11-20-2018

Early Life History Response of Reef Building Coral, Orbicella faveolata, to Ocean Acidification and Warming

Kelly A. Pitts

pittsakelly@gmail.com

Follow this and additional works at: https://nsuworks.nova.edu/occ_stuetd

Part of the Marine Biology Commons, and the Oceanography and Atmospheric Sciences and Meteorology Commons

Share Feedback About This Item

Thesis of
Kelly A. Pitts

Submitted in Partial Fulfillment of the Requirements for the Degree of

Master of Science

M.S. Marine Biology

Nova Southeastern University
Halmos College of Natural Sciences and Oceanography

November 2018

Approved:
Thesis Committee

Major Professor: Nicole D. Fogarty, Ph.D.

Committee Member: Justin Campbell, Ph.D.

Committee Member: Joana Figueiredo, Ph.D.

HALMOS COLLEGE OF NATURAL SCIENCES AND OCEANOGRAPHY

EARLY LIFE HISTORY RESPONSE OF REEF BUILDING CORAL, *ORBICELLA FAVEOLATA*, TO OCEAN ACIDIFICATION AND WARMING

By

Kelly A. Pitts

Submitted to the Faculty of

Halmos College of Natural Sciences and Oceanography

in partial fulfillment of the requirements for the degree of Master of Science with a specialty in:

Marine Science

Nova Southeastern University

ACKNOWLEDGEMENTS

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

ABSTRACT

Ocean warming and acidification pose major threats to coral reef organisms. It is unknown how the early life history stages of Atlantic corals cope with the combined effects of these two global environmental stressors. Here, I investigate how these stressors influence the fertilization success, larval survivorship, and settlement of the threatened Atlantic coral, *Orbicella faveolata*. Gametes from *O. faveolata* were subjected to a factorial combination of present and future scenarios of oceanic temperatures (28.5° C and 30° C) and pH (8.2 and 8.0) predicted to occur by 2050. Results indicate that treatment type did not significantly affect fertilization success. Elevated temperature caused complete larval mortality and inhibited the settlement of *O. faveolata*. Interestingly, these negative effects of high temperature were partially mitigated when combined with ocean acidification. Overall, both the larval survivorship and settlement in the combined treatment was reduced to approximately half when compared to ambient treatment. Although ocean acidification may partially mitigate the negative effects of ocean warming during the larval stage, the overall reduced survival and settlement of larvae under future oceanic conditions, coupled to reduced calcification in adults, portends devastating effects on the health of this threatened species.

CHAPTER 1: INTRODUCTION

1.1 Status of Coral Reef Ecosystems

      Although coral reefs only cover approximately 0.5% of the ocean floor (Copper 1994), they support more species than any other marine environment and contribute 5% to global diversity (Odum and Odum 1955; Reaka-Kudla 1997). These ecosystems can host a staggering amount of diversity because they provide unique habitat and a source of essential nutrients for marine food chains in an oligotrophic environment (Froelich 1983; D'Elia 1988; Opitz 1996; Allgeier et al. 2016). Not only are these ecosystems vital to maintain biodiversity, but they also buffer shorelines from wave activity (Moberg and Folke 1999; Elliff and Silva 2017), provide sustenance to millions of people (Salvat 1992; Whittingham et al. 2003; Sadovy 2005), and offer over $30 billion in commercial value annually (Costanza et al. 1998; Hoegh-Guldberg 2004; Chen et al. 2015).

      Despite their importance, the majority of coral reefs face the serious threat of extinction from an array of anthropogenic stressors (Halpern et al. 2008). Local stressors include habitat destruction, disease, eutrophication, sedimentation, and overfishing, which reduce the resilience of corals against global stressors, such as ocean warming (OW), ocean acidification (OA), and storm intensification (Hughes et al. 2003; Pandolfi et al. 2003; Wilkinson 2004; Hoegh-Guldberg et al. 2007). Although disturbance is important for maintaining biodiversity, the increase in scale and frequency of these stressors have led to the destruction of coral reef ecosystems (Done 1992; Hughes 1994; Mumby et al. 2007). Both local and global pressures have contributed to a 60% decline in coral reefs worldwide, leaving the remaining one third of all reefs at elevated risk of extinction (Carpenter et al. 2008; Jackson 2008). Even corals with the greatest level of protection are approaching extinction (Pandolfi et al. 2005). If this rate of loss continues unabated, mass extinction of coral reef ecosystems is predicted to occur by 2050 (Burke et al. 2011).

1.2 Ocean Warming (OW)

The recent increase in atmospheric carbon dioxide (CO_2), mostly from the burning of fossil fuels, represents one of the most detrimental disturbances to coral reef ecosystems worldwide. Since the Industrial Revolution, atmospheric CO_2 has increased from approximately 280 parts per million by volume (ppmv) to over 400 ppmv (Solomon 2007; Meinshausen et al. 2011; Gattuso et al. 2015), an amount that is 30% higher than what has naturally occurred over the past 650,000 years (Siegenthaler et al. 2005). As a result of the increased concentration of this greenhouse gas, heat becomes trapped within the atmosphere, thus warming sea surface waters. Consequently, the oceans are expected to increase in temperature by 1.2 - 3.2°C by the end of the century (Solomon 2007; Meinshausen et al. 2011; Gattuso et al. 2015), affecting the vast majority of coral reef organisms.

Coral reefs are located in shallow waters close to their upper thermal tolerance limits, making them one of the most vulnerable ecosystems to global climate change (Hoegh-Guldberg 1999). As a result, coral organisms express sensitivity to even a 1°C increase in seawater temperature (Donner et al. 2005; Hoegh-Guldberg et al. 2007; Baker et al. 2008). According to Sammarco and Strychar (2013), host corals can tolerate fluxes in temperature more so than their algal symbionts, *Symbiodinium* spp. High temperature or irradiance can damage the photosynthetic machinery of the *Symbiodinium* spp., causing the overproduction of oxygen radicals. These radicals can harm both the coral host and *Symbiodinium* spp, leading to the degeneration of their symbiotic relationship and the expulsion of algae from the host (Lesser 2006). This process, termed coral bleaching, can cause a range of physiological effects, including reductions in growth, reproduction, and survival of the coral host (Brown 1997; McClanahan et al. 2009). In the Caribbean, McWilliams et al. (2005) suggest that even a 0.1°C increase in sea surface temperature can result in a 42% increase in bleaching intensity, as well as a 35% increase in the number of areas that have reported bleaching. Since the 1980s, bleaching events have been reported from almost all coral reef supporting regions, often with whole ocean basins affected (Baker et al. 2008).

1.3 Ocean Acidification (OA)

The oceans' absorption of more than 30% of atmospheric carbon dioxide (CO_2) emitted by human activity (OA) represents another detrimental disturbance to coral reef ecosystems worldwide. Once absorbed, CO_2 reacts with water to form carbonic acid (H_2CO_3). By losing hydrogen ions, this weak acid can dissociate to form bicarbonate ions (HCO_3^-) and further, to form carbonate ions (CO_3^{2-}) as seen in the following reactions:

$$CO_{2(atmos)} \leftrightarrow CO_{2(aq)} + H_2O \leftrightarrow H_2CO_3 \leftrightarrow H^+ + HCO_3^- \leftrightarrow 2H^+ + CO_3^{2-}$$

These reactions are reversible and near equilibrium (Millero et al. 2002; Doney et al. 2009). However, when CO_2 is added to seawater, bicarbonate ion and hydrogen ion concentrations increase, causing the oceans to become more acidic. Carbonate ion concentrations decline as they combine with H^+ to form HCO_3^-, pushing the above equation from right towards center. As a result, this increase in anthropogenic atmospheric CO_2 since preindustrial times has reduced both seawater pH and carbonate ion concentrations (CO_3^{2-}) (Chave and Suess 1970), by 0.1 units (Raven et al. 2005) and 30 µmolkg^1 (Hoegh-Guldberg et al. 2007), respectively. If anthropogenic atmospheric CO_2 continues to increase at the current rate, oceanic pH is projected to decrease 0.3-0.4 pH units by the end of the century. This represents a 150% increase in H+ and 50% decrease in carbonate concentrations (Caldeira and Wickett 2003; Orr et al. 2005; Raven et al. 2005; Stocker et al. 2013).

Ocean acidification is of tremendous concern for marine calcifying organisms, such as reef-building corals, that rely on carbonate ions to form their calcium carbonate structural skeletons (Smith and Buddemeier 1992). The current average calcium carbonate concentration is approximately 250 µmol kg^{-1} (Field and Van Aalst 2014). If concentrations fall below 200 µmol kg^{-1}, coral reef carbonate accretion will approach zero or become negative (Hoegh-Guldberg et al. 2007). Many studies have examined the direct relationship of reduced coral calcification in response to decreased carbonate ion concentration (Gattuso et al. 1998; Schneider and Erez 2006; Anthony et al. 2008; Marubini et al. 2008). For example, Langdon et al. (2000) studied coral reef organisms at a community level over the course of 3.8 years and found community calcification as a linear function of calcium and carbonate ion concentrations. As a result of OA, it is

expected that coral calcification rates will decline 20-60% by 2100 (Andersson et al. 2005; Kleypas et al. 2005; Langdon and Atkinson 2005; Parry et al. 2007; Chan and Connolly 2013). In addition to decreased calcium carbonate production rates, coral skeleton dissolution rates also increase in acidic conditions, presenting another challenge for reef-building corals (Langdon et al. 2000; Yates and Halley 2006). When rates of dissolution become greater than calcification, whole coral reef ecosystems collapse (Erez et al. 2011).

1.4 OW and OA on Reef-building Corals

It is clear that both OW and OA can have detrimental effects on numerous reef-building corals. However, even though these global stressors occur simultaneously, their synergistic effects on coral organisms are poorly understood. Analysis of coral colony cores between 1988 and 2003 depict a 21% decline in calcification, much lower than expected from OA alone. These results suggest that multiple environmental stressors, including OW, may have compounding effects with OA on reef-building corals (Carpenter et al. 2008). Further, while OW may allow for corals to migrate to less tropical latitudes (Precht and Aronson 2004), the decreased carbonate concentrations in these areas may restrict reef development, combating the ability of coral organisms to escape thermal stress (Kleypas et al. 2001; Guinotte et al. 2003). Other impacts of OW and OA when combined include increased bioerosion (Reyes-Nivia et al. 2013), bleaching (Erez et al. 2011), and the narrowing of thermal tolerance windows (Pörtner 2008). Alternatively, McCulloch et al. (2012b) suggest that some corals display increased resilience to OW and OA by pH up-regulation within the coral tissue. McNeil et al. (2004) also suggest that coral organisms have increased resilience to OW and OA. As calcification rates increased in OW, despite OA, they predict that calcification rates for 2100 will exceed pre-industrial calcification rates by 35%. Overall, conflicting results suggest that tolerance to these environmental stressors may be species specific.

The recovery and persistence of coral reef ecosystems depends on the ability of recruitment to keep pace with adult population mortality (Richmond 1997; Hughes and Tanner 2000). Anecdotal evidence suggests that the early life history stages of corals may be more sensitive to environmental stressors than adults. However, due to the

difficulties associated with rearing and interpreting larval behaviors, few studies have focused on the effects of OW or OA on the early life history stages of corals, and only five studies have investigated their combined effects. All five of these studies have focused on reef-building corals of the Indian or Pacific Oceans (Anlauf et al. 2011; Albright and Mason 2013; Chua et al. 2013b; Cumbo et al. 2013; Baria et al. 2015; Foster et al. 2015), so the effects of OW and OA on early life history stages for all Atlantic reef-building coral species remains unknown. Further, the techniques employed to investigate this topic, and their results obtained for various species have been dissimilar (Appendix A).

The majority of reef-building coral species are hermaphroditic broadcast spawning corals that reproduce by releasing sperm and eggs into the water column where they drift for approximately 30 minutes before fertilization (Harrison 2011). This process of external fertilization leaves sperm and eggs vulnerable to the chemical composition of the surrounding ocean water (Ritson-Williams et al. 2009). For example, Negri et al. (2007) found that *Acropora millepora* exhibited a reduction in fertilization when exposed to higher temperatures expected for the next century. However, three other species tested did not display vulnerability to OW, suggesting that some coral species may be able to cope with higher temperatures more so than others. Albright and Mason (2013) determined that as levels of OA increased, the coral *Acropora tenuis* required higher concentrations of sperm for fertilization, presumably because of a reduction in sperm to egg connections or contact efficiency. It is also possible that OA may reduce sperm motility and thereby decrease sperm effectiveness (Suwa et al. 2010). Only two studies have investigated the effects of both stressors simultaneously on fertilization and the results are conflicting. Albright and Mason (2013) suggests that these negative effects of OW and OA are amplified when gametes are subjected to both stressors concurrently, as eggs required higher concentrations of sperm for optimal fertilization. However, Chua et al. (2013b) found that *A. millipora* and *A. tenuis* were not significantly impacted by OW and OA in combination. Both studies suggest that the effects of OW and OA on fertilization will vary among species, as corals require different sperm concentrations to optimize fertilization.

After an egg is fertilized, the embryo undergoes gastrulation and eventually develops into a ciliated planula larva that is equipped for dispersal (Richmond and Hunter 1990). Ocean warming has been observed to increase the rate of larval metabolism (Woolsey et al. 2013; Figueiredo et al. 2014), embryonic deformities (Bassim et al. 2002; Negri et al. 2007), and mortality (Edmunds et al. 2001; Putnam et al. 2008; Randall and Szmant 2009a, 2009b; Figueiredo et al. 2014; Baria et al. 2015). It is suggested that the accelerated development may cause more errors in cell division, increasing the rate of larval mortality (Woolsey et al. 2013). It is also possible that mortality increases as a result of an increase in metabolism, which causes larvae to exhaust their energy reserves before they become competent to settle (Edmunds et al. 2011; Figueiredo et al. 2014). Like OW, OA has also been found to decrease successful embryological development (Nakamura et al. 2011). However, unlike OW, there is evidence that OA decreases larval metabolism (Albright and Langdon 2011; Nakamura et al. 2011). This reaction to OA seems to be species specific as Chua et al. (2013a) found no significant effect of OA on survivorship of three species of *Acropora*. Only two studies have investigated the simultaneous effects of OW and OA on larval survivorship, and their results are species specific. Both stressors combined had no effect on larval survivorship of *A. millipora* and *A. tenuis* (Chua et al. 2013b), but decreased the survivorship of *Pocillopora damicornis* larvae (Cumbo et al. 2013). It is clear there are numerous knowledge gaps of the effects of these two global stressors on coral larvae while in the water column.

Larvae can swim for days before settling and seeding a surrounding reef (Harrison 2011). If the larvae survive the planktonic stage, they will then form a flattened disc for attachment to the reef substrate upon reception of proper settlement cues (Harrison and Wallace 1990). Ocean warming has been found to accelerate the acquisition of competency (Nozawa and Harrison 2002; Nozawa and Harrison 2007; Figueiredo et al. 2014), increase the proportion of settlement (Randall and Szmant 2009b), as well as increase post-settlement mortality (Randall and Szmant 2009a; Figueiredo et al. 2014). As a result, a shorter pre-competency period may increase local retention, therefore debilitating long distance dispersal (Nozawa and Harrison 2002; Figueiredo et al. 2014). Contrarily, OA has been found to either decrease (Albright et al. 2010; Albright and

6

Langdon 2011) or have no affect (Albright et al. 2008) the amount of larval settlement. Altered settlement behavior may be a result of indirect effects, such as OA, limiting the availability of settlement cues (Albright and Langdon 2011). When combined, OW and OA have not been known to affect coral settlement (Anlauf et al. 2011; Foster et al. 2015).

1.5 Importance and Objectives

It is clear by the immense increase in the number of studies on the effects of OW and/or OA on reef-building corals within the last few decades that this topic is multifaceted and of great importance. Many reef-building corals spawn once or twice a year, restricting the amount of time available for manipulative experiments. Further, the typically large mortality rates associated with gametes and larvae present additional difficulties when researching early life history stages of corals. Thus, there are only a few species of corals where OA and OW have been concurrently investigated, all of which are from the Indian and Pacific oceans. Given the inconsistent results from prior work, more research is needed to better understand larval behavior when subjected to the combined global stressors expected within the century.

Although coral reef recovery is critically dependent upon the success of early life history stages, no study has examined the effects of future climate scenarios on any early life history stage of Atlantic reef-building corals, due primarily to the difficulties rearing and interpreting larval behaviors. Here, I follow the Atlantic coral species, *Orbicella faveolata* throughout three early life history stages (fertilization, larval survivorship, and larval settlement) when exposed to OW and OA expected for the next century in order to investigate the following:

Q1: Does OW and/or OA influence *Orbicella faveolata* fertilization success across various sperm concentrations?

> H_0: OW and/or OA has no effect on fertilization success across various sperm concentrations.

> H_a: OW and/or OA reduce fertilization success while eggs require higher concentrations of sperm for fertilization. These effects are amplified when stressors are combined.

Q2: Does OW and/or OA influence timing to settlement?

> H_0: OW and/or OA do not affect the timing to settlement.

> H_a: OW decreases time to settlement. OA increases the time to settlement. OW and OA have no effect on timing to settlement when in combination.

Q3: Does OW and/or OA influence the total percentage of settlement?

> H_0: OW and/or OA do not affect the total percentage of larvae settled.

> H_a: OW increases the percentage of settlement. OA decreases the percentage of settlement. OW and OA do not affect the percentage of settlement when in combination.

CHAPTER 2: PUBLICATION

2.1 Introduction

Rising atmospheric carbon dioxide (CO_2) has a profound effect on marine ecosystems by altering physiochemical parameters of oceans (Doney et al. 2011). Perhaps the most threatening consequences include ocean warming with an increase in temperature by 0.7°C and ocean acidification with a decrease in pH by 0.1 units. Since the Industrial revolution, anthropogenic atmospheric CO_2 has increased from ~280 to 390 ppm (Solomon 2007). As atmospheric CO_2 increases to 560 ppm by 2050, ocean surface waters are expected to further increase in temperature by 1.5°C and decrease by 0.2 pH units (Gattuso et al. 2015).

These oceanic conditions are expected to have the greatest effect on calcifying marine organisms that thrive close to their thermal tolerance limits. Consequently, ecosystems with calcifying, stenothermal organisms as the foundation species, such as coral reefs, are among the most vulnerable (Hoegh-Guldberg 1999). Coral reefs face extinction as oceans warm because they are sensitive to even a 1°C increase in temperature (Donner et al. 2005; Hoegh-Guldberg et al. 2007). As a result of ocean warming, the coral's symbiotic relationship with the *Symbiodinium* spp. degenerates, leading to bleaching (the expulsion of the endosymbiont allowing the white skeleton to be visible through the coral's translucent tissue). Bleaching can cause a range of detrimental effects, including reductions in growth, reproduction, and survival of the coral host (Brown 1997; McClanahan et al. 2009). Ocean acidification can also have negative physiological effects through reduced calcification and growth due to the reduction of oceanic carbonate ion (CO_3^{2-}) concentrations (Chave and Suess 1970; Smith and Buddemeier 1992; McCulloch et al. 2012a; Kornder et al. 2018). Both of these global stressors reduce the resilience of corals against local stressors, such as habitat destruction, eutrophication, sedimentation, and overfishing (Hughes et al. 2003; Pandolfi et al. 2003; Wilkinson 2004; Hoegh-Guldberg et al. 2007). As a result, global and local threats have contributed to a 60% decline in coral reefs worldwide, leaving the remaining one third of all reefs at an elevated risk of extinction (Carpenter et al. 2008; Jackson 2008).

Due to difficulties associated with rearing and interpreting larval behaviors, few studies have focused on the effects of ocean warming or acidification on the early life history stages of corals. Hermaphroditic, broadcast spawning coral species reproduce by releasing gamete bundles of both sperm and eggs, which float to the surface, dissipate, and fertilize (Harrison 2011). The fertilized egg develops into a ciliated planula larva that remains planktonic for days before settling (Richmond and Hunter 1990; Harrison 2011). Settlement on a suitable substrate is induced by chemical cues produced by bacterial biofilms and crustose coralline algae (CCA) (Morse et al. 1988; Sneed et al. 2014; Tebben et al. 2015). Surviving larvae form a flattened disc for attachment, and metamorphose to form a primary polyp that begins to calcify (Harrison and Wallace 1990).

Although sexual reproduction is vital for recruitment to reefs as well as for maintenance and enhancement of genetic diversity (Richmond 1997; Ayre and Hughes 2000), the process of external fertilization in the case of broadcast spawning, leaves sperm and eggs exposed to the chemical composition of the surrounding ocean water (Ritson-Williams et al. 2009). For example, temperature stress can cause embryonic deformities (Bassim et al. 2002; Negri et al. 2007), decrease larval survivorship (Edmunds et al. 2001; Randall and Szmant 2009a; Woolsey et al. 2013; Figueiredo et al. 2014), and accelerate the acquisition of competency (Nozawa and Harrison 2002; Nozawa and Harrison 2007; Figueiredo et al. 2014). However, responses to ocean warming have varied in another study which found no significant effect on larval survivorship or settlement (Ross et al. 2013). Likewise, ocean acidification has been found to decrease fertilization (Albright et al. 2010; Morita et al. 2010), settlement (Albright et al. 2010), and post-settlement growth (Albright et al. 2010; Morita et al. 2010; Suwa et al. 2010), while responses have varied in other studies in which ocean acidification had no impact on fertilization (Chua et al. 2013a), larval survivorship (Chua et al. 2013a; Baria et al. 2015), or settlement (Foster et al. 2015).

Although ocean acidification and warming are predicted to occur simultaneously, few studies have investigated the combined effects of these stressors on the early life history stages of broadcast spawning corals. To date, these have only focused on corals

of the Indian and Pacific oceans and have found that the concurrent exposure to both stressors decreases fertilization or causes eggs to require higher concentrations of sperm for fertilization (Albright and Mason 2013). However, these stressors have shown no effect on larval survivorship (Chua et al. 2013b; Baria et al. 2015) or settlement (Foster et al. 2015). The ability of corals in the Western Atlantic to tolerate these combined conditions during the earliest life history stages is currently unknown. Here we report the independent and combined effects of ocean warming and acidification on the early life history stages of a threatened reef-building coral, *Orbicella faveolata* (Ellis and Solander 1786; NMFS 2014). Our research is unique in that we investigate the effects of these stressors on multiple consecutive early life history stages including fertilization, larval survivorship, and settlement on a Western Atlantic coral species. Understanding the most vulnerable early life history stages of corals is the first step in protecting these fragile, highly biodiverse, and environmentally critical coral reef ecosystems.

2.2 Methodology

2.2.1 Gamete Collection

Gamete bundles from five *Orbicella faveolata* colonies were collected from the Meso-American Barrier Reef in Belize (16°48'06.0"N, 88°04'57.9"W) on September 12th, 2017. These colonies spawned 200 to 215 minutes after sunset, six days after the full moon. Colonies selected for collection were at least 5 m apart. Bundles were transferred to the laboratory for separation of sperm from eggs. Investigating *O. faveolata* is particularly important, as it is an essential reef building species that is listed as threatened under the U.S. Endangered Species Act (NMFS 2014), and its early life history response to global stressors remains unknown.

2.2.2 Fertilization

We employed four different treatments based off of the ambient temperature and pH of the reef in September of 2017 and the 'business as usual' RCP8.5 scenario projections predicted by year 2050 (Gattuso et al. 2015). The four treatments included (1) AMB: ambient temperature/ambient pCO_2, (2) OW: high temperature/ambient pCO_2, (3) OA: ambient temperature/high pCO_2, and (4) OAW: high temperature/high pCO_2 (Table 1). All fertilization assays were conducted in 100mL glass jars. Each of the four

treatments had one water bath maintained at the appropriate temperature. The proper pH was achieved by bubbling CO_2 into 0.2µL filtered seawater and distributing 60mL of pH treated seawater to each jar immediately before introducing the gametes. As Albright and Mason (2013) found that eggs required higher concentrations of sperm for fertilization in ocean acidification and warming conditions, we created serial dilutions of sperm for each *O. faveolata* cross in order to determine the optimal sperm concentration for each treatment. To do so, 3mL of sperm was added to the first of a series of three jars to create a serial dilution of sperm concentrations. The first jar was mixed and then 3mL was transferred to the second jar; this process was repeated for the third jar. Approximately 200 eggs were added to each jar of various sperm concentrations for a total of six crosses between *O. faveolata* individuals. Two of the crosses were reciprocals, meaning egg and sperm from a single colony was mixed in both directions (Table 1). Every 30 minutes throughout fertilization, three jars containing gametes were monitored for pH and temperature. These jars were not included in our dataset because of concerns that the pH measurements might alter fertilization success. Controls consisted of eggs only to confirm that no fertilization had occurred *in situ* before gametes were separated and subjected to treatments. After three hours, the number of fertilized and unfertilized eggs within each jar was determined using a dissecting microscope. The three jars for each of the six crosses were pooled and reared in 400mL polypropylene tripour beakers. These tripours were housed in 18.9L buckets with corresponding treatment conditions (details in next section). Each tripour, which had a mesh bottom to allow for the flow of treated seawater, was placed on an eggcrate shelf so that just the top remained above the water.

Table 1. *O. faveolata* individuals used to make six crosses for experimentation.

Cross	Female	Male
1	A	B
2	B	A
3	C	A
4	D	E
5	B	E
6	E	B

2.2.3 Larval Survivorship

Larval survivorship was assessed in 18.9L buckets with three independent replicates per treatment. All buckets were initially filled with seawater collected from the backreef (1m depth) and the OA and OAW buckets were dosed with CO_2 gas (using a pH stat system) to achieve appropriate treatment conditions. A main computer (Aqua Medic) monitored pH inside the OA and OAW buckets using a lab grade double junction pH probe (Neptune Systems) and pH was adjusted with the periodic bubbling of 100% gaseous CO_2 via magnetic solenoids. AMB and OW buckets did not receive a pH probe, and thus were not connected

Figure 1. Treatment buckets depicting six flow through tripours for survivorship and settlement experiments, a) settlement tiles in each tripour, b) a heater to maintain temperature, and c) a pH probe to maintain pH.

to the Aqua Medic controller. The pH in these buckets was independently monitored and manually adjusted twice a day with small additions of sodium hydroxide solution to maintain ambient pH levels. Heaters were used to elevate temperature within the OW and OAW buckets (Table 2). All buckets contained an air stone to circulate the water. The pH (NBS scale) and temperature were measured three times per day with an Orion Ross combination electrode to ensure proper calibration and setpoints of the pH stat system. Embryos from the fertilization experiment were reared for 32 hours in tripours in the treatments, after which, 50 larvae were counted out and placed back into the tripours. The treatment that the larvae were exposed to in the fertilization experiment remained the same throughout the larval survivorship and settlement experiments. Each tripour corresponded to a fertilization cross for a total of 6 tripours per bucket (Fig. 1). Surviving larvae in all tripours were counted daily over an additional five days.

2.2.4 Settlement

As recruitment to suitable substrates is induced by chemical settlement cues (Morse et al. 1988; Sneed et al. 2014; Tebben et al. 2015), aragonite settlement disks (2.5cm in diameter) were preconditioned in close proximity to the reef for the 2 months prior to experimentation in order to acquire settlement cues. One disk was placed in each of the tripours (Fig. 1) starting the first day of the survivorship experiment. The number of swimming

Figure 2. Microscopic view of a a) settler that is stuck and b) recruit that is metamorphosed to the aragonite tile.

larvae, settlers (attached to the tile), and recruits (metamorphosed on tile) were counted each day using a dissecting microscope (Fig. 2).

2.2.5 Data Analysis

Treatment parameters for the fertilization, survivorship, and settlement experiments were each tested with a one way ANOVA. Parametric assumptions were not met so we instead analyzed the data using a Kruskal-Wallis rank sum tests. The effect of treatment on fertilization was analyzed with an ANCOVA with sperm concentration as a covariate. The effect of cross on fertilization was analyzed using a one way ANOVA and then Kruskal-wallis rank sum test when parametric assumptions were not met. The effects of treatment and cross on the time to death was analyzed using a Cox model and log rank test. The time to settlement was tested using a Mantel-Haenszel log-rank test.

2.3 Results

2.3.1 Experimental Conditions

The chemical conditions of the fertilization, larval survivorship, and settlement experiments were monitored daily. Treatments remained stable throughout experimentation (Table 2&3).

Table 2. Summary of experimental conditions (means ± SE) across fertilization and survivorship and settlement experiments.

Treatment	Temperature (°C)	pH_{NBS}	Salinity (ppm)
Fertilization Experiment Sep. 12th-13th 2017			
AMB	28.28 ± 0.13	8.19 ± 0.001	
OA	28.30 ± 0.13	8.01 ± 0.003	
OW	29.86 ± 0.17	8.19 ± 0.001	
OAW	29.86 ± 0.14	8.01 ± 0.003	
Survivorship and Settlement Experiment Sep 14th-19th 2017			
AMB	28.81 ± 0.08	8.20 ± 0.01	35.33 ± 0.27
OA	28.95 ± 0.08	8.02 ± 0.01	35.00 ± 0.00
OW	30.35 ± 0.07	8.20 ± 0.01	35.33 ± 0.27
OAW	30.28 ± 0.08	8.03 ± 0.01	35.66 ± 0.27

Table 3. Kruskal-Wallis rank sum test results of chemical conditions during the fertilization and larval survivorship and settlement experiments.

		Treatment				χ^2	df	*P*
		AMB	OA	OW	OAW			
Fertilization	Temperature	a	a	b	b	17.34	3	<0.001
	pH	a	b	a	b	39.18	3	<0.001
Survivorship + Settlement	Temperature	a	a	b	b	126.72	3	<0.001
	pH	a	b	a	b	122.28	3	<0.001

2.3.2 Fertilization

Six crosses were created using five *O. faveolata* individuals to investigate the effect of treatment on fertilization success (Table 1). Each cross was formed using three different concentrations of sperm to determine the optimal concentration for fertilization. Treatment alone did not affect fertilization. Fertilization was significantly higher with higher sperm concentrations (Table 4; Fig. 3). There was little evidence of polyspermy (i.e., decreased fertilization at the highest sperm concentrations from developmental failure after more than one sperm fertilizes an egg). The cross of *O. faveolata* individuals significantly affected fertilization success (Fig. 4; Kruskal-Wallis: $\chi^2 = 44.83$, df = 5, p = 1.57×10^{-8}).
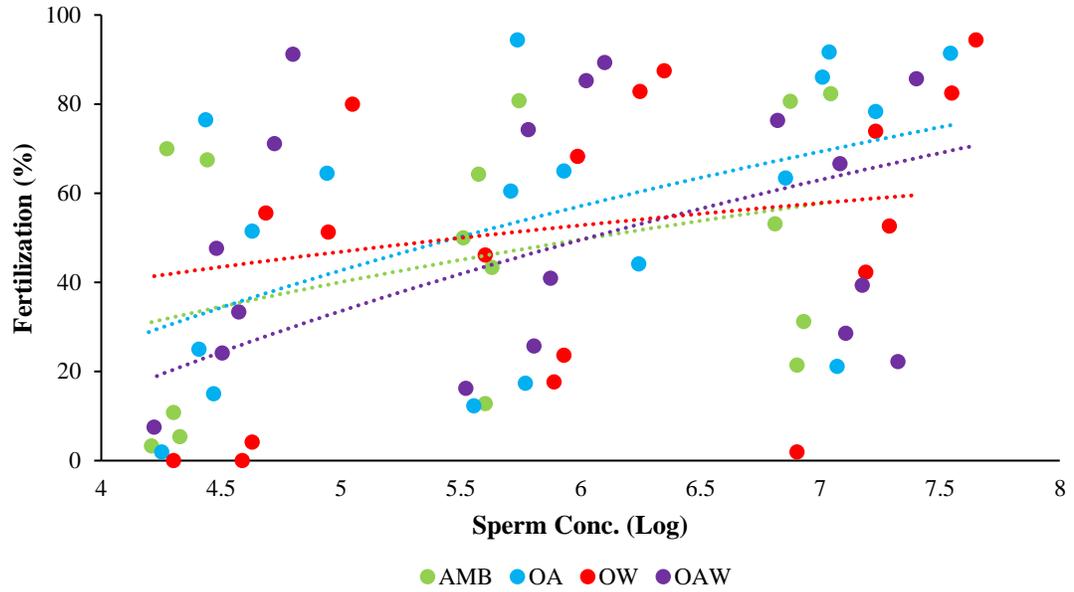
Figure 3. Effect of treatment on fertilization success of *Orbicella faveolata*.

Table 4. ANCOVA results of fertilization experiment.

Source	df	SS	ms	*F*	*P*
Log Sperm	1	4013.997		12.2046	0.009
Treatment	3	859.3733		0.8659	0.2644
Error	55	18089.01	328.89		
Total	59	22707.64			
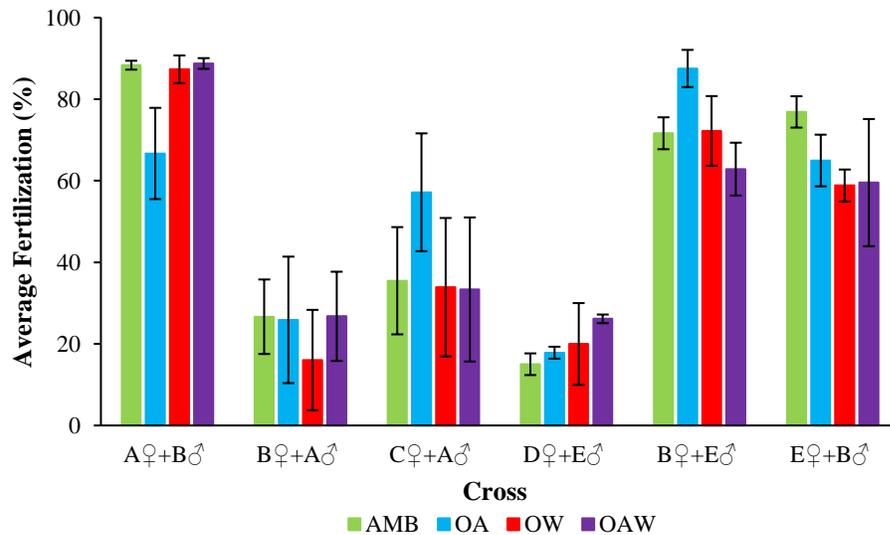
Figure 4. Effect of cross on fertilization success (means ± SE) of *Orbicella faveolata*.

2.3.3 Larval Survivorship

All six crosses from the fertilization experiment were maintained within the same treatments for six days post spawn. The cross of *O. faveolata* individuals significantly affected larval survivorship (Fig. 5; Cox model: $z = -2.44$, $p = 0.0147$).
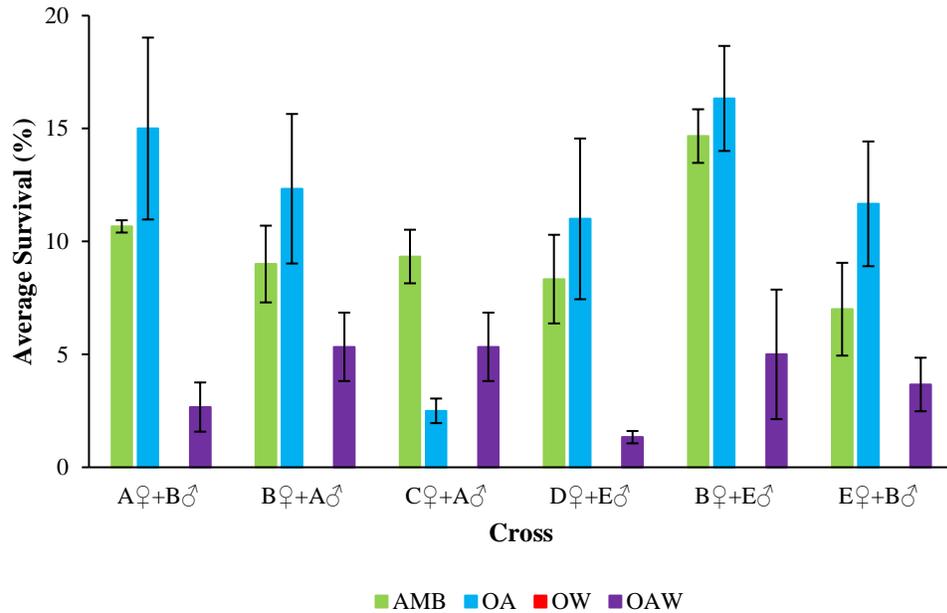
Figure 5. Effect of cross on larval survivorship (means ± SE) of *Orbicella faveolata* on the 7th day post spawn.

Treatment also had a significant effect on survival of *O. faveolata* larvae (Fig. 6A; Cox model: $z = -20.80$ $p < 0.01$). OA did not significantly differ from AMB (Log-Rank test, $p = 0.42$), while OW caused complete mortality by the 7th day, making the effect of ocean warming significantly different from all other treatments (Log-Rank test, $p < 0.0001$). Increasing CO_2 partially mitigated this detrimental effect of OW in the combined treatment, such that OAW was significantly different from all other treatments (Log-Rank test, $p < 0.0001$). As a result, larval survivorship in OAW was 415% higher three days after spawning and 567% higher six days after spawning than in OW. Still, the combined treatment exhibited less than half of the survivorship seen in the AMB treatment.
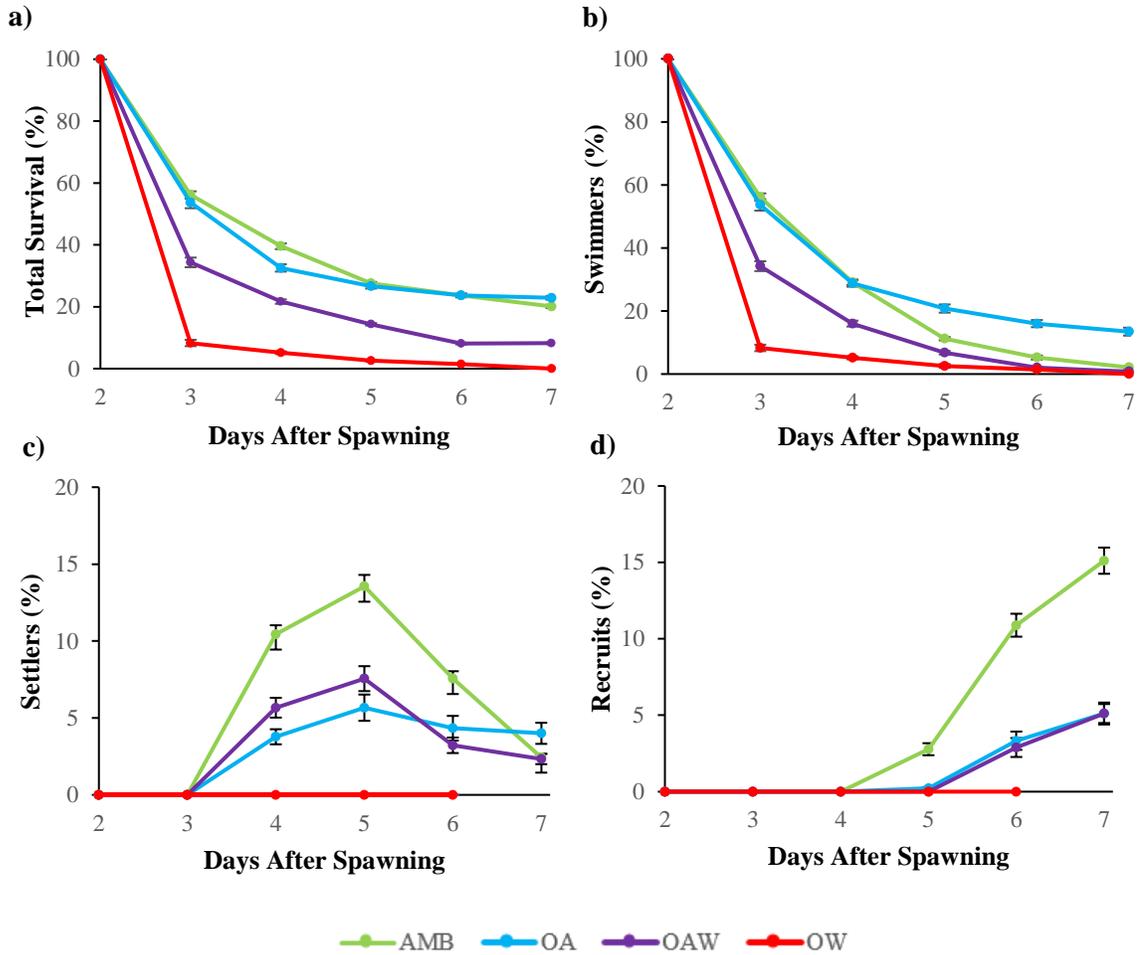
Figure 6. Survival (means ± SE) of *Orbicella faveolata* depicting percentage of a) total survival, b) swimmers, c) settlers, and d) recruits for each treatment.

2.3.4 Settlement

Settlement in terms of total settlers (Fig. 6C) plus total recruits (Fig. 6D) were counted daily for six days post spawn. Treatment had a significant effect on *O. faveolata* settlement (Fig. 7; Mantel-Haenszel: $\chi^2 = 59.9$, df = 3, p = 6.06×10^{-13}). Settlement was highest in AMB and significantly differed from the OA (Log-Rank test, p = 4.3×10^{-5}), OAW (p = 4.3×10^{-5}), as well as OW (p = 6.8×10^{-14}) treatments. The temperature stress treatment completely inhibited settlement. OA caused settlement to decrease by approximately half compared to the AMB treatment. Interestingly, OA partially mitigated the negative effects of OW in the combined treatment, making settlement statistically similar between the OA and OAW treatments (p = 0.978).
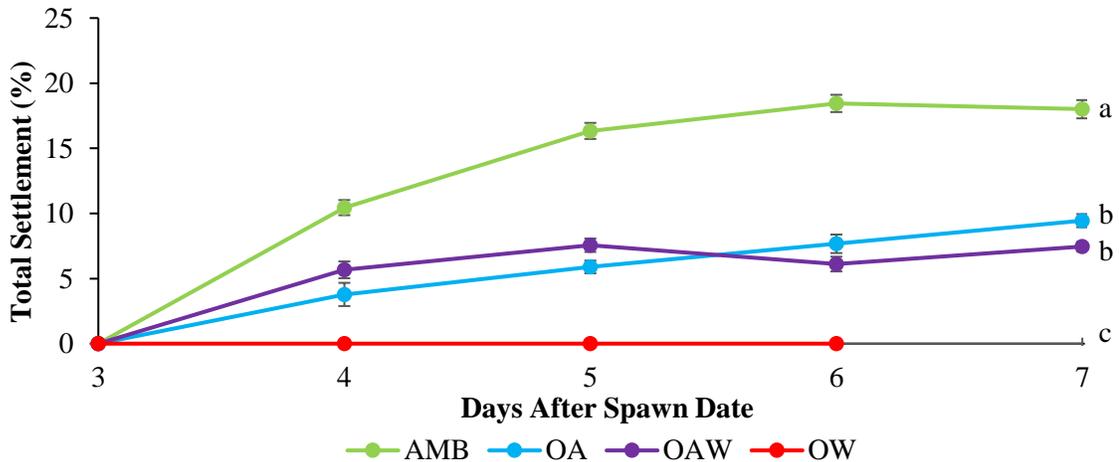
Figure 7. Total of *Orbicella faveolata* settlers plus recruits (means ± SE) across each treatment for seven days post spawn.

2.4 Discussion

It is not surprising that reef-building corals are sensitive to ocean warming and acidification as these organisms naturally live near their upper thermal tolerance limits (Hoegh-Guldberg 1999) and rely on a carbonate saturation state above 4 for calcification (Kleypas et al. 1999; Doney et al. 2009). What remains less understood is the ability of reef-building corals to cope with ocean acidification and warming during their earliest life history stages. This project investigated the effects of ocean warming and acidification predicted for 2050 on the Western Atlantic coral, *Orbicella faveolata*. Prior to this study, nothing was known about this important reef-building species' ability to withstand these two global stressors in its early life. As coral species worldwide are faced with mass extinction (Burke et al. 2011) and replenishment of coral populations relies heavily on successful reproduction and recruitment to the reef (Richmond 1997; Hughes and Tanner 2000), it is critical to understand the influence of global climate change during the earliest life history stages.

Fertilization was not affected by ocean acidification, warming, or the combination expected by year 2050. Previous studies on other species have revealed contrasting results, suggesting that fertilization success under global environmental stressors may be species specific (Albright et al. 2010; Morita et al. 2010; Albright and Mason 2013; Chua

et al. 2013b), as demonstrated for some invertebrates (Byrne and Przeslawski 2013). Therefore, if some species are more resilient than others, ocean acidification and warming may influence faunal shifts, community function, and species invasion (Gibson et al. 2011). This study also highlights the significant effects of different crosses of *O. faveolata* individuals on fertilization success. It is therefore possible that a history of environmental stress of the parental individuals chosen for this study may influence gametic quality (Michalek-Wagner and Willis 2001; Omori et al. 2001; Ward et al. 2002) or genetic differences may influence gametic compatibility (Negri et al. 2007; Baums et al. 2013). In addition to natural differences between species and individuals, these varying responses may have occurred as a result of discrepancies between methodologies. Consequently, it is vital for future studies to employ ocean acidification and warming treatments based on projections from the same time period in the future. Like Albright and Mason (2013), our current study also supports the importance of testing varying sperm concentrations as higher concentrations of sperm allowed for greater *O. faveolata* fertilization success. If *O. faveolata* populations further decline so that sperm availability in the water column becomes limiting, fertilization success may act as a bottleneck, preventing population maintenance and growth (Pennington 1985; Levitan and Petersen 1995). The success of sperm is also influenced by *in situ* factors, such as wind, current, and time after spawning. When these *in situ* factors are unfavorable, sperm concentration and/or fertilization rates become limiting for most broadcast spawning sessile organisms (Levitan and Petersen 1995), a concept that is largely understudied because *in situ* fertilization studies are difficult to accomplish.

Difference in *O. faveolata* crosses significantly affected larval survivorship. It is therefore perhaps a difference in parental health or genotype that continues to impact larval success after fertilization. These results highlight the importance genotypic diversity on the reef as well as testing multiple individuals in future studies. Treatment also had a significant effect on larval survivorship demonstrating that both cross and treatment interact to impact larval success. Ocean warming caused 100% mortality by the end of the experiment. Previous studies that investigate ocean warming on coral larvae mostly complement these results as temperature stress has been found to reduce larval survivorship (Edmunds et al. 2001; Randall and Szmant 2009a, 2009b; Chua et al. 2013b;

Cumbo et al. 2013). Figueiredo et al. (2014) suggest that the metabolism of larvae is augmented as a result of increased enzymatic activity in higher temperatures. Larvae can therefore exhaust their energy reserves prior to settlement, leading to mortality. On the other hand, larval survivorship of *O. faveolata* was not affected by ocean acidification. These results are comparable to previous studies, suggesting that the larvae of multiple species of broadcast spawning corals can better cope with ocean acidification compared to their adult stages when calcification occurs (Suwa et al. 2010; Nakamura et al. 2011; Chua et al. 2013b; Baria et al. 2015). However, it is possible that the metabolism of larvae decreases with ocean acidification (Albright and Langdon 2011). Larval survivorship of *O. faveolata* in the combined treatment representing predictions for 2050 was 41% of the survivorship from the ambient pH and temperature of 2017. It is perhaps the balance of an increased metabolism from ocean warming and lowered metabolism from ocean acidification that allows the combined treatment to partially mitigate the high mortality found in the ocean warming treatment.

Ocean acidification reduced settlement by about half compared to the ambient treatment, which is supported by previous studies where settlement was greatly reduced by ocean acidification (Albright et al. 2010; Albright and Langdon 2011; Doropoulos et al. 2012; Doropoulos and Diaz-Pulido 2013). Two of these studies suggest this reduction in settlement could be attributed to a disruption in the interactions between the microbes located on the substrate and larvae (Doropoulos et al. 2012; Doropoulos and Diaz-Pulido 2013). As ocean acidification allowed for high survivorship but decreased settlement, it is also possible that the *Orbicella faveolata* larvae were sluggish to settle and may have eventually settled. This hypothesis is further supported by Albright and Langdon (2011) who suggest that ocean acidification reduces larval metabolism, making them slower to settle. Contrarily, ocean warming completely inhibited all settlement of *O. faveolata*. These results are more extreme than other studies in which the proportion of settlement decreased (Randall and Szmant 2009a, 2009b) or the time to competency was shortened (Nozawa and Harrison 2002; Nozawa and Harrison 2007; Figueiredo et al. 2014). It is possible that the increased metabolism of *O. faveolata* in higher temperatures caused the larvae to prematurely exhaust energy reserves required for settlement. Once again, ocean acidification partially mitigated this negative impact of ocean warming on settlement in

the combined treatment. The possible reduction in larval metabolism caused by ocean acidification may have helped to balance the heightened metabolism caused by ocean warming such that the larvae did not completely exhaust their energy reserves before settlement.

The work demonstrates how *Orbicella faveolata* may respond to warmer, more acidic conditions that are expected for 2050. Our data suggests that fertilization may not be directly impacted by these global stressors. However, if adult populations continue to decline, the availability of sperm may limit fertilization success regardless of oceanic conditions. Larval survivorship will be greatly reduced by future oceanic conditions. If the bottleneck for the persistence of this species becomes embryonic thermal tolerance, then the question of compromised settlement may no longer be relevant. Regardless, settlement for this species in both ocean acidification and warming projected for 2050 was approximately half of the settlement that was during the present day. Overall, a reduction in the success of early life history stages will greatly impact the ability of these corals to survive, reproduce, and recruit to the reef. If more species of corals experience similar responses to these global stressors, the already decimated Caribbean reefs will be further forced into decline.

CHAPTER 3: DISCUSSION

3.1 Importance

As corals live close to their upper thermal tolerance limits (Hoegh-Guldberg 1999) and rely on carbonate saturation for calcification (Doney et al. 2009), ocean acidification and warming represent two of the largest threats to coral reef organisms. Although populations of adult corals have declined by 60% worldwide (Carpenter et al. 2008; Jackson 2008), it is not well understood how these global stressors impact corals in the earliest, and potentially most vulnerable life history stages. This project investigated the effects of ocean acidification and warming predicted for 2050 on the Western Atlantic coral, *Orbicella faveolata*. This is the first experiment to examine the effects of both stressors on any early life history stage of this important reef building species. The comparison of the results of this study to others provide insight on species specific responses to these global stressors and how a shift in community structure may be possible in the future. As replenishment of coral populations relies heavily on successful reproduction and recruitment to the reef (Richmond 1997; Hughes and Tanner 2000), research could not be of greater importance at this vulnerable time of mass coral reef extinction (Burke et al. 2011).

3.2 Fertilization

Fertilization was the first early life history stage of *O. faveolata* investigated in this study. The ability of eggs to become fertilized was not affected by OW, OA, or the combination expected by year 2050 (Fig. 3). Chua et al. (2013b) also found that these stressors had no effect on two acroporid species native to the Indo-Pacific. These complimentary results suggest that fertilization may not be the bottleneck early life history stage of multiple species. Contrarily, two previous studies found that OA decreases fertilization of *Acropora digitifera* by reducing sperm motility (Morita et al. 2010; Nakamura et al. 2011). As treatment had no effect on *O. faveolata* fertilization, it does not appear as though these stressors impacted male gametic success. Further, OA was found to decrease fertilization of *Acropora palmata* (Albright et al. 2010), while both OW and OA decreases fertilization of *Acropora tenuis* (Albright and Mason 2013). The

results of these studies suggest that the effects of global stressors, such as ocean acidification and warming may be species specific.

Although high fertilization success was achieved across all treatments, variability in fertilization between *O. faveolata* crosses indicates that some parental colonies produced more successful gametes than others (Fig. 4). This may be due to genetic differences (Negri et al. 2007; Baums et al. 2013) or a history of environmental stress (Szmant and Gassman 1990; Michalek-Wagner and Willis 2001; Omori et al. 2001; Ward et al. 2002) of the parental individuals. Though these adult colonies appeared healthy while spawning, it is possible OW or OA impacted the early life history stages of corals prior to spawning by affecting gamete production. It is also possible that dissimilarities of results may have occurred from discrepancies in methodologies. It is essential for future studies to employ OW and OA treatments based on projections from the same time period in the future to allow for comparisons. Testing multiple sperm concentrations is also important for study comparison. For example, Chua et al. (2013b) found that *Acropora millepora* fertilization was lower at 29°C compared to 27°C. However, this study only investigated one concentration of sperm for fertilization, making it difficult to compare their conclusions with this current study.

Regardless of treatment, the concentration of sperm significantly affected fertilization success of *O. faveolata* with greater fertilization occurring at the highest sperm concentrations (Fig. 3). Typically, sperm is not motile until it encounters egg-derived compounds while drifting throughout the water column in close proximity to eggs (Morita et al. 2006). These compounds attach to the sperm and cause a cascade of reactions to initiate motility (Coll et al. 1994; Morita et al. 2006). These reactions depend on the internal pH of the sperm; therefore, it is through these processes in which OA can impact sperm success. As a result of this mechanism, Morita et al. (2010) found that OA decreased sperm motility of *Acropora digitifera*. The fertilization of *O. faveolata*, on the other hand, was not affected by OA. This may be because we used pH projections for 2050 compared to more extreme OA treatments for 2100. Contrarily, not much is understood about the ability of coral sperm to endure thermal stress. Though higher temperatures increase sperm activity in different invertebrates (Byrne 2010), Negri et al.

(2007) did not find an effect of temperature on coral sperm motility. As the fertilization of *O. faveolata* was not impacted by temperature stress, it is possible that the sperm of this species was also not impacted by OW. It is important to note that even though OW and OA did not impact fertilization in this study, it is possible that an increase in stressor intensity by the end of the century may have more severe consequences for fertilization. Finally, according to Edwards and Richardson (2004), an increase in temperature or acidity may induce adult corals to spawn earlier in the year. This may cause complications as abundances of predators or competitors may be greater during this time (Harley et al. 2006).

3.3 Larval Survivorship

Difference in cross significantly impacted *O. faveolata* larval survivorship (Fig. 5). These results suggest that differences in parental health or genetics not only impact coral gametes during fertilization, but also continue to impact the survival of larvae days after fertilization. It is therefore vital for future populations to be genetically diverse to increase the likelihood of withstanding future global stressors to maintain recruitment to Caribbean reefs. In addition, it is often that the difference in cross success is overlooked as many studies are conducted from batch cultures. Our findings highlight the importance of conducting future studies using multiple individuals to better understand how whole reef populations may be impacted by future stressors.

Larval survivorship of *O. faveolata* was not affected by OA (Fig. 6A). These results are comparable to previous studies, suggesting that the larvae of multiple species of broadcast spawning corals can cope with OA better than their calcifying adult stages (Suwa et al. 2010; Nakamura et al. 2011; Chua et al. 2013b; Baria et al. 2015). However, Cumbo et al. (2013) found that OA decreases survival of *Pocillopora damicornis*, and propose that coral species with longer pelagic durations may be more severely impacted by global stressors. OA has also been found to reduce the metabolism of coral larvae, thus slowing their rate of development (Suwa et al. 2010; Albright and Langdon 2011; Nakamura et al. 2011). OW, on the other hand, caused 100% mortality of *O. faveolata* by day seven (Fig. 6). These results complement prior studies in which temperature stress reduced larval survivorship (Edmunds et al. 2001; Randall and Szmant 2009a, 2009b;

Chua et al. 2013b; Cumbo et al. 2013). Figueiredo et al. (2014) suggest that the metabolism of larvae augments due to increased enzymatic activity in higher temperatures. Although heightened metabolism quickens the rate of development, this process also causes higher rates of mortality as larvae exhaust their energy reserves before settlement. Interestingly, larval survivorship in the OAW treatment was 41% of the survivorship in the ambient treatment by day seven (Fig. 6A). It is therefore perhaps the balance of metabolism that allows OA to partially mitigate the increased mortality caused by OW in the combined treatment. These results indicate that some *O. faveolata* larvae may be able to survive future oceanic conditions expected for 2050 as both OW and OA serve as concurrent stressors. However, it is still unclear the long term or latent effects of OAW has on early post-settlement survival.

3.4 Settlement

Ocean acidification reduced settlement to 52% compared to the ambient treatment by day seven (Fig. 7), which is supported by previous studies where settlement was greatly reduced by ocean acidification (Albright et al. 2010; Albright and Langdon 2011; Doropoulos et al. 2012; Doropoulos and Diaz-Pulido 2013). Two of these studies suggest that this reduction in settlement could be attributed to a disruption in the interactions between the microbes located on the substrate and larvae (Doropoulos et al. 2012; Doropoulos and Diaz-Pulido 2013). As OA allowed for high survival but decreased settlement (Fig. 6D and 7), it is also possible that the *Orbicella faveolata* larvae were slow to or did not get the chance to settle. This hypothesis is further supported by Albright and Langdon (2011) who suggest that OA reduces larval metabolism, making the initiation to settlement more sluggish. Therefore, future studies should investigate settlement over a longer period of time to account for slower settlement. Unlike OA, OW completely inhibited all settlement of *O. faveolata*. It is possible that the increased metabolism of *O. faveolata* in higher temperatures causes the larvae to prematurely exhaust energy reserves required for settlement. These results are more extreme than other studies in which the proportion of settlement decreased (Randall and Szmant 2009a, 2009b) or the time to competency was shortened (Nozawa and Harrison 2002; Nozawa and Harrison 2007; Figueiredo et al. 2014). Figueiredo et al. (2014) suggest that a

heightened metabolism increases larval rate of development, forcing larvae to settle faster. This reaction to OW causes the dispersal distances to decrease, thus increasing local retention of coral reefs. Although the magnitude of the impact of OW depends on the species studied, it is clear that a change in metabolism by either OA or OW greatly impacts community wide dynamics. Finally, OA partially mitigated the negative impact of OW on settlement in the OAW treatment. The possible reduction in larval metabolism caused by ocean acidification may have helped to balance the quickened metabolism caused by ocean warming such that the larvae did not completely exhaust their energy reserves before settlement. However, as the success of *Orbicella* species reproduction decreases following mass bleaching events (Levitan et al. 2014), and bleaching events are predicted to increase to 100% with an increase in 3°C (Berkelmans et al. 2004), it is reasonable to believe that ocean acidification and warming conditions in 2100 will be too severe to allow for successful reproduction of *O. faveolata*. It is also important to note that even though OA helped to partially mitigate the effects of OW, it has been well documented that OA has deleterious effects on coral calcification.

3.5 Species Specific Responses

It is clear from comparing the results of this study to previous studies that responses to both ocean warming and ocean acidification are species specific; there is still no general consensus of predictable outcomes of these two global stressors on coral early life history stages. The magnitude of this impact for each species seems to vary based on different factors. For example, various species of corals spend longer durations of time in the larval survivorship early life history stage. As coral larvae are typically confined to the top meter of the water column after fertilization where they experience large fluctuations in daily temperature and carbonate chemistry (Gilmour et al. 2009), it is possible that these species of larvae are better equipped to cope with a wider range of temperature and pH (Foster et al. 2015). Further, species with shorter larval stages are less affected by ocean acidification (Widdicombe and Spicer 2008). Not only does endurance depend on different durations of early life history stages, but also on geographical location. Surprisingly, heat tolerant middle and high intertidal corals may be more vulnerable to climate change than species that are deeper and less heat tolerant.

This trend can also be seen when comparing low and high latitude species. Typically, species that are closer to their thermal tolerance window do not quickly adapt to temperatures outside of this window over a prolonged period of time (Harley et al. 2006). In fact, corals of the Arabian Gulf can tolerate a range of 20°C where most tropical reef species can only tolerate a range of 5-7°C (Coles and Jokiel 1977; Schoepf et al. 2015). Foster et al. (2015) suggests that these trends of thermal plasticity in adults may extend to early life history stages of corals.

Species specific responses to ocean acidification and warming have also been seen in other marine organisms (Kurihara 2008; Byrne and Przeslawski 2013). The planktonic and early life history stages of these organisms are particularly vulnerable to these global stressors (Pechenik 1987; Gosselin and Qian 1997). In general, it appears as though thermal stress increases the metabolism of species until a lethal threshold in temperature or duration of exposure is reached (Pechenik 1987; Byrne 2010). Ocean acidification typically reduces growth and survival (Byrne and Przeslawski 2013). However, there have been many studies that show adverse reactions to OA. As examples, the survivorship of some gastropod species has been found to increase (Davis et al. 2013), *Amphibalanus improvises* has displayed greater shell strength (Pansch et al. 2013), *Saccostrea glomerata* shows increased growth (Parker et al. 2010), and crustacean larvae appear to be fairly resilient (Byrne and Przeslawski 2013) in elevated temperatures. Likewise, larval crustaceans, as well as juvenile amphipods, barnacles, and crabs appear more tolerant to ocean acidification (Byrne and Przeslawski 2013). According to Widdicombe and Spicer (2008), smaller bodied organisms may be more vulnerable to OA within a generation; however, larger bodied species will be more susceptible throughout evolutionary timescales. From these various responses, it seems as though there may be winners as well as losers in future oceanic conditions. If some species are more resilient than others, future ocean acidification and warming may influence faunal shifts, community function, and species invasion (Gibson et al. 2011).

3.6 Conclusions

The study of the early life history stages of corals is challenging for researchers worldwide. This topic is well under examined and therefore less understood, so

methodologies have greatly varied from study to study. All of the experiments conducted to date utilize different predictions for future environmental stressors to investigate their effects on corals, making it extremely difficult to compare conclusions across studies. It is therefore of utmost importance that forthcoming studies examining the effects these two global stressors on corals utilize OW projections that complement OA projections for the same future time period as the effects of these stressors interact to impact corals. This study also highlights the importance of employing a greater magnitude of sperm concentrations for fertilization, as well as testing settlement for a longer duration. These factors should be incorporated in future studies so that researchers can continue to prefect methodologies.

This current study is the first to investigate the impacts of both ocean warming and ocean acidification on an Atlantic coral species. Our data suggests that fertilization may not be directly impacted by these global stressors. However, if adult populations continue to decline, the availability of sperm may limit fertilization success. Further, *Orbicella faveolata* larval survivorship is expected to decline by more than half by 2050. If the bottleneck for the persistence of this species becomes embryonic thermal tolerance, then the question of comprised settlement may no longer be relevant. Regardless, settlement for this species in both OW and OA declined by half in the projected 2050 scenario. All three of the early life history stages investigated in this study were greatly impacted by future global stressors. A reduction in the success of early life history stages will greatly impact the ability of these corals to survive, reproduce and recruit to the reef. In comparison to other studies, it appears that the effect of these stressors is species specific. If other coral species experience similar responses to these global stressors, Caribbean reefs will likely be subject to additional decline. More research on the effects of both ocean acidification and warming on early life history stages of a diverse array of coral organisms is absolutely vital at this pivotal time in climate history in order to understand the future of the world's coral reefs.

LITERATURE CITED

Albright, R, B Mason, and C Langdon. 2008. "Effect of aragonite saturation state on settlement and post-settlement growth of Porites astreoides larvae." *Coral Reefs* 27 (3): 485-490.

Albright, R., B. Mason, M. Miller, and C. Langdon. 2010. "Ocean acidification compromises recruitment success of the threatened Caribbean coral Acropora palmata." *Proceedings of the National Academy of Sciences of the United States of America* 107 (47): 20400-20404. https://doi.org/10.1073/pnas.1007273107. <Go to ISI>://WOS:000284529000048.

Albright, Rebecca, and Chris Langdon. 2011. "Ocean acidification impacts multiple early life history processes of the Caribbean coral Porites astreoides." *Global Change Biology* 17 (7): 2478-2487.

Albright, Rebecca, and Benjamin Mason. 2013. "Projected near-future levels of temperature and p CO 2 reduce coral fertilization success." *PLoS One* 8 (2): e56468.

Allgeier, Jacob E, Abel Valdivia, Courtney Cox, and Craig A Layman. 2016. "Fishing down nutrients on coral reefs." *Nature communications* 7: 12461.

Andersson, A. J., F. T. Mackenzie, and A. Lerman. 2005. "Coastal ocean and carbonate systems in the high CO2 world of the anthropocene." *American Journal of Science* 305 (9): 875-918. https://doi.org/10.2475/ajs.305.9.875. <Go to ISI>://WOS:000236181100001.

Anlauf, Holger, Luis D'Croz, and Aaron O'Dea. 2011. "A corrosive concoction: The combined effects of ocean warming and acidification on the early growth of a stony coral are multiplicative." *Journal of Experimental Marine Biology and Ecology* 397 (1): 13-20. https://doi.org/https://doi.org/10.1016/j.jembe.2010.11.009.

Anthony, K. R. N., D. I. Kline, G. Diaz-Pulido, S. Dove, and O. Hoegh-Guldberg. 2008. "Ocean acidification causes bleaching and productivity loss in coral reef builders." *Proceedings of the National Academy of Sciences of the United States of America* 105 (45): 17442-17446. https://doi.org/10.1073/pnas.0804478105. <Go to ISI>://WOS:000260981800051.

Ayre, David J, and Terence P Hughes. 2000. "Genotypic diversity and gene flow in brooding and spawning corals along the Great Barrier Reef, Australia." *Evolution* 54 (5): 1590-1605.

Baker, Andrew C, Peter W Glynn, and Bernhard Riegl. 2008. "Climate change and coral reef bleaching: An ecological assessment of long-term impacts, recovery trends and future outlook." *Estuarine, coastal and shelf science* 80 (4): 435-471.

Baria, M. V. B., H. Kurihara, and S. Harii. 2015. "Tolerance to Elevated Temperature and Ocean Acidification of the Larvae of the Solitary Corals Fungia fungites (Linnaues, 1758) and Lithophyllon repanda (Dana, 1846)." *Zoological Science* 32 (5): 447-454. https://doi.org/10.2108/zs150036. <Go to ISI>://WOS:000361955400005.

Bassim, K., P. Sammarco, and T. Snell. 2002. "Effects of temperature on success of (self and non-self) fertilization and embryogenesis in Diploria strigosa (Cnidaria, Scleractinia)." *Marine Biology* 140 (3): 479-488. https://doi.org/10.1007/s00227-001-0722-4.

Baums, IB, MK Devlin-Durante, NR Polato, D Xu, S Giri, NS Altman, D Ruiz, JE Parkinson, and JN Boulay. 2013. "Genotypic variation influences reproductive success and thermal stress tolerance in the reef building coral, Acropora palmata." *Coral Reefs* 32 (3): 703-717.

Berkelmans, Ray, Glenn De'ath, Stuart Kininmonth, and William J Skirving. 2004. "A comparison of the 1998 and 2002 coral bleaching events on the Great Barrier Reef: spatial correlation, patterns, and predictions." *Coral reefs* 23 (1): 74-83.

Brown, BE. 1997. "Coral bleaching: causes and consequences." *Coral reefs* 16 (1): S129-S138.

Burke, Lauretta, Kathleen Reytar, Mark Spalding, and Allison Perry. 2011. *Reefs at risk revisited*.

Byrne, M. 2010. "Impact of climate change stressors on marine invertebrate life histories with a focus on the Mollusca and Echinodermata." *Climate alert: climate change monitoring and strategy. University of Sydney Press, Sydney*: 142-185.

Byrne, Maria, and Rachel Przeslawski. 2013. "Multistressor impacts of warming and acidification of the ocean on marine invertebrates' life histories." *Integrative and comparative biology* 53 (4): 582-596.

Caldeira, Ken, and Michael E Wickett. 2003. "Oceanography: anthropogenic carbon and ocean pH." *Nature* 425 (6956): 365.

Carpenter, K. E., M. Abrar, G. Aeby, R. B. Aronson, S. Banks, A. Bruckner, A. Chiriboga, J. Cortes, J. C. Delbeek, L. DeVantier, G. J. Edgar, A. J. Edwards, D. Fenner, H. M. Guzman, B. W. Hoeksema, G. Hodgson, O. Johan, W. Y. Licuanan, S. R. Livingstone, E. R. Lovell, J. A. Moore, D. O. Obura, D. Ochavillo, B. A. Polidoro, W. F. Precht, M. C. Quibilan, C. Reboton, Z. T. Richards, A. D. Rogers, J. Sanciangco, A. Sheppard, C. Sheppard, J. Smith, S. Stuart, E. Turak, J. E. N. Veron, C. Wallace, E. Weil, and E. Wood. 2008. "One-third of reef-building corals face elevated extinction risk from climate change and local impacts." *Science* 321 (5888): 560-563.

Chan, Neil CS, and Sean R Connolly. 2013. "Sensitivity of coral calcification to ocean acidification: a meta-analysis." *Global Change Biology* 19 (1): 282-290.

Chave, Keith E, and Erwin Suess. 1970. "Calcium carbonate saturation in seawater: effects of dissolved organic matter." *Limnology and Oceanography* 15 (4): 633-637.

Chen, P. Y., C. C. Chen, L. Chu, and B. McCarl. 2015. "Evaluating the economic damage of climate change on global coral reefs." *Global Environmental Change-Human and Policy Dimensions* 30: 12-20. https://doi.org/10.1016/j.gloenvcha.2014.10.011. <Go to ISI>://WOS:000347863300002.

Chua, C. M., W. Leggat, A. Moya, and A. H. Baird. 2013a. "Near-future reductions in pH will have no consistent ecological effects on the early life-history stages of reef corals." *Marine Ecology Progress Series* 486: 143-151. https://doi.org/10.3354/meps10318. <Go to ISI>://WOS:000321776600012.

---. 2013b. "Temperature affects the early life history stages of corals more than near future ocean acidification." *Marine Ecology Progress Series* 475: 85-92. https://doi.org/10.3354/meps10077. <Go to ISI>://WOS:000314935000006.

Coles, SL, and PL Jokiel. 1977. "Effects of temperature on photosynthesis and respiration in hermatypic corals." *Marine biology* 43 (3): 209-216.

Coll, JC, BF Bowden, GV Meehan, GM Konig, AR Carroll, DM Tapiolas, PM Alino, A Heaton, R De Nys, and PA Leone. 1994. "Chemical aspects of mass spawning in corals. I. Sperm-attractant molecules in the eggs of the scleractinian coral Montipora digitata." *Marine Biology* 118 (2): 177-182.

Copper, P. 1994. "Ancient reef ecosystem expansion and collapse." *Coral reefs* 13 (1): 3-11.

Costanza, R., R. d'Arge, R. de Groot, S. Farber, M. Grasso, B. Hannon, K. Limburg, S. Naeem, R. V. O'Neill, J. Paruelo, R. G. Raskin, P. Sutton, and M. van den Belt. 1998. "The value of the world's ecosystem services and natural capital (Reprinted from Nature, vol 387, pg 253, 1997)." *Ecological Economics* 25 (1): 3-15. https://doi.org/10.1016/s0921-8009(98)00020-2. <Go to ISI>://WOS:000073896700002.

Cumbo, VR, TY Fan, and PJ Edmunds. 2013. "Effects of exposure duration on the response of Pocillopora damicornis larvae to elevated temperature and high pCO 2." *Journal of Experimental Marine Biology and Ecology* 439: 100-107.

D'Elia, Christopher F. 1988. "The cycling of essential elements in coral reefs." In *Concepts of ecosystem ecology*. 195-230. Springer.

Davis, Andrew R, Daniel Coleman, Allison Broad, Maria Byrne, Symon A Dworjanyn, and Rachel Przeslawski. 2013. "Complex responses of intertidal molluscan embryos to a warming and acidifying ocean in the presence of UV radiation." *PloS one* 8 (2): e55939.

Done, Terry J. 1992. "Phase shifts in coral reef communities and their ecological significance." *Hydrobiologia* 247 (1-3): 121-132.

Doney, Scott C, Victoria J Fabry, Richard A Feely, and Joan A Kleypas. 2009. "Ocean acidification: the other CO2 problem."

Doney, Scott C, Mary Ruckelshaus, J Emmett Duffy, James P Barry, Francis Chan, Chad A English, Heather M Galindo, Jacqueline M Grebmeier, Anne B Hollowed, and Nancy Knowlton. 2011. "Climate change impacts on marine ecosystems."

Donner, Simon D, William J Skirving, Christopher M Little, Michael Oppenheimer, and OVE Hoegh-Guldberg. 2005. "Global assessment of coral bleaching and required rates of adaptation under climate change." *Global Change Biology* 11 (12): 2251-2265.

Doropoulos, C., and G. Diaz-Pulido. 2013. "High CO2 reduces the settlement of a spawning coral on three common species of crustose coralline algae." *Marine Ecology Progress Series* 475: 93-99. https://doi.org/10.3354/meps10096. <Go to ISI>://WOS:000314935000007.

Doropoulos, C., S. Ward, G. Diaz-Pulido, O. Hoegh-Guldberg, and P. J. Mumby. 2012. "Ocean acidification reduces coral recruitment by disrupting intimate larval-algal settlement interactions." *Ecology Letters* 15 (4): 338-346. https://doi.org/10.1111/j.1461-0248.2012.01743.x. <Go to ISI>://WOS:000301349600006.

Edmunds, P, R Gates, and D Gleason. 2001. "The biology of larvae from the reef coral Porites astreoides, and their response to temperature disturbances." *Marine Biology* 139 (5): 981-989.

Edmunds, Peter J, Vivian Cumbo, and Tung-Yung Fan. 2011. "Effects of temperature on the respiration of brooded larvae from tropical reef corals." *Journal of Experimental Biology* 214 (16): 2783-2790.

Edwards, Martin, and Anthony J Richardson. 2004. "Impact of climate change on marine pelagic phenology and trophic mismatch." *Nature* 430 (7002): 881.

Elliff, C. I., and I. R. Silva. 2017. "Coral reefs as the first line of defense: Shoreline protection in face of climate change." *Marine Environmental Research* 127: 148-154. https://doi.org/10.1016/j.marenvres.2017.03.007. <Go to ISI>://WOS:000402212400015.

Ellis, John, and Daniel Charles Solander. 1786. *The natural history of many curious and uncommon zoophytes : collected from various parts of the globe*. London :: Printed for Benjamin White and Son ... and Peter Elmsly ...

Erez, Jonathan, Stéphanie Reynaud, Jacob Silverman, Kenneth Schneider, and Denis Allemand. 2011. "Coral calcification under ocean acidification and global change." In *Coral reefs: an ecosystem in transition*. 151-176. Springer.

Field, Christopher, and Maarten Van Aalst. 2014. *Climate change 2014: impacts, adaptation, and vulnerability*. Vol. 1. IPCC.

Figueiredo, J., A. H. Baird, S. Harii, and S. R. Connolly. 2014. "Increased local retention of reef coral larvae as a result of ocean warming." *Nature Climate Change* 4 (6): 498-502. https://doi.org/10.1038/nclimate2210. <Go to ISI>://WOS:000337138700028.

Foster, T, JP Gilmour, CM Chua, JL Falter, and MT McCulloch. 2015. "Effect of ocean warming and acidification on the early life stages of subtropical Acropora spicifera." *Coral Reefs* 34 (4): 1217-1226.

Froelich, Alina Szmant. 1983. "Functional aspects of nutrient cycling on coral reefs." The ecology of deep shallow coral reefs, NOAA Symp Ser Undersea Res., edited by: Rosenstiel School of Marine and Atmospheric Science University of Miami, Rockville, MD, NOAA Undersea Research Program.

Gattuso, J P, A Magnan, R Billé, WWL Cheung, EL Howes, F Joos, D Allemand, L Bopp, SR Cooley, and CM Eakin. 2015. "Contrasting futures for ocean and society from different anthropogenic CO2 emissions scenarios." *Science* 349 (6243): aac4722. http://science.sciencemag.org/content/sci/349/6243/aac4722.full.pdf.

Gattuso, J. P., M. Frankignoulle, I. Bourge, S. Romaine, and R. W. Buddemeier. 1998. "Effect of calcium carbonate saturation of seawater on coral calcification." *Global and Planetary Change* 18 (1-2): 37-46. https://doi.org/10.1016/s0921-8181(98)00035-6. <Go to ISI>://WOS:000074699700003.

Gibson, R, R Atkinson, J Gordon, I Smith, and D Hughes. 2011. "Impact of ocean warming and ocean acidification on marine invertebrate life history stages: vulnerabilities and potential for persistence in a changing ocean." *Oceanogr Mar Biol Annu Rev* 49: 1-42.

Gilmour, James P, Luke D Smith, and Richard M Brinkman. 2009. "Biannual spawning, rapid larval development and evidence of self-seeding for scleractinian corals at an isolated system of reefs." *Marine Biology* 156 (6): 1297-1309.

Gosselin, Louis A, and Pei-Yuan Qian. 1997. "Juvenile mortality in benthic marine invertebrates." *Marine Ecology Progress Series* 146: 265-282.

Guinotte, JM, RW Buddemeier, and JA Kleypas. 2003. "Future coral reef habitat marginality: temporal and spatial effects of climate change in the Pacific basin." *Coral reefs* 22 (4): 551-558.

Halpern, Benjamin S, Shaun Walbridge, Kimberly A Selkoe, Carrie V Kappel, Fiorenza Micheli, Caterina D'agrosa, John F Bruno, Kenneth S Casey, Colin Ebert, and Helen E Fox. 2008. "A global map of human impact on marine ecosystems." *Science* 319 (5865): 948-952.

Harley, Christopher DG, A Randall Hughes, Kristin M Hultgren, Benjamin G Miner, Cascade JB Sorte, Carol S Thornber, Laura F Rodriguez, Lars Tomanek, and Susan L Williams. 2006. "The impacts of climate change in coastal marine systems." *Ecology letters* 9 (2): 228-241.

Harrison, Peter L. 2011. "Sexual reproduction of scleractinian corals." In *Coral reefs: an ecosystem in transition*. 59-85. Springer.

Harrison, PL, and CC Wallace. 1990. "Reproduction, dispersal and recruitment of scleractinian corals." *Ecosystems of the world* 25: 133-207.

Hoegh-Guldberg, O. 2004. "Coral reefs in a century of rapid environmental change." *Symbiosis* 37 (1-3): 1-31. <Go to ISI>://WOS:000223474000002.

Hoegh-Guldberg, Ove. 1999. "Climate change, coral bleaching and the future of the world's coral reefs." *Marine and freshwater research* 50 (8): 839-866.

Hoegh-Guldberg, Ove, Peter J Mumby, Anthony J Hooten, Robert S Steneck, Paul Greenfield, E Gomez, C Drew Harvell, Peter F Sale, Aladdair J Edwards, and Ken Caldeira. 2007. "Coral reefs under rapid climate change and ocean acidification." *science* 318 (5857): 1737-1742. http://science.sciencemag.org/content/sci/318/5857/1737.full.pdf.

Hughes, Terence P. 1994. "Catastrophes, phase shifts, and large-scale degradation of a Caribbean coral reef." *Science* 265 (5178): 1547-1551.

Hughes, Terence P, and Jason E Tanner. 2000. "Recruitment failure, life histories, and long-term decline of Caribbean corals." *Ecology* 81 (8): 2250-2263.

Hughes, Terry P, Andrew H Baird, David R Bellwood, Margaret Card, Sean R Connolly, Carl Folke, Richard Grosberg, Ove Hoegh-Guldberg, Jeremy BC Jackson, and Janice Kleypas. 2003. "Climate change, human impacts, and the resilience of coral reefs." *science* 301 (5635): 929-933.

Jackson, Jeremy BC. 2008. "Ecological extinction and evolution in the brave new ocean." *Proceedings of the National Academy of Sciences* 105 (Supplement 1): 11458-11465.

Kleypas, Joan A, Robert W Buddemeier, David Archer, Jean-Pierre Gattuso, Chris Langdon, and Bradley N Opdyke. 1999. "Geochemical consequences of increased atmospheric carbon dioxide on coral reefs." *science* 284 (5411): 118-120.

Kleypas, Joan A, Robert W Buddemeier, and Jean-Pierre Gattuso. 2001. "The future of coral reefs in an age of global change." *International Journal of Earth Sciences* 90 (2): 426-437.

Kleypas, Joan A, Richard A Feely, Victoria J Fabry, Chris Langdon, Christopher L Sabine, and Lisa L Robbins. 2005. "Impacts of ocean acidification on coral reefs and other marine calcifiers: a guide for future research." Report of a workshop held.

Kornder, Niklas A, Bernhard M Riegl, and Joana Figueiredo. 2018. "Thresholds and drivers of coral calcification responses to climate change." *Global change biology*.

Kurihara, Haruko. 2008. "Effects of CO2-driven ocean acidification on the early developmental stages of invertebrates." *Marine Ecology Progress Series* 373: 275-284.

Langdon, C, and MJ Atkinson. 2005. "Effect of elevated pCO2 on photosynthesis and calcification of corals and interactions with seasonal change in temperature/irradiance and nutrient enrichment." *Journal of Geophysical Research: Oceans* 110 (C9).

Langdon, C., T. Takahashi, C. Sweeney, D. Chipman, J. Goddard, F. Marubini, H. Aceves, H. Barnett, and M. J. Atkinson. 2000. "Effect of calcium carbonate saturation state on the calcification rate of an experimental coral reef." *Global Biogeochemical Cycles* 14 (2): 639-654. https://doi.org/10.1029/1999gb001195. <Go to ISI>://WOS:000087586100009.

Lesser, Michael P. 2006. "Oxidative stress in marine environments: biochemistry and physiological ecology." *Annu. Rev. Physiol.* 68: 253-278.

Levitan, D. R., and C. Petersen. 1995. "Sperm Limitation in the Sea." *Trends in Ecology & Evolution* 10 (6): 228-231. https://doi.org/10.1016/s0169-5347(00)89071-0. <Go to ISI>://WOS:A1995QZ11700005.

Levitan, Don R, William Boudreau, Javier Jara, and Nancy Knowlton. 2014. "Long-term reduced spawning in Orbicella coral species due to temperature stress." *Marine Ecology Progress Series* 515: 1-10.

Marubini, F., C. Ferrier-Pages, P. Furla, and D. Allemand. 2008. "Coral calcification responds to seawater acidification: a working hypothesis towards a physiological mechanism." *Coral Reefs* 27 (3): 491-499. https://doi.org/10.1007/s00338-008-0375-6. <Go to ISI>://WOS:000258085900005.

McClanahan, TR, E Weil, J Cortés, AH Baird, and M Ateweberhan. 2009. "Consequences of coral bleaching for sessile reef organisms." In *Coral bleaching*. 121-138. Springer.

McCulloch, M., J. Falter, J. Trotter, and P. Montagna. 2012a. "Coral resilience to ocean acidification and global warming through pH up-regulation." *Nature Climate Change* 2 (8): 623-633. https://doi.org/10.1038/nclimate1473. <Go to ISI>://WOS:000307369300021.

McCulloch, Malcolm, Jim Falter, Julie Trotter, and Paolo Montagna. 2012b. "Coral resilience to ocean acidification and global warming through pH up-regulation." *Nature Climate Change* 2: 623. http://dx.doi.org/10.1038/nclimate1473.

McNeil, Ben I, Richard J Matear, and David J Barnes. 2004. "Coral reef calcification and climate change: The effect of ocean warming." *Geophysical Research Letters* 31 (22).

McWilliams, John P, Isabelle M Côté, Jennifer A Gill, William J Sutherland, and Andrew R Watkinson. 2005. "Accelerating impacts of temperature-induced coral bleaching in the Caribbean." *Ecology* 86 (8): 2055-2060.

Meinshausen, Malte, Steven J Smith, K Calvin, John S Daniel, MLT Kainuma, JF Lamarque, K Matsumoto, SA Montzka, SCB Raper, and K Riahi. 2011. "The RCP greenhouse gas concentrations and their extensions from 1765 to 2300." *Climatic change* 109 (1-2): 213-241.

Michalek-Wagner, K, and BL Willis. 2001. "Impacts of bleaching on the soft coral Lobophytum compactum. I. Fecundity, fertilization and offspring viability." *Coral Reefs* 19 (3): 231-239.

Millero, Frank J, Denis Pierrot, Kitack Lee, Rik Wanninkhof, Richard Feely, Christopher L Sabine, Robert M Key, and Taro Takahashi. 2002. "Dissociation constants for carbonic acid determined from field measurements." *Deep Sea Research Part I: Oceanographic Research Papers* 49 (10): 1705-1723.

Moberg, Fredrik, and Carl Folke. 1999. "Ecological goods and services of coral reef ecosystems." *Ecological Economics* 29 (2): 215-233. https://doi.org/http://doi.org/10.1016/S0921-8009(99)00009-9.

Morita, Masaya, Akira Nishikawa, Ayako Nakajima, Akira Iguchi, Kazuhiko Sakai, Akihiro Takemura, and Makoto Okuno. 2006. "Eggs regulate sperm flagellar motility initiation, chemotaxis and inhibition in the coral Acropora digitifera, A. gemmifera and A. tenuis." *Journal of Experimental Biology* 209 (22): 4574-4579.

Morita, Masaya, Ryota Suwa, Akira Iguchi, Masako Nakamura, Kazuaki Shimada, Kazuhiko Sakai, and Atsushi Suzuki. 2010. "Ocean acidification reduces sperm flagellar motility in broadcast spawning reef invertebrates." *Zygote* 18 (2): 103-107.

Morse, Daniel E, Neal Hooker, Aileen NC Morse, and Rebecca A Jensen. 1988. "Control of larval metamorphosis and recruitment in sympatric agariciid corals." *Journal of Experimental Marine Biology and Ecology* 116 (3): 193-217.

Mumby, Peter J., Alan Hastings, and Helen J. Edwards. 2007. "Thresholds and the resilience of Caribbean coral reefs." *Nature* 450: 98. https://doi.org/10.1038/nature06252.

Nakamura, Masako, Shun Ohki, Atsushi Suzuki, and Kazuhiko Sakai. 2011. "Coral larvae under ocean acidification: survival, metabolism, and metamorphosis." *PLoS One* 6 (1): e14521.

Negri, AP, PA Marshall, and AJ Heyward. 2007. "Differing effects of thermal stress on coral fertilization and early embryogenesis in four Indo Pacific species." *Coral Reefs* 26 (4): 759-763.

NMFS. 2014. "Final listing determinations on proposal to list 66 reef-building coral species and to reclassify elkhorn and staghorn corals, final rule 79, Federal Register 53852–54123."

Nozawa, Y, and PL Harrison. 2002. "Larval settlement patterns, dispersal potential, and the effect of temperature on settlement of larvae of the reef coral, Platygyra daedalea, from the Great Barrier Reef." Proc. 9th Int. Coral Reef Symp.

Nozawa, Yoko, and Peter L Harrison. 2007. "Effects of elevated temperature on larval settlement and post-settlement survival in scleractinian corals, Acropora solitaryensis and Favites chinensis." *Marine Biology* 152 (5): 1181-1185.

Odum, Howard T., and Eugene P. Odum. 1955. "Trophic Structure and Productivity of a Windward Coral Reef Community on Eniwetok Atoll." *Ecological Monographs* 25 (3): 291-320. https://doi.org/10.2307/1943285.

Omori, Makoto, Hironobu Fukami, Hisao Kobinata, and Masayuki Hatta. 2001. "Significant drop of fertilization of Acropora corals in 1999: An after-effect of heavy coral bleaching?" *Limnology and Oceanography* 46 (3): 704-706.

Opitz, Silvia. 1996. *Trophic interactions in Caribbean coral reefs*. Vol. 1085. WorldFish.

Orr, James C, Victoria J Fabry, Olivier Aumont, Laurent Bopp, Scott C Doney, Richard A Feely, Anand Gnanadesikan, Nicolas Gruber, Akio Ishida, and Fortunat Joos. 2005. "Anthropogenic ocean acidification over the twenty-first century and its impact on calcifying organisms." *Nature* 437 (7059): 681.

Pandolfi, J. M., R. H. Bradbury, E. Sala, T. P. Hughes, K. A. Bjorndal, R. G. Cooke, D. McArdle, L. McClenachan, M. J. H. Newman, G. Paredes, R. R. Warner, and J. B. C. Jackson. 2003. "Global trajectories of the long-term decline of coral reef ecosystems." *Science* 301 (5635): 955-958. https://doi.org/10.1126/science.1085706. <Go to ISI>://WOS:000184755900036.

Pandolfi, John M, Jeremy BC Jackson, N Baron, Roger H Bradbury, Hector M Guzman, Terence P Hughes, CV Kappel, F Micheli, John C Ogden, and Hugh P Possingham. 2005. Are US coral reefs on the slippery slope to slime? : American Association for the Advancement of Science.

Pansch, Christian, Ali Nasrolahi, Yasmin Shirin Appelhans, and Martin Wahl. 2013. "Tolerance of juvenile barnacles (Amphibalanus improvisus) to warming and elevated pCO2." *Marine Biology* 160 (8): 2023-2035.

Parker, Laura M, Pauline M Ross, and Wayne A O'Connor. 2010. "Comparing the effect of elevated pCO2 and temperature on the fertilization and early development of two species of oysters." *Marine Biology* 157 (11): 2435-2452.

Parry, Martin, Martin L Parry, Osvaldo Canziani, Jean Palutikof, Paul Van der Linden, and Clair Hanson. 2007. *Climate change 2007-impacts, adaptation and vulnerability: Working group II contribution to the fourth assessment report of the IPCC*. Vol. 4. Cambridge University Press.

Pechenik, Jan A. 1987. "Environmental influences on larval survival and development." *Reproduction of marine invertebrates* 9: 551-608.

Pennington, J Timothy. 1985. "The ecology of fertilization of echinoid eggs: the consequences of sperm dilution, adult aggregation, and synchronous spawning." *The Biological Bulletin* 169 (2): 417-430.

Pörtner, Hans-O. 2008. "Ecosystem effects of ocean acidification in times of ocean warming: a physiologist's view." *Marine Ecology Progress Series* 373: 203-217.

Precht, William F, and Richard B Aronson. 2004. "Climate flickers and range shifts of reef corals." *Frontiers in Ecology and the Environment* 2 (6): 307-314.

Putnam, Hollie M, Peter J Edmunds, and Tung-Yung Fan. 2008. "Effect of temperature on the settlement choice and photophysiology of larvae from the reef coral Stylophora pistillata." *The Biological Bulletin* 215 (2): 135-142.

Randall, C. J., and A. M. Szmant. 2009a. "Elevated temperature affects development, survivorship, and settlement of the elkhorn coral, Acropora palmata (Lamarck 1816)." *The Biological Bulletin* 217 (3): 269-282.

---. 2009b. "Elevated temperature reduces survivorship and settlement of the larvae of the Caribbean scleractinian coral, Favia fragum (Esper)." *Coral Reefs* 28 (2): 537-545. https://doi.org/10.1007/s00338-009-0482-z. <Go to ISI>://WOS:000265832100028.

Raven, John, Ken Caldeira, Harry Elderfield, Ove Hoegh-Guldberg, Peter Liss, Ulf Riebesell, John Shepherd, Carol Turley, and Andrew Watson. 2005. *Ocean acidification due to increasing atmospheric carbon dioxide*. The Royal Society.

Reaka-Kudla, M. D.E. Wilson, E. O. Wilson. 1997. "The global biodiversity of coral reefs: a comparison with rain forests. In:." *Reaka-Kudla, M., D.E. Wilson, E.O. Wilson (eds.), Biodiversity II: Understanding and Protecting our Biological Resources. Washington, D.C.: Joseph Henry Press. pp. 83-108.*

Reyes-Nivia, Catalina, Guillermo Diaz-Pulido, David Kline, Ove-Hoegh Guldberg, and Sophie Dove. 2013. "Ocean acidification and warming scenarios increase microbioerosion of coral skeletons." *Global Change Biology* 19 (6): 1919-1929.

Richmond, Robert H. 1997. "Reproduction and recruitment in corals: critical links in the persistence of reefs." *Life and death of coral reefs. Chapman & Hall, New York*: 175-197.

Richmond, Robert H, and Cynthia L Hunter. 1990. "Reproduction and recruitment of corals: comparisons among the Caribbean, the Tropical Pacific, and the Red Sea." *Marine ecology progress series. Oldendorf* 60 (1): 185-203.

Ritson-Williams, Raphael, Suzanne N Arnold, Nicole D Fogarty, Robert S Steneck, Mark JA Vermeij, and Valerie J Paul. 2009. "New perspectives on ecological mechanisms affecting coral recruitment on reefs." *Smithsonian Contributions to the Marine Sciences* (38): 437.

Ross, C, R Ritson-Williams, K Olsen, and VJ Paul. 2013. "Short-term and latent post-settlement effects associated with elevated temperature and oxidative stress on larvae from the coral Porites astreoides." *Coral Reefs* 32 (1): 71-79.

Sadovy, Y. 2005. "Trouble on the reef: the imperative for managing vulnerable and valuable fisheries." *Fish and Fisheries* 6 (3): 167-185. https://doi.org/10.1111/j.1467-2979.2005.00186.x. <Go to ISI>://WOS:000232248000002.

Salvat, Bernard. 1992. "Coral reefs — a challenging ecosystem for human societies." *Global Environmental Change* 2 (1): 12-18. https://doi.org/http://dx.doi.org/10.1016/0959-3780(92)90032-3.

Sammarco, Paul W, and Kevin B Strychar. 2013. "Responses to high seawater temperatures in zooxanthellate octocorals." *PloS one* 8 (2): e54989.

Schneider, Kenneth, and Jonathan Erez. 2006. "The effect of carbonate chemistry on calcification and photosynthesis in the hermatypic coral Acropora eurystoma." *Limnology and Oceanography* 51 (3): 1284-1293.

Schoepf, Verena, Michael Stat, James L Falter, and Malcolm T McCulloch. 2015. "Limits to the thermal tolerance of corals adapted to a highly fluctuating, naturally extreme temperature environment." *Scientific reports* 5: 17639.

Siegenthaler, Urs, Thomas F Stocker, Eric Monnin, Dieter Lüthi, Jakob Schwander, Bernhard Stauffer, Dominique Raynaud, Jean-Marc Barnola, Hubertus Fischer,

and Valérie Masson-Delmotte. 2005. "Stable carbon cycle–climate relationship during the late Pleistocene." *Science* 310 (5752): 1313-1317.

Smith, Stephen V, and RW Buddemeier. 1992. "Global change and coral reef ecosystems." *Annual Review of Ecology and Systematics* 23: 89-118.

Sneed, Jennifer M, Koty H Sharp, Kimberly B Ritchie, and Valerie J Paul. 2014. "The chemical cue tetrabromopyrrole from a biofilm bacterium induces settlement of multiple Caribbean corals." *Proceedings of the Royal Society of London B: Biological Sciences* 281 (1786): 20133086.

Solomon, Susan. 2007. *Climate change 2007-the physical science basis: Working group I contribution to the fourth assessment report of the IPCC*. Vol. 4. Cambridge University Press.

Stocker, TF, D Qin, GK Plattner, M Tignor, SK Allen, J Boschung, A Nauels, Y Xia, V Bex, and PM Midgley. 2013. IPCC, 2013: Climate Change 2013: The Physical Science Basis. Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change, 1535 pp. Cambridge Univ. Press, Cambridge, UK, and New York.

Suwa, Ryota, Masako Nakamura, Masaya Morita, Kazuaki Shimada, Akira Iguchi, Kazuhiko Sakai, and Atsushi Suzuki. 2010. "Effects of acidified seawater on early life stages of scleractinian corals (Genus Acropora)." *Fisheries Science* 76 (1): 93-99.

Szmant, AMt, and NJ Gassman. 1990. "The effects of prolonged "bleaching" on the tissue biomass and reproduction of the reef coral Montastrea annularis." *Coral reefs* 8 (4): 217-224.

Tebben, J, CA Motti, Nahshon Siboni, DM Tapiolas, AP Negri, PJ Schupp, Makoto Kitamura, Masayuki Hatta, Peter David Steinberg, and T Harder. 2015. "Chemical mediation of coral larval settlement by crustose coralline algae." *Scientific reports* 5: 10803.

Ward, Selina, P Harrison, and Ove Hoegh-Guldberg. 2002. "Coral bleaching reduces reproduction of scleractinian corals and increases susceptibility to future stress." Proceedings of the Ninth International Coral Reef Symposium, Bali, 23-27 October 2000.

Whittingham, Emma, Jock Campbell, and Philip Townsley. 2003. *Poverty and reefs*. IMM Limited.

Widdicombe, Stephen, and John I. Spicer. 2008. "Predicting the impact of ocean acidification on benthic biodiversity: What can animal physiology tell us?" *Journal of Experimental Marine Biology and Ecology* 366 (1): 187-197.

Wilkinson, Clive CR. 2004. *Status of coral reefs of the world: 2004*. Australian Institute of Marine Science (AIMS).

Woolsey, E. S., M. Byrne, and A. H. Baird. 2013. "The effects of temperature on embryonic development and larval survival in two scleractinian corals." *Marine Ecology Progress Series* 493: 179-184. https://doi.org/10.3354/meps10499.

Yates, KK, and RB Halley. 2006. "CO 2 3 concentration and pCO 2 thresholds for calcification and dissolution on the Molokai reef flat, Hawaii." *Biogeosciences Discussions* 3 (1): 123-154.

Appendix A. Summary of studies on the response of coral early life history stages to ocean warming (OW) and ocean acidification (OA).

Author	Year	Journal	Genus	Species	Spawn Type	Development Stage	Temperature (°C)	Atmospheric CO_2 (µatm)	Findings
Edmunds et al.	2001	Mar. Biol.	*Porites*	*astreoides*	Brood	Larval survivorship, motility, and development	26, 28, and 33	*	Highest temperature treatments increased mortality and metamorphosis. No treatment significantly impacted motility. Highest and lowest treatments reduced gross photosynthesis. Photosynthesis/respiration ratio decreased to <1 in highest treatment.
Bassim et al.	2002	Mar. Biol.	*Psuedo-diploria*	*strigosa*	Broadcast	Fertilization, development	30, 31, and 32	*	Fertilization was high for all treatments. Higher temperatures caused more larval abnormalities.
Nozawa and Harrison	2002	ICRS	*Platygyra*	*daedalea*	Broadcast	Settlement	27 and 29	*	Elevated treatment accelerated the acquisition of competency and larval attachment. However, time to maximum larval settlement-competency period was delayed.
Negri et al.	2007	Coral Reefs	*Acropora* *Favites* *Favites* *Mycedium*	*millepora* *abdita* *chinensis* *elephantotus*	Broadcast	Fertilization, development	25.5-34.1	*	All species had high fertilization and normal development at all temperatures until the 5th cell cleavage. *Acropora millepora* was the only species that had reduced fertilization and more deformities at higher temperatures.
Nozawa and Harrison	2007	Mar. Biol.	*Acropora* *Favites*	*solitaryensis* *chinensis*	Broadcast Broadcast	Settlement, post-settlement	20, 23, 26, and 29	*	Time to competency was shortened at higher temperatures for both species. *F. chinesis* displayed low post-settlement mortality across all treatment. Post-settlement mortality of *A. solitaryensis* was approximately 90% in the highest temperature treatment.
Putnam et al.	2008	Bio. Bulletin	*Stylophora*	*pistillata*	Brood	Settlement	23, 25, and 29	*	OW increased the number of larvae settling on CCA 7-fold, reflecting a temperature-mediated choice over plastic or limestone. Maximum quantum yield of PSII was 4% lower in larvae compared to parents.

*Not Tested

43

Appendix A. Continued

Author	Year	Journal	Genus	Species	Spawn Type	Development Stage	Temperature (°C)	Atmospheric CO_2 (µatm)	Findings
Rodriguez-Lanetty et al.	2009	Mol. Eco.	*Acropora*	*millepora*	Broadcast	Larval survivorship	24, 28, and 31	*	Expression of heat shock proteins increased while fluorescent protein expression decreased when subjected to OW. Heat stress may compromise coral immune defense in the larval stage. Oxidative stress genes may require the presence of algal symbiont reactive oxygen species.
Randall and Szmant	2009a	Coral Reefs	*Favia*	*fragum*	Brood	Survivorship, settlement	28, 29, and 31	*	Survivorship decreased 13% after 156 hrs at the highest temperature. Survivorship of settled larvae decreased by 27%.
Randall and Szmant	2009b	Bio. Bulletin	*Acropora*	*palmata*	Broadcast	Development, survivorship, settlement	27.5, 28, 30 and 31.5	*	Development accelerated causing abnormalities. The highest mortality occurred during gastrulation. Survivorship decreased 8-fold at higher temperatures. Settlement (%) decreased at higher temperatures.
Putnam et al.	2010	Invert. Biol.	*Pocillopora* *Seriatopora*	*damicornis* *hystrix*	Both Brood	Larval survivorship	21, 28 and 30	*	Larvae varied in size, *Symbiodinium* content, and quantum yield of photosystem II, suggesting that adults may produce broods of functionally variable larvae in order to combat unusual environmental conditions.
Edmunds et al.	2011	Exp. Biol	*Pocillopora* *Seriatopora* *Stylophora*	*damicornis* *hystrix* *pistillata*	Both Brood Brood	Larval release, larval survivorship	26.4-29.6	*	Peak larval release and the thermal threshold for respiration coincided. Respiration rates were highest at 28°C and decreased thereafter. More than half of the larvae studied were released between a narrow temperature range (27.5-28.9°C).
Ross et al.	2012	Coral Reefs	*Porites*	*astreoides*	Brood	Laval survivorship, settlement, and metamorphosis	27 and 30	*	Higher temperatures did not affect larval survivorship, settlement, or metamorphosis. Respiration or photochemical efficiency was not affected by high temperatures.

*Not Tested

Appendix A. Continued

Author	Year	Journal	Genus	Species	Spawn Type	Development Stage	Temperature (°C)	Atmospheric CO_2 (µatm)	Findings
Woolsey et al.	2013	MEPS	*Acropora* *Goniastrea*	*spathulata* *favulus*	Broadcast Broadcast	Development, larval survivorship	20, 22, 24, 26, and 28	*	Temperature treatments below ambient did not significantly affect larval survivorship. Larvae took significantly less time to become motile at higher temperatures. Each species displayed differences in survivorship suggesting *A. spathulata* larvae are more sensitive to OW than *G. favulus*.
Figueiredo et al.	2014	NCC	*Cyphastrea* *Acropora* *Favites*	*japonica* *millepora* *stylifera*	Broadcast Broadcast Broadcast	Development, larval survivorship, settlement	27, 29, and 31	*	Higher temperature accelerates development (shorter pre-competency time). Local retention and mortality increase with increasing temperature. Local retention time is also augmented for species with a longer time to competency and larger eggs.
Albright et al.	2008	Coral Reefs	*Porites*	*astreoides*	Brood	Settlement, post-settlement	*	380, 560, and 720	Settlement (%) was not affected by high OA treatments. However, mid and high OA treatments decreased post-settlement skeletal extension rate by approximately 50 ad 78%, respectively.
Albright et al.	2010	PNAS	*Acropora*	*palmata*	Broadcast	Fertilization, settlement and post-settlement growth	*	400, 560, and 800	All life stages were negatively impacted by increasing OA treatments. A reduction in sperm concentration further reduced fertilization success. Settlement declined more than 50% in high compared to low OA treatments. Linear extension during post-settlement growth decreased 39% in the mid-range and 50% in the high-range OA treatment.
Suwa et al.	2010	Fish. Science	*Acropora*	*spp.*	Broadcast	Survival, and post-settlement	*	400–475 905–1660 2115–3585	Survival was not affected by OA. Polyp growth and algal symbiont infection rates decreased in more acidic treatments.

*Not Tested

Author	Year	Journal	Genus	Species	Spawn Type	Development Stage	Temperature (°C)	Atmospheric CO_2 (µatm)	Findings
Nakamura et al.	2010	Fish. Science	*Acropora*	*digitifera*	Broadcast	Fertilization, development, metabolism, post-settlement	*	~34, ~119, and ~295	OA decreased fertilization via reducing sperm motility. Recruitment also declined as a result of a decline in successful embryological development. Post-settlement growth reduced through a loss of skeletal productivity.
Morita et al.	2010	Zygote	*Acropora*	*digitifera*	Broadcast	Fertilization	*	400–475 775–1005 930–1260 905–1660 2115–3585 12600–21100	Sperm motility was impaired by OA.
Albright and Langdon	2011	GCB	*Porites*	*astreoides*	Brood	Metabolism, settlement, post-settlement	*	380, 560, and 800	Larval metabolism suppressed by 27% and 63% in 560 and 800 µatm respectively compared to controls. Settlement was reduced by 42-45% and 55-60% in 560 and 800 µatm respectively relative to controls. Post-settlement reduced by 16 and 35% in 560 and 800 µatm respectively compared to controls.
Nakamura et al.	2011	PLoS One	*Acropora*	*digitifera*	Broadcast	Larval survivorship, metamorphosis	*	33.5, 118.8, and 295.0	Oxygen consumption was suppressed with increased OA (although not significantly). Metamorphosis significantly decreased in OA conditions in both short (2h) and long term exposure (7d).
Chua et al.	2013a	MEPS	*Acropora* *Acropora* *Acropora*	*tenuis* *hyacinthus* *millepora*	Broadcast	Embryonic development, survivorship, metamorphosis	*	380, 550, 750, and 1000	OA did not significantly affect any of these three early life history stages.
Yuan et al.	2018	Scientific Reports	*Acropora*	*gemmifera*	Broadcast	Settlement, post-settlement	*	389, 700, and 1214	OA decreased settlement (%). Size of recruits decreased as a result of slowed development.

*Not Tested

Appendix A. Continued

Author	Year	Journal	Genus	Species	Spawn Type	Development Stage	Temperature (°C)	Atmospheric CO_2 (μatm)	Findings
Anlauf et al.	2011	EMBE	*Porites*	*panamensis*	Brood	Settlement, post-settlement	28.4-29.9	487-546 and 861-1006	Settlement (%) was not affected by OW or OA. Growth reduced minimally when exposed to OA but significantly when exposed to OW and OA. OW reduced zooxanthellae densities while both OW and OA reduced polyp biomass.
Albright and Mason	2013	PLoS One	*Acropora*	*tenuis*	Broadcast	Fertilization	27 and 30	400 and 800	To obtain 50% of maximum fertilization, sperm concentrations increased 6-8 fold with addition of one factor (temperature or OA) and 50 fold with addition of both factors.
Chua et al.	2013b	MEPS	*Acropora* *Acropora*	*millepora* *tenuis*	Broadcast Broadcast	Fertilization, development, larval survivorship, metamorphosis	27 and 29	421-521 and 653-759	OA had no effect on early life stages alone, or in combination with OW. Elevated temperature increased rates of metamorphosis. However, OW had no consistent effect on the other early life stages.
Cumbo et al.	2013	EMBE	*Pocillopora*	*damicornis*	Brood	Larval survivorship	24 and 30.49	487.5 and 850.7	OW and OA did not affect protein content or *Symbiodinium* density. Respiration increased with elevated temperature (but not OA). Survival decreased in all treatments compared to ambient treatments.
Baria et al.	2015	Zoo. Science	*Fungia* *Lithophyllon*	*fungites* *repanda*	Broadcast Broadcast	Larval survivorship	28, 31, and 34	400-500, 1000-1300, 1700-2200	*L. repanda* survival decreased with increasing OW. However, *L. repanda* was not significantly affected by OA. Survivorship of *F. fungites* was not affected by OW or OA, and therefore displayed a higher percent mean survival. A >99% mortality rate was observed for *L. repanda* exposed to 34°C. Diameter of *F. fungites* was double that of *L. repanda*.

*Not Tested

Appendix A. Continued

Author	Year	Journal	Genus	Species	Spawn Type	Development Stage	Temperature (°C)	Atmospheric CO_2 (µatm)	Findings
Foster et al.	2015	Coral Reefs	*Acropora*	*spicifera*	Broadcast	Settlement, post-settlement	24 and 27	250 and 900	Settlement (%) was not affected by OW, high OA or the combination. Post-settlement survival was consistent among treatments. High OA treatments reduced skeletal development. Although not significantly, high temperatures somewhat mitigated the effect of high OA on calcification.

*Not Tested