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REPORT

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Impacts of bleaching on the soft coral *Lobophytum compactum*. I. Fecundity, fertilization and offspring viability

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Abstract We document long-term effects of a simulated bleaching event on the reproductive output and offspring viability of the soft coral *Lobophytum compactum*. Corals were subjected to temperature and solar radiation treatments to produce both moderately (48–60%) and heavily (90–95%) bleached colonies. Although bleached colonies recovered their zooxanthellae within 10 to 18 weeks, impacts on reproductive output were significant for at least two annual spawning seasons. In the first year, both polyp fecundity and mean oocyte diameter were reduced and inversely correlated with the degree of bleaching, with complete failure of fertilization in the group of heavily bleached colonies. For moderately bleached soft corals, survival and growth of sexual offspring did not differ significantly from those of unbleached colonies. Although no further reductions in zooxanthellae densities in experimental soft corals were recorded throughout the subsequent second year, egg size and fecundity of the heavily bleached soft corals were still significantly reduced 20 months later. Severe bleaching clearly has long-term sub-lethal impacts, reducing overall reproductive output for at least two spawning seasons.

Key words Bleaching · Soft coral · Reproduction · Fecundity · Fertilization

Introduction

Coral bleaching events have been recorded for decades, but bleaching events of unprecedented scale and intensity have been reported in recent years (e.g. Williams and Bunkley-Williams 1990; Berkelmans and Oliver 1999; Hoegh-Guldberg 1999). Bleaching is a stress response during which the symbiosis between the coral host and its symbiotic dinoflagellates (zooxanthellae) is disrupted, resulting in loss of zooxanthellae from the association and/or loss of photosynthetic pigments within the algal partner. Bleaching may be evoked by a variety of environmental factors, however, increased seawater temperature has been implicated as the main stress factor in recent large-scale bleaching events (e.g. Fitt et al. 1993; Glynn et al. 1996). High solar irradiance and ultraviolet radiation (UVR) in particular have also been implicated as a bleaching stimulus and have the potential to increase adverse impacts dramatically by acting synergistically with increased temperature (Jokiel and Coles 1990; Drollet et al. 1994).

An understanding of the underlying biochemical mechanisms that lead to bleaching, particularly the basis for the interaction between temperature and solar radiation, is only just emerging. Increases in temperature result in a decreased capacity of zooxanthellae to process the excitation energy coming from the dark reactions of photosynthesis (Jones et al. 1998). This leaves zooxanthellae secondarily more sensitive to light and leads eventually to destruction of chloroplasts and photoinhibition (Jones et al. 1998). Subsequent discarding of thermally damaged and dysfunctional zooxanthellae from the coral association presents an alternative to previous suggestions that zooxanthellae are expelled to reduce reactive oxygen species in host tissues as a damage-limiting response (Kühl et al. 1995; Lesser 1997). Regardless of the mechanism, any loss of zooxanthellae constitutes a nutritional constraint, because the algal partner translocates up to 95% of its photosynthates to the coral host, thereby providing up to 143% of its daily energetic costs (Muscatine et al. 1984; Davies 1991). Consequently, bleaching results in decreased lipid and protein concentrations in host tissues (Fitt et al. 1993), reduced calcification and growth (Clausen and Roth 1975; Leder et al. 1991; Szmant and Gassman 1990) and, in extreme cases, in death of the coral (e.g. Glynn et al. 1996; Hoegh-Guldberg 1999).

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While the primary effects of bleaching are well documented, studies on longer-term sub-lethal consequences have been scarce. Only one study (Szmant and Gassman 1990) has investigated the possible effects on gametogenesis and provides the first evidence that bleaching has the potential to disrupt the reproductive cycle. Given the important role that sexual reproduction plays in the maintenance and replenishment of reefs, studies of the possible longer-term, sub-lethal impacts of bleaching on reproduction are clearly required.

In this study we simulated a moderate and strong bleaching event and monitored the effects of the disturbances on reproductive output of the common, soft coral, *Lobophytum compactum*, for the two subsequent spawning seasons. This paper documents the impact of the disturbance on adult soft corals (fecundity and egg size), their gametes (fertilization) and their offspring (survival and growth of juveniles). A second paper (Michalek-Wagner and Willis 2000) reports the impact of the simulated disturbance on biochemical parameters associated with fitness and reproduction in experimental adults and their gametes.

Materials and methods

Site and species descriptions

This study took place between October 1995 and December 1997 in Pioneer Bay adjacent to the Orpheus Island Research Station, on the Great Barrier Reef (18°34′S; 146°29′E). All soft corals used in this study were collected from the reef slope at 3- to 4-m depth and subsequently returned to the same site during the recovery phase. *Lobophytum compactum* (Tixier-Durivault 1958), a common reef flat soft coral on the inner and mid-shelf reefs of the Great Barrier Reef (Dinesen 1983; K. Michalek-Wagner, unpublished), was used in the experimental manipulations described below. As is typical for this genus, polyps of *Lobophytum compactum* are dimorphic with autozooids functioning as feeding polyps and bearing gonads, whereas siphononzoids are reduced in size and function solely to circulate water throughout the colony (Tixier-Durivault 1958). *L. compactum* is gonochoric and has a 2-year oogenic cycle (Aliño and Coll 1989) so that large and small eggs, representing two different year cohorts, are present simultaneously within autozooids (Aliño and Coll 1989). In contrast, spermatogenesis requires only 1 year (Aliño and Coll 1989). Thus, mature oocytes are produced every year in synchrony with the annual cycle of sperm production in male colonies but mature females carry two generations of oocytes at any one time. The species typically spawns on the 4th day after the November full moon at Orpheus Island, with egg release starting around 18:30 h and ending around 20:30 h (Aliño and Coll 1989).

Collection and preparation of experimental colonies

Ten randomly selected female colonies of *Lobophytum compactum* were divided with a chisel in situ into four approximately equal-sized fragments. Only female colonies of a similar initial diameter were used. To avoid reversed puberty associated with reduction in colony size below a minimum threshold, all females were approximately 1 m^2 in size and fragments were 36–40 cm in diameter. Each fragment was randomly assigned to one of four different experimental treatments (A–D). After tagging, all soft coral fragments were left to recover at their site of origin for 5 months. Group A remained in situ for the duration of the study (handling controls), whereas group B were transported to flow-through tanks where they were maintained at ambient temperatures and light (tank controls). Groups C and D were subjected to increased solar radiation and temperature to simulate moderate and severe bleaching events respectively. In addition, ten random colonies (group E) from the same site and depth as experimental colonies were tagged and left in situ as undisturbed field controls (chiseling controls).

Bleaching experiments

In order to simulate a moderate bleaching event (approximately 50% loss of zooxanthellae), group C were subjected to an enhanced solar radiation and temperature treatment for 8 days. The simulation of a comparatively strong bleaching event (90–95% loss of zooxanthellae) was accomplished by exposing group D to the same experimental treatment for 12 days. Temperatures in flow-through experimental tanks at Orpheus Island Research Station were increased from 29–30 °C (ambient) to 31 °C ± 0.5 °C [see Berkelmans and Willis 1999 for details of experimental setup]. Photosynthetically active radiation (PAR) and ultraviolet radiation (UVR) were increased through transplantation of soft corals from 3–4 m in situ to 50 cm in the experimental tanks. This transplantation was approximately equivalent to an increase of 50% in PAR and 33% in UVR, respectively, according to light profiles recorded in Pioneer Bay using a Li-Cor light sensor and UV sensor. Control colonies were shaded under a solar weave roof, which provided light conditions equivalent to PAR at 4–5 m in Pioneer Bay. Fluxes were approximately 8% lower for UV-A and 14% lower for UV-B than those experienced by corals in their natural environment on a summer day, which was designated as ambient for the purposes of this experiment (calculations are based on UVR profiles carried out in Pioneer Bay). The timing of the experiment, March 1996, was set to coincide with the most likely timing (late Austral summer) for a natural bleaching event.

At the conclusion of the bleaching treatment, soft corals were returned to the site of collection and their recovery was monitored initially at two-weekly and then at monthly intervals between March 1996 and November 1997. Each month, tissue samples (five lobes in the range of 1–2 g wet weight/colony) were collected and frozen at −20 °C prior to determination of zooxanthellae densities.

Zooxanthellae densities were monitored as indicators of bleaching and recovery of host tissues. Tissue samples for the analysis were fully homogenized in 0.45-μm filtered and autoclaved seawater. Aliquots were fixed in formalin and stored at 4 °C until analysed. Zooxanthellae densities were calculated from quadruplicate hemocytometer counts for each of two subsamples per colony and normalized to soft coral wet weight.

Reproductive parameters

Eggs were quantitatively collected by placing egg nets fitted with collecting jars on top of each experimental and control female colony. Egg nets were deployed approximately 1 h prior to spawning (17:00) and retrieved 3 h later (20:00). To collect sperm, male colonies were placed in well-aerated flow-through aquaria at Orpheus Island Research Station 4 days prior to spawning and placed individually in highly aerated containers 2 h prior to spawning. Four male colonies of *L. compactum* were collected randomly and thus their bleaching histories were unknown. Sperm water was decanted immediately after spawning and diluted to concentrations found to optimize fertilization (10^6 sperm/ml; Willis et al. 1997).

To determine polyp fecundity and mean egg size, tissue samples at least 3 cm long were collected from the center of each colony immediately prior to spawning in all experimental treatments. Samples were fixed in the field with 10% seawater formalin for 24 h, rinsed in freshwater and then stored in 70% ethanol (Jokiel and Coles 1990; Szmant 1991). Ten polyps per colony were dissected to estimate polyp fecundity. In each polyp, the diameters of

ten stage III oocytes (mature oocytes) were measured using a calibrated ocular micrometer. Oocyte stages were categorized according to Yamazato et al. (1981). Only oocytes over 580 μm were scored as mature.

To test the hypothesis that bleaching disturbances affect the fertilization potential of developing eggs, spawned eggs from all soft corals were collected in egg nets and washed three times in millipore-filtered seawater (0.45 μm). Eggs were combined with sperm from each of the four males, i.e. four egg-sperm combinations per female. For each combination, eggs were incubated in quadruplicate vials with sperm at a concentration of 1.2×10^6 sperm/ml. After 6 h, sperm-water was discarded, the fertilized eggs were washed in millipore-filtered seawater, fixed in Bouins solution for 24 h and then stored in 70% ethanol. One hundred eggs per vial were examined and those that had undergone cleavage were scored as fertilized. Fertilization experiments were only carried out during the 1996 breeding season.

To compare larval survival and juvenile growth for offspring from experimental and control groups, approximately 500 larvae from the moderately bleached group and each of the control groups (combined from all female colonies within each group) were reared in separate 10-l aquaria supplied with 1-μm-filtered flow-through seawater and maintained under temperature controlled (25–29 °C) conditions. Metal-halide lights provided light in the PAR region (approximately 800 $\mu E\ m^{-2}\ s^{-1}$) to each aquarium and were set on a 12-h light: 12-h dark cycle. Previously conditioned clay tiles served as settlement substratum for the coral larvae. After larvae had metamorphosed, gymnodinoid swarmers and non-motile coccoid zooxanthellae derived from *Lobophytum compactum* (maternal strain) and kept in culture at James Cook University, were added to each of the four treatment tanks on a daily basis for 2 weeks. Colony growth was assessed on a 2-weekly basis for 5 months after settlement of larvae and recorded as the number of polyps per colony.

Statistical analysis

Differences in fertilization success, fecundity, egg sizes and growth of polyps were tested for significance by one-way ANOVA followed by multiple comparisons (Tukey's HSD test) using the SPSS 7.5 software package.

Results

Coral survival and recovery of zooxanthellae

Comparison of zooxanthellae densities before and after experimental treatment revealed that the moderately and strongly bleached corals lost approximately 49 and 93% of their zooxanthellae populations, respectively (Fig. 1). In contrast, no colonies in any of the control groups underwent significant bleaching during the experimental period and no visible effect of handling could be discerned. None of the test corals, regardless of whether they were bleached or unbleached, handled or not handled, died during the experiment.

The length of time required for zooxanthellae to return to background densities was strongly correlated with the degree of bleaching ($r^2 = 0.96$). While the moderately bleached group recovered within 10 weeks, zooxanthellae densities in colonies that were strongly bleached returned to background levels only after 18 weeks (Fig. 1). With the exception of a slight loss of zooxanthellae during the summer of 1997 (February/March, $< 7\%$ decrease), no other natural loss of zooxanthellae occurred during the 20 months.

Oogenic cycle

Bleaching had a major impact on the oogenic cycle of experimental soft corals. By the first spawning season (November 1996), gametes in their second year of development from females that had been severely bleached, were at a stage normally reached in May, which means that their development lagged behind controls by 5 months. Interestingly, the unspawned eggs did not change in size or resume development until April 1997, when they were once more in phase with the normal oogenic cycle. Maturation of oocytes in their second year of development in all other treatment and control groups was accompanied by a gradual color change from white to bright pink (Fig. 2b), which is due to a protein-bound carotenoid in the eggs (B. Bowden, personal communication).

General details of oogenesis were similar in all field and laboratory control colonies of *Lobophytum compactum*. We found gonads in the autozooids but not in the siphonozooids, although typically only autozooids in the center of colonies were fertile. Gonad maturation occurred synchronously within and between colonies.

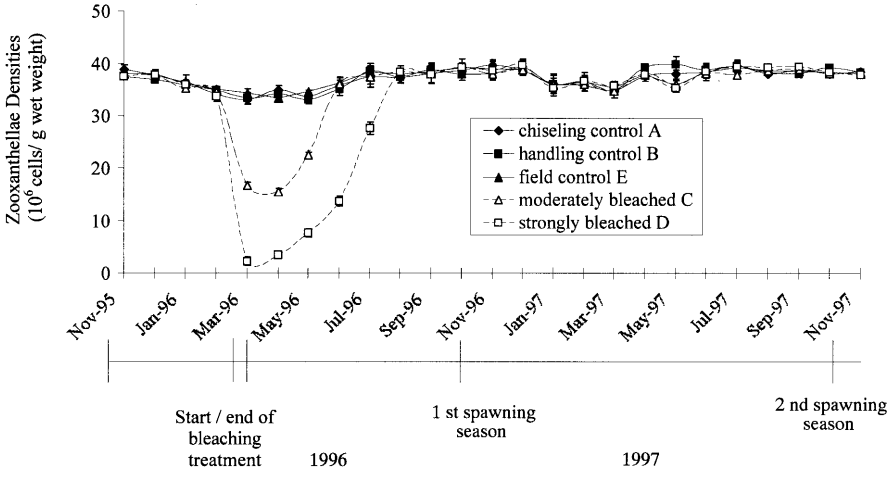

Fig. 1 Mean zooxanthellae densities (± SE) in three control and two experimental groups of *Lobophytum compactum* between November 1995 and November 1997. $n = 10$ colonies per treatment. *Vertical bars* on the time scale denote the initiation of the experiment, the beginning (1 March 1996) and end (15 March 1996) of the bleaching treatment, and the spawnings in November 1996 and 1997

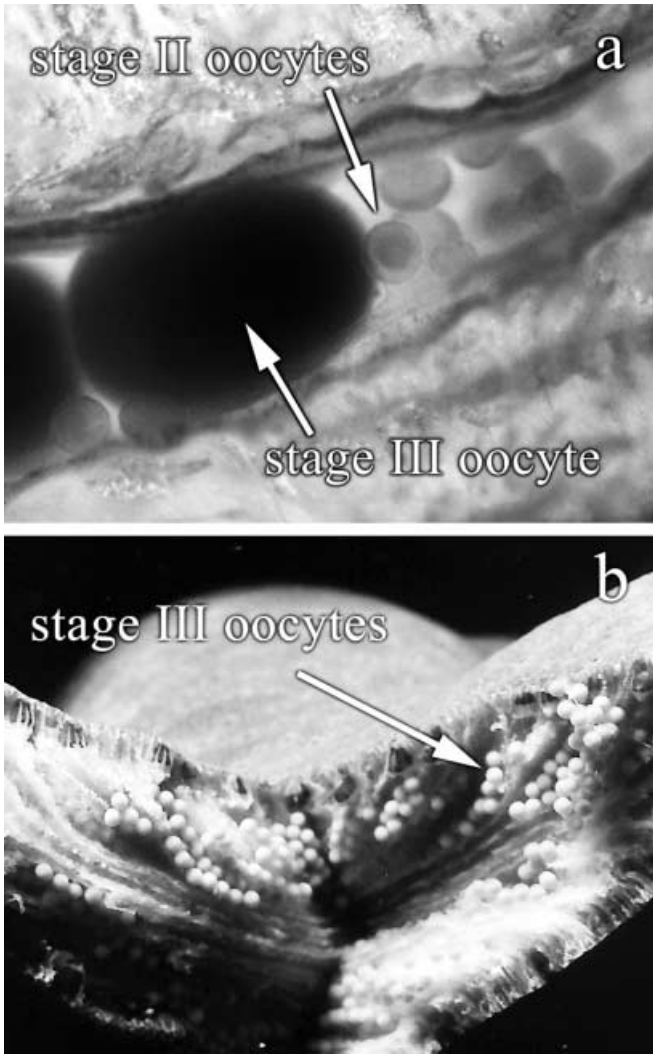

Fig. 2 Oocytes in the tissue of *Lobophytum compactum*. **a** Histological section showing stage II (immature) and stage III (mature) oocytes. **b** Dissected colony from the control group showing stage III oocytes prior to spawning

Both immature stage II oocytes (Fig. 2a) and mature stage III oocytes (Fig. 2b) were present in autozooids just prior to spawning in both 1996 and 1997. Mature stage III oocytes (diameter of 600–620 μm) were first recorded around September, that is 2–3 months prior to spawning and 22–23 months after first appearing as stage II oocytes with an initial diameter of 50 μm (K. Michalek-Wagner, unpublished data). Autozooids bore gonads on up to six of the eight mesenteries, with stage II oocytes developing proximally and stage III oocytes distally on mesenteries relative to the oral disc of the polyp (Fig. 2b). The mean diameters of the large and small oocytes at spawning were 630 ± 1.5 μm ($n = 1000$) and 110 ± 1.3 μm ($n = 1000$) respectively. No parental provision of zooxanthellae was detected in eggs of *L. compactum*. Uptake of zooxanthellae and establishment of a symbiosis occurred only after fertilization and polyp development.

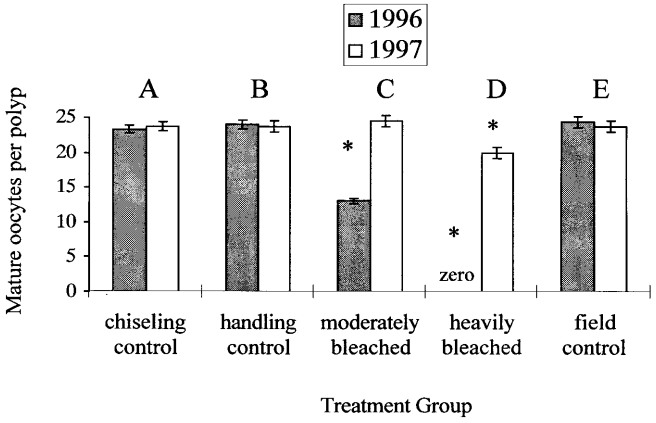

Fig. 3 Mean polyp fecundity (±SE) in bleached and unbleached colonies of *Lobophytum compactum,* one (1996) and two (1997) spawning seasons after experimental treatment. $n = 100$ polyps per group. *Asterisks* denote significant reductions in fecundities (relative to controls). Letters denote experimental groups (see text)

Polyp fecundity

Chiseling and handling of coral colonies had no significant effect on their fecundity (Fig. 3). In 1996, however, the mean fecundity of the moderately bleached colonies (13 ± 0.4, $n = 100$) was approximately half that of the chiseling controls (23 ± 0.6, $n = 100$). The heavily bleached group failed to produce any mature oocytes in the first spawning season (Fig. 3). In the second year following experimental treatment, fecundity of the moderately bleached group was equivalent to that of the controls (Tukey's HSD test, $p = 0.95$). However, the reproductive output of the heavily bleached group was still significantly reduced (Tukey's HSD test, $p = 0.003$), by approximately 20% (Fig. 3). A strong negative relationship was found between the degree of bleaching and the number of mature eggs (stage III oocytes) in the gonads of *Lobophytum compactum* immediately prior to the first spawning season (Fig. 4; $r^2 = 0.92$, $F = 587.5$, $p < 0.001$).

Egg size comparisons

The diameters of stage III oocytes immediately prior to spawning were normally distributed in all control treatments, with the majority of eggs in control groups falling into the 605- to 655-μm size class (Fig. 5). However, we found a highly significant difference in egg size between control and experimental groups in the first (1996) spawning season ($F = 1101.3$, $p < 0.001$). Egg sizes of the moderately and severely bleached groups differed both from the controls (Tukey's HSD test, both $p < 0.0001$) and from each other (Tukey's HSD test, $p < 0.0001$). Chiseling and handling of the colonies did not significantly affect egg size. The most striking difference in the size-frequency distribution of eggs from moderately bleached colonies (in comparison to control colonies) was the strong decrease in the number of eggs

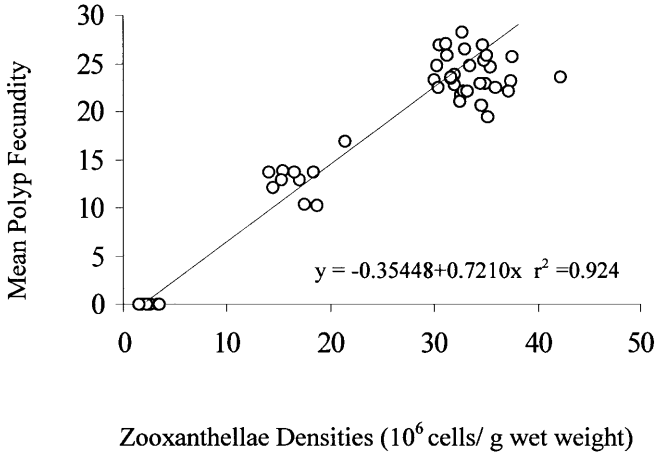

Fig. 4 Relationship between polyp fecundity (number of mature oocytes/polyp) and zooxanthellae densities in *Lobophytum compactum*. Mean values were used to calculate the correlation coefficient, $n = 10$ colonies for determinations of zooxanthellae densities and $n = 100$ polyps for fecundity estimates per treatment

in the two largest size classes. Despite this loss of large eggs, the modal size class of 605–655 μm was the same as that found in distributions for all of the control groups. In contrast, the modal size class for soft corals that had been heavily bleached decreased to 455–505 μm. Moreover, we found no eggs greater than 555 μm in diameter (Fig. 5). Typically, a diameter of approximately 580 μm is the minimum size required for eggs to be spawned (K. Michalek-Wagner, unpublished data). With a mean diameter of 468.1 ± 1.5 μm, the eggs from heavily bleached corals were approximately 26% smaller in diameter and 59% smaller in volume than control eggs (mean diameter = 633.4 ± 1.9 μm; Fig. 5).

A significant difference continued to occur in mean egg size among control and experimental groups in the second spawning season following treatment ($F = 60.2$, $p < 0.001$). Eggs from heavily bleached colonies were still significantly smaller in diameter and volume than those from control colonies (Tukey's HSD test, $p < 0.001$), by approximately 5% (Fig. 5) and 13% respectively. By the second breeding season, however, eggs from moderately bleached soft corals were not significantly different from those of control colonies (Tukey's HSD test, $p = 0.94$).

Spawning, fertilization and survival

With the exception of the heavily bleached colonies of *Lobophytum compactum*, colonies in all experimental and control groups released all of their stage III oocytes in November 1996. In the heavily bleached group only eight of the ten colonies spawned in November, and these colonies released only a few eggs. In November 1997, seven of the ten colonies in the heavily bleached group released eggs. Although gonads of the three unspawned colonies contained mature-sized pink eggs, no spawning was detected during the following 3 months.

Mean fertilization success differed significantly among treatments ($F = 2125.9$, $p < 0.001$). This was entirely because eggs collected from the heavily bleached group did not fertilize (Fig. 6). Consequently, no statistical differences in fertilization success were found between gametes derived from the moderately bleached corals and those of the three control groups ($F = 0.49$, $p = 0.69$).

No differences in survivorship or growth were detected between juveniles originating from the moderately bleached group and any of the control groups of corals (Table 1). Larvae (Fig. 7a) started to settle on the clay tiles 4 days after fertilization and approximately 80% had settled after 1 week. Development of the primary polyp followed 3–4 days after settlement. Post-settlement development began with the opening of the 'mouth' (actinopharynx), followed by development of the tentacles and pinnules (Fig. 7b). Juveniles reached the four-polyp stage after approximately 4 months (Fig. 7c). Uptake of zooxanthellae followed immediately after the primary polyp developed tentacles and significant densities were visible within 2 weeks.

Discussion

This study shows that the reproductive output of soft corals may be affected by bleaching events, and that the degree of impact varies with the intensity of the disturbance. Moderate bleaching reduced both the number and size of mature oocytes in experimental colonies of the soft coral *Lobophytum compactum*. Given that lipids comprise up to 65% of the dry weight of eggs (Michalek-Wagner and Willis 2000), smaller mean egg sizes mean that larvae are energetically less well-equipped for survival once eggs are fertilized. Severe bleaching reduced the mean size of mature oocytes, and they were retained for an entire year beyond the normal time of release. Although mature-sized eggs developed in all severely bleached females in the second breeding season following experimental treatment, lack of spawning in 30% of

Table 1 Juvenile survival and size, measured as the number of polyps per colony 5 months after spawning. A total of 500 larvae was monitored in each treatment. Heavily bleached soft corals (*D*) did not produce larvae

Treatment	Number of surviving juveniles after 5 months	Multiple polyp stage				Mean number of polyps/ colony (±SE)
		1	2	3	4	
Chiseling control A	36	2	7	10	17	3.16 ± 0.16
Handling control B	30	1	4	7	18	3.18 ± 0.16
Field control E	33	1	4	9	19	3.39 ± 0.14
Moderately bleached colonies C	34	3	2	8	21	3.38 ± 0.16

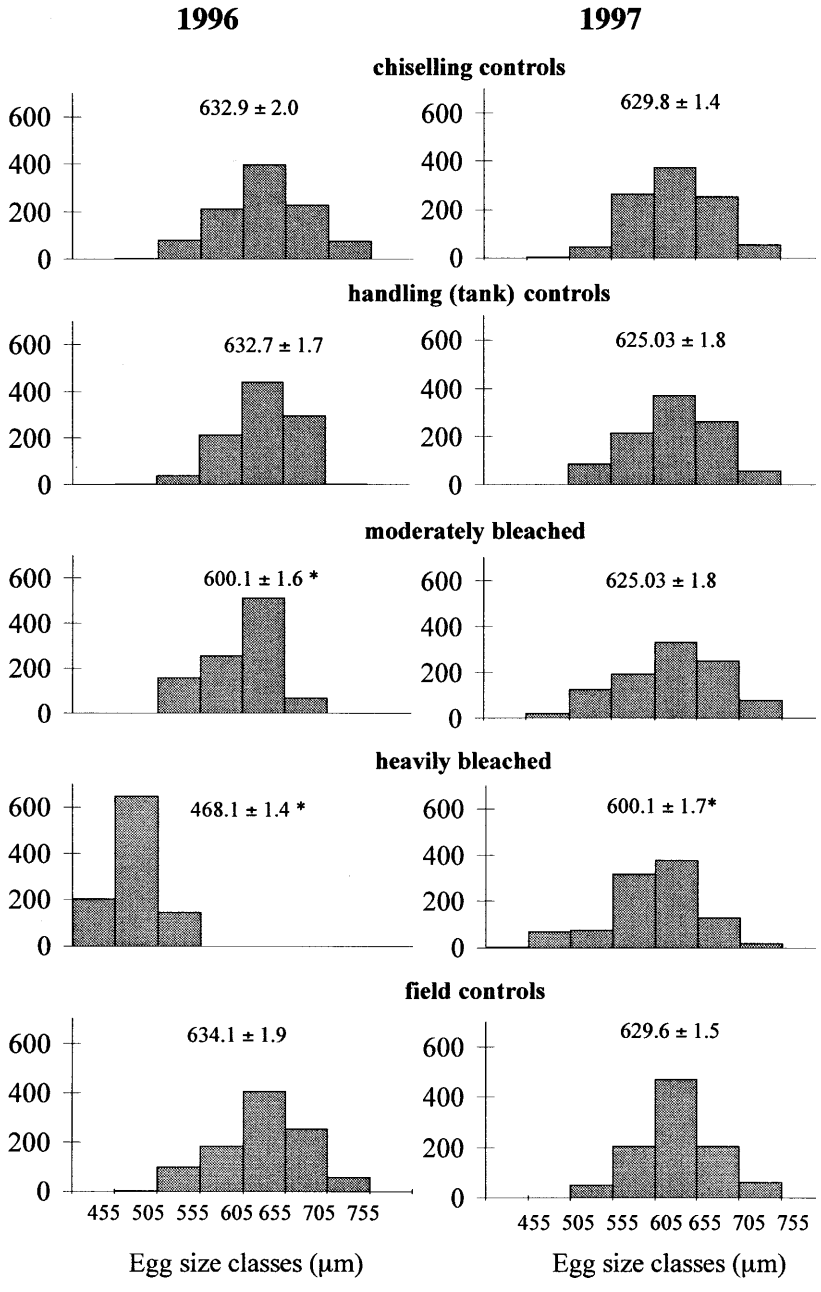

Fig. 5 Size-frequency distributions of stage III eggs derived from bleached and unbleached colonies of *Lobophytum compactum* immediately prior to the 1996 and 1997 spawning seasons. $n = 1000$ eggs per treatment (i.e. 10 eggs × 10 polyps × 10 colonies). *Numbers* above each graph denote mean egg diameter (μm) ± SE. *Asterisks* denote a significant difference from the field controls

these females demonstrates that the impact of such disturbances can extend beyond 20 months.

We also demonstrated that the rate of zooxanthellae recovery depends on the degree of bleaching experienced by the soft coral host. Recovery of algal stocks in the moderately and strongly bleached groups of experimental soft corals took approximately 70 and 126 days, respectively. Davies (1991) estimated that corals could survive periods of decreased photosynthetic productivity for 28 to 114 days through catabolism of lipid reserves. Although lipid reserves were sufficient to allow the recovery of all severely bleached colonies of *Lobophytum compactum* in our study without any (even partial) mortality, the reduced fecundity of these colonies indicates that survival occurred at a significant cost to resources normally allocated to reproduction.

The 45% reduction in fecundity of *Lobophytum compactum* in the moderately bleached group and complete failure to produce mature eggs in the severely bleached group in the first year clearly demonstrate that fecundity is a good indicator of sub-lethal stress in *Lobophytum compactum*. Similarly, differences in egg sizes between bleaching treatments suggest that egg size could also be used to gauge the severity of natural bleaching disturbances. Reproductive failure can be induced in hard corals by stresses such as turbidity, sedimentation (Kojis and Quinn 1984), high seawater temperatures (Jokiel and Guinther 1978) and pollution

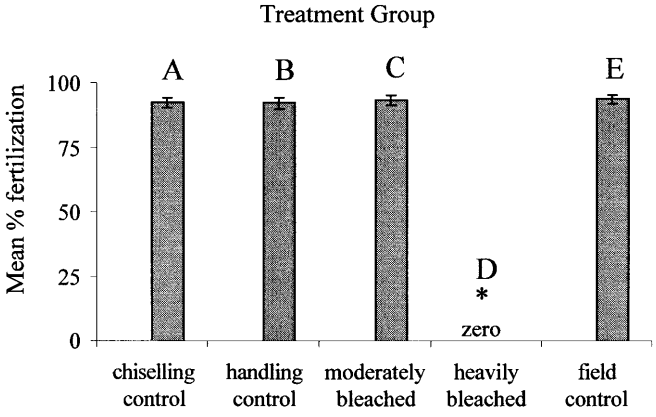

Fig. 6 Mean fertilization success (±SE) for eggs collected from bleached and unbleached colonies of *Lobophytum compactum* in the first spawning season (1996) following experimental treatment. $n = 400$ eggs per treatment. The *asterisk* denotes significantly different fertilization success

(Loya and Rinkevich 1979). While fecundity can be used as an indicator of stress (Kojis and Quinn 1984; Harrison and Wallace 1990), it is generally not easy to separate sub-lethal impacts on reproduction from natural variation in fecundity due to factors such as the differing size and age of colonies that are sampled (Szmant 1991; Sier and Olive 1994; Slattery et al. 1999). We reduced potential sources of natural variation in fecundity by standardizing both the size of experimental colonies and the location of sampling within a colony. The low variation in fecundity we found between colonies within a treatment and between the 2 years, suggests that standardization of sampling may allow fecundity to be used more widely as an indicator of stress.

The fecundities of moderately bleached *Lobophytum compactum* were reduced (13 ± 0.4 mature eggs/polyp) in comparison to control colonies (24 ± 0.7), even though the bleaching event occurred after the typical complement of oocytes had developed (i.e. midway through the oogenic cycle), suggesting that some middle-stage oocytes had been resorbed to allow development of the remaining ones. Thus, energy allocated to reproduction was apparently directed towards maintaining fewer eggs than normal to ensure that they attained a mature size. Yamazato and co-workers (1981) also noted that some reduction in the number of oocytes may occur in early oogenesis in *L. crassum*, even in the absence of detectable stress, the reduction presumably being linked to re-allocation of energy to support remaining oocytes.

Although resorption of some early and middle-stage eggs also apparently occurred in strongly bleached *Lobophytum compactum*, any redirection of reserves was not sufficient to allow production of mature eggs in the first year. Eggs that were produced were 26% smaller in diameter (and 59% smaller in volume) than controls, and were retained until the next (1997) spawning season. The almost complete failure to spawn in all strongly bleached females in 1996, 8 months after experimental treatment, is consistent with the interpretation that developmental delays associated with recovery from the disturbance prevented oocytes from attaining maturity by the time of the breeding season.

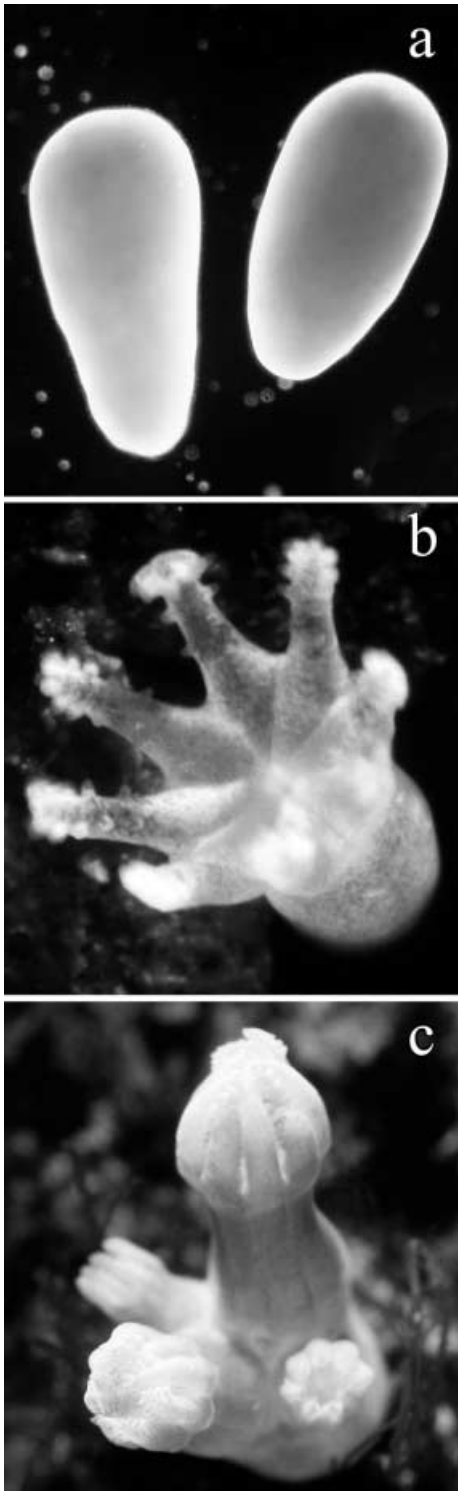

Fig. 7 Developmental stages of *Lobophytum compactum*. **a** Planulae 48 h after fertilization; **b** 1-month-old primary polyp; **c** 4-month-old juvenile (four-polyp stage)

The retention of most stage III oocytes for a full year beyond their expected release by strongly bleached soft corals suggests that there are inherent benefits in retaining nearly mature eggs until the next mass spawning period (e.g. increased sperm availability and reduced mortality because of increased potential for predator satiation: Babcock et al. 1986; Johnson 1992). Although mature oocytes may be resorbed following incomplete spawning in hard corals (Rinkevich and Loya 1979; Szmant and Gassman 1990; Sier and Olive 1994), this may not always be the optimal solution. Resorption of a full complement of oocytes, relatively advanced in their development, followed by *de novo* gametogenesis is unlikely to be as energetically favorable as retention of late stage oocytes for a full year. Lack of development of under-sized oocytes in severely bleached soft corals until oogenesis was in phase with field populations suggests that energy allocation strategies of soft corals are highly plastic. Both mature and immature oocytes may be resorbed to provide energy for remaining oocytes, or the soft coral may suspend oogenesis altogether until it is once more in phase with annual gametogenic cycles.

Differences in fertilization success of eggs between severely bleached and control colonies in the first spawning season following experimental treatment were most likely due to differences in mean sizes of gametes and associated maturity factors. The smaller eggs of severely bleached females had zero fertilization success. Sperm-egg histo-incompatibility can be ruled out as an explanation for the lack of fertilization because all crosses were replicated using the same clone combinations in all treatments. Since heavily bleached colonies retained the majority of their eggs for a further year, it is unlikely that eggs had undergone the final maturation steps required to become receptive to sperm. Although eggs from moderately bleached colonies were 5% smaller than controls, they had comparable fertilization success (93 vs 92% fertilization success, respectively). Thus, despite an approximate 45% reduction in the number of spawned eggs in moderately bleached colonies, eggs that were spawned were able to fertilize and develop normally. Survival and growth rates of offspring did not differ significantly between moderately bleached and control colonies. The reduced number of eggs available for fertilization and development from bleached soft corals is consistent with observations of reduced recruitment following natural bleaching events (Glynn et al. 1996) and reduced representation of families in recruitment assemblages that are most affected by bleaching events when compared to non-bleaching years (Gleason 1996).

In conclusion, our results demonstrate that bleaching has the potential to decrease soft coral reproductive output or suspend gametogenesis entirely, resulting in reproductive failure in the subsequent breeding season. We also infer that soft corals may recover from bleaching by re-allocating energy reserves that would normally be directed to reproduction. Although zooxanthellae densities recovered within a few months, reproductive output was negatively affected for at least another 20 months in cases of severe bleaching. Thus, the time-course of recovery of zooxanthellae to normal densities can be shorter than that of host physiological processes and does not reflect full recovery by the host. We suggest that zooxanthellae densities should only be used as an indicator of coral health in conjunction with other indicators of sub-lethal stress such as fecundity. If bleaching episodes occur with increasing intensity and at shorter intervals in the future (see Williams and Bunkley-Williams 1990; Jones et al. 1997; Hoegh-Guldberg 1999), then the longer term implications of our study are that sustained reductions in reproductive output and fertilization success may impede replenishment of coral assemblages.

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