

Gametogenetic cycles of three corals in Singapore

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Abstract. Among life functions of coral, reproduction appears to have the narrowest tolerance to stress, while being critical for maintenance of populations. However, relatively little is known about the effects of environmental stressors on reproductive output, especially in equatorial regions. In this study, the gametogenetic cycles and reproductive output of three common broadcasting scleractinian corals *Hydnophora exesa*, *Merulina ampliata* and *Echinopora lamellosa* were investigated at three fringing reefs south of Singapore. All three species showed strong seasonality and broadly similar patterns of gametogenesis, with bi-annual peaks in fecundity occurring primarily in April, followed by a smaller secondary peak in October. Both periods coincide with the inter-monsoon, during which tidal flushing is poorest. Fecundity in all three species significantly declined from 2009 to 2011, although spatial effects were also prominent. Results indicate that oogenesis occurred over two to three months, during which fecundity metrics also elucidated negative relationships with sea surface temperature, total nitrogen and total suspended sediments and positive relationships with salinity, total organic carbon and chlorophyll-a. The directionality of relationships between fecundity, turbidity faecal coliforms were variable among species, with positive associations for *H. exesa* and negative associations for *E. lamellosa* in both cases. A bleaching event in mid-2010 had large effects on reproductive output, with reproductive failure in all three species in October 2010. This suggests these coral species are sensitive and susceptible to deteriorating water quality within the relatively short time frame of the three months associated with set. Thence we have shown that, variations in fecundity are good indicators of sub-lethal coral stress, indicating that the monitoring of coral reproductive output is useful for coral reef management.

Key words: Reproductive Seasonality, Coral Fecundity, Coral Stressors, Singapore.

Introduction

Sexual reproduction is a critical component of coral reef resilience (*sensu* Hughes *et al.*, 2007), particularly as it provides the genetic variability to survive in changing environments (Tirado, 2006) and presents new recruits to then replace corals that die or break from predation, storm damage, algal competition, disease and human impacts (Ward *et al.* 2002).

Reproduction has a narrower tolerance to stress than any other life function (Harrison & Wallace, 1990) and certain stressors can cause a major decline in coral fecundity, therefore coral reproduction also has a pivotal role in the success or failure of the populations (Kinne, 1963; Kojis & Quinn, 1984; Harrison, 2011). In synchronous spawners, reproduction typically occurs annually or bi-annually (Baird *et al.*, 2009), and major disruption to these may result in recruitment failure for the following six months.

A suite of natural and anthropogenic stressors such as thermal stress (Baird & Marshall 2002), salinity (Vermeij *et al.* 2006; Li *et al.* 2008), sedimentation and turbidity (Kojis & Quinn, 1984; Peters & Pilon, 1985; Harrison 2011), nutrients (Pastorok & Bilyard, 1985; Tomascik & Sander, 1987) and macroalgal

competition (Tanner, 1995) have been shown to have significant negative effects on fecundity and oocyte size. In Singapore, many coral species spawn synchronously during two discrete periods (March/April and to a much lesser extent in October) (Guest *et al.* 2002) which coincide with periods between the dominant (NE and SW) monsoon seasons. The inter-monsoon is characterised by having relatively higher temperatures (compared to that of the NE monsoon), but also by having the lowest net transport changes (Chen *et al.*, 2005), and therefore the greatest retention of pollutants in the system. Depending on the length of the gametogenetic cycle, there is potential for poor water quality to negatively affect reproductive success and this warrants investigation.

The aims of this study are therefore: (a) to examine the gametogenetic cycle of *Merulina ampliata*, *Hydnophora exesa* and *Echinopora lamellosa*, three scleractinian coral species for which reproductive cycles have not yet been documented locally; (b) examine the variability in fecundity at sites with different exposure to anthropogenic stresses and distance from mainland) and (c) environmental condition on the reproductive output of these at reefs around Singapore's southern islands.

Material and Methods

Patterns of coral reproduction were investigated on reefs fringing three islands (Raffles Lighthouse, Kusu Island and Pulau Hantu) south of mainland Singapore between April 2009 and July 2011 by histological examination of coral tissue.

At each reef, coral clippings of the three coral species, *H. exesa*, *M. ampliata* and *E. lamellosa* were collected quarterly (sampling months shown on Fig. 2) from five mature colonies (i.e. $\geq 30\text{cm}$) that were randomly selected at each sampling occasion to measure inter-colony variation in gamete maturity. Three individual branches (3-6 cm in length) were broken from the centre of each colony to avoid sterile zones on the periphery (Baird & Marshall, 2002). Coral clippings were then preserved and prepared for histological examination as per Chornesky & Peters (1987). For each polyp, up to 10-14 slides (with 4-5 sequential sections per slide) of gonadal tissue (e.g. Fig 1) were examined under the microscope to determine oocyte frequencies and staging, using the developmental stages classified by Szmant-Froelich *et al.* (1980), Szmant-Froelich *et al.* (1985) and Tirado (2006). Environmental data was acquired from a long-term water quality monitoring programme undertaken by TMSI, from which monthly data was available at monitoring stations ~500m from the studied sites.

A fully-factorial analysis of variance (ANOVA) were used to test the effects of year and site on coral fecundity during April, during which all three species were found to have high numbers of oocytes and proportionally the greatest amount of late-stage eggs.

Best subset multiple regressions were carried out separately for each species as a preliminary investigation to identify if key water quality variables affect coral reproductive output (only fecundity estimates at maturity were used for this test). All statistical analyses were conducted using STATISTICA v10 (StatSoft 2010).

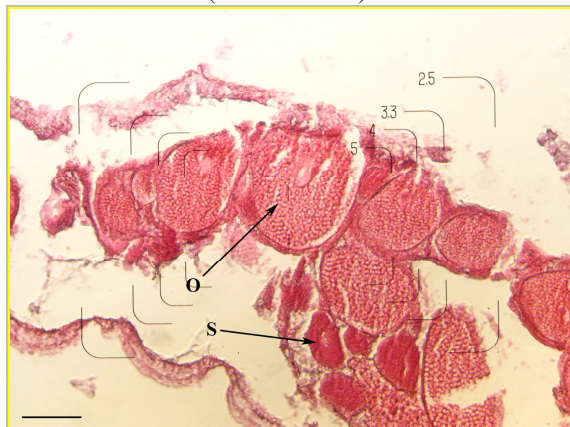


Figure 1: Example of a tissue section of *M. ampliata* showing oocyte developmental stage IV (O) and late-staged spermatocytes (S) within the mesentery (x10 magnification). Scale bar 100 μm .

Results

All three species had a large amount of mature colonies within their polyps, in April and October at all three sites (Fig. 3). In all other remaining months (November 2009, January 2010, July 2010 and 2011, February 2011) (Fig. 2), corals had either no discernible gonadal material or only early-stage oocytes present (Fig. 3). Late-stage oocytes were present in all the colonies collected, in April and October for all sampling years whilst lower frequencies of early-staged oocytes or no gonadal material were present in all other months.(Fig. 2).

The absence and very low abundances of oocytes in January 2010 and February 2011 (respectively) suggests that the duration of set may be fairly rapid, possibly occurring within two months or less, given the complete absence of oocytes at Raffles in February 2011 (Fig. 2).

In both *M. ampliata* and *H. exesa* samples, higher numbers of oocytes per polyp were observed in April in all sampled years and lower or zero reproductive output in the remaining months. At all sites, oocytes in April (2009-2011) were mainly comprised of late-stage (III and IV) oocytes (apart from an anomaly in April 2009, where a small amount of S-II oocytes were present in *H. exesa* samples in Hantu) (Fig. 2-3).

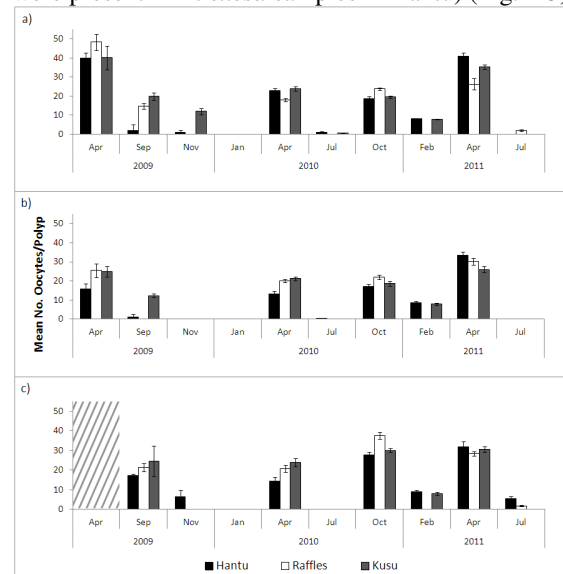


Figure 2: Column graph showing fecundity of a) *M. ampliata*, b) *H. exesa* and c) *E. lamellosa* at Hantu fringing, Raffles Lighthouse and Kusu from April 2009 to Jul 2011. (*E. lamellosa* sampling commenced in Sept 2009) (Mean \pm S.E. a) and b) n=50, c) n=45).

Patterns of fecundity in *Echinopora lamellosa* were similar to that observed for the other two species (although collection of this species only started from September 2009 onwards). Stage II-III oocytes were present in September 2009 while corals collected in April (2010 and 2011) and October 2010 comprised of late-stage oocytes.

Across all species and sites, there were significant main effects of sampling year on fecundity of *M. ampliata* ($F_{2,44}=15.58$; $p<0.001$), *H. exesa* ($F_{2,44}=7.81$; $p<0.01$), and for *E. lamellosa* ($F_{1,29}=10.55$; $p<0.01$). In all three, fecundity in 2010 was significantly lower than in other years sampled. No main or interactive effects of site were detected on the fecundity of the three species examined.

The domain-wide decrease in fecundity in 2010 was likely to be a result of a bleaching event, possibly linked to a global increase in sea surface temperatures (SST). Temperature in May 2010 peaked to 30.5-31.5°C in but was approximately 0.5°C lower the previous year. Fecundity of *M. ampliata*, *H. exesa* and *E. lamellosa* in 2011 were generally indicative of recovery from the bleaching stress due to SST in 2010, comparable to or exceeding the levels measured in 2009. However, recovery of *M. ampliata* appeared to be slower at Raffles Lighthouse, with 2011 levels more similar to 2010 than 2009.

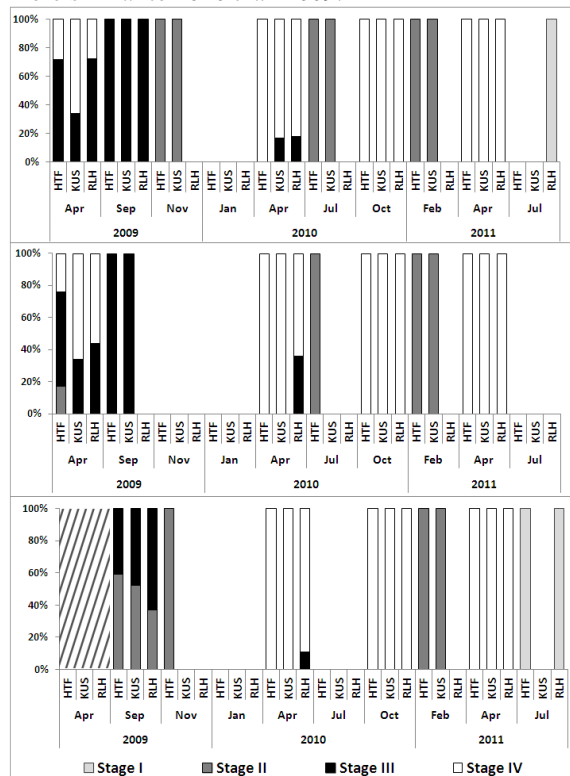


Figure 3: Percentage composition of oocyte developmental stages I-IV as in Szmant-Froelich et al. 1980 in a) *M. ampliata*, b) *H. exesa* and c) *E. lamellosa* at Hantu Fringing (HTF), Kusu (KUS) and Raffles Lighthouse (RLH) from Apr 2009 to Jul 2011 (*E. lamellosa* sampling commenced in September 2009).

In all species, reproductive output was significantly related to at least two indicators of environmental condition, but no single parameter was consistently important for all three (Table 1). *Hydnophora exesa* appeared most sensitive to a range of water quality

parameters (Table 1), and this may offer some explanation as to the consistently low fecundity and greater frequency with which oocytes were absent in this species (Fig. 2).

Temperature (SST), Total Nitrogen (TN) and Total Suspended Solids (TSS) all had significant, negative effects on the reproductive output of *H. exesa* and *M. ampliata* (Table 1). In addition, significant positive relationships were detected between fecundity in *H. exesa* and Total Phosphorus (TP), Chlorophyll a (Chl-a), Total Organic Carbon (TOC), Salinity (Sal), Turbidity (Turb) and Faecal Coliforms (FC). Of these, only Salinity and TOC had similar effects on reproduction in *E. lamellosa*, whilst the directionality of partial coefficients for FC and Turbidity were reversed.

	<i>M. ampliata</i>		<i>H. exesa</i>		<i>E. lamellosa</i>	
	β	R^2	β	R^2	β	R^2
SST	-1.00	0.49	-2.22	0.27	-	-
Sal	-	-	1.44	0.27	1.32	0.26
Turb	-	-	0.44	0.27	-0.59	0.26
TSS	-0.31	0.49	-0.86	0.27	-	-
TN	-0.43	0.49	-1.22	0.27	-	-
TP	-	-	1.38	0.27	-	-
TOC	-	-	0.45	0.27	0.74	0.26
Chl-a	-	-	0.48	0.27	-	-
FC	-	-	1.09	0.27	-1.01	0.26

Table 1: Partial regression coefficients and R^2 for water quality parameters identified by best subset multiple regression as being influential on coral fecundity at $p<0.01$.

Discussion

The data suggests that all three species spawned twice per year; these are consistent with broad patterns previously described for other coral species in Singapore by Guest (2004) and Guest *et al.* (2005).

It is likely that reproductive effort is unequal between April and October, with greater fecundity recorded in April than later in the year, but late-stage oocytes were still found in all colonies in October which provides sound evidence that they are spawning twice per year although unfortunately, coral fecundities in October were only sampled in one year (2010) during which reproductive output was depressed. As such, conclusions on unequal effort during the two spawning seasons will require more data and intra-colony monitoring (i.e. sampling the same colonies throughout the year) is necessary.

Reproductive seasonality and synchrony maximises fertilisation rates by increasing the chance of conspecific individuals meeting in the water column and therefore increasing fertilisation success (Guest *et al.*, 2005). Oocyte maturation seemed to coincide with an annual increase in SST following the NE and SW monsoons, and it has been suggested that SST plays a major role in the seasonal timing of coral spawning in Singapore (Guest, 2004).

One noticeable finding of the study was significantly lower fecundity detected in April 2010, as compared to the same month of 2009 and 2011. This was most likely the result of anomalous elevated temperatures that similarly triggered extensive coral bleaching throughout the Northern Indian Ocean and SE Asian regions (Goreau, 2010; Guest *et al.* 2012).

However, prolonged elevated SST is known to be detrimental to coral health (Kojis & Quinn, 1984; McClanahan *et al.* 2009) and temperature in this study was also shown to have negative effects on fecundity of *M. ampliata* and *H. exesa*. Significantly lower fecundity was also recorded for all three species in 2010, when temperatures were higher and severe bleaching was observed for many species. Fecundity of all three taxa in October 2010 were generally indicative of recovery from the bleaching, comparable to or exceeding the levels measured in April of the same year.

The concentrations of total suspended solids were also found to have negative effects on the fecundities of *M. ampliata* and *H. exesa*. The negative effects of suspended particulate matter on the reproductive biology of certain scleractinian corals have been extensively documented and probably results from the diversion of energy resources towards cleaning at the expense of growth or reproduction (Kojis & Quinn 1984, Tomascik & Sander 1987; Harrison & Wallace 1990; Guzmán & Holst, 1993; Fabricius, 2005).

It is unclear why fecundity of *E. lamellosa* appeared to be independent of TSS concentrations. While this may be a function of species tolerances, fecundity was negatively associated with turbidity, which is often used as a proxy for water clarity and suspended particulate load. This is perhaps suggestive of a relationship between fecundity in this species and types of suspended particles, since the relationship between TSS and turbidity depend strongly on the particle composition. Under certain conditions (e.g. increased SPM concentrations), corals (namely *Pocillopora damicornis*, *Montipora digitata* and *Acropora millepora*) can employ heterotrophic strategies to compensate for reduced photosynthetic efficiency (Anthony, 1999).

Increased SST and TSS are not the only factors that can negatively affect coral fecundity; exposure to elevated nutrients alone may be enough to have noticeable effects too (Guest, 2004), although the patterns detected in this study were highly variable among species. An *in situ* study by Ward and Harrison (2000) revealed that even small increases in nitrogen and phosphorus concentrations can have dramatic changes on the reproductive activity in several species of scleractinian corals, namely *Acropora* spp. Exposed to elevated levels of nitrogen, the corals produced significantly smaller and fewer

eggs and contained less testes but when exposed to elevated levels of phosphorus, the corals produced more eggs (but consistently smaller) and more testes material. Manipulative laboratory experiments involving elevated levels of nitrates and phosphates will be carried out to assess the effects they have on coral fecundity.

While the investigation of environmental influences was not intended to be conclusive, patterns identified nonetheless provided insights into relative sensitivities of the three species that were supported by field data. It was apparent that *H. exesa* was the most sensitive species of coral in this study, as the fecundity data demonstrated that during the periods of low (but measurable) reproductive output for the other two species, oocytes are completely absent in *H. exesa*. Benthic community data at these sites also indicated that *H. exesa* coral abundance is significantly lower than *M. ampliata* and *E. lamellosa* (Oh & Sin, in prep.); however this could also be due to pre- or post-settlement mortality.

Additionally, *H. exesa* fecundity was also the most sensitive to environmental parameters, showing to have a negative relationship with SST, TSS and TN but positively correlated to salinity, TP, TOC, Chl-*a* and FC, which suggests that coral fecundity would be a useful bio-indicator of sub-lethal stress.

M. ampliata had the highest fecundity of the studied species and was sensitive to very few of the measured environmental parameters (i.e. SST, TSS and TN). Studies also demonstrate that this species is an efficient space competitor, which often dominates reef slopes (Dai, 1990; Fan & Dai, 1998; Veron, 2000) and tolerates sediment deposition through heavy mucous secretion and sloughing (Dikou & Woesik, 2006). This evidence therefore suggests that *M. ampliata* is a relatively resilient species.

E. lamellosa is also considered to be a widely distributed and common scleractinian in the Indo-Pacific region (Veron, 2000) where it dominates certain areas of the reef (Veron *et al.*, 1977; Sheppard, 1980; Fan & Dai, 1995) and was sensitive to four of the measured environmental parameters, such as Turbidity, TOC, FC and Salinity.

Salinity is commonly known to have negative effects on coral reproduction, where as in this study, it had the opposite effect. One explanation may be that the studied sites salinity ranged from approximately 27.5 to 34.5ppt and this may not have been excessive enough to lead to detrimental effects on coral health in this region. A study by Li *et al.* (2008) indicates that combined effects of elevated temperature and low salinity aggravate and damage the coral having negative effects on the photosynthesis of the symbiotic algae; however the corals in Li *et al.*'s study were subjected to salinity as extreme as 25ppt.

This study was designed to be a preliminary investigation into the key environmental parameters impacting these species' reproductive output; subsequent extensive environmental monitoring over the whole set shall be carried out to examine how various parameters at particular times may have the most influence on coral fecundity within each gametogenic cycle.

Kojis and Quinn (1984) discovered that fecundity in *Acropora palifera* begun developing two months earlier than usual when there was a prolonged temperature increase, which means is a risk that mature oocytes could be overlooked in the current sampling times. Increasing sampling times from quarterly to monthly collections is thence required to further elucidate the coral's reproductive seasonality and gametogenic cycle in more detail. This should ideally help to create a clearer picture of reproductive seasonality of these species in this region and thus contribute to successful coral reef management.

While random sampling is the most suitable approach for testing the effect of environmental variables on fecundity; monthly monitoring of tagged colonies will also be carried out to get an even more accurate idea of these species' gametogenic cycles and to measure intra-colony variation of gamete maturity and to identify whether the same colonies are spawning twice per year or if they are spawning in one of the two opportunities per year.

In equatorial regions, coral reefs are continuously exposed to temperatures close to their upper thermal tolerance limits and the lack of knowledge on species-specific responses to environmental conditions could have extensive implications for biodiversity conservation. This study supplements the current limited species-specific knowledge on the reproductive output of *Hydnophora exesa*, *Merulina ampliata* and *Echinopora lamellosa* within South-East Asia, with the exception on the latter two species in sub-tropical Taiwan (Fan & Dai, 1995; 1998).

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