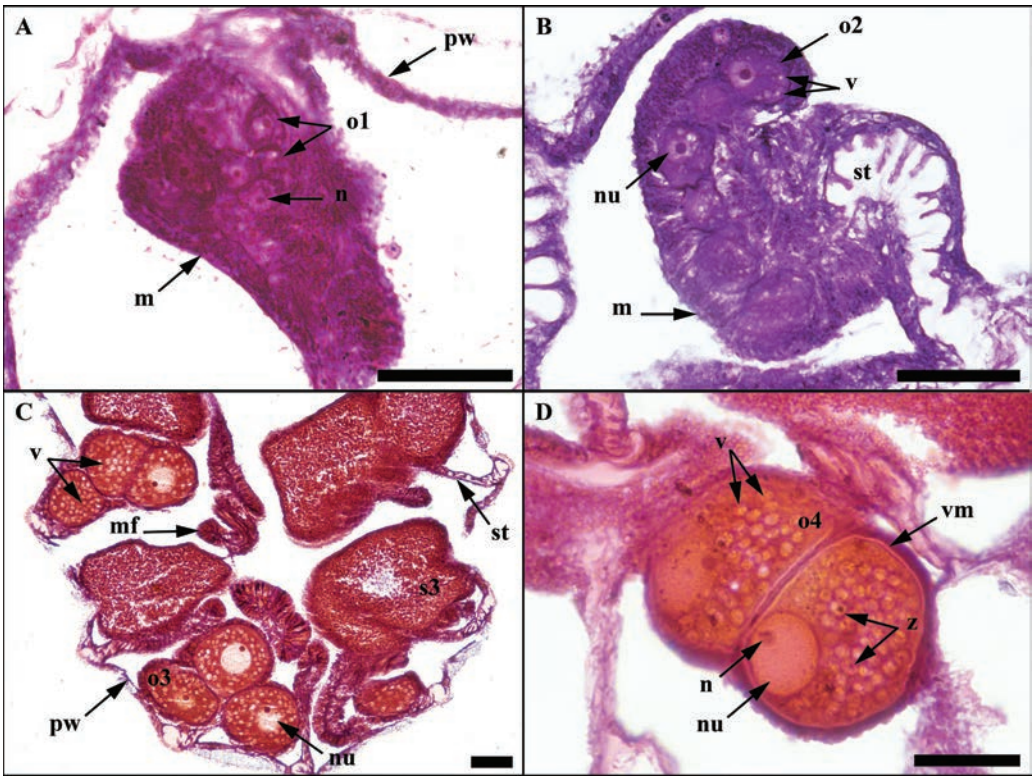

Figure 1. Oocyte maturation in *Pocillopora damicornis* off Durban. A, Early ovary containing Stage I oocytes. B, Stage II oocytes in a "seedpod"-like ovary. C, Stage III oocytes undergoing vitellogenesis adjacent to Stage III spermaries. D, Mature Stage IV oocytes containing zooxanthellae. m, mesentery; mf, mesenterial filament; n, nucleolus; nu, nucleus; o1, o2, o3, o4, oocytes Stage I, II, III, IV respectively; pw, polyp wall; s3, spermary Stage III; st, mesenterial stalk; v, vitellogenic reserves; vm, vitellogenic membrane; z, zooxanthellae. Scale bars are 50 µm.

from Stage I to Stage IV, while the average number of spermaries per polyp increased by 61% from Stage I to Stage IV. This may be attributable to difficulty in identifying early stage spermaries and/or to their rapid transition from early to late stages during spermatogenesis. Mature Stage IV oocytes and spermaries were observed for the first time in December 2007. A decline in the number of mature oocytes was observed in January 2008, an artefact of sampling as two colonies with low fecundity were sampled that month, and was not accompanied by a decline in the number of mature spermaries. Spawning was inferred from the simultaneous disappearance of mature gametes in March-April 2008 which occurred between the sampling dates of March the 3rd and April the 6th.

Environmental factors and the timing of reproduction

During the study period, the monthly mean SST off Durban rose slowly from 20.8°C in September 2007 to 24.7°C in February 2008 (Fig. 4). The SST reached a maximum of 26.5°C for a few days in February 2008 before gradually decreasing from March to May 2008. The rise in SST was strongly correlated with the increase in oocyte (r^2=0.79, $p<0.05$) and spermary (r^2=0.89, $p<0.05$) size. Mature gametes were prevalent on the polyp mesenteries when the water temperature was the highest. However, spawning occurred more than a month after the summer peak in temperature, i.e. when the monthly average SST was 24.0°C in March 2008. Day length

and light intensity rose one to two months earlier than the SST and peaked respectively in December and January. No correlations were found between these environmental factors and the increase in gamete size ($p>0.05$). Spawning was inferred by the disappearance of the gametes between March and April 2008 and might have occurred during the full moon period of March 2008; more intensive sampling would be needed to determine the influence of lunar phase on *P. damicornis* off Durban.

DISCUSSION

The rocky reefs off Durban constitute a marginal environment with conditions that fall beyond the threshold needed for typical coral development (see Kleypas *et al*. 1999). In contrast with the tropics, these high-latitude reefs are subjected to the natural stresses of lower temperatures in winter, higher seasonal variation in SST and exposure to strong wave action. Under such conditions, corals are expected to manifest low survival and limited reproduction (Veron *et al*. 1974; Veron & Done 1979; Johannes *et al*. 1983; Harriott 1999). *P. damicornis* nevertheless proved to be fecund off Durban, close to its southernmost distribution on the East African coast. Histology revealed that 74% of the colonies contained gametes during the study period and all of them had produced mature oocytes and spermaries by March 2008. This level of activity fell within the range recorded for gravid *P. damicornis* colonies on tropical reefs in the eastern Pacific i.e. 32-90% (Glynn *et al*. 1991), and was higher than that of 35% found for the same species on the Great Barrier Reef (Harriott 1983). Furthermore, the number of mature oocytes per polyp in *P. damicornis* was high off Durban. Prior to spawning, polyps contained an average (±SE) of 8.5 (±1.3) Stage IV oocytes and 3.3 (±0.4) Stage IV spermaries (Table 1). A maximum of 24 Stage IV oocytes and 5 Stage IV spermaries was observed in a polyp in March 2008. In comparison, the average (±SD) number of oocytes in *P. damicornis* at Uva Island in Panama (8°N) ranged between 2.2 (±2.2) and 6.1 (±5.0) oocytes per polyp (Glynn *et al*. 1991). This suggests that the environmental conditions off Durban do not adversely affect the fecundity and proportion of gravid colonies in this species.

Gametogenesis in *P. damicornis* off Durban was variable between colonies during the first four months of gametogenesis. Oogenesis was initiated one to two months prior to spermatogenesis; however, this lag in male development was not found in other histological studies on *P. damicornis* but does occur in another pocilloporid coral, *Stylophora pistillata*, in the Red Sea (Rinkevich & Loya 1979). Here, oocyte development commenced three months before that of the spermaries. Conversely, Harriot (1983) found that spermaries appeared to develop and mature before oocytes in brooding colonies of *P. damicornis* on the Great Barrier Reef.

Variation in the synchronisation of oocyte and spermary development in *P. damicornis* thus does not seem to be related to latitude. It may, however, reveal local adaptation of this species to environmental conditions. Oocytes are lipid-rich compared to spermatozoa and therefore require more energy for their production (Richmond 1981, 1987). Since light intensity is reduced at high-latitude

Table 1. Mean number and size of the gametogenic stages in *Pocillopora damicornis* off Durban. Mean number per polyp was calculated when a gametogenic stage was dominant in the polyp mesenteries.

	Oocyte		**Spermary**	
	Mean no per polyp (SE)	Mean diameter µm (SE)	Mean no per polyp (SE)	Mean diameter µm (SE)
Stage I	13.6 (2.5)	17.0 (2.0)	1.6 (0.2)	27.6 (0.3)
Stage II	14.3 (3.1)	30.3 (1.4)	3.0 (0.7)	54.5 (0.2)
Stage III	8.8 (1.2)	54.2 (1.1)	2.7 (0.6)	126.6 (0.2)
Stage IV	8.5 (1.3)	83.3 (1.3)	3.3 (0.4)	176.6 (0.4)

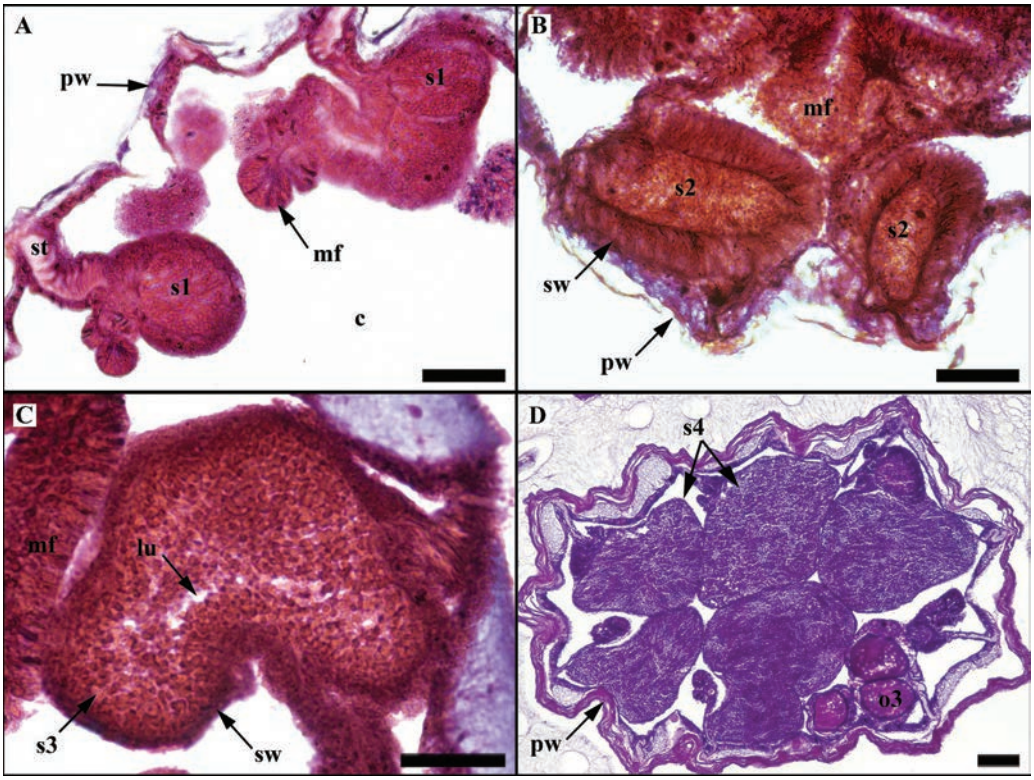

Figure 2. Spermary maturation in Pocillopora damicornis off Durban. A, Stage I spermaries. B, Stage II spermaries. C,Stage III spermary with lumen. D, Mature Stage IV spermaries. c, coelenteron; lu, lumen; mf, mesenterial filament;o3, oocytes Stage III; pw, polyp wall; s1, s2, s3, s4, spermaries Stages I ,II, III and IV respectively; st, mesenterial stalk; sw, spermatogonial wall. Scale bars are 50 µm.

(Kleypas *et al*. 1999), sub-tropical corals may undergo reduced photosynthesis and slower energy production compared to those in the tropics. This may account for the delay in the onset of spermatogenesis and the slower development of oocytes in *P. damicornis* off Durban. To date, no study has compared the variation in the energy budget between tropical and subtropical coral species and further research on the subject is needed.

The arrangement and size of gametes in *P. damicornis* colonies off South Africa matched those reported in the literature (Stoddart & Black 1985; Glynn *et al*. 1991; Diah Permata *et al*. 2000). However, the duration of gametogenesis was longer off Durban (6-7months) than on more tropical reefs (3-6 months; Glynn *et al*. 1991; Chavez-Romo & Reyes-Bonilla 2007). In addition, only one gametogenic cycle was observed in the present study while several overlapping cycles were reported in broadcast spawning colonies in tropical localities (Glynn *et al*. 1991; Chavez-Romo & Reyes-Bonilla 2007). The duration and annual nature of reproduction in *P. damicornis* off South Africa was, however, similar to that found in broadcast-spawning colonies of this species on the high-latitude reefs of Rottnest Island (Ward 1992).

No evidence of brooding was found in the *P. damicornis* samples collected off Durban; all indications were that it is a hermaphroditic broadcast spawner. It released its gametes between March and April and no planulae were found developing within the polyp mesenteries. However, planula development in brooding corals may be short in duration, taking two to three weeks (Stoddart & Black 1985; Diah Permata *et al*. 2000). If it had occurred off Durban during the sampling

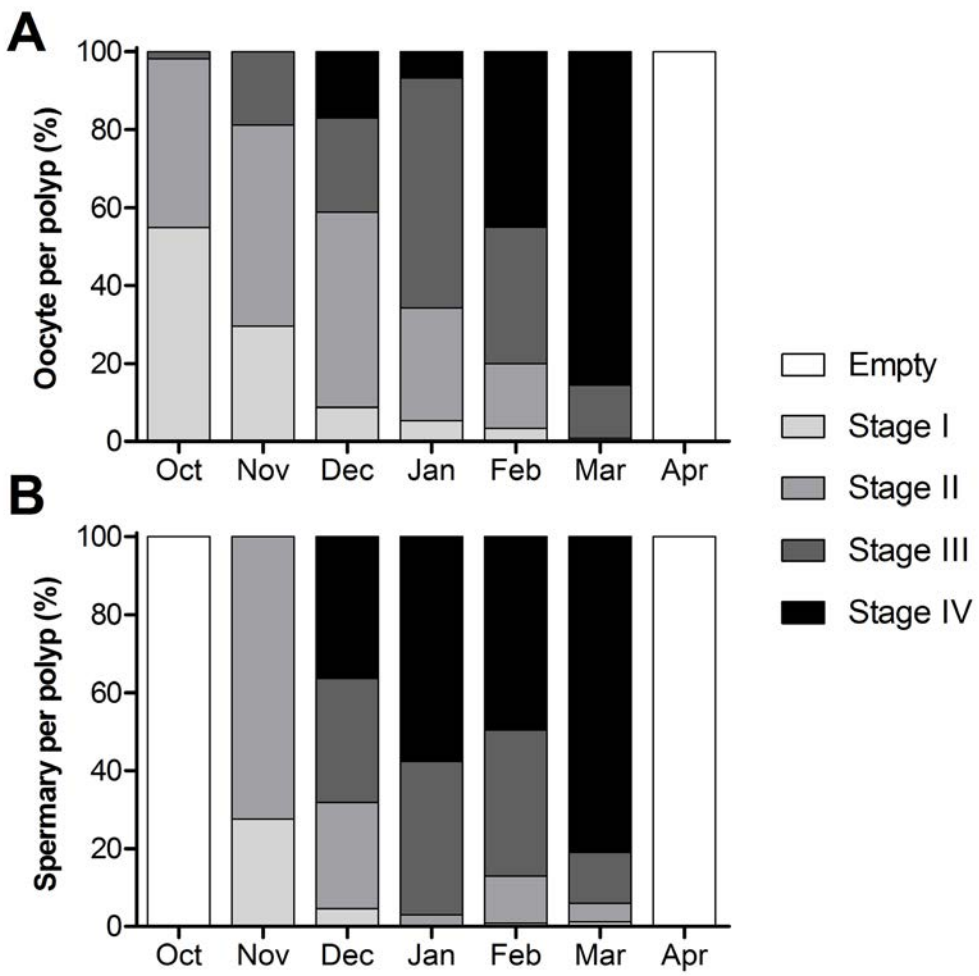

Figure 3. Gamete development in *Pocillopora damicornis* off Durban. A: Oogenesis; B: Spermatogenesis. Spawning was inferred from the disappearance of the gametes.

period, this would have necessitated the release of sperm just after sampling in March and planulation before sampling in April. This scenario is unlikely as brooding colonies of *P. damicornis* elsewhere undergo repetitive planulation which overlaps gamete development (Harriott 1983; Stoddart & Black 1985; Diah Permata *et al*. 2000); no such pattern was found in our samples. They manifested a single, extended gametogenic cycle, with retention of the mature oocytes in the polyp mesenteries for three months without undergoing any change. Furthermore, the presence of planulae in the polyps causes distension of the gastro-vascular cavity (Stoddart & Black 1985), another feature not found in our samples in which the polyps were crowded with eggs and spermaries.

Broadcast spawning has been observed in both tropical (Glynn *et al*. 1991; Chavez-Romo & Reyes-Bonilla 2007) and high-latitude colonies (Ward 1992). Therefore, variability in the reproductive mode in *P. damicornis* does not appear to be latitude-related. Both modes of reproduction have advantages depending on local conditions on the reefs. In marginal habitats, broadcast spawning may allow coral larvae to escape a crowded environment and colonise more suitable reefs that are some distance away (Johannes *et al*. 1983; Karlson *et al*. 1996). However, this mode of reproduction may

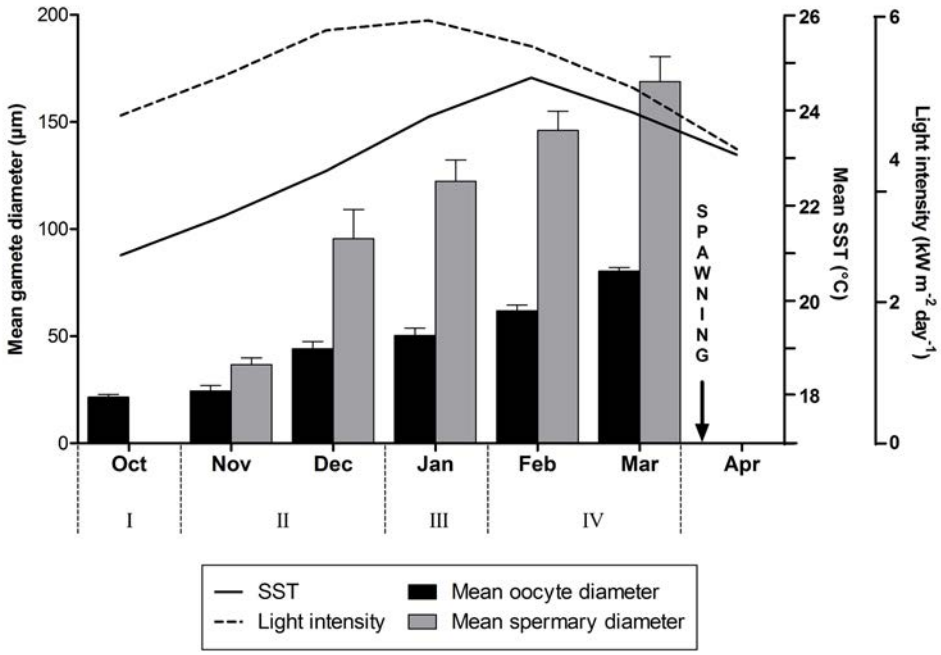

Figure 4. Mean monthly gamete size in *Pocillopora damicornis* off Durban relative to SST and light intensity. Latin numbers represent the dominant gametogenic stage of oocyte in the polyps. Spawning was inferred from the disappearance of the gametes.

be costly since planular survival under such circumstances may be low. Conversely, turbulence on reefs may favour brooding of planulae since it enables more rapid settlement and metamorphosis of coral larvae after release (Stimson 1978; Fadlallah 1983; Gilmour *et al*. 2004). The benefits of one mode of reproduction over 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 nature.

Disturbance on reefs may favour asexual reproduction in corals (see e.g. Gilmour *et al*. 2004; Sherman *et al*. 2006). However, no evidence of colony fragmentation or the asexual production of planulae was observed in *P. damicornis* on the Durban reefs. The sampled colonies had small branches that were densely crowded, a growth form that would not favour fragmentation. This suggests that *P. damicornis* in Durban may rely mainly on sexual reproduction for its propagation. Further genetic analysis on the level of clonality in *P. damicornis* on Durban reefs is needed to confirm this.

The timing of gametogenesis and spawning in corals is known to be linked to environmental cues such as SST, solar insolation, and lunar phase (see Babcock *et al*. 1986; Penland *et al*. 2004; van Woesik *et al*. 2006). Sea temperature and/or solar insolation may influence the time of year of spawning (Babcock *et al*. 1986; Penland *et al*. 2004; van Woesik *et al*. 2006), while lunar cycles regulate the time of month (Babcock *et al*. 1986). In this study, an increase in oocyte and spermary size was strongly correlated with an increase in SST. The latter thus seems to control the timing of reproduction and gamete development in *P. damicornis* at high latitude as no correlation was found between the variation in gamete size and light intensity or day length. The onset of gametogenesis in *P. damicornis* off Durban occurred during the rise in light intensity and day-length (Fig. 4), yet spawning occurred in April 2008, three months after the peak in light intensity and day length. The influence of these parameters on reproduction in *P. damicornis* has not been investigated in other studies but it is unlikely that they influence the time of spawning.

At a finer scale, lunar periodicity is known to influence the month of spawning in *P. damicornis* and numerous studies have demonstrated its influence on the release of spawn or planulae (Richmond & Jokiel 1984; Jokiel 1985; Villanueva *et al*. 2008). Broadcast spawning colonies of *P. damicornis* off Costa Rica, Panama and Galapagos Islands spawn during full moon (Glynn *et al*. 1991) and this might have occurred off Durban during the full moon in March 2009. In contrast, colonies of *P. damicornis* in south Western Australia release their gametes during the last lunar quarter or the new moon (Stoddart & Black 1985; Ward 1992). These results thus suggest that spawning in *P. damicornis* is not closely governed by lunar phase.

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