

# Sedimentation and the Reproductive Biology of the Hawaiian Reef-Building Coral *Montipora capitata*

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**Abstract.** Environmental conditions can influence the physiology of marine organisms and have important implications for their reproductive performance and capacity to supply new recruits. This study examined the seasonal reproductive patterns of the coral *Montipora capitata* in habitats exposed to different sedimentation regimes. Although *M. capitata* is a main reef-building coral in the Hawaiian Archipelago, little is known about the gametogenic cycle and reproductive ecology of this important species. Our results indicate that gamete production in *M. capitata* is a resilient process; no differences in gamete development or fecundity were observed among sites with very different sedimentation regimes. The gametogenic cycle of *M. capitata* lasts between 10 and 11 months, with spawning occurring over 3–5 months during warmer months (May–September). Oocytes were found throughout the year, but spermatocysts were only found April–August. The largest increases in oocyte size occurred during February to May, the months when solar radiation increased rapidly. The largest variation in oocyte sizes was found during July and August; during this period individual colonies contained mature oocytes for immediate spawning and new oocytes being formed for spawning the next year. The capacity of *M. capitata* to reproduce in areas with high sedimentation is an interesting finding highlighting the potential of the species for acclimatization, adaptation, or both. Despite this optimistic finding, the management of terrestrial runoff and the restoration of habitat quality for corals remains a top

priority to ensure the renewal and maintenance of coral populations.

## Introduction

Recognizing what factors influence the supply and success of new recruits is of vital importance to understanding the ecology of coral reefs and in predicting the response of these important ecosystems to anthropogenic impacts such as coastal pollution due to terrestrial runoff (Fabricius, 2005) and global change (McClanahan *et al.*, 2009). Reproductive fitness in corals reflects condition, energy reserves, and maintenance demands of the adult colony, which can all vary spatially and temporally (Willis *et al.*, 1985; Rinkevich and Loya, 1987; Harrison and Wallace, 1990; Leuzinger *et al.*, 2012; Padilla-Gamiño and Gates, 2012). Under stressful conditions, energy allocation for reproduction can be diverted to somatic growth and maintenance, reducing reproductive fitness (Maltby, 1999). Environmental factors such as sedimentation (Kojis and Quinn, 1984; Gilmour, 1999; Fabricius, 2005), nutrients (Ward and Harrison, 2000; Cox and Ward, 2002), oil pollution (Guzman and Holst, 1993), and elevated temperature (Szmant and Gassman, 1990; Mendes and Woodley, 2002; McClanahan *et al.*, 2009) can affect coral’s physiology and significantly impair gamete development, fecundity, and overall reproductive success. Thus, it is important to understand how the environment influences the reproductive biology of corals, particularly of reef-building species that can play a major ecological role in structuring the ecosystem.

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Hawaiian coral reef ecosystems are threatened by reductions in the water quality that reflect extensive urban development in coastal environments (Smith *et al.*, 1981; Hunter and Evans, 1995). Sedimentation, as a result of both natural processes and human activities, can significantly impact coral population structures and be one of the main drivers of reef degradation (Rogers, 1990). Increased sediment loading of coastal waters can increase water turbidity and can lead to lower light available for photosynthesis (Rogers, 1990; Philipp and Fabricius, 2003), increase nutrients (Fabricius, 2005), reduce feeding surfaces responsible for catching prey (Telesnicki and Goldberg, 1995), and in extreme cases, bury entire coral colonies (Jokiel *et al.*, 1993). Coral reproduction and recruitment can also be affected by terrestrial runoff (Fabricius, 2005). Nutrient enrichment has been shown to affect fecundity, oocyte sizes, fertilization rates, and embryo development in acroporids (Ward and Harrison, 2000; Harrison and Ward, 2001; Cox and Ward, 2002), and sedimentation has been shown to affect processes such as larval settlement, recruit survival, and juvenile growth (Rogers, 1990; Te, 1992; Gilmour, 1999; Fabricius, 2005). Of the few previous studies that have explored the effects of sedimentation on coral health in Hawai'i, most have focused on coral growth and physiological performance (Piniak and Brown, 2008; Piniak and Storlazzi, 2008), and very little is known about how sedimentation affects the reproductive biology of corals in the central Pacific.

In this study we explored how sedimentation affects the reproductive biology of the rice coral *Montipora capitata*, Dana 1846 (synonym *M. verrucosa*), which is a main reef-building coral species in Hawaiian reef ecosystems. The genus *Montipora* (Blainville, 1830) is the second largest genus in the family Acroporidae and has a cosmopolitan distribution. Species of this genus can inhabit a wide range of habitats and are major contributors of coral reef formations around the world (Veron, 2000). Despite the ubiquitous and ecological importance of this species-rich genus, information on the reproductive biology of this group is scarce. Although spawning times for many *Montipora* species can be predicted at locations around the world (Heyward and Collins, 1985; Willis *et al.*, 1985; Babcock *et al.*, 1986; Heyward, 1986; Hodgson, 1988; Stobart *et al.*, 1992; Hayashibara *et al.*, 1993; Kolinski and Cox, 2003; Penland *et al.*, 2004), we know very little about the duration of their reproductive cycle, synchrony in gamete development, or how the environment affects reproductive processes. Both annual and biannual cycles of gametogenesis have been observed for *Montipora* species in the Pacific (Heyward and Collins, 1985; Stobart *et al.*, 1992). In Hawai'i, *M. capitata* has been observed to spawn during the summer months (Heyward, 1986; Hunter, 1988; Kolinski and Cox, 2003; Padilla-Gamiño and Gates, 2012); however, there is no information on the length of the gametogenic cycle or on seasonal spawning in single individuals.

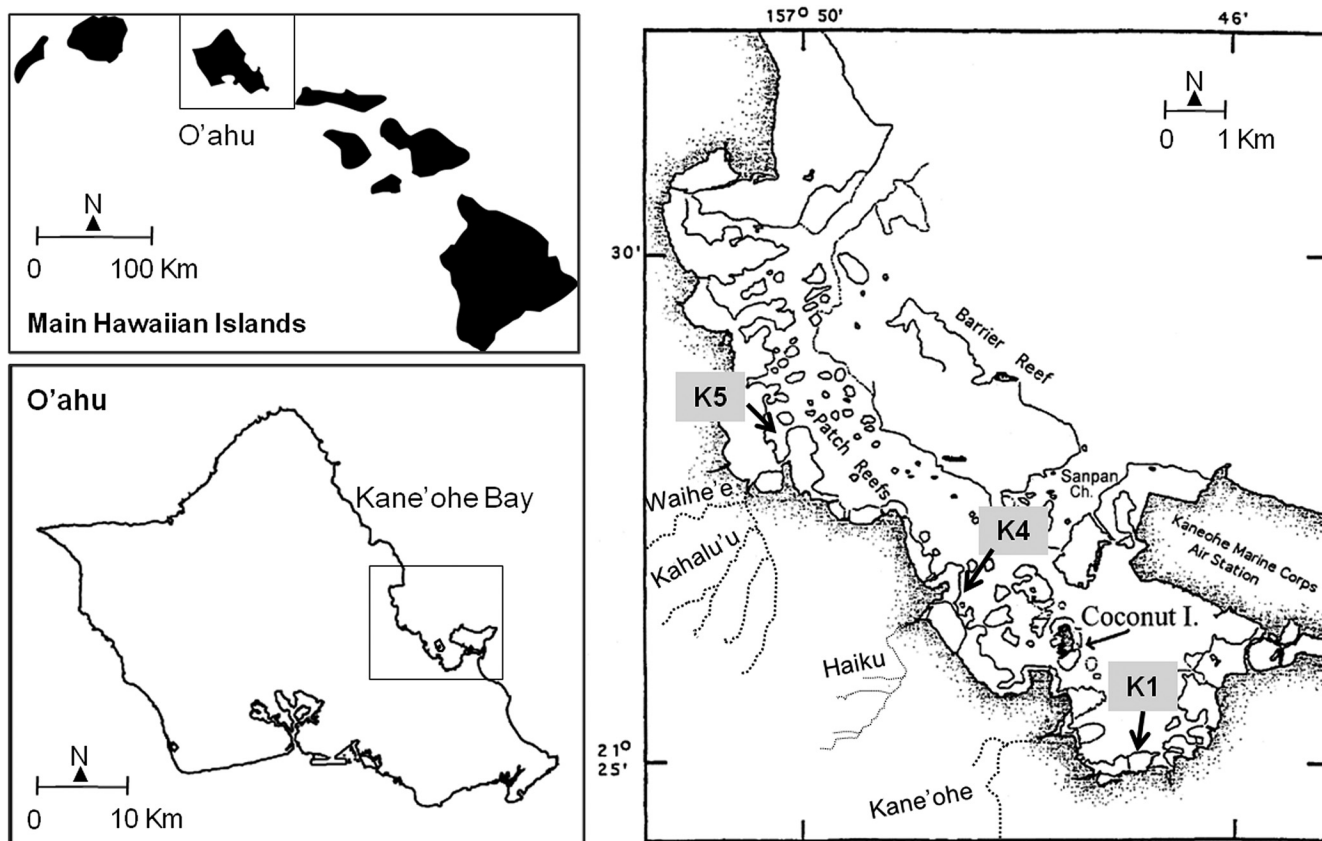
To determine if differences in the environment influence reproduction, we investigated the reproductive biology of *M. capitata* in different habitats. The specific objectives of this study were to (i) characterize the complete gametogenic cycle (oocyte and spermatocyte) of *Montipora capitata* in Hawai'i and (ii) determine if the reproductive cycle (colony synchrony and fecundity) differs among sites with distinct sedimentation conditions. Understanding gamete development and length of the reproductive season in foundation species such as *M. capitata* can provide a much-needed context to assess changes in reproductive status over time and in the face of local anthropogenic disturbances with important implications for reef conservation. Further, changes in coral reproductive status may represent a powerful tool with which to monitor the sublethal impacts of declining habitat quality and to implement changes in land use practices that improve the health of the coral reef ecosystems in Hawai'i.

## Materials and Methods

### Location of study and sample collections

The study was performed at three fringing reefs in Kaneohe Bay (O'ahu Hawai'i, Fig. 1). This bay is a complex estuarine system with a large barrier reef, numerous patch reefs, fringing reefs, and several riverine inputs (about a dozen streams empty into the bay). Three sites representing fringing reefs with different environmental characteristics were chosen for this study. The first site (K1; 21°25'263"N, 157°47'277"W) was located in the southern part of the bay, which is partially enclosed and has more restricted circulation (Bathen, 1968; Smith *et al.*, 1973). The second site (K4; 21°26'684"N, 157°48'362"W) was located in the central part of the bay, closer to the Sampan channel and exposed to more flow exchange; and the third site (K5; 21°28'032"N, 157°49'977"W) was located in the northern part of the bay near the He'eia fishpond and the output of the Waihe'e and Kahalu'u streams.

To provide insights into the environmental fluctuations at these sites, temperature sensors and sediment traps were deployed at each site. Temperature was measured using StowAway Tidbits (accurate to  $\pm 0.2$  °C; Onset Computer Corp.) and recorded every 15 min. Sediment traps (6:1 aspect ratio,  $n = 4$  per site) were deployed and collected monthly (February 2008–August 2009) to estimate sedimentation rates at the three selected sites. Sediment trap content was rinsed with distilled water to remove salts, and dried at 60 °C until constant weight was achieved. Sun-plus-sky radiation at Coconut island was measured hourly with a silicon pyranometer (model L12 00X-L, Campbell Scientific), which had a sensitivity of  $0.2 \text{ kW m}^{-2} \text{ mV}^{-1}$ , and UV radiation was measured with a total UV radiometer (model TUVR, Eppley Laboratory), which had a sensitivity of  $150 \text{ } \mu\text{V/Wm}^{-2}$ .



**Figure 1.** Location of fringing reefs where environmental monitoring and coral collections were performed. Kane'ohe Bay is a complex estuarine system located on the windward coast of the island of O'ahu, Hawai'i.

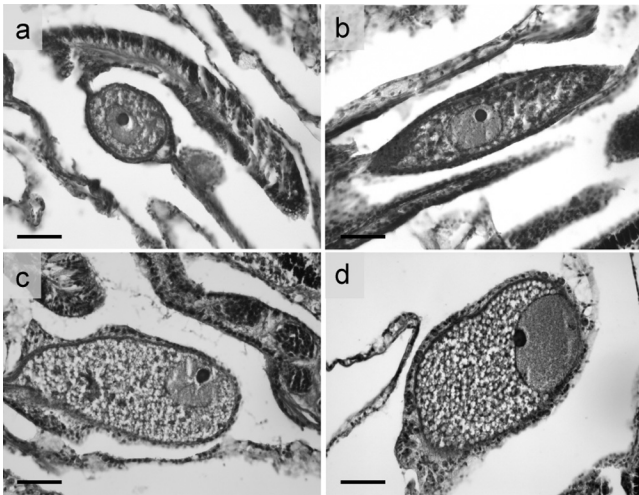
Coral samples ( $n = 7-8$  per site) were collected almost every month from October 2008 to September 2009. Coral fragments of *M. capitata* were obtained randomly from medium-large colonies (1–2 m in diameter) displaying the most common morphotype—branching at the center and plating at the edge of the colony. Fragments were obtained only from the branching part of the center of the colony at least 4 cm away from the tips where polyps were expected to be reproductively active (Wallace, 1985). Immediately after collection, samples were fixed in the field using buffered zinc formalin fixative (Z-fix, Anatech Ltd) diluted in 0.2- $\mu\text{m}$  filtered seawater (1:4). Corals were fixed for at least 48 h and then transferred to 70% ethanol (diluted in DI water) until processing.

### Histology

A 2–3-cm-long portion of the fixed coral sample was decalcified using a buffered 10% hydrochloric acid solution for  $\sim 24$  h. The samples were then dehydrated through a series of alcohols and xylene and embedded in paraffin (Paraplast Plus, SPI Supplies) to obtain both cross and longitudinal sections. Serial sections, 5–7- $\mu\text{m}$ -thick and

spaced 70  $\mu\text{m}$  apart, were cut using a Leica RM 2155 rotary microtome (Leica Microsystems GmbH) and stained with Masson's Trichrome. Stained slides were observed and photographed using a compound microscope with camera attachment (Olympus BX51, Olympus Corp.). Developmental stage of gametes was followed based on cell size and morphology criteria (Szmant-Froelich *et al.*, 1980; Szmant-Froelich, 1985; Glynn *et al.*, 1996) (Figs. 2 and 3). Feret's Statistical Diameter was used to estimate the size of the oocytes using ImageJ software ver. 1.42 (Abramoff *et al.*, 2004). Size measurements were performed only in oocytes sectioned through the nucleus in order to standardize measurements to the widest axis of oocytes and ensure no duplicate measurements (Davis, 1982; Parker *et al.*, 1997). For station K4, oocyte size was measured every month, whereas for stations K1 and K5, oocytes were measured only in December, March, June, and September. Coral fecundity from all three sites was estimated from samples, collected in June, in which oocytes from six polyps per coral had been staged (previtellogenic *versus* vitellogenic) and counted.

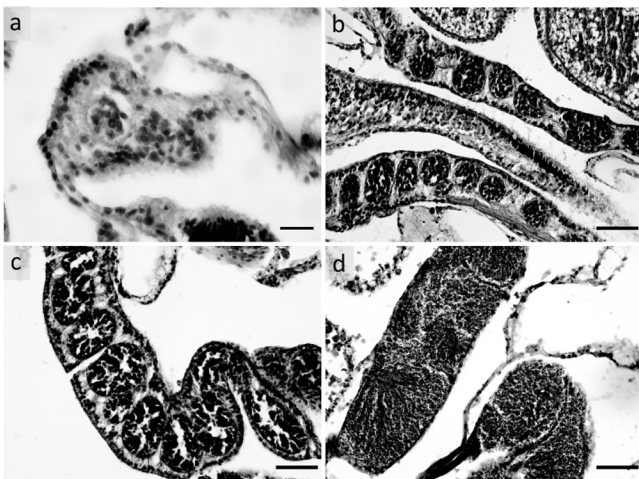




**Figure 2.** Oocyte development in *Montipora capitata*. (a) Stage I: oocyte embedded in the mesoglea, nucleus and nucleolus present (20–70  $\mu\text{m}$ ); (b) Stage II: more oval shape, onset of vitellogenesis, cytoplasm a little more granular (40–300  $\mu\text{m}$ ); (c) Stage III: oocytes filled with lipid vesicles, nucleus has moved to the periphery of the oocyte (200–600  $\mu\text{m}$ ); (d) Stage IV: nucleolus on the edge of nucleus, *Symbiodinium* infection starts (300–600  $\mu\text{m}$ ). Scale bar = 50  $\mu\text{m}$ .

#### Statistical analyses

Friedman tests were conducted on oocyte size to test for synchrony between stations for a given month. Mean monthly oocyte sizes were tested for association with monthly means of environmental parameters (light, temperature, and sedimentation) using Pearson product-moment correlations. Fecundity differences between sites were evaluated using one-way ANOVA with site as fixed factor.



**Figure 3.** Spermatocyst development in *Montipora capitata*. (a) Stage I: unbound irregularly shaped cells closely associated with the mesoglea; (b) Stage II: well-organized clusters, nuclei peripherally aligned; (c) Stage III: conspicuous peripheral arrangement, prominent central laminae; (d) Stage IV: bouquet of spermatozoa, tails in uniform direction. Scale bar: 15  $\mu\text{m}$  for stage I; 50  $\mu\text{m}$  for stages II, III, and IV.

## Results

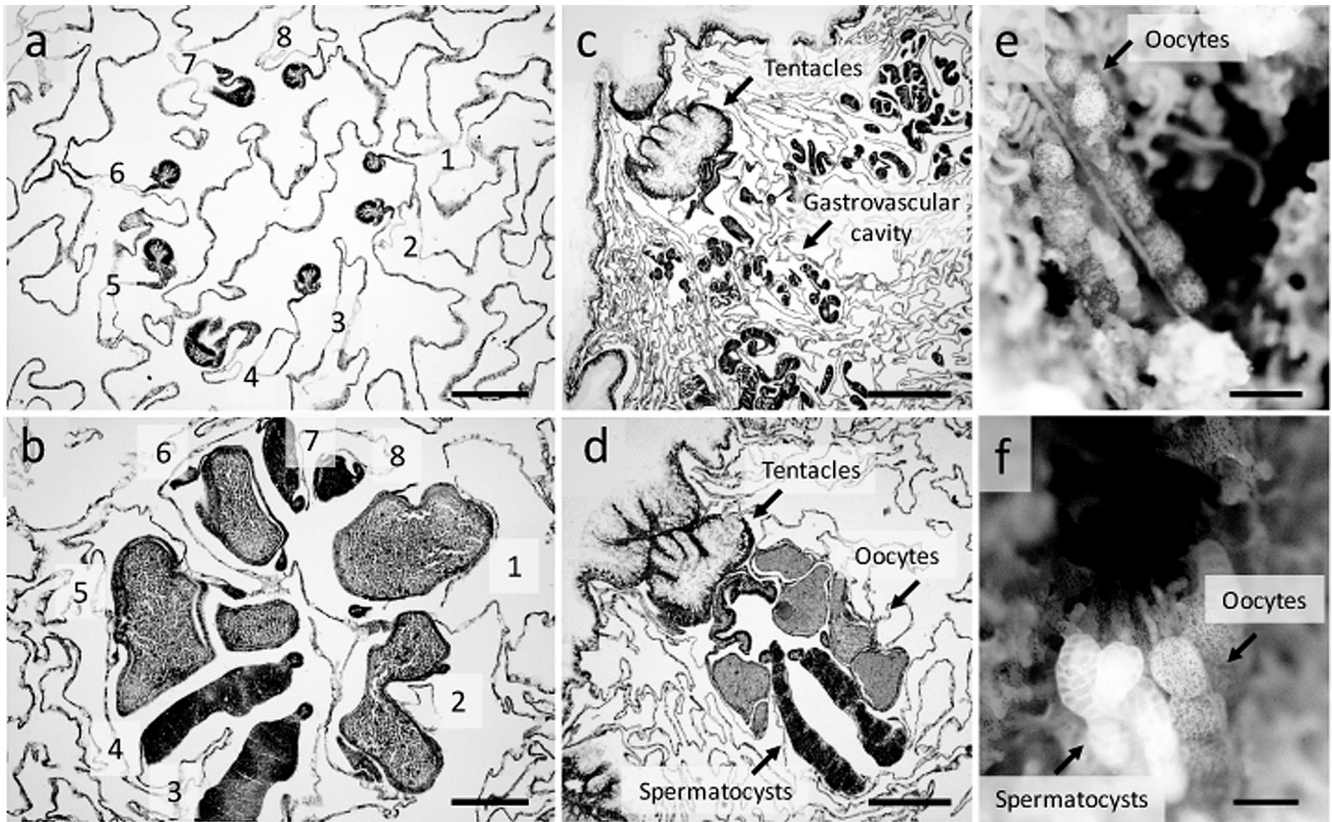
### Gamete development and synchronicity

*Montipora capitata* is a simultaneous hermaphrodite with an annual gametogenic cycle. Oocytes and spermatocysts develop deep in the skeleton along eight mesenteries, two male alternating with two female (Fig. 4). Oogenesis lasts about 9–10 mon and generally starts during July–October (Fig. 5). Oocytes within a single polyp were at a similar stage of development, but at each site, we found that development within and among individuals could differ. Oocytes acquire *Symbiodinium* (symbiotic dinoflagellate algae) late in development; during this period, the mesenterial layer surrounding the oocyte thickens and *Symbiodinium* cells are transmitted throughout the oocyte (Fig. 6). Some individuals had mature oocytes already infected by *Symbiodinium* during June, whereas others did not acquire symbionts until August. The largest variation in oocyte sizes was found during the months of July and August, ranging from 26 to 790  $\mu\text{m}$  (Fig. 5). During these months it is apparent that there are individuals with early and late oocytes, most likely representing oocytes that will still be spawned that season as well as a new developing cohort for the next year. Oocytes within a single polyp were all at the same stage, but intra-colony variation was observed (*i.e.*, some polyps contained vitellogenic oocytes, and some contained only previtellogenic oocytes). Spermatogenesis lasts about 5 mon and starts during April (Fig. 7). Similar to oocytes, spermatocysts were at a similar stage of development within a single individual, but at each site, stage of development could differ among individuals.

Oocyte development did not differ between stations (Fig. 8,  $S = 0$ ,  $\text{df} = 2$ ,  $P = 1$ ; Friedman test). At all sites, oocyte development started in July–October and similar development rates were observed during the different months. Average fecundity for K1, K4, and K5 was 13.2, 11.1, and 13.2 oocytes per polyp, respectively. A one-way ANOVA showed no significant difference in average fecundity between the three sites ( $F_{2,12} = 0.836$ ,  $P < 0.05$ ). Interestingly, spermatocyst development was slightly different between stations (Fig. 7). At station K1, male gamete development was faster than at stations K4 and K5, showing higher percentages of late-stage spermatocysts in June.

### Environment and reproduction

Solar radiation was the lowest during December–February ( $\sim 100 \text{ W/m}^2$ ) and the highest during June–September ( $\sim 250 \text{ W/m}^2$ ) (Fig. 9a). Seasonal variation of temperature was very similar among the three investigated stations. The coldest temperatures were found during March and April ( $\sim 23^\circ\text{C}$ ) and the warmest temperatures during June through October ( $\sim 27\text{--}28^\circ\text{C}$ ) (Fig. 9a). Sedimentation



**Figure 4.** Polyp cross sections showing (a) mesenterial arrangement with no gametes present and (b) oocytes and spermatocysts arranged in eight mesenteries, two females (1, 2, 5, 6) alternating with two males (3, 4, 7, 8). Polyp sagittal sections showing (c) polyp with no gametes present and (d) polyp with oocytes and spermatocysts present. Dissections on fresh specimens showing (e) oocytes growing along the mesenteries and (f) oocytes and spermatocysts developing deep into the skeleton. Pictures in Fig. 4a, c were taken from samples collected at station K4 during September 2009. Pictures in Fig. 4b, d, e, f were taken from samples collected at station K4 during June 2009. Scale bar: 200  $\mu\text{m}$  for panels (a) and (b); 500  $\mu\text{m}$  for (c), (d), and (e); and 400  $\mu\text{m}$  for (f).

rates differed between sites (Fig. 9b). K5 had higher sedimentation rates throughout the year, with a monthly sedimentation rate ranging from 8.1 to 42.7  $\text{mg}/\text{cm}^2/\text{day}$ ; K1 had a medium sediment deposition rate, ranging from 8 to 24.87  $\text{mg}/\text{cm}^2/\text{day}$ ; and K4 had the lowest sediment deposition rate, ranging from 1.2 to 10.2  $\text{mg}/\text{cm}^2/\text{day}$ .

Spawning season (and largest oocytes sizes) coincided with high solar radiation, warm temperatures, and low sedimentation rates (Fig. 9,  $S = 9$ ,  $\text{df} = 3$ ,  $P = 0.029$ ). Pearson moment correlations indicated that oocyte size had a significant positive correlation with light ( $r = 0.636$ ,  $P = 0.035$ ), a negative correlation with sedimentation ( $r = -0.722$ ,  $P = 0.028$ ), and no significant correlation with temperature ( $r = 0.391$ ,  $P = 0.234$ ).

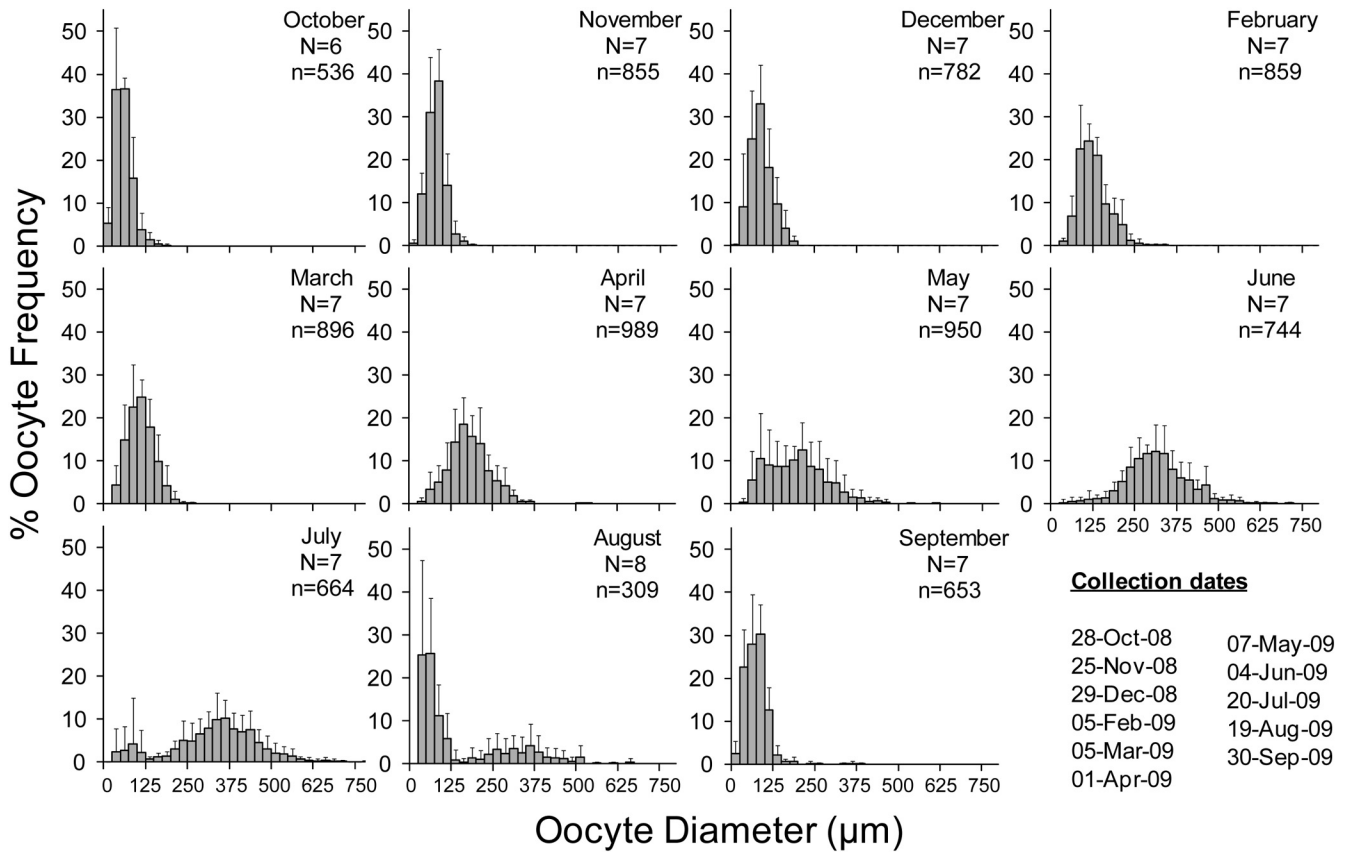
## Discussion

### Gamete development and synchrony

Successful reproduction has important consequences for the maintenance and replenishment of coral populations and

the future of reef ecosystems (Hughes *et al.*, 2000). This study characterized the reproductive biology of an important reef builder in the central Pacific and explored how spatial and temporal variability in the environment can affect the onset of gametogenesis and gamete maturation. We found that *Montipora capitata* in Hawai'i is a simultaneous hermaphrodite with a single annual cycle of gametogenesis. Oogenesis occurred for 10–11 months from June to September or May to September and spermatogenesis for 4–5 months from April to August. Spawning season of *M. capitata* most likely occurred in the summer season (from June to August), during the warmer seawater temperatures of the year. In contrast to other regions in the Pacific (Palau, Penland *et al.*, 2004; Great Barrier Reef, Stobart *et al.*, 1992), no evidence of biannual spawning (two gametogenic cycles per year) was detected. Interestingly, despite differences in timing of spawning, annual temperature variation between sites, or number of gametogenic cycles per year, spawning of *Montipora* spp. at all locations occurred at similar environmental temperatures  $\sim 27\text{--}30^\circ\text{C}$  (Stobart *et*





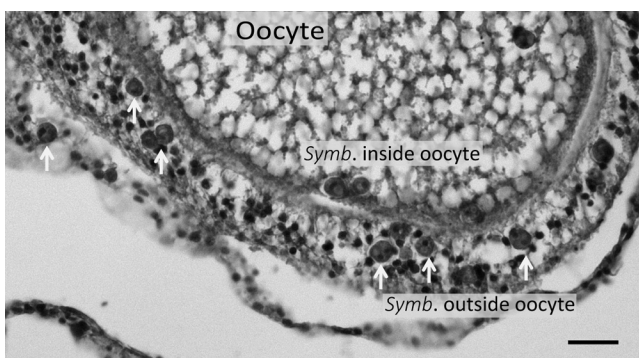
**Figure 5.** Oocyte size-frequency distribution for *Montipora capitata* in Kane'ohe Bay, Hawai'i. Samples were collected monthly for one year at station K4.

*al.*, 1992; Penland *et al.*, 2004; Padilla-Gamiño and Gates, 2012; this study). This suggests that spawning within this temperature range may have an adaptive value for gamete development, spawning synchrony, or optimal larval survival, growth, and recruitment.

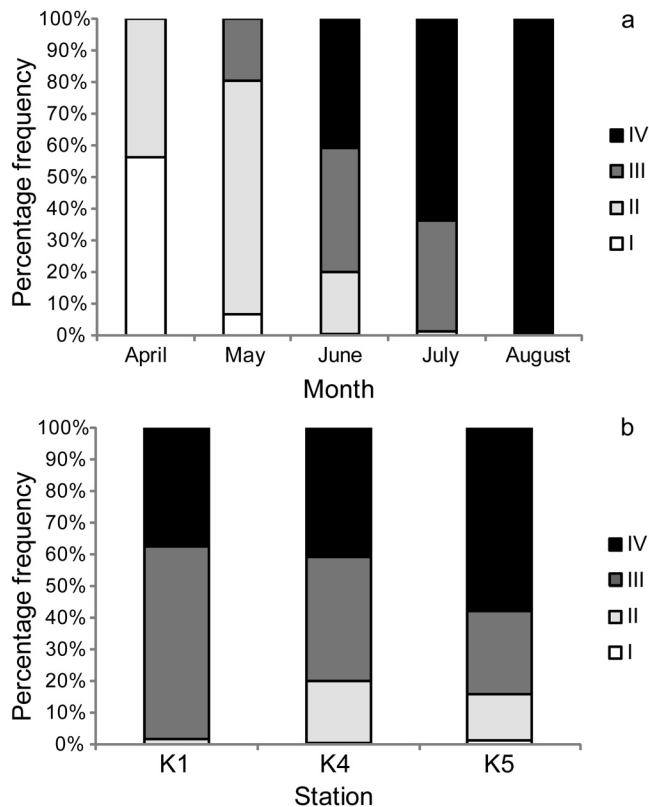
The largest increase in oocyte size occurred during the months when solar radiation increased rapidly (February–

May). This response was very consistent across several reefs in Kane'ohe Bay with very different environmental characteristics (*e.g.*, differences in turbidity due to sedimentation, Figs. 8 and 9), which suggests it may be the relative change in irradiance cycles rather than the absolute value in solar irradiance that triggers vitellogenesis and oocyte maturation in *M. capitata* (Penland *et al.*, 2004; Fiorillo *et al.*, 2013).

Dinoflagellate endosymbionts (*Symbiodinium* spp.) were transferred to the oocytes at the end of the maturation cycle, and during this period, symbiont cells from the mesenteries were incorporated over the entire oocyte cell surface and randomly distributed within the oocytes. Although the mechanisms of dinoflagellate symbiont transmission remain unknown, it is likely that symbionts enter through follicle cells surrounding the oocytes in temporary gaps formed in the mesoglea (Hirose *et al.*, 2001). Further investigation is necessary to understand the mechanisms of symbiont acquisition and to examine the physicochemical cues that corals use to recognize the right timing for symbiont transmission to the oocytes and whether this process is mostly mediated by the symbiont, the host, or both (Padilla-Gamiño *et al.*, 2012).



**Figure 6.** Oocyte acquiring *Symbiodinium* cells in the coral *Montipora capitata*. White arrows show *Symbiodinium* cells in the mesenteries surrounding the oocyte. Scale bar = 15 μm.



**Figure 7.** Frequency in the spermatocyst developmental stages of *Montipora capitata*: (a) throughout one gametogenic cycle at station K4; (b) between stations during the month of June.

Interestingly, during the spawning season (June–August) not all the spermatocysts were at the same developmental stage (Fig. 7a), and spermatocyst development differed between sites (Fig. 7b). This is consistent with the finding that egg-sperm bundles released during spawning events can contain spermatozoa at different stages of development (Padilla-Gamiño *et al.*, 2011) and suggests that fertilization success could differ temporally and spatially depending on the availability of mature spermatozoa. Egg-sperm bundles released later in the spawning season have higher chances of containing more mature sperm than bundles released earlier in the season. It is important to note, however, that fertilization success also depends on other factors such as the number of colonies participating in the spawning event, the rate of sperm diffusion, and oocyte-sperm interactions (Levitan and Petersen, 1995). In Hawai'i, *M. capitata* spawning events are more intense (higher reproductive output and number of colonies participating in the events) earlier in the reproductive season (Padilla-Gamiño and Gates, 2012), and spawning at this time could be advantageous due to higher gamete density in the water column. This could counteract the presence of immature spermatozoa and maximize the chances of fertilization.

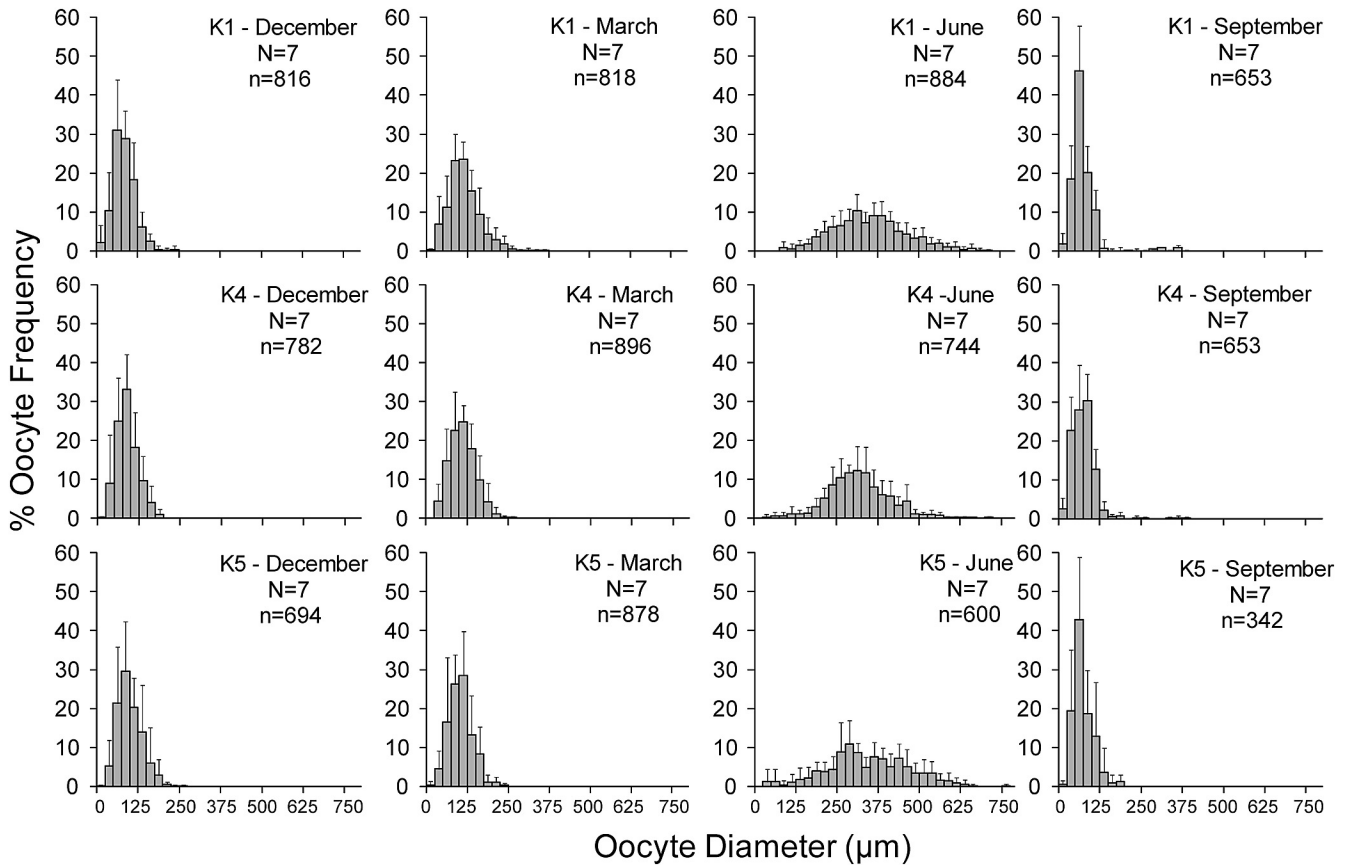
In our study we found high variability in gamete devel-

opment between colonies at each site and within colonies, most likely reflecting the occurrence of split spawning within the populations and partial spawning within individual colonies. These spawning patterns may constitute a strategy to increase the chances of successful fertilization over a longer period of time, reduce interspecific competition among new recruits, increase genetic diversity (increased chances of mating with differing colonies), and reduce the risk of failure of the population's entire reproductive output due to a single catastrophic event (Harrison *et al.*, 1984; Shlesinger and Loya, 1985; Willis *et al.*, 1985; Hodgson, 1988; Harrison and Wallace, 1990; Richmond and Hunter, 1990). Additionally, split spawning could also serve as a mechanism to provide opportunity for colonies with different physiological condition and reproductive state to participate in a spawning event (Shimoike *et al.*, 1992; Van Veghel, 1994) and reproduce successfully.

Lastly, the fact that oocytes were present and developing year-round, not just prior to summer spawning months, is a significant finding with important implications for reef protection and conservation. Anthropogenic impacts even during months outside the spawning season could affect gamete development, compromise the reproductive capacity in the following summer, and have significant consequences for the population dynamics and recovery of reef systems.

#### *Environment and reproduction (different stations)*

Environmental conditions can significantly impact the physiological state of coral colonies and, in turn, affect their capacity to reproduce. Our study sites had very similar temperature regimes, but sedimentation rates differed greatly, especially during the rainy season. During this period, sedimentation rates at some stations were 4 to 8 times higher (reaching 42.7 mg/cm<sup>2</sup>/day) than the rates at the station with the lowest sedimentation. Surprisingly, despite the large variation in sedimentation rates between sites, no difference was observed in the oocyte development or fecundity between *M. capitata* populations exposed to these different sedimentation regimes. This suggests that *M. capitata* reproduction is not compromised by sedimentation effects at these sites (*i.e.*, nutrients, particulate organic matter, low light levels due to turbidity) and that this species can recognize reproductive cues under very different environmental conditions. Other studies have also found high resilience in the reproductive capacity of this species. For example, reproductive output and number of eggs per bundle (polyp fecundity) were not different in *M. capitata* colonies exposed to elevated ammonia (Cox and Ward, 2002) or those that bleached during early oocyte development (Cox, 2007). Moreover, the biochemical composition of eggs from *M. capitata* populations exposed to very different light and temperature regimes did not show differences in the amount of energy reserves and antioxidant



**Figure 8.** Oocyte size-frequency distribution for *Montipora capitata* at three stations in Kane'ohe Bay, Hawai'i, during December, March, June, and September of 2009.

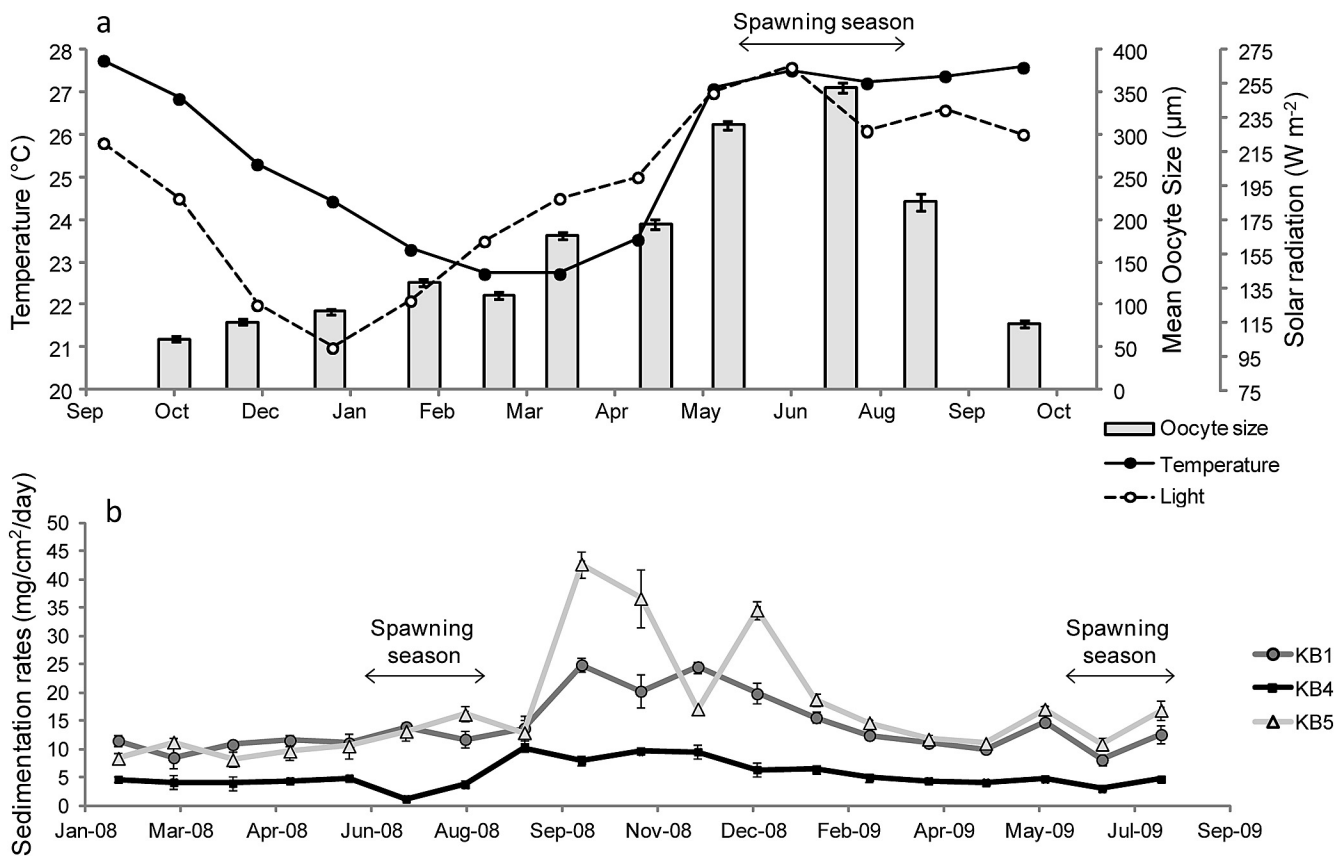
levels (Padilla-Gamiño *et al.*, 2013). It is likely that the capacity to successfully produce gametes under different environmental conditions is linked to this coral's ability to use both heterotrophic and autotrophic sources of energy to sustain metabolic functions and maintain lipid reserves for gamete development (Anthony, 2000; Anthony and Fabricius, 2000; Grottoli *et al.*, 2006; Cox, 2007). *M. capitata* has been observed to increase its heterotrophic feeding rates in response to experimental bleaching and to replenish biomass and energy reserves within short time scales (weeks) (Grottoli *et al.*, 2006). This strategy could give *M. capitata* the physiological flexibility necessary to live and successfully reproduce in areas with high sedimentation and low turbidity and become less dependent on autotrophic energy acquisition by symbiont photosynthesis.

To date, no study has examined the energy allocation to reproduction in *M. capitata* in relation to energy derived from both photosynthesis and heterotrophy. However, energy cost estimates based on energy uptake by photosynthesis suggest that gamete production in *M. capitata* is an inexpensive process accounting for only 2%–3.5% of annual net photosynthetic productivity, which can be replaced within weeks (Kolinski, 2004). In contrast, other processes

such as growth and mucus production can account for up to 21% and 48%, respectively (Kolinski, 2004). Thus, the high capacity to successfully produce gametes in *M. capitata* under different environments may be attributed to both a high physiological flexibility for energy acquisition and an inexpensive cost of gamete production.

It is important to consider that the rates of sediment deposition reported in the present study are considerably lower than those reported from other areas in Hawai'i. For example, fringing reefs in Molokai Island can reach sedimentation values higher than 740 g/cm<sup>2</sup>/day during Kona storms (Bothner *et al.*, 2006), and these extreme impacts can impose greater physiological demands (*i.e.*, production of mucus) that could compromise the reproductive biology of *M. capitata*. Previous studies in other coral species have found that gametogenesis, fecundity, and planulation can be compromised by sedimentation and eutrophication effects (Kojis and Quinn, 1984; Tomascik and Sander, 1987). Furthermore, production of gametes and larvae is only the first step in the reproductive cycle and does not guarantee successful survival of the new recruits. Recruitment in areas with high sedimentation could be severely compromised by low gamete quality, lower fertilization rates, reduced area of





**Figure 9.** (a) Temperature, solar radiation, and oocyte size in *Montipora capitata* from September 2008 to October 2009. (b) Sedimentation rates at study sites from February 2008 to August 2009. Arrows indicate spawning months.

sea floor suitable for settlement, and alteration of chemical cues in the environment (Rogers, 1990; Babcock and Davies, 1991; Gilmour, 1999; Fabricius, 2005). More studies are also needed to understand how parental history influences the quality of gametes and survival capacity of larvae and recruits.

Increased sedimentation caused by coastal development and poor land management is a major threat facing coral reefs throughout the world today (Rogers, 1990; Fabricius, 2005). Our results indicate that *M. capitata* has the potential to live in areas with different sedimentation regimes without compromising its capacity to produce gametes. Despite large differences between sites and individuals, the gametogenic cycle lasted between 10 and 11 mon at all sites, and oocyte growth was mainly correlated to solar radiation. This is a significant and optimistic finding that highlights the resilience of *M. capitata* and the importance of habitat restoration for coral recruitment. Future experimental studies, using long-term reciprocal transplants from a more heavily sedimented environment, should be conducted to explore reproductive thresholds in response to sedimentation stress and monitor sublethal impacts of declining water quality. This will facilitate the design and implementation

of appropriate land practices to maintain habitat quality at a level that allows for successful reproduction and the replenishment of the reef.

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