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Short Communication

Effect of elevated temperature on fecundity and reproductive timing in the coral *Acropora digitifera*

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Summary

The synchrony of spawning is of paramount importance to successful coral reproduction. The precise timing of spawning is thought to be controlled by a set of interacting environmental factors, including regional wind field patterns, timing of the sunset, and sea surface temperatures (SST). Climate change is resulting in increased SST, which is causing physiological stress in corals and could also be altering spawning synchrony and timing. In this study, we examined the effect of increasing seawater temperature by 2°C for 1 month prior to the predicted spawning time on reproduction in the coral *Acropora digitifera.* This short period of elevated temperature caused spawning to advance by 1 day. In animals incubated at elevated temperature, egg number per egg bundle did not change, however, egg volume significantly decreased as did sperm number. Our results indicate that temperature is acting both as a proximate cue to accelerate timing and as a stressor on gametogenesis to reduce fecundity. This finding suggests that increasing SSTs could play a dramatic role in altering reproductive timing and the success of corals in an era of climate change.

Keywords: *Acropora digitifera*, Climate change, Corals, Gametogenesis, Spawning

Introduction

Scleractinian corals exhibit a diversity of reproductive patterns that occur along a continuum that ranges from highly synchronized mass spawning events to discrete temporal reproductive isolation. These patterns vary widely with species, biogeography and the environment [reviewed in Harrison (2011) and Nozawa (2012)]. In all locations, synchrony of coral spawning for the same species is paramount, as most coral species do not self-fertilize and therefore rely on neighbouring colonies for fertilization (Heyward & Babcock, 1986).

There are two primary aspects of coral reproduction that are regulated: the progression of gametogenesis and the precise timing of spawning. The mechanisms that control and regulate coral reproduction are not fully understood but are thought to include an interaction of environmental selective pressures that regulates the progression of gametogenesis and proximate cues that determine the timing of spawning (Oliver *et al.*, 1988). Many factors have been found to influence environmental selective pressures including global wind field patterns and solar irradiation (van Woesik *et al.*, 2006; van Woesik, 2010). Proximate cues that influence spawning timing include moonlight and day length (Hunter, 1988; Brady *et al.*, 2009).

Sea surface temperature can play a role in both gametogenesis and spawning. Some studies that compared reproductive timing on colder, offshore reefs with warmer, inshore reefs have shown a positive correlation between SST and the timing of spawning

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and larval release in the brooding coral *Pocillopora damicornis* (Harrison *et al.*, 1984; Crowder *et al.* 2014). Others studies on shallow reefs, where SST fluctuates widely on a monthly and even daily basis, showed no such relationship (Kojis, 1986; van Woesik *et al.*, 2006). Increased SST also acts as a stressor to corals, causing physiological stress that can slow growth, compromise health and cause bleaching (Hoegh-Guldberg *et al.*, 2007; Abdo *et al.*, 2012). SST may therefore be acting as an environmental selective pressure, a proximate cue and/or a stressor to coral development.

Global climate change is increasing SSTs, and the future health of coral reefs will be dependent on the rate of temperature increase and the ability of corals to adapt (Donner, 2009). At present, the effect of elevated temperature on spawning in corals has not been experimentally investigated. SST is expected to rise by approximately 2°C over the next 100 years (Donner, 2009). Will this increase act as a proximal cue that accelerates the timing of spawning or will it act as a stressor and inhibit gametogenesis and spawning? To determine if elevated temperature affects the timing of coral reproduction, we exposed the coral *Acropora digitifera* to a 2°C increase above ambient temperature for 1 month prior to the predicted spawning and then quantified changes in timing of spawning and in fecundity.

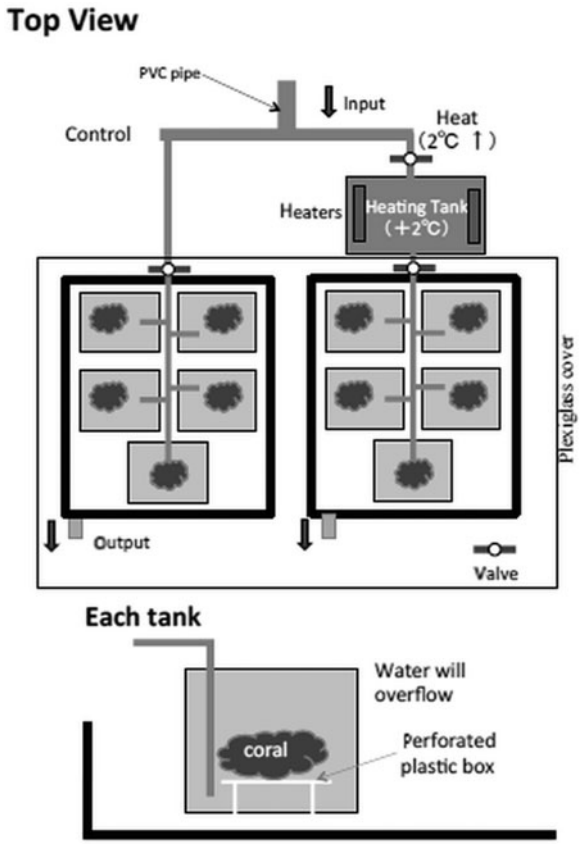

Figure 1 Experiment was set up to have seawater directly pumped to experimental station where it was divided to control tanks or a temperature treatment centre to increases temperature by 2°C and then flowed into the 2°C tanks. For each condition there where five experimental overflow tanks (A–E) with a raised perforated platform where coral ramets where placed. Water from overflow tanks flowed into a containment tub for each condition before draining.

Materials and methods

Five mature colonies of *A. digitifera* were collected (~30 cm in diameter) from Sesoko Island, Okinawa, Japan (26°38′13.29″N, 127°52′0.42″E) on 15 April 2013 and kept in running seawater tanks at Sesoko Station, Tropical Biosphere Research Station, University of the Ryukyus. Corals previously collected 3 or more months before the annual cycle failed to spawn (data not shown), therefore for this experiment corals were collected no more then 2 months prior to the predicted spawning cycle in either May or June of 2013. Each colony (A–E) was divided into two ramets. One of the two was placed in one of five control (ambient) tanks and the other in one of five tanks destined to be elevated (2°C above ambient) temperature tanks. Treatment tanks were outside, exposed to ambient light but protected from rain with by a single Plexiglass cover (Fig. 1). The ramets were allowed to acclimatize in running seawater at ambient temperature for 10 days prior to the start of the experiment. Approximately 1 month before the full moon (25 May 2013), running seawater temperature in the treated tanks was increased to 2°C above ambient temperature by heating water with four Power safe limit +300 Heaters (Nissso, Saitama, Japan) in a holding tank that then flowed into the treatment tanks. Temperature in both tanks was measured every 30 min with a Tidbit v2 Temp logger (Onset, MA, USA).

Starting 1 week prior to and extending to 1 week after the full moon in May, running seawater was turned off from 18:00 to 24:00. Using a red light to minimize light exposure (Gorbunov and Falkowski, 2002), corals were monitored every 30 min for signs of spawning. Once gamete bundles were observed, spawning was continually monitored for 1 h.

Ten egg-sperm bundles were collected from ramets of colonies A–D after spawning. Bundles from colony E were not collected because they started to separate immediately after release thereby preventing accurate quantification of sperm. To aid in quantification, bundles were preserved and stained. Bundles were incubated in 900 µl seawater and gently broken up manually by shaking, then preserved by the addition of 100 µl of Coomassie Blue R250 0.5% in 10% acetic acid/50% methanol. Egg number was quantified

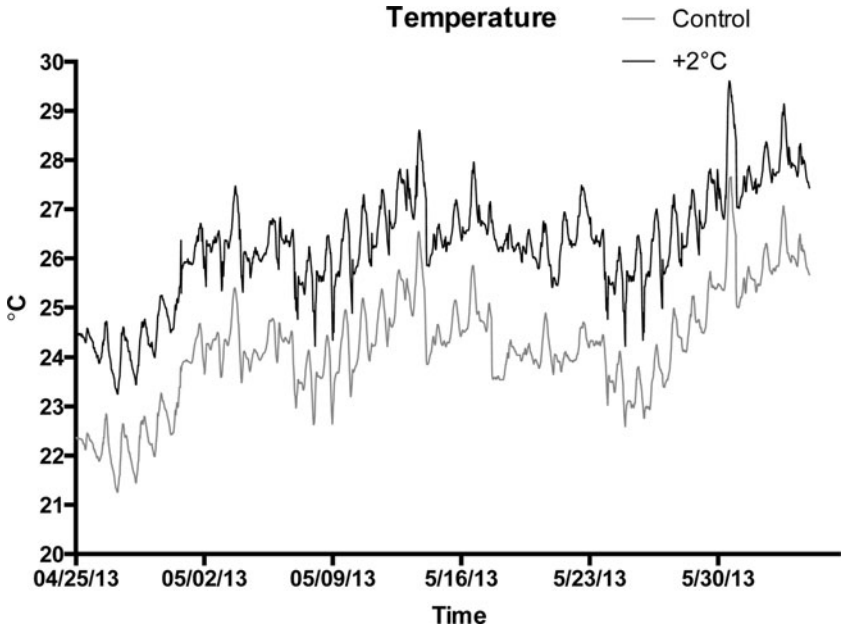

Figure 2 Temperatures in the control and temperature-treated tanks for the days after the full moon. Temperature was measured every 30 min with a data logger.

under a stereomicroscope. Egg volume was calculated using the elliptical integral equation $V = (4/3)\pi ab^2$ where a = ½ egg length and b = ½ egg width (n = 15 eggs per ramet) (Van Moorsel, 1983). The number of sperm was determined using haemocytometer counts (Erma, Tokyo, Japan).

All data were tested for normality and homoscedasticity before being analyzed by a two-tailed *T*-test or two-way analysis of variance (ANOVA). *T*-tests with a Bonferroni correction were employed when multiple comparisons were made (GraphPad, La Jolla, CA, USA). Data are presented as means ± standard error of the mean (SEM). All observations were comparisons from at least four independent samples. Significance was set at $P < 0.05$.

Results and Discussion

The temperature differences between the control and experimental tanks (+2°C were maintained throughout the ($N = 1919$, $t = 335.8$, $P < 0.0001$; Fig. 2). Starting 1 week before the May full moon, water flow was turned off to the tanks for 6 h from 18:00 to 24:00 to prevent the overflow of spawning bundles. To examine the possibility that the cessation of flow affected temperature in the treatment tanks, temperatures in the two tanks were compared from 18:00 to 24:00 in the 7 days before and the 7 days after the flow cessation started. Temperature was found to be significantly different in a two-way ANOVA for the control tanks ($P = 0.0129$) and the elevated temperature tanks ($P = 0.0103$) when comparing these days. However, the 2°C degree difference between treatments was maintained throughout this time period. Five days after the full moon (DAFM), colonies of *A. digitifera* began to spawn. All colonies spawned between 22:00 and 22:30, 160–190 min after sunset. Four out of five ramets in the +2°C tank spawned 1 day earlier than their corresponding ramets in the control tank (Table 1). Colony C was the only colony for which control and +2°C-treated ramets spawned on the same night. Two of the +2°C ramets spawned on 5 DAFM while the remaining spawned 6 DAFM. Three of the control ramets also spawned 6 DAFM with the remaining two ramets spawning 7 DAFM. The advancement in spawning time with increased temperature could occur via a Q_{10} effect that accelerates coral bioregulatory processes. There is evidence that steroid hormone-like molecules play a role in reproduction (Twan *et al.*, 2006) and homologues to some genes in mammalian

Table 1 Day after the full moon on which control and temperature-treated corals spawn

	Days after the full moon		
Colonies	5	6	7
A		+	0
B	+	0	
C		0, +	
D		+	0
E	+	0	

Control = 0; temperature treated = +.

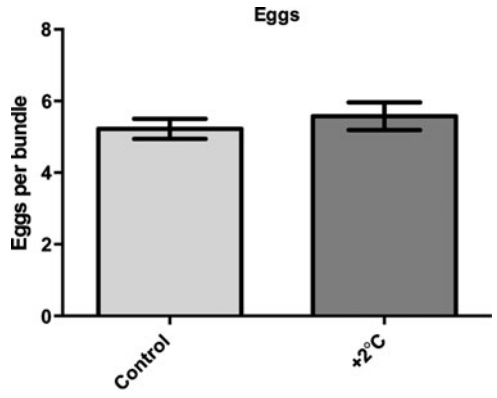

Figure 3 Number of eggs per bundle for coral ramets in control and temperature treatment conditions. Average number of eggs was calculated from 10 bundles of four separate colonies.

reproductive hormone pathways have been identified (Tarrant *et al.*, 2009). Future work examining the role of hormones in reproductive regulation and the effect of temperature on these processes will help gain insight into the impact of global warming on regulation of reproduction and reproductive timing.

Fecundity also differed between ramets in the two temperature treatments. There was no significant difference in egg number per bundle between the control and +2°C-treatment ramets (Fig. 3). However there was a significant decrease in egg volume in corals from the +2°C treatments ($N = 60$, $t = 6.044$, $P < 0.0001$, Fig. 4*a*). Three of the four ramets displayed significant differences in egg volume. The exception was once again colony C (Fig. 4*b*). The number of spermatozoa in the control ramets was on average 1.71 times greater than that in the temperature-treated ramets ($N = 40$, $t = 9.661$, $P < 0.0001$) (Fig. 5*a*). Colony comparison analysis revealed, once again, that colony C did not display a difference between the two treatment conditions (Fig. 5*b*).

Gametogenesis of *in situ Acropora* spp. occurs over a period of several months. The process begins with the development of oocytes, followed a few months later by spermatocytes. Spermatozoa are not present until spermaries reach developmental Stage IV which occurs approximately 14 days before spawning (Vargas-Ángel *et al.*, 2006). Egg number is established early in oocytes but final development from Stage III to Stage IV ova takes place in the last week before spawning (Vargas-Ángel *et al.*, 2006). In elevated temperature incubations, energy normally devoted to gametogenesis could be redirected to protective functions, in attempt to mitigate temperature stress. Our data suggest that normal gametogenesis was disrupted in animals incubated in the elevated temperature treatment. We hypothesize that egg number was set but that less energy was available for both final egg and sperm development, and thus egg volume and sperm number were low relative to control ramets. This decrease in fecundity could result in a reduction of fertilization success, larval number and survivorship. The fact that colony C displayed no difference between treatment conditions suggests that it was not affected by the temperature increase and could indicate a higher heat tolerance relative to the other colonies.

In summary, this study shows that even a short-term elevation in seawater temperature has a significant impact on both coral reproductive timing and fecundity, suggesting that temperature functions as both an environmental selective pressure regulating the rate of gametogenesis and a proximate cue affecting the timing of coral spawning. How impacts of temperature interact with unchanging reproductive cues such as solar irradiation, lunar periodicity and tidal height is a critical topic for future study. The study also points to the potential importance of genetic variability in the ability of corals to adapt to environmental change. The lack of response to temperature by colony C

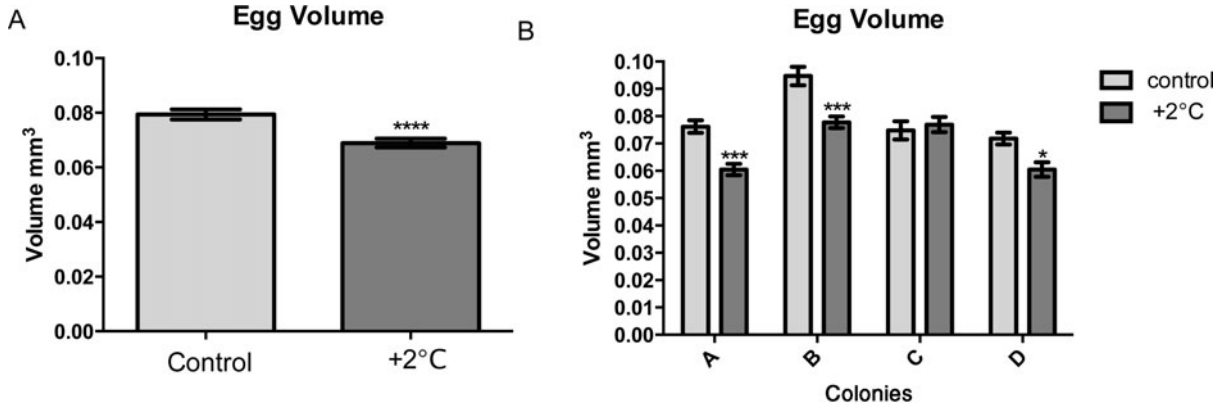

Figure 4 Egg volume from coral ramets in control and temperature treatment conditions. (*a*) Volume of 15 eggs from 10 bundles of four separate colonies. (*b*) The comparison of colonies for each condition $^{*}P < 0.05$, $^{***}P < 0.001$, $^{****}P < 0.0001$.

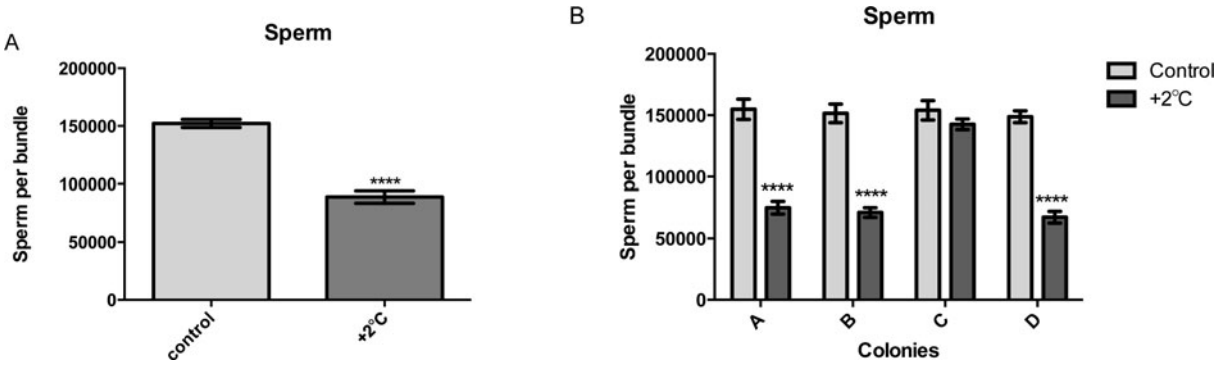

Figure 5 Number of sperm per bundle form coral ramets in control and temperature treatment conditions calculated using a haemocytometer. (*a*) Average number of sperm from 10 bundles of four separate colonies. (*b*) The comparison of ramets for each condition $^{****}P < 0.0001$.

could represent such variability that would allow some corals to adapt to and survive a rapidly changing climate.

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Statement of interest

None

Ethical standards

The authors assert that all procedures contributing to this work comply with the ethical standards of the relevant national and institutional guides on the care and use of laboratory animals.

References

Abdo, D.A., Bellchambers, L.M. & Evans, S.N. (2012). Turning up the heat: increasing temperature and coral bleaching at the high latitude coral reefs of the Houtman Abrolhos Islands. *PLoS One* **7**, e43878.

Brady, A.K., Hilton, J.D. & Vize, P.D. (2009). Coral spawn timing is a direct response to solar light cycles and is not an entrained circadian response. *Coral Reefs* **28**, 677–80.

Crowder, C.M., Liang, W.L., Weis, V.M. & Fan, T.Y. (2014). Elevated temperature alters the lunar timing of planulation in the brooding coral *Pocillopora damicornis*. *PLoS One* **9**, e107906.

Donner, S.D. (2009). Coping with commitment: projected thermal stress on coral reefs under different future scenarios. *PLoS One* **4**, e5712.

Gorbunov, M.Y. & Falkowski, P.G. (2002). Photoreceptors in the cnidarian hosts allow symbiotic corals to sense blue moonlight. *Limnol. Oceanogr.* **47**, 309–15.

Harrison, P.L. (2011). Sexual reproduction of scleractinian corals. In *Coral Reefs: An Ecosystem in Transition* (eds Z. Dubinsky & N. Stambler), pp. 59–85. New York: Springer.

Harrison, P.L., Babcock, R.C., Bull, G.D., Oliver, J.K., Wallace, C.C. & Willis, B.L. (1984). Mass spawning in tropical reef corals. *Science* **223**, 1186–9.

Hayashibara, T., Shimoike, K., Kimura, T., Hosaka, S., Heyward, A., Harrison, P., Kudo, K. & Omori, M. (1993). Patterns of coral spawning at Akajima Island, Okinawa, Japan. *Mar. Ecol. Prog. Ser.* **101**, 253–62.

Heyward, A.J. & Babcock, R.C. (1986). Self- and cross-fertilization in scleractinian corals. *Mar. Biol.* **90**, 191–5.

Hoegh-Guldberg, O., Mumby, P., Hooten, A., Steneck, R., Greenfield, P., Gomez, E., Harvell, C.D., Sale, P.F., Edwards, A.J., Caldeira, K., Knowlton, N., Eakin, C.M., Iglesias-Prieto, R., Muthiga, N., Bradbury, R.H., Dubi, A. & Hatziolos, M.E. (2007). Coral reefs under rapid climate change and ocean acidification. *Science* **318**, 1737–42.

Hunter, C. (1988). Environmental cues controlling spawning in two Hawaiian corals, *Montipora verrucosa* and *M. dilatata*. In *Proceedings of the 6th International Coral Reef Symposium Townsville, Australia* (eds J.H. Choat & D. Barnes), **2**, 727–32.

Kojis, B. (1986). Sexual reproduction in *Acropora* (*Isopora*) (Coelenterata: Scleractinia). *Mar. Biol.* **91**, 311–8.

Nozawa, Y. (2012). Annual variation in the timing of coral spawning in a high-latitude environment: influence of temperature. *Biol. Bull.* **222**, 192–202.

Oliver, J., Babcock, R., Harrison, P. & Willis, B. (1988). Geographic extent of mass coral spawning: clues to ultimate causal factors. In *Proceedings of the 6th International Coral Reef Symposium Townsville, Australia* (eds J.H. Choat & D. Barnes), **2**, 803–10.

Tarrant, A.M., Reitzel, A.M., Blomquist, C.H., Haller, F., Tokarz, J. & Adamski, J. (2009). Steroid metabolism in cnidarians: insights from *Nematostella vectensis*. *Mol. Cell. Endocrinol.* **301**, 27–36.

Twan, W-H., Hwang, J-S., Lee, Y-H., Wu, H-F., Tung, Y-H. & Chang, C-F. (2006). Hormones and reproduction in scleractinian corals. *Comp. Biochem. Phys. A* **144**, 247–53.

Van Moorsel, G. (1983). Reproductive strategies in two closely related stony corals (Agaricia, Scleractinia). *Mar. Ecol. Prog. Ser.* **13**, 273–83.

van Woesik, R. (2010). Calm before the spawn: global coral spawning patterns are explained by regional wind fields. *Proc. Roy. Soc. Lond. B Bio.* **277**, 715–22.

van Woesik, R., Lacharmoise, F. & Köksal, S. (2006). Annual cycles of solar insolation predict spawning times of Caribbean corals. *Ecol. Lett.* **9**, 390–8.

Vargas-Ángel, B., Colley, S., Hoke, S.M. & Thomas, J. (2006). The reproductive seasonality and gametogenic cycle of *Acropora cervicornis* off Broward County, Florida, USA. *Coral Reefs* **25**, 110–22.