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Competitive effects of macroalgae on the fecundity of the reef-building coral *Montastraea annularis*

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ABSTRACT: In recent decades, a rise in coral mortality, attributed to increased frequency of mass-bleaching events, increased prevalence of disease, and more frequent and severe hurricanes, has contributed to a rapid proliferation of macroalgae across many Caribbean reefs. As a consequence, the frequency of coral–algal interactions has risen. Here, we document the effects of 2 dominant Caribbean macroalgae, *Dictyota* spp. and *Lobophora variegata*, and a mixed algal community on the fecundity of a massive coral. *Montastraea annularis* is a dominant Caribbean reef-building coral characterised by a low recruitment rate. To investigate the effects of macroalgae on coral fecundity, algal contact was experimentally manipulated around the perimeter of *M. annularis* patches. Fecundity was measured as the diameter of eggs (ES), the number of eggs per gonad (E#) and the number of gonads per polyp (G#). Algal contact was shown to significantly reduce the diameter of eggs at both the coral–algal boundary and at the centre of coral patches. The presence of *Dictyota* spp. or a mixed algal community was shown to have more detrimental effects on ES than the presence of *L. variegata*. Removal of algal contact immediately prior to gametogenesis increased the reproductive output of polyps directly adjacent to the cleared areas, with an increase in ES, E# and G#. Our results imply that algal competitors can reduce the fecundity of *M. annularis* through mechanical and/or allelochemical damage of polyps directly adjacent to the algae and by causing the reallocation of energy within the coral patch from reproduction to defence and repair.

KEY WORDS: Fecundity · Competition · Coral · Macroalgae · Energy allocation

INTRODUCTION

The critical balance between algae and corals in reef ecosystems has recently been disturbed as a consequence of natural and anthropogenic perturbations, resulting in a shift from coral-dominated to algal-dominated reefs in many regions of the Caribbean (Hughes 1994, Aronson & Precht 2001). While some macroalgae are an integral component of coral reefs providing food and habitat for numerous species, the dominance of algae is typically associated with a decline in reef health. A rise in coral mortality attributed to the increased frequency of mass-bleaching events (Hoegh-Guldberg 2004), increased frequency and prevalence of disease (Harvell et al. 1999), and more frequent and severe hurricanes (Holland & Webster 2007), has contributed to the rapid proliferation of macroalgae on many reefs because dead coral is rapidly colonised by algal recruits or fragments (Walters et al. 2002, Diaz-Pulido & McCook 2004). If grazing levels are unable to compensate for the increase in algal colonisation, then a more mature algal successional phase may arise (Szmant 2002, Hughes et al. 2007).

One consequence of increased macroalgal biomass on reefs is a rise in the frequency and duration of contact between algal species and other sessile taxa such as corals (Lirman 2001). This has, in part, stimulated new studies of coral–algal competition (reviewed in McCook et al. 2001). While the observed decline in coral cover over recent decades coincided with the rapid proliferation of macroalgae on many reefs,

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macroalgal blooms are mostly a consequence of coral mortality, rather than the prime cause (McCook et al. 2001, Diaz-Pulido & McCook 2002). Algal recruits are hypothesised to rapidly pre-empt coral settlement space and may settle directly onto stressed or dead coral tissue, rather than overgrowing healthy coral tissue (McCook et al. 2001, Diaz-Pulido & McCook 2002, 2004), although direct overgrowth of healthy coral tissue has been observed (Hughes et al. 2007). Macroalgae have been shown to inhibit coral recruitment (Kuffner et al. 2006), and coral–algal interactions can result in reduced coral growth rates and increased tissue mortality (Lirman 2001, River & Edmunds 2001, Jompa & McCook 2002, Nugues & Bak 2006, Box & Mumby 2007). Furthermore, the presence of algae around coral colonies has also been documented to reduce the fecundity of the entire coral colony (Tanner 1995, Hughes et al. 2007). While mortality of coral tissue is likely due to the mechanical and/or allelochemical effects of direct contact with the algal fronds (River & Edmunds 2001, Jompa & McCook 2003), a reduction in growth rate or colony fecundity suggests a possible diversion of energy away from reproduction or growth and towards defence and repair of damaged tissue (Tanner 1995, Rinkevich 1995).

Any organism has a finite amount of energy available to partition between growth, maintenance and reproduction (Pianka 1983). Physiological trade-offs in energy allocation occur when 2 or more functions compete directly for limited resources within one individual (Stearns 1992). For example, the energetically costly process of forming gametes is likely to be at the expense of maintenance and growth processes (Calow 1985). Changes in ecological or environmental conditions that result in a higher energy requirement for growth or maintenance may thus result in a decrease in reproductive output. Such trade-offs in energy allocation have been observed directly and indirectly in coral species, particularly in physiologically stressful environments (Ward 1995, Anthony et al. 2002). Sexual reproduction in corals may be impaired by the process of regeneration of damaged tissue (Rinkevich 1996). As a result, the reproductive output of the entire colony may be reduced and/or growth rates may be retarded. Such reductions in fundamental processes within a coral colony may decrease the capacity of the entire population to cope with increasing ecological and environmental change occurring on reefs. Sexually generated larvae are a vital source of genetic diversity within populations and provide sessile organisms, such as corals, with the ability to disperse beyond the natal population, perhaps to more favourable habitats (Stocklin & Winkler 2004). Paucity of viable larvae may ultimately lead to a decline in population size and persistence.

Montastraea annularis sensu strictu (Ellis & Solander 1786) is a long-lived, dominant reef-building coral of the Caribbean that forms massive colonies, frequently over 1 m in diameter. In recent decades, the abundance of *M. annularis* colonies on many reefs across the Caribbean has been observed to decline and more opportunistic, faster-growing coral species have become more widespread (Jackson 2001). Populations of *M. annularis* are characterised by low recruitment rates (Bak & Engel 1979, Mumby 1999), despite an annual mass-spawning of gametes in late summer (Szmant 1991), and are therefore predicted to take many decades to recover to previous levels (Hughes & Tanner 2000). Size-based demographic models have demonstrated that the low rates of sexual recruitment typical of *M. annularis* populations may not be sufficient to sustain population recovery once colony abundance declines beyond a certain point (Edmunds & Elahi 2007). If the fecundity of *M. annularis* colonies is impaired by macroalgal blooms, then the bleak predictions for sustainability of this coral could become worse. Here, we investigate the effects of 2 dominant Caribbean macroalgae, *Lobophora variegata* (Phaeophyta, Dictyotales) and *Dictyota* spp. (Phaeophyta, Dictyotales), and a mixed algal community on the fecundity of *M. annularis*. Typically in the Caribbean, *L. variegata* (a corticated macroalga) has a flat, creeping life-form, whereas *Dictyota* (a corticated foliose alga) has an erect, branching morphology (Steneck & Dethier 1994, Littler & Littler 2000). The mixed algal community was composed of turf algae, predominantly *Derbesia* spp. (Chlorophyta, Caulerpales), and will be referred to as such from here on. During the study, we manipulated the presence of *Dictyota* spp., *L. variegata* and *Derbesia* spp. in contact with the perimeter of coral patches of *M. annularis* during gametogenesis to test the hypothesis that the presence of algal competitors will reduce polyp fecundity. In addition, we test the hypothesis that reductions in polyp fecundity observed in *M. annularis* during gametogenesis are sensitive to the type of algal competitor (*Dictyota* spp., *L. variegata* or *Derbesia* spp.).

While previous studies demonstrated the negative effects of macroalgae on coral fecundity (Tanner 1995, Hughes et al. 2007), we specifically manipulated algal contact for the entire period of gametogenesis within a massive coral species and investigated both whole-patch effects and the effects on individual polyps.

MATERIALS AND METHODS

Study site. The study was undertaken on the north coast of Roatan, Honduras between May 23 and September 4, 2004. A study site was established at

Seaquest (16° 17′ 39″ N, 86° 36′ 00″ W) on a large *Montastraea* reef located between 8 and 11 m of depth.

Experimental design. For the purpose of this study, a discrete aggregate of lobes was defined as a colony, and a coral patch was defined as an autonomous area of tissue on a single lobe. Fifty-four coral patches with high algal contact (>80%) were selected from 18 colonies of *Montastraea annularis* (3 patches per colony). To ensure that coral patches were fully reproductive, only patches with a 2-dimensional area >100 cm^2 were selected from colonies with a 2-dimensional area >200 cm^2. To eliminate the effects of systematic differences in colony fecundity, each set of treatments was assigned to separate colonies, rather than randomly assigning them across patches. The treatments were as follows: (1) all algae along the perimeter of the coral patch were removed and the cleared area was maintained every 2 wk (0% algal contact), (2) 50% of the algae along the perimeter of the coral patch was removed and the same cleared area was maintained every 2 wk (50% algal contact), (3) all algae along the perimeter of the coral patch were left intact and maintained at the same % contact for the whole experiment (control: 100% algal contact). All 3 treatments were repeated for 3 algal taxa: *Dictyota* spp. (principally *D. pulchella*), *Lobophora variegata* and *Derbesia* spp. Colonies were assigned to an algal taxon based on the most common alga surrounding the perimeter of coral patches. In summary, 6 colonies were assigned to each algal taxon (*Dictyota*, *Lobophora* and *Derbesia*), and each colony possessed 3 coral patches (1 per algal removal treatment). Thus, each combination of algal taxon and removal treatment was replicated 6 times (Table 1). Although assignment of algal taxa was not random, colonies were evenly distributed over the reef.

Approximately 20 polyps were collected from the edge and the centre of each coral patch. For patches assigned to 0% algal contact, 2 samples were collected per coral patch: 0%-EDGE-CLEAR and 0%-CENTRE (Table 1). For patches assigned to 50% algal contact, polyps were sampled from the edge adjacent to algae (50%-EDGE-ALGAE), from the edge cleared of algae (50%-EDGE-CLEAR) and from the centre of the coral patch (50%-CENTRE) (Table 1). For patches assigned to 100% algal contact, 2 samples were collected per coral patch: 100%-EDGE-ALGAE and 100%-CENTRE (Table 1).

Sampling and fecundity measurements. Fecundity of *Montastraea annularis* was monitored in non-experimental colonies to enable sampling to be conducted on fully developed gametes. A small piece of coral was chiselled from a coral patch and inspected for the presence of pinkish eggs, visible to the naked eye. Sampling of all experimental coral patches took place between 25 August and 4 September 2004, just prior to the date of predicted spawning. Approximately 20 polyps were collected from the edge and the centre of each coral patch. It has been estimated that there are approximately 12 gonads per polyp and that each gonad produces between 5 and 14 eggs in mature colonies (Szmant 1986). The polyps collected from the edge of the coral patches were taken from within the first 5 rows of polyps.

Polyps were collected using a hammer and chisel and placed in labelled plastic tubes. On returning to the shore, the samples were immediately fixed in 10% seawater formalin (a solution of 1 part 37% formaldehyde and 9 parts seawater) and left in the fixative for a minimum of 2 h. The fixative was then poured off and the sample rinsed under running tap water for approximately 15 min. Samples were then stored in 70% isopropanol with 1% glycerin, and transported back to the UK for further analysis. Due to logistical problems, colony breakage and missing tags, it was not possible to collect all samples. In total, 51 out of 54 patches were sampled (a total of 117 samples).

Samples of polyps were decalcified using a weak acid solution (1 l = 900 ml water, 80 ml hydrochloric acid and 20 ml formaldehyde). For each sample, the isopropanol was drained off and the sample was placed in a 100 ml Pyrex beaker and washed under running tap water for 15 min. Approximately 25 to 50 ml of weak acid solution was added

Table 1. *Montastraea annularis.* Summary of algal removal treatments and samples collected for each algal taxon. Each algal taxon was located on a separate colony and each algal removal treatment was applied to a separate coral patch (CP) within the colony. This design was replicated 6 times, using 54 coral patches on 18 colonies. CENTRE: centre polyps; EDGE-ALGAE: polyps adjacent to algae; EDGE-CLEAR: polyps adjacent to cleared area; +: samples; –: no samples

Colony	Algal taxon	Samples	Algal contact		
			CP1 (0%)	CP2 (50%)	CP3 (100%)
1	*Dictyota* spp.	CENTRE	+	+	+
		EDGE-ALGAE	–	+	+
		EDGE-CLEAR	+	+	–
2	*Lobophora variegata*	CENTRE	+	+	+
		EDGE-ALGAE	–	+	+
		EDGE-CLEAR	+	+	–
3	*Derbesia* spp.	CENTRE	+	+	+
		EDGE-ALGAE	–	+	+
		EDGE-CLEAR	+	+	–

to the beaker and the skeleton was allowed to dissolve completely (between 24 and 160 h depending on size). Decalcification was complete when the soft tissue floated to the surface of the solution. The acidity of the solution was checked with litmus paper every 24 h and the solution was changed every 48 h, or earlier if required, to ensure adequate acidity. Once decalcified, the sample was placed in a labelled tissue capsule and washed under running water for a minimum of 2 h. The sample was then placed in a labelled tube and preserved in 80% ethanol prior to dissection.

For each sample, fecundity was estimated as the diameter of each egg (i.e. egg size, ES), the number of eggs produced per gonad (E#), and the number of gonads produced per polyp (G#). Such measures of gametic characteristics have been demonstrated as useful indices of reproductive effort (Villinski 2003), and changes in these indices can be an indication of sublethal stress in corals (Ward & Harrison 2000). Individual polyps were randomly removed from each sample and individually dissected. The polyp was cut down the longitudinal axis and opened up into 2 halves (Fig. 1a). Gonads were carefully extracted (Fig. 1b), counted and measured in terms of length (µm) and width (µm) using an eyepiece graticule calibrated with a stage micrometer. Each egg within the gonad was counted and its diameter (µm) recorded. Where possible, a minimum of 6 polyps was dissected for each sample. All gonads and eggs within each polyp were counted and sized.

Statistical analysis. Linear mixed effects models with a normal distribution were used to analyse all data for ES (continuous data), and generalised linear mixed effects models with a Poisson distribution were used to analyse all data for E# and G# (count data) (Crawley 2002). For CENTRE polyps, ES, E# and G# comparisons were made among the 3 algal treatments (0, 50 and 100%) and among the 3 algal taxa (*Lobophora variegata*, *Dictyota* spp. and *Derbesia* spp.), with contact and algal taxa as fixed effects and colony and coral patch as random effects (to account for natural variation among colonies). Within treatment 2, ES, E# and G# were compared among the 3 sample types (50%-CENTRE, 50%-EDGE-ALGAE and 50%-EDGE-CLEAR), with sample type as the fixed effect and colony as a random effect. When comparing edge polyps alone, data were pooled for edge polyps adjacent to algae (50%-EDGE-ALGAE + 100%-EDGE-ALGAE = EDGE-ALGAE-ALL) and for edge polyps adjacent to cleared areas (50%-EDGE-CLEAR + 0%-EDGE-CLEAR = EDGE-CLEAR-ALL). ES, E# and G# were compared between EDGE-ALGAE-ALL and EDGE-CLEAR-ALL, with sample type as a fixed effect and colony and coral patch as random effects.

The adequacy of all models was evaluated by plotting standardised residuals against fitted values to test for heteroscedasticity and against standard normal deviates to test for normality. None of these assumptions were violated by the data.

Fig. 1. *Montastraea annularis.* (a) Cross-section of a polyp. Gonads containing eggs, surrounded by opaque spermary tissue, attached to the mesenterial filaments. Scale bar = 1000 µm. (b) Gonad containing 5 eggs surrounded by opaque spermary tissue. Scale bar = 250 µm

RESULTS

A summary of significant results is shown in Table 2.

Egg diameter

Across algal taxa, ES was found to be significantly smaller within 100%-CENTRE polyps compared to 0%-CENTRE polyps (Fig. 2a, Table 3). Removal of only 50% of the algal contact had no significant effect on ES (Fig. 2a, Table 3). *Dictyota* spp. and *Derbesia* spp. both had greater, negative effects on ES at all algal contacts compared to *Lobophora variegata* (Fig. 3, Table 3). For patches within treatment 2, ES within 50%-CENTRE and within 50%-EDGE-CLEAR polyps was larger than ES within 50%-EDGE-ALGAE polyps (Fig. 2b, Table 3). Using data pooled from all treatments, direct comparison of ES in edge polyps showed that EDGE-ALGAE-ALL polyps had smaller eggs than EDGE-CLEAR-ALL polyps (Table 3).

Number of eggs per gonad

The effect of algal contact on E# varied among algal taxa (see interaction term, Table 4). E# was lower within 100%-CENTRE polyps surrounded by *Derbesia* spp. compared to 50%-CENTRE or 0%-CENTRE polyps surrounded by *Derbesia* spp. (Fig. 4). However, the opposite was observed for coral patches surrounded by *Dictyota* spp., where E# was lower in 0%-CENTRE polyps compared to 50%-CENTRE or 100%-CENTRE polyps (Fig. 4). Irrespective of algal taxa, the 3 sample types collected within treatment 2 differed significantly. 50%-CENTRE and 50%-EDGE-CLEAR polyps contained more eggs per gonad than 50%-EDGE-ALGAE polyps (Fig. 2c, Table 4).

Number of gonads per polyp

Algal treatment had no effect on G# within CENTRE polyps of coral patches (Table 5). Irrespective of algal taxa, the 3 sample types collected within treatment 2 differed significantly. 50%-CENTRE polyps contained more gonads than 50%-EDGE-CLEAR and 50%-EDGE-ALGAE polyps (Fig. 2d, Table 5). Using pooled data, direct comparison of G# within edge polyps showed that EDGE-ALGAE-ALL polyps had fewer gonads than EDGE-CLEAR-ALL polyps (Table 5).

Table 2. *Montastraea annularis.* Summary of significant results observed for each fecundity index testing the effects of algal contact on polyps. CENTRE: centre polyps; EDGE-ALGAE: polyps adjacent to algae; EDGE-CLEAR: polyps adjacent to cleared area; ES: egg size; E#: no. of eggs per gonad; G#: no. of gonads per polyp; -ALL: pooled samples

Fecundity index	Significant result
ES	For all algal genera, 100%-CENTRE polyps produced smaller diameter eggs than 0%-CENTRE polyps (Fig. 2a, Table 3)
	At all algal contacts, polyps adjacent to *Dictyota* spp. or *Derbesia* spp. had smaller eggs than polyps adjacent to *Lobophora variegata* (Fig. 3, Table 3)
	50%-EDGE-ALGAE polyps had smaller eggs than 50%-CENTRE and 50%-EDGE-CLEAR polyps (Fig. 2b, Table 3)
	EDGE-ALGAE-ALL polyps had smaller eggs than EDGE-CLEAR-ALL polyps (Table 3)
E#	Effect of algal contact on egg number varied among algal taxa (Fig. 4, Table 4)
	100%-CENTRE polyps with *Derbesia* spp. had fewer eggs than 50%-CENTRE or 0%-CENTRE polyps with *Derbesia* spp. (Fig. 4, Table 4)
	0%-CENTRE polyps with *Dictyota* spp. had less eggs than 50%-CENTRE or 100%-CENTRE polyps with *Dictyota* spp. (Fig. 4, Table 4)
	50%-EDGE-ALGAE polyps had less eggs than 50% CENTRE and 50%-EDGE-CLEAR polyps (Fig. 2c, Table 4)
G#	50%-CENTRE polyps had more gonads than 50%-EDGE-ALGAE and 50%-EDGE-CLEAR polyps (Fig. 2d, Table 5)
	EDGE-ALGAE-ALL polyps had less gonads than EDGE-CLEAR-ALL polyps (Table 5)

DISCUSSION

The presence of macroalgae was found to affect the fecundity of both adjacent coral polyps and those in the centre of coral patches. Therefore, the hypothesis that the presence of algal competitors will reduce polyp fecundity is accepted. A reduction in egg size within central polyps implies that algal impacts are not local and that energy may be diverted away from reproduction and re-allocated towards defence and repair mechanisms within polyps on the edge of patches. Previous studies have already demonstrated that macroalgal contact can damage polyps and induce tissue mortality, so the mechanism behind possible energy re-allocation is supported (River & Edmunds 2001, Nugues & Bak 2006). Shifts in the allocation of energy between reproduction and maintenance or repair under stressful conditions have been proposed before. Tanner (1995) observed whole colony effects in the species *Acropora palifera*, where larval output decreased by 50% in colonies in the presence of macroalgae. Tanner (1995) attributed

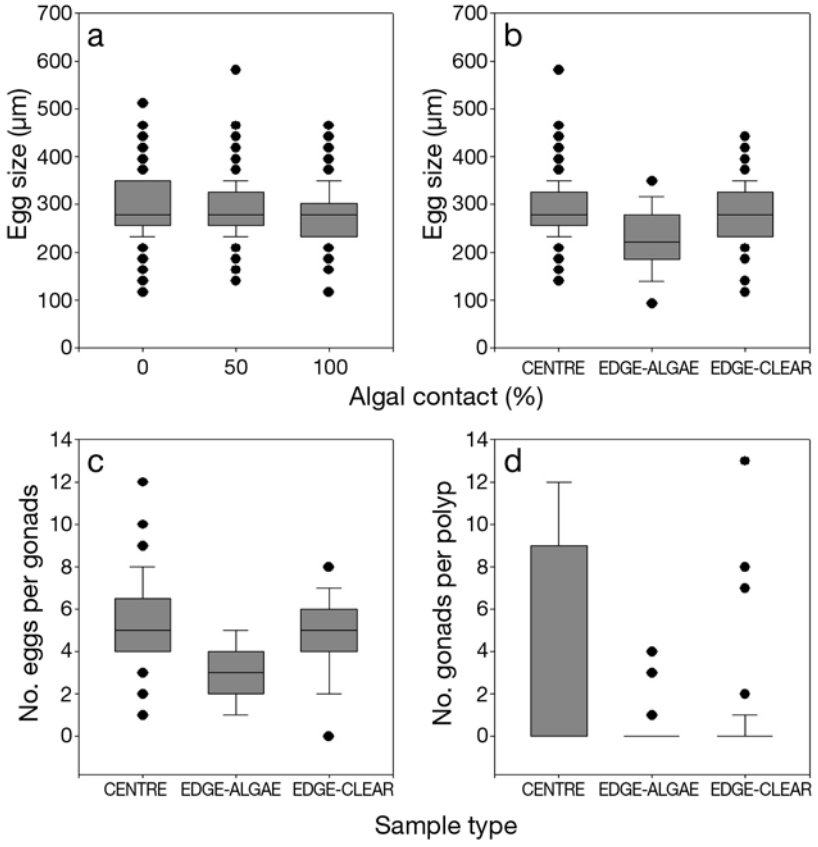

Fig. 2. *Montastraea annularis.* (a) Egg size (µm) within centre polyps of patches with 0, 50, and 100% algal contact. (b) Egg size (µm) within polyps of patches with 50% algal contact. (c) Number of eggs per gonad within polyps of patches with 50% algal contact. (d) Number of gonads within polyps of patches with 50% algal contact. Box represents median with 25th and 75th percentiles. Whiskers denote 10th and 90th percentiles. Black dots denote all outliers. Sample type represents location of polyps within patch: CENTRE, centre polyps; EDGE-ALGAE, polyps adjacent to algae; EDGE-CLEAR, polyps adjacent to cleared area

Table 3. *Montastraea annularis.* Summary of linear mixed effects models testing for the effects of algal contact and taxa on egg size (ES, µm). Model conditions to which coefficients are compared are shown in the intercept row. df: degrees of freedom; *t*: test statistic; p: associated probability; CENTRE: centre polyps; EDGE-ALGAE: polyps adjacent to algae; EDGE-CLEAR: polyps adjacent to cleared area; significant p-values ($p < 0.005$) are marked with an asterisk

Model and Source	Coefficient	df	*t*	p
ES vs. contact				
0%-CENTRE contact (Intercept)	295.04	4376	72.55	<0.001*
50%-CENTRE contact	−6.36	6	−1.22	0.2679
100%-CENTRE contact	−13.32	6	−2.63	0.0391*
50%-CENTRE vs. 100%-CENTRE	−6.96	6	−1.36	0.2219
ES vs. Algal taxa				
Dictyota spp. (Intercept)	279.90	4377	89.60	<0.001*
Lobophora variegata	14.25	4377	6.25	<0.001*
Derbesia spp.	4.67	4377	1.68	0.093
Derbesia spp. vs. *Lobophora variegata*	−9.58	4377	−4.03	<0.001*
ES: 50%-CENTRE vs. 50%-EDGE-ALGAE vs. 50%-EDGE-CLEAR				
50%-CENTRE (Intercept)	288.85	1429	77.67	<0.001*
50%-EDGE-ALGAE	−65.32	1429	−6.52	<0.001*
50%-EDGE-CLEAR	−0.09	1429	−0.02	0.984
50%-EDGE-CLEAR vs 50%-EDGE-ALGAE	65.23	1429	6.15	<0.001*
ES: EDGE-ALGAE-ALL vs. EDGE-CLEAR-ALL				
EDGE-ALGAE-ALL (Intercept)	177.86	379	6.94	<0.001*
EDGE-CLEAR-ALL	74.24	379	5.90	<0.001*

the decline in larval output to an increase in energy expenditure within the colonies due to competition with the macroalgae. Hughes et al. (2007) also documented a reduction in egg size, number of eggs per polyp, and number of reproductive polyps cm^{-2} in colonies of *Montipora digitata* placed beneath algal canopies compared to colonies in unshaded controls. Within the species *Montastraea annularis*, lesions have also been shown to reduce reproductive output. Van Veghel & Bak (1994) observed a reduction in the number of eggs and gonads per polyp in those polyps directly bordering the damaged tissue. The results presented here provide the first evidence of the negative effects of algal competitors on fecundity within a massive coral species and demonstrate that the effects are not localised to polyps adjacent to the macroalgae.

An alternative theory to energy tradeoff within colonies has been proposed in which energy allocation to various biological functions is hierarchical and preset, with sexual reproduction taking precedence over other functions such as growth, or vice versa (Harrison & Wallace 1990). While our results do not discount the theory of a preset hierarchy of biological functions within corals, they do suggest that, within colonies of *Montastraea annularis*, defence of polyps takes precedence over sexual reproduction in the presence of algal competitors.

The impact of algal competition on coral fecundity differs among algal

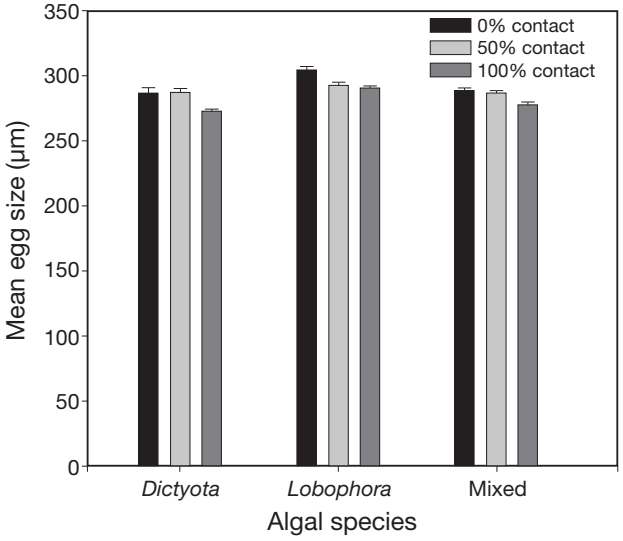

Fig. 3. *Montastraea annularis.* Mean (±1 SE) egg size within centre polyps of coral patches in contact with *Dictyota* spp., *Lobophora variegata* and *Derbesia* spp. for each algal treatment (0, 50, and 100% contact)

Table 4. *Montastraea annularis.* Summary of generalised linear mixed effects models testing for the effects of algal contact and taxa on the number of eggs per gonad (E#). Model conditions to which coefficients are compared are shown in the intercept row. df: degrees of freedom; *t*: test statistic; p: associated probability; CENTRE: centre polyps; EDGE-ALGAE: polyps adjacent to algae; EDGE-CLEAR: polyps adjacent to cleared area; significant p-values (p <0.005) are marked with an asterisk

Model and Source	Coefficient	df	*t*	p
E# vs. Contact				
0%-CENTRE contact (intercept)	1.63	761	22.27	<0.001*
50%-CENTRE contact	0.05	6	0.59	0.5763
100%-CENTRE contact	0.13	6	1.79	0.1245
50%-CENTRE vs. 100%-CENTRE	0.09	6	1.17	0.2882
E# vs. Algal taxa				
Dictyota spp. (intercept)	1.83	759	25.88	<0.001*
Lobophora variegata	−0.13	759	−4.14	<0.001*
Derbesia spp.	−0.25	759	−6.25	<0.001*
Derbesia spp. vs. *Lobophora variegata*	−0.11	759	−3.34	<0.001*
E# vs. Contact × Algal taxa				
0%-CENTRE contact – *Dictyota* spp. (intercept)	1.31	755	14.27	<0.001*
50%-CENTRE × *Lobophora variegata*	−0.60	755	−7.09	<0.001*
100%-CENTRE × *Lobophora variegata*	−0.52	755	−6.40	<0.001*
50%-CENTRE × *Derbesia* spp.	−0.78	755	−6.90	<0.001*
100%-CENTRE × *Derbesia* spp.	−0.97	755	−9.93	<0.001*
E#: 50%-CENTRE vs. 50%-EDGE-ALGAE vs. 50%-EDGE-CLEAR				
50%-CENTRE (Intercept)	1.64	263	16.04	<0.001*
50%-EDGE-ALGAE	−0.67	263	−4.72	<0.001*
50%-EDGE-CLEAR	−0.27	263	−4.33	<0.001*
50%-EDGE-CLEAR vs. 50%-EDGE-ALGAE	0.40	263	2.68	0.0077*
E#: EDGE-ALGAE-ALL vs. EDGE-CLEAR-ALL				
EDGE-ALGAE-ALL (Intercept)	0.94	87	3.28	0.0015*
EDGE-CLEAR-ALL	0.35	87	1.64	0.1044

taxa. While all taxa were found to reduce the size of eggs in coral patches surrounded by 100% algal contact, the presence of *Dictyota* spp. or *Derbesia* spp. had a greater effect on the diameter of eggs compared to that of *Lobophora variegata*. Thus, the hypothesis that reductions in polyp fecundity observed in *Montastraea annularis* during gametogenesis are sensitive to the type of algal competitor can also be accepted. In addition, *Derbesia* spp. was observed to have the greatest negative effect on egg number compared to *Dictyota* spp. or *L. variegata.* The effects of algal competitors will likely vary according to the physical, biological and chemical properties of the alga (McCook et al. 2001, Jompa & McCook 2003). The branching morphology of *Dictyota* spp. and the filamentous nature of the dominant turf algae *Derbesia* spp. within the mixed communities may be particularly problematic for corals, because their corticated branches oscillate more frequently with currents and surges, thereby abrading adjacent coral polyps (Coyer et al. 1993). In contrast, the creeping blades of *L. variegata* are flatter and less motile, thereby having a greater impact through overgrowth and shading, rather than through the mechanical effects of abrasion (Nugues & Bak 2006). Such effects have been observed previously; *Dictyota pulchella* was shown to have a greater effect on the growth of juvenile coral species when in close proximity compared to *L. variegata* (Box & Mumby 2007).

Two measures of fecundity (egg number and gonad number) in the centre of coral patches were less affected by the extent of algal contact. While this measure reflects reproductive output of a coral colony, egg size is suggested to be more sensitive to the effects of sub-lethal stress, such as algal contact (Ward & Harrison 2000). Nevertheless, differences were observed between centre polyps and those adjacent to algae and cleared areas. Those polyps in direct contact with macroalgae had the smallest egg size and fewest gonads, and whilst polyps on the edge of colonies are typically less fecund than centre polyps (Szmant 1991), our results indicate that direct macroalgal contact can further reduce the fecundity of polyps in the peripheral zone. Polyps in direct contact with algae may be subject to both mechanical

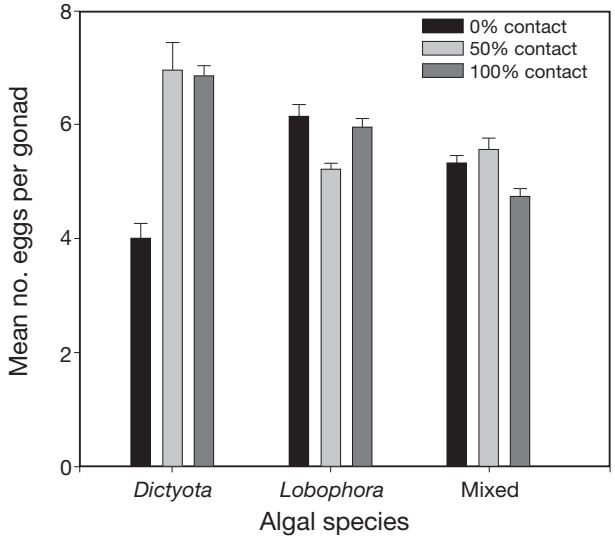

Fig. 4. *Montastraea annularis.* Mean (±1 SE) number of eggs per polyp within centre polyps of coral patches in contact with *Dictyota* spp., *Lobophora variegata* and *Derbesia* spp. for each algal treatment (0, 50 and 100% contact)

and allelochemical effects of the macroalgae which have been suggested to cause polyp retraction and eventually tissue mortality (River & Edmunds 2001, Jompa & McCook 2003). Given the energy required for gamete production, algal stress is likely to be most critical during the period of gametogenesis. Removal of algal competitors immediately prior to the onset of gametogenesis increased the reproductive output of polyps directly adjacent to the cleared areas. However, elimination of adjacent algae a few weeks or months prior to the onset of gametogenesis may further enhance fecundity levels by allowing sufficient time for damaged polyps to recover before energy is required for reproduction and gamete development.

Given the increase in algal abundance observed on many reefs of the Caribbean in recent decades (Hughes 1994, Gardner et al. 2003), the effects of algae on fecundity may have significant implications for the ecological function (reef building) carried out by *Montastraea annularis* populations across the Caribbean. Smaller eggs may potentially result in reduced fertilisation rates and/or lower larval survival, and a reduction in egg number may result in reduced larval numbers. The relative effects of egg size versus egg number have not been systematically evaluated in corals, but a reduction in egg number may outweigh effects of reduced egg size as fewer larvae will be produced. Paucity of sexually generated larvae can restrict population recovery following disturbances and may inhibit dispersal to more favourable environments (Eriksson 2000). Furthermore, low numbers of sexually generated recruits may lead to a reduction in the genetic diversity of populations and, subsequently, a reduction in the resistance of populations to biotic stress (Pianka 1983, Honnay & Bossuyt 2005). Nevertheless, there is evidence that egg size can be important in terms of fertilisation success and larval survival in broadcast spawning marine organisms (Marshall et al. 2000, Levitan 2002). Further research is required to determine the effects of reduced egg size and egg number on fertilisation success in *M. annularis.*

Table 5. *Montastraea annularis.* Summary of generalised linear mixed effects models testing for the effects of algal contact and taxa on the number of gonads per polyp (G#). Model conditions to which coefficients are compared are shown in the intercept row. df: degrees of freedom; *t*: test statistic; p: associated probability; CENTRE: centre polyps; EDGE-ALGAE: polyps adjacent to algae; EDGE-CLEAR: polyps adjacent to cleared area

Model and Source	Coefficient	df	*t*	p
G# vs. Contact				
0%-CENTRE contact (intercept)	1.39	168	5.37	<0.001*
50%-CENTRE contact	−0.08	7	−0.36	0.7192
100%-CENTRE contact	0.13	7	0.67	0.5227
50%-CENTRE vs 100%-CENTRE	0.21	7	1.04	0.3326
G# vs. Algal taxa				
Dictyota spp. (intercept)	0.84	167	3.01	0.003*
Lobophora variegata	0.68	167	3.34	0.001*
Derbesia spp.	1.06	167	4.20	<0.001*
Derbesia spp. vs. *Lobophora variegata*	0.37	167	1.80	0.0739
G#: 50%-CENTRE vs. 50%-EDGE-ALGAE vs. 50%-EDGE-CLEAR				
50%-CENTRE (intercept)	1.26	173	3.83	<0.001*
50%-EDGE-ALGAE	−3.27	173	−4.17	<0.001*
50%-EDGE-CLEAR	−1.75	173	−4.38	<0.001*
50%-EDGE-CLEAR vs. 50%-EDGE-ALGAE	1.52	173	1.77	0.0781
G#: EDGE-ALGAE-ALL vs. EDGE-CLEAR-ALL				
EDGE-ALGAE-ALL (intercept)	−1.93	225	−3.76	<0.001*
EDGE-CLEAR-ALL	1.31	225	2.31	0.0219*

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