Combined effects of water quality and temperature on the early life history stages of the broadcast spawning coral *Acropora tenuis*

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Statement of contributions of others

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Abstract

Coastal developments and increased agricultural activities are causing long-term changes to marine ecosystems at local scales through exposure to elevated levels of sediments and nutrients. At global scales, marine ecosystems are also experiencing warming seawater temperatures due to climate change. Coral reproduction is vulnerable to both declining water quality and warming temperatures, with simultaneous exposures likely to compound their negative impacts and further inhibit successful replenishment of coral populations. A quantitative evaluation of the effects of nutrient enrichment, suspended sediments and warming temperatures, and of interactions among these stressors, on the early life history stages of corals is crucial to understand how local (i.e. water quality) and global stressors (i.e., temperature) directly affect replenishment of coral populations. This research was conducted experimentally under controlled conditions, using *Acropora tenuis,* a common species in the Indo-Pacific and the Red Sea, as a model species. Results provide important evidence that processes during the early life of hard corals are directly and negatively affected by water quality declines, warming temperatures and their interactions, and that thresholds for stress are dependent on specific combinations of these stressors.

As single stressors, nutrient enrichment, suspended sediments and elevated temperatures are each known to reduce coral cover and biodiversity; but their combined effects on early life history processes are unknown. In **Chapter 2,** a series of experiments were conducted to test the individual and combined effects of nutrient enrichment (three levels: 0, 0.3 and 0.6 mg organic carbon l^{-1}) and elevated seawater temperature (up to five levels: 27, 29, 30, 31 and 32°C) on the early life history stages of *Acropora tenuis*. Gamete fertilization, larval survivorship and larval settlement were all significantly reduced as temperature increased, but only fertilization was further affected by simultaneous nutrient enrichment. Combinations of high temperatures and nutrient enrichment affected fertilization in an additive manner, whereas embryo abnormalities increased synergistically. Higher than normal temperatures (32 ℃) increased coral juvenile growth rates 1.6-fold, but mortality also increased by 50%. However, when the high temperatures co-occurred with nutrient enrichment, juvenile mortality declined from 50% to 36%, ameliorating temperature stress (antagonistic interaction). Overall, the types of effect

(additive vs synergistic or antagonistic) and their magnitude varied among life stages. Gamete and embryo stages were more affected by temperature stress and, in some cases, also by nutrient enrichment than the juvenile corals. Results suggest that coastal runoff events are likely to exacerbate the impacts of warming temperatures on fertilization if these events co-occur during corals spawning. The cumulative impacts of simultaneous exposure to nutrient enrichment and elevated temperatures over all early life history stages increases the likelihood for failure of larval supply and recruitment for this coral species.

Chapter 3 complemented Chapter 2, and contains data on how early life history processes (gamete fertilization, larval survival and larval settlement) of the coral *A. tenuis*, responded to environmentally-relevant levels of suspended sediments (up to five levels: 0, 5, 10, 30 and 100 mg l^{-1}), when tested both individually and in combination with either elevated nutrients (three levels: 0, 0.3 and 0.6 mg organic carbon l^{-1}) or temperatures (three levels: 27, 30 and 32°C). Results reveal that key early life processes differ greatly in their sensitivities to these pressures. Fertilization success was reduced by as much as 80% by sediments, and up to 24% by temperature, but the addition of nutrients had no further impact. Larval survivorship was unaffected by any of these treatments. However, the settlement success of larvae developing from treatment-exposed embryos was negatively affected by all three stressors: by 33% for nutrient enrichment, 14% for increased temperature and up to 55% for suspended sediments. When exposed to treatments only during later larval stages, larval settlement success was affected only by temperature, decreasing by 23% at 32°C. In combination, sediments and temperature had the greatest impacts, affecting more processes than the combined impacts of suspended sediments and nutrients. The combined effects of suspended sediments and nutrients, and of suspended sediments and temperature, on early life stages were additive, indicating that cumulative pressures aggravate negative impacts on coral recruitment in nearshore environments. Results suggest that management strategies to maintain suspended sediments at low concentrations in inshore areas during coral spawning events could ameliorate the impacts of thermal stress likely to be experienced with climate change.

Chapter 4 contains data on the effects of co-exposing juveniles of three coral species (*Acropora tenuis*, *Acropora millepora* and *Pocillopora acuta*), common on inshore Indo-Pacific and Red Sea reefs, to suspended sediments (four levels: 0, 10, 30 and 100 mg l^{-1}) and nutrient enrichment (two levels: 0 and 0.6 mg organic carbon l^{-1}) for

40 days. Effects of the treatments on survival, growth and physiology varied among species, indicating species-specific strategies to cope with stress. Suspended sediments reduced survival in *A. millepora* to 64% at 100 mg l^{-1} but did not affect survival in *A. tenuis* or *P. acuta*, instead reducing their growth rates to 73 and 60%, respectively, compared with rates under control conditions. Suspended sediments did not affect maximum quantum yields in any of the three species, but increased the effective quantum yield in *A. millepora* and *A. tenuis* by 30 and 40%, respectively; no effects were obtained for *P. acuta*. High levels of suspended sediments (100 mg l^{-1}) also enhanced respiration rates by 13 and 64%, evidence of an energy cost associated with exposure to suspended sediments. Nutrient enrichment up to a concentration of 0.6 mg organic carbon l^{-1} did not have any significant effect on any of the variables measured, suggesting resilience of juveniles to this stressor.

To improve understanding of the effects of early life history stages on coral population dynamics, a size-based model considering all life history stages (i.e. from gametes to adult colonies) was built for *Acropora tenuis* in **Chapter 5**. The model was constructed based on empirical published data of the demography of juveniles and adult coral colonies from inshore reefs of the Great Barrier Reef, together with the experimental information of early life history stages (gamete fertilization, larval survivorship and settlement success; Chapter 2 and 3) were used to construct the model. Impacts of contrasting water quality (i.e., nutrient enrichment and suspended sediments) and stress-inducing high temperatures were modelled during the period of coral spawning, to examine their potential effects on the annual population growth rates. This theoretical exercise provides new insight into the effects of local (i.e. water quality) and global (i.e. temperature) stressors during the development of early life history stages on coral population dynamics. Results highlight the importance of considering early life history stages in demographic analyses aimed at understanding how coral cover is likely to change when spawning events are affected by local and global stressors.

Collectively, this research provides important evidence that early life history stages and processes of hard corals are directly affected by water quality declines, warming temperatures and their interactions, and that clear threshold values exist for the effects of these combined stressors. The additive nature of simultaneous exposure to these stressors during gamete fertilization, larval development, larval settlement juvenile physiology and fitness underscore the need to improve water quality associated with river

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Chapter 1: General introduction

Coral reefs under stress: the effects of co-occurring water quality and thermal stressors

1.1. Stressors on coral reefs

Coral reefs are one of the most diverse, socioeconomically important, and threatened ecosystems in the world (Carpenter et al. 2008, Wilkinson 2008, Hoegh-Guldberg 2011), harboring thousands of species and providing food and livelihoods for millions of people, while also safeguarding coastal populations from storms and waves (Burke et al. 2011). Despite substantial national and international conservation efforts, coral cover has declined globally by ~19% in the last few decades (Wilkinson 2008), and between 60% to 75% of reefs are currently threatened by direct human pressures (Mora et al. 2016). Striking declines in coral cover have been attributed to a combination of environmental stressors, at both global scales from warming and acidifying oceans associated with climate change, and local scales due to widespread urban expansion, modification of coastal areas, exploitation of marine resources, colonization by invasive species, and degradation of habitats through fishing and runoff from agriculture and sewage outfalls (Bruno and Selig 2007). Such environmental changes cause deleterious responses at individual, population and community levels. The simultaneous co-occurrence of natural and anthropogenic stressors increases the urgency for better understanding of their effects on coral reef organisms, populations and communities.

During the last decade, interactions among multiple stressors and their resulting cumulative impacts have been identified as a research priority for marine ecosystems by a range of researchers (Darling et al. 2013, Brown et al. 2014, Clarke Murray et al. 2014, Rudd 2014, Cote et al. 2016), and also by management and regulatory bodies (Canada 2008, PICES 2012, Great Barrier Reef Marine Park Authority 2014, NOAA 2016). For coral reefs, simultaneous exposure to multiple stress factors is known to cause rapid, dramatic, and global-scale losses of coral cover (Hoegh-Guldberg et al. 2007b, Wilkinson 2008, De'ath and Fabricius 2010, De'ath et al. 2012, Pendleton et al. 2016), emphasizing

the urgent need to understand stressor interactions in order to implement effective management and restoration plans in coastal areas (Allan et al. 2013).

1.2. Interactive effects of multiple stressors: concepts and experimental approaches

Although a large number of studies have addressed the combined effects of multiple stressors on coral reefs, few studies have quantitatively examined interactions and clearly demonstrated the presence or absence of synergistic effects (but see Crain et al. 2008, Ban et al. 2014, Cote et al. 2016). Experimental difficulties associated with exposing reef organisms to several levels of more than one stress factor have been an impediment to the development of fully factorial experimental designs. Nonetheless, advances in diving and technical equipment, experimental aquarium techniques and infrastructure, and knowledge about the natural history of coral reef organisms now enables field and laboratory studies to effectively test the effects of multiple stressors with environmentally realistic treatment levels. However, in order to conclude whether responses are linear or non-linear, experimental designs testing the effects of multiple stressors need to have sufficient numbers of treatment levels (i.e., several levels for each stressor, with their respective controls and treatment combinations) and adequate replication, aspects of experimental design that are rarely accomplished.

One factor that has limited robust study of the effects of multiple stressors and their interactions is related to the interpretation of interactive effects (Folt et al. 1999, Crain et al. 2008, Uthicke et al. 2016). To interpret sizes and types of effects (additive, synergistic or antagonistic effects, multiplicative antagonisms or multiplicative synergisms), one needs to consider the statistical model used (i.e., comparative, additive or multiplicative), as the classification of effects differs among statistical models (Crain et al. 2008, Cote et al. 2016). Under a simple comparative model, the effect of multiple stressors typically approximates the effect of the dominant stressor (Fig. 1.1, Bruland et al. 1991). When the combined effect is greater or less than the effect of the single worst stressor, the interactions are either synergistic or antagonistic, respectively. Under an additive model, the effects of multiple stressors are classified as additive if there is no statistical interaction, and the combined effect of multiple stressors will be similar to the sum of the individual effects of all single stressors (Fig. 1.1). If the effects of stressors are found to be additive, then stressors are operating independently from each other. Alternatively, if

the effect of one stressor is affected by the presence or intensity of another stressor, i.e., the statistical interaction is significant, then the joint effect of stressors could be either be synergistic (greater than the sum of their individual effects) or antagonistic (less than expected for additivity, Hay et al. 1994). The preceding description summarize the most common scientific usage of the terms additive, synergism and antagonism and the most frequently used model. An important limitation of the additive model is that synergisms cannot be detected when the sum of the individual effects exceeds 100% (Pennings 1996). When responses are non-linear or have non-constant variance, and data transformation is necessary to approximate linearity or meet model assumptions, a multiplicative model is used. Under a multiplicative model, effects that are greater or less than the product of individual effects are designated as multiplicative synergisms or multiplicative antagonisms respectively. The multiplicative model is commonly applied in the field of ecotoxicology, where it is referred to as the Response Addition model of Independent Action (De Zwart and Posthuma 2005).

The vast majority of studies addressing the impacts of simultaneous stressors on coral reefs have used analysis of variance (ANOVA) to study the size and type of effects, and to detect interactions between stressors (Ban et al. 2014). In order to meet ANOVA assumptions, most studies apply transformations to the data, changing the type of model being tested (from additive to multiplicative). To avoid incorrect interpretations of results and erroneous conclusions, the model used needs to be carefully considered, because multiplicative relationships may become additive after transformation. Therefore the type of effect (additive, synergistic or antagonistic) needs to be defined according to the scale of the parameter used in the model and not at the scale measured (Uthicke et al. 2016). Transparent use of appropriate null models to study and classify the types of effects and interactions among stressors is needed, both to promote the development of knowledge in the area, and because of the importance of implications of the results for ecosystem management and conservation actions.

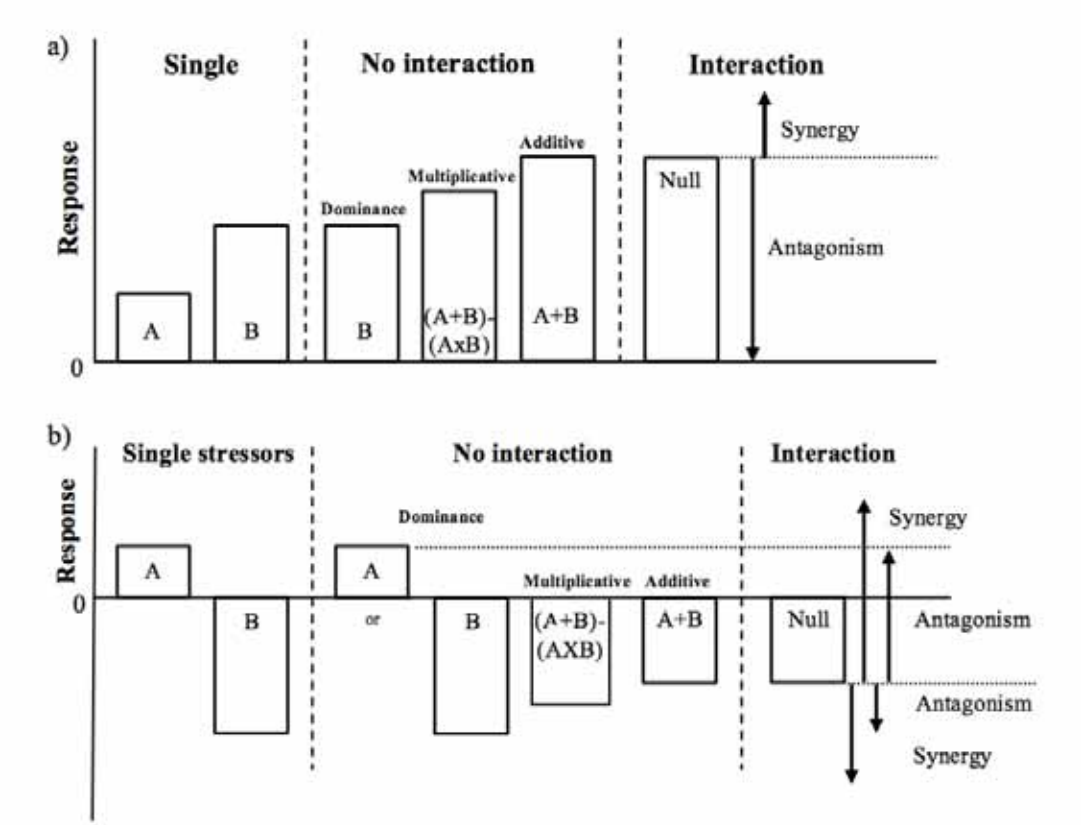

Figure 1.1: Schematic comparing statistical models that test for ecological synergies and other interactions among multiple stressors. a) Two stressors (A and B) impact a biological response in the same direction when acting separately. Under a comparative model, their combined effects could simply be equal to the effect of one of the stressors i.e., dominance effect, or be additive, i.e., the sum of the two stressor effects, with or without a multiplicative correction. Alternatively, stressors can interact either antagonistically or synergistically. Null models (additive expectation as the null model here) provide the threshold for distinguishing between these interactions. Interaction type becomes more difficult to interpret when the combined response is in the opposite direction to that of the individual stressors. b) Two stressors have opposing effects on a biological response (modified from Cote et al. 2016).

1.3. Interactions between stressors on coral reefs with special emphasis on the Great Barrier Reef

Determining if a stressor acts independently or interacts with another stressor is a complex task in marine ecosystems due to: i) the large number of stressors that potentially co-occur, especially on coral reefs (Table 1.1), ii) their spatial and temporal variability, and iii) the different responses that they can affect (from gene expression to biodiversity), each having different implications at physiological and ecological levels. Overall, general conclusions about the frequency and types of stressors and their interactions in nature are

difficult, more so considering that the addition of stressors can change their effects and type of interaction (Crain et al. 2008). Simple linear changes in perturbed ecosystems are rare, and it is likely that ecological responses under multiple stressors are different to physiological responses observed under single stressors. Similarly, it is also likely that the effects of single or several stressors vary among life stages of a single organism (Przeslawski et al. 2015), with different implications at individual and population levels.

Table 1.1: List of pressures relevant for the Great Barrier Reef. Only those threats identified in the GBR Outlook Report (Great Barrier Reef Marine Park Authority 2014) as "Very High" or "High" risk to the GBR Region's ecosystem are listed. Parentheses indicate causes considered to be secondary.

Stressor	**Local cause (L) vs. global cause (G)**
Ocean warming	G
Ocean acidification	G
Sea level rise	G
Cyclones/altered weather patterns	L (G)
Pesticide pollution	L (G)
Marine debris	L (G)
Nutrient runoff	L
Sediment runoff	L
Disposal of dredge material	L
Coastal habitat modification	L
Barriers to flow	L
Illegal fishing and poaching	L
Incidental catch of species of conservation concern	L
Discarded catch	L
Outbreak of Crown of Thorns Seastars	L
Outbreak of diseases	L (G)
Extraction of predators	L
Extraction from spawning aggregations	L

There is an extensive body of literature concerning the effects of single and multiple stressors on coral reefs (see references in Crain et al. 2008, Ban et al. 2014, Pendleton et al. 2016, Uthicke et al. 2016). Ban et al. (2014) conducted a meta-analysis of over 170 studies, finding that of these, 111 used statistical methods that allowed quantification of the types of interactive effects. Most studies (54%) described a synergistic effect, with additivity (30%) and antagonistic effects (15%) being less common. Uthicke et al. (2016) conducted a complementary meta-analysis on 77 fully factorial studies that focused on

interactions between global stressors (sea surface temperature increase and ocean acidification) and local stressors (pollution and sediments related to land runoff), including a wider range of tropical reef organisms. Antagonistic effects were only reported in 4% of studies, synergisms in 59%, and no effects or additivity were reported in 37% of the studies reviewed. The number of levels of each factor used in the majority of these studies was the minimum required for a fully factorial design (two levels of a global stressors, two of a local one), with a minimum replication effort (n = 3 per treatment combination). The review highlights the dearth of experiments on coral reef organisms that include levels of a factor that are sufficient (≥ 5) to describe full stress-response curves and reliably identify thresholds for combined factors. Additionally, the majority of studies of multiple stressors in corals have been done on adult stages or by exposing only one life history stage (either larvae, recruits, juveniles, or adults) or process (e.g., gametogenesis, gamete fertilization, survivorship, growth or physiology of any of these stages) to the stressor in question.

On the GBR, accumulating acute and chronic stressors have both local and global causes (Table 1.1). On inshore reefs, water quality is considered a key stressor at local scales, reducing coral cover and ecosystem resilience (Fabricius and De'ath 2004). At a global scale, stressors are the result of increased emission of greenhouse gases through fossil fuel burning, leading to ocean warming and acidification (Hoegh-Guldberg 2011). The GBR Outlook Report 2014 acknowledges that climate change is likely to represent the greatest global stressor to this ecosystem (Great Barrier Reef Marine Park Authority 2014). Local and regional stressors are related to land use and modifications to catchments and coastal areas, urban development, and the use of marine resources and services (Table 1.1). Since 1998, nine severe cyclones (category 3 or above) have impacted the GBR (Great Barrier Reef Marine Park Authority 2014), and three severe bleaching events have occurred (Berkelmans et al. 2004, Normile 2016). If the trend of the past few decades continues, coral reefs of the GBR will be increasingly exposed to local and global stressors, requiring innovative management strategies that need to be based on assessments of cumulative stressors in order to mitigate the effects of anthropogenic activities in the face of climate change.

1.4. Coral early life history stages and processes and their susceptibility to stressors

Scleractinian corals vary in their breeding system; they can either broadcast spawn gametes for external fertilization or brood internally fertilized eggs. Around 63% of scleractinian corals are broadcast-spawners (Fig. 1.2), simultaneously releasing gametes (buoyant eggs and sperm) into the water column (Guest et al. 2008, Baird et al. 2009), with subsequent planktonic embryo and larval development. After gamete fertilization, cell cleavage takes place by progressive furrow formation and the embryos of most species undergo a relatively unordered, irregular division cycle (Ball et al. 2002). Thirty-six hours after fertilization, embryos of the genus *Acropora* become roughly spherical in shape, and epidermal cilia begin to beat synchronously, imparting mobility to the larvae. In brooding species, embryo development is internal (within the polyp) and developed larvae are later released into the water column. Once larvae from brooders and broadcasting species have developed, they become progressively elongated and begin searching for suitable settlement substrata. Once attached, larvae undergo metamorphosis to form the primary polyp, which subsequently divides to found a colony.

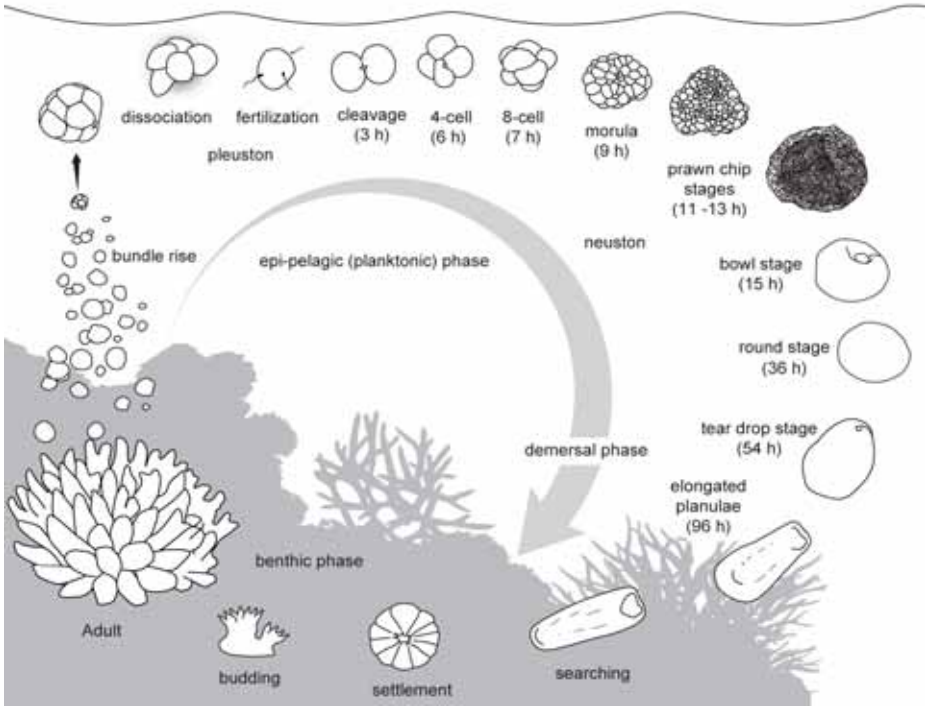

Figure 1. 1: Schematic representation of the reproductive cycle of a broadcast spawning species of *Acropora* (from Jones et al. 2015b).

The early life-history stages of corals are susceptible to a range of water quality and climate pressures (Hoegh-Guldberg et al. 2007a, Jones et al. 2015b), which is concerning, as reproduction and recruitment underpin the maintenance and resilience of reef communities (Harrison et al. 1984, Richmond 1997, Hughes et al. 2000). Spawning of the majority of species takes place in early summer (from October to December on the GBR, Babcock et al. 1986), which may coincide with sediment and nutrient discharges driven by major river flood events during the summer monsoonal wet season (from October to April in North Queensland; Devlin et al. 2001). Heat stress and floods can therefore co-occur and overlap with broadcast spawning, placing the sensitive early life history stages of hard corals (gametes, embryos, larvae and recruits) at risk. Despite the perception that early life history stages of corals are more sensitive to environmental change and pollution than adult stages (Fabricius 2005), few studies have empirically addressed their susceptibility to individual and co-occurring pressures (but see Harrison and Ward 2001, Bassim and Sammarco 2003, Humphrey et al. 2008, Negri and Hoogenboom 2011, Miin Chua et al. 2013). Moreover, the effects of stressors on early life history stages will vary with their duration, intensity and the number of stressors co-occurring simultaneously. The exposure of successive early life history processes to multiple stressors might enhance their detrimental impacts due to carry-on effects from one stage to the next, an aspect that has not been studied in hard corals.

1.6. Research aims and objectives

The overarching aim of this study was to experimentally investigate the individual and combined effects of multiple stressors on the early life history stages of hard corals (Fig. 1.2). Information obtained from this study will provide new management-relevant insights into the susceptibility of early life history stages of corals, which are key to the distribution and abundance of coral cover and the long-term persistence of coral reefs (Hughes *et al.* 1999, Kuo & Soong 2010).

Acropora tenuis (Dana, 1846) was chosen as the model species because it is an abundant broadcast spawning species on inshore, mid-shelf and outer-shelf reefs of the GBR and other reefs and throughout the Indo-Pacific. Both its mobile (i.e., gametes, embryos and larvae) and sessile (i.e., recruits, juveniles and adults) life stages have the potential to be exposed to changes in water quality and warming temperatures simultaneously. *A. tenuis* is commonly used as a model species in studies of early life

histories, since protocols for gamete separation, gamete fertilization, larvae rearing and settlement are well-established in the literature and result in successful performance under laboratory conditions (Negri and Heyward 2000). The following chapters present the findings of a series of experiments conducted from 2014-2016 using combinations of two stressors at realistic environmental levels (i.e. pairwise combinations of nutrient enrichment, suspended sediments and temperature) in fully crossed designs. Results are written as stand-alone chapters based on prepared, submitted or published manuscripts. A significant characteristic that separates this study from previous works is the methods employed to prepare the nutrient enrichment and suspended sediment treatments, which preserved the stoichiometric composition of nutrients and trace elements in seawater and sediments surrounding river-exposed inshore reefs, exposing early life history stages to realistic levels of organic and inorganic nutrients and suspended sediment concentrations.

Accordingly, in **Chapter 2,** I determine the individual and combined effects of nutrient enrichment and temperature on early life history processes of *A. tenuis* (i.e., on gamete fertilization, embryo development, larval survivorship, larval settlement and juvenile survivorship, growth and photophysiology). The effects of exposing only one stage to stressors versus consecutive exposure of several stages were compared, and their cumulative effects on the survivorship of juveniles in a coral population were explored.

In **Chapter 3,** I investigate the effects of suspended sediments as a single stressor or when combined with either nutrient enrichment or temperature on early life history processes of *A. tenuis* (i.e., gamete fertilization, embryo development, larval survivorship and larval settlement). This chapter provided insights into which of the combinations of stressors (i.e., suspended sediments with nutrient enrichment, or suspended sediments with elevated temperature) has the greatest effect on the reproductive success of this species. Additionally, threshold levels of stressors were identified in order to provide guidelines to management authorities of inshore areas that are exposed to environmental threats.

In **Chapter 4**, I examine individual and combined effects of suspended sediments and nutrient enrichment on the fitness and physiology of juveniles of the species *Acropora tenuis*, *A. millepora* and *Pocillopora acuta*. Understanding the impacts of nutrient-enriched sediments on the early survivorship, growth rates and physiology of juveniles during their first months of life will help to predict the susceptibility of coral

juveniles to projected environmental changes in coastal areas and their implications for coral cover.

Finally, **Chapter 5** represents a theoretical exercise to explore the implications of disturbance events on early life history stages or processes, by assessing the impact of water quality declines and warming temperatures on hard coral populations of inshore reefs. By combining data available in the literature and from Chapters 2 and 3, and applying these to a size-structured population model, this study predicts how changes in nutrient enrichment, suspended sediments and warming temperature can affect coral population dynamics.

Chapter 2: Cumulative effects of nutrient enrichment and elevated temperature compromise the early life history stages of the coral *Acropora tenuis*

This chapter is published as:

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2.1. Introduction

Coral reefs around the world are facing increasing pressures from coastal human activities and climate change (Hoegh-Guldberg 2011), with warming sea surface temperatures (SST) and nutrient enrichment among their most harmful stressors (Halpern et al. 2008). The simultaneous and cumulative effects of elevated SST and nutrient enrichment on demographic processes may lead to significant declines in coral cover (Hoegh-Guldberg and Bruno 2010). This highlights the importance of studying their joint effects, particularly on the sensitive early life history stages that maintain and replenish coral populations, including gamete fertilization, larval supply, settlement and juvenile survivorship (Ritson-Williams et al. 2010).

Since the beginning of the 20th century SST has risen by a global average of ~1°C (Brohan et al. 2006) and it is projected to increase by a further 2 to 3°C by the end of the century under a moderate Representative Concentration Scenario of the Intergovernmental Panel on Climate Change (IPCC RCP 4.5 scenario, Meissner et al. 2012). Such increases in SST alone would endanger many coral species, which typically live close to their upper thermal tolerance limit (Berkelmans and Willis 1999). Additionally, coral reefs are increasingly exposed to elevated nutrients associated with terrestrial runoff from expanding agriculture and associated fertilizers and the loss of top soils (Devlin and Brodie 2005). Increases in the concentrations of nutrients (organic and inorganic) in a water body, which can enhance the algal production, turbidity,

sedimentation of particulate matter and in severe cases can deplete oxygen concentrations is known as eutrophication (Lincoln et al. 1998, GESAMP 2001). River runoff, resulting in the eutrophication of nearshore tropical marine habitats has been reported to cause: reductions in coral biodiversity (De'ath and Fabricius 2010), increases in macroalgae cover (Fabricius 2005), proliferation of macro-bioeroding organisms (i.e., sponges, molluscs, polychaetes and sipunculans) that weaken the structural integrity of coral reefs (Le Grand and Fabricius 2011), increases in the frequency and severity of coral diseases (Bruno et al. 2003), and changes in the composition of biofilms that provide conditioned surfaces for larval settlement and metamorphosis of many sessile organisms (Wieczorek and Todd 1998, Webster et al. 2004, Sawall et al. 2012).

Since European settlement in 1850, the development of Australia's North Queensland catchments adjacent to the Great Barrier Reef (GBR) has led to significant changes in the quality and quantity of water discharges into the GBR lagoon (McCulloch et al. 2003, Kroon et al. 2012). Expansion of agricultural and grazing activities, the clearing of vegetation leading to widespread soil erosion, and the application of fertilizers has increased river discharges of dissolved and particulate organic and inorganic nutrients and trace elements in the region (Furnas 2003, Devlin and Brodie 2005, Brodie et al. 2010, Kroon et al. 2012). Inorganic nutrients from anthropogenic sources generally only persist in the GBR lagoon for periods of days to weeks (Brodie et al. 2010), as they are rapidly taken up by microbial and planktonic communities. They are then transformed into organic matter and undergo complex cycling between particulate and dissolved forms, organic and inorganic forms, and undergo repeated deposition-resuspension cycling (Grossart and Ploug 2001, Angly et al. 2016). Recent studies estimate that nutrient loads of rivers discharging into the GBR lagoon have increased by a factor of 5.7 for nitrogen and 8.9 for phosphorus since European settlement (Kroon et al. 2012), leading to significant organic enrichment in inshore waters (Weber et al. 2012). For the foreseeable future, coastal marine ecosystems are likely to face further increases in eutrophication (inorganic and organic enrichment) as a consequence of nutrient inputs from river runoff (Smith and Schindler 2009), as well as increases in SST due to climate change (Meissner et al. 2012).

Several studies on tropical coral species of the Caribbean and the Indo-Pacific have demonstrated detrimental impacts of nutrient enrichment (Fabricius 2005, Vega Thurber et al. 2014, Lam et al. 2015) or elevated seawater temperatures (Michalek-

Wagner and Willis 2001, Edmunds 2004, Edmunds 2005, Randall and Szmant 2009, Heyward and Negri 2010) on coral reproduction, growth, health and survivorship. Moreover, eutrophication renders adult corals more susceptible to thermal bleaching, as nutrient enrichment enhances the abundance of algal symbionts (Marubini and Davies 1996), increasing the ratio of symbiont to host cells, which can increase the vulnerability of this symbiotic partnership to disruption associated with high sea temperatures (Cunning and Baker 2012, Wiedenmann et al. 2012, Vega Thurber et al. 2014). While evidence is mounting that interactions between elevated SST and nutrient enrichment might have important deleterious effects at the population level (Crain et al. 2008, Fabricius et al. 2013a, Ban et al. 2014), no studies have investigated the combined effects of these stressors on the early life history stages and processes of corals (from gamete fertilization to coral juveniles).

An improved understanding of how present and future combinations of stressors are likely to affect early life history stages of hard corals is needed to adequately assess and develop management policies for coral reef ecosystems (Mumby 2009). Here I describe a series of experiments that tested the effects of elevated temperature and nutrient enrichment (mimicking eutrophication) on the fertilization success of coral gametes, development and settlement of coral larvae, and the growth, photophysiology and survivorship of 4-month-old coral juveniles. The study was conducted with the common inshore coral species *Acropora tenuis*, and aimed to: 1) understand the combined effects of elevated temperature and nutrient enrichment when they co-occur; 2) identify the most sensitive early life history stages to elevated temperatures and nutrient enrichment, and 3) provide a minimum estimate of their combined effects on population replenishment.

2.2. Materials and methods

2.2.1. Obtaining coral gametes and juveniles

Gravid colonies (> 20 cm diameter) of the broadcast spawning coral *Acropora tenuis* (Dana, 1846), an abundant species on shallow inshore coral reefs of the GBR, were collected from Magnetic Island (19° 06'S, 146° 51'E) at ~6 m depth on the 5th of November 2014 under the permit G12/35236.1 issued by the Great Barrier Reef Marine Park Authority. Colonies were transferred to outdoor flow-through temperature-

controlled aquaria at the National Sea Simulator at the Australian Institute of Marine Science (AIMS), where seawater temperatures were set to ambient reef temperatures on the day of collection (27ºC). Following spawning 5 days after full moon (at ~19:30), egg-sperm bundles from 6 colonies were gently scooped from the surface of the water, and eggs were separated from sperm using a 100 µm mesh filter and gently washed five times in 0.2 µm filtered sea water (FSW), as described in Negri and Heyward (2000). Concentrated sperm water was diluted to achieve a working stock mixture of ~1 x 10^7 sperm ml^{-1} to optimise fertilization success (Willis et al. 1997). A subsample of gametes was used for the fertilization experiment (Experiment 2.1), and the remaining gametes were mixed and fertilized (Negri and Heyward 2000). Bulk larval cultures were reared for the larval settlement and juvenile experiments (2.2 and 2.3) in 500 l flow-through tanks using 1 µm-filtered seawater at 27°C.

2.2.2. Experimental setups

Three experiments were conducted to investigate the combined effects of nutrient enrichment (organic and inorganic nutrient enrichment) and elevated seawater temperatures on early life history stages and processes (from gamete fertilization to 4-month-old juveniles) of *A. tenuis*. Experiments were designed to mimic the impact of nutrient enrichment as a consequence of river plumes and terrestrial runoff events, which wash nutrients and trace elements onto inshore reefs, where they are taken up by plankton communities and converted into organic matter. Experimental concentrations of nutrients were chosen to lie within the range of those measured on inshore GBR reefs (Kroon et al. 2012, Schaffelke et al. 2012, Waters et al. 2014). Temperature treatments corresponded to increases of +2 to +5°C above ambient temperatures recorded during coral spawning periods on reefs of the GBR (Keith et al. 2016). Experiments were conducted to test the effects of nutrient enrichment (three levels) together with temperature (up to five levels) on: 1) gamete fertilization, embryo development and larval settlement (Experiment 2.1, Fig. 2.1), 2) settlement of 5-day-old larvae when no preceding stages were exposed to treatment conditions (Experiment 2.2, Fig. 2.1) and 3) the photophysiology, growth, and survivorship of 4-month-old coral juveniles when no preceding stages were exposed to treatment conditions (Experiment 2.3, Fig. 2.1). The small size of recently settled coral recruits (~1 mm) makes it difficult to measure physiological variables, and they were therefore allowed to grow for four months before commencing this experiment.

2.2.3. Preparation of nutrient enrichment and temperature treatments

For Experiments 2.1 and 2.2, nutrient enrichment treatments were prepared by adding inorganic and organic nutrients derived from inshore organic matter and plankton to FSW. Inshore nutrients were collected with a plankton net (mesh size 100 µm) over the reefs of Orpheus Island (18° 36'S, 146° 29'E). On the inshore of the GBR, suspended particulate matter mostly consists of decayed detritus resuspended from the seafloor, and zooplankton (Fabricius et al. 2014). The bulk material caught with the net was sieved to remove large fragments (> 26 µm), homogenized with a blender and frozen until use. Two replicate glass Schott bottles (each 2 l) were used to incubate the nutrient enriched seawater for each treatment for 48 h at 200-µmol photons m^{-2} s^{-1} light intensity (12 h:12 h diurnal cycle) at the target temperatures (27, 29, 30, 31 and 32°C, S2.1 Table). Incubations were conducted to allow the microbial communities to take up the bioavailable fraction of the inorganic nutrients and transform it into organic nutrients (Arrigo 2005), a process that is accelerated as temperatures increase (Nogales et al. 2011). Previous studies have successfully applied this method for studying the effects of nutrient enrichment on corals (Fabricius et al. 2003b, Weber et al. 2012), with incubations of 48 h being required for the microbial community to develop (McCarren et al. 2010, Fabricius 2011, Bryson et al. 2016). Nutrient enrichment treatments were performed using decaying natural plankton in order to maintain a realistic stoichiometric composition of nutrients and trace elements. Based on the total organic carbon (OC) present in the collected nutrient mixture, three nutrient enrichment treatments were prepared by adding the required volume of the mixture to FSW, at a nominal concentration of +0, +0.3, or +0.6 mg OC l^{-1} FSW. Such organic carbon enrichment levels are environmentally relevant for river-influenced inshore reefs in the GBR (Schaffelke et al. 2012, Table 2.1).

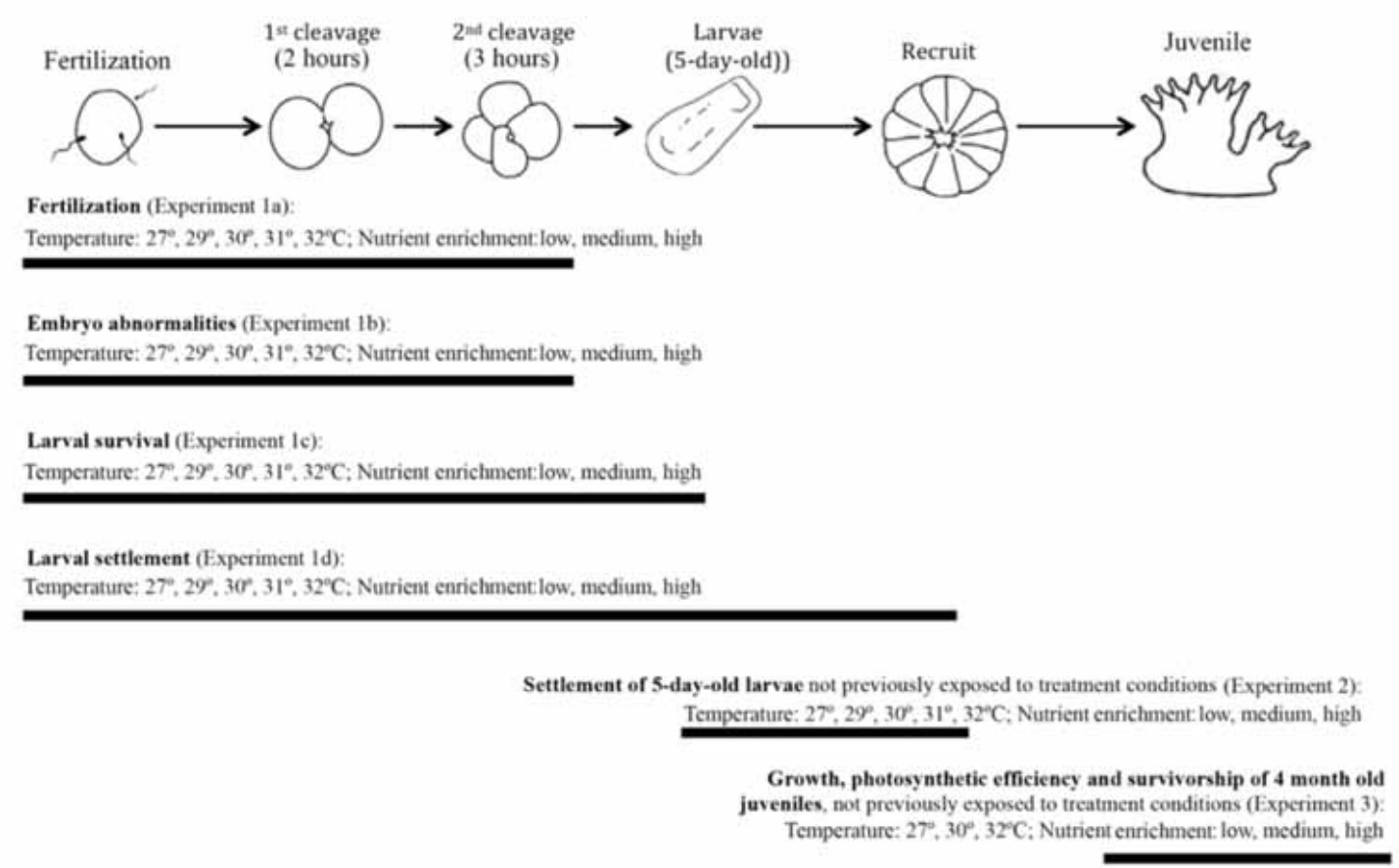


Figure 2.1: Experiments performed with early life history stages of *Acropora tenuis* exposed to different treatments of temperature and nutrient enrichment. Black bars indicate the stages involved in each experiment.

In Experiment 2.3, nutrient enriched treatments were prepared and incubated in 4 l polyethylene tanks with gentle aeration. Tanks were placed in temperature-controlled water baths (six tanks per water bath, at temperatures: 27, 30 and 32°C, S2.1 Table) and illuminated as in Experiment 2.2. Coral juveniles were kept in 18 gently aerated experimental tanks (4 l) in water baths (at temperatures: 27, 30 and 32°C), but under 60 μmol photons m^{-2} s^{-1} light. Seawater in the experimental tanks was replaced every two days with seawater that had been enriched with nutrients and incubated over the previous 48 h.

To characterize water quality of the different nutrient enrichment treatments, concentrations of total organic carbon, dissolved organic carbon, particulate organic carbon, total dissolved phosphorus, dissolved organic nitrogen, total particulate nitrogen, ammonium, phosphate, nitrate, and nitrite, were measured at the end of the incubation in duplicate subsamples from all Schott Bottle replicates in Experiments 2.1 and 2.2, and on a weekly basis after incubation in all replicates in Experiment 2.3. In this way, water quality parameters of the different treatments were always measured after the incubations, at the start of each experiment. Water quality samples were taken following standard protocols as described in detail in Schaffelke et al. (2012) and analysed by the Analytical Services laboratory at AIMS.

The addition of nutrients to FSW increased the concentrations of all water quality variables measured in each of the three Experiments (Table 2.1). Nutrient concentrations varied after the incubation between experiments, therefore nutrient enrichment treatments were designated as 'low', 'medium' and 'high' nutrient enrichment, corresponding to the addition of +0, +0.3, and +0.6 mg OC l^{-1} FSW. In all experiments the treatment with 'low' nutrient enrichment and at temperature = 27°C was considered as the control.

2.2.4. Elevated temperature and nutrient enrichment effects on gamete fertilization, embryo development and larval settlement (Experiment 2.1)

Fertilization experiments (Experiment 2.1a, Fig. 2.1, Table 2.2) were conducted in six-well polystyrene tissue culture plates (NuncTM, Denmark), with each treatment having six replicate wells. A total of 15 treatments were established, with three levels of nutrient enrichment (+0, +0.3, +0.6 mg OC l^{-1} FSW) and five levels of temperature (27, 29, 30, 31 and 32°C). Plates were maintained in temperature incubators (S2.1 Table) 60 min before the start of each experiment and throughout the duration of the experiment.

Experiment	Temperature	Nutrients	DOC (µM)	TOC (µM)	NH_4 (µM)	NO_2+NO_3 (µM)	NO_2 (µM)	TDN (µM)	TN (µM)	PO_4 (µM)	TDP (µM)	O_2 (mgl^{-1})
Schaffelke et al 2012 (Schaffelke et al. 2012)			42.8-195.7	3.9-70.5	0-0.8	NA	NA	2.3-11.5	0.5-2.8	0.02-0.6	0-1.01	
1a, b	27	Low	84.1±0.1	8.5±3.6	0.5±0.1	0.5±0.1	0.2±0.1	8.8±0.5	0.9±0.1	0.1±0.1	0.2±0.1	8.0±0.2
		Medium	92.5±4.0	8.7±1.8	4.4±0.1	1.3±0.1	0.8±0.1	15.7±1.6	1.2±0.1	0.4±0.1	0.5±0.1	7.8±0.1
		High	99.2±4.8	8.7±3.4	8.9±0.1	1.4±0.1	0.8±0.1	23.0±0.1	1.5±0.1	0.7±0.1	0.7±0.1	7.7±0.1
	29	Low	86.3±2.6	5.0±3.4	0.8±0.4	0.7±0.1	0.2±0.1	9.3±0.2	0.8±0.3	0.1±0.1	0.2±0.1	7.9±0.1
		Medium	91.2±0.2	7.7±2.7	4.4±0.1	1.3±0.1	0.7±0.1	15.9±0.8	1.5±0.3	0.4±0.1	0.5±0.1	7.6±0.1
		High	92.9±5.3	9.6±6.1	9.2±0.1	1.4±0.1	0.8±0.1	22.4±1.6	1.8±0.4	0.6±0.1	0.7±0.1	7.8±0.3
	30	Low	91.5±0.1	2.3±1.2	0.7±0.1	0.8±0.1	0.2±0.1	10.2±0.6	0.8±0.1	0.1±0.1	0.3±0.1	7.8±0.1
		Medium	92.5±1.6	5.3±1.2	4.6±0.1	1.2±0.1	0.5±0.1	15.4±0.7	1.5±0.3	0.4±0.1	0.6±0.1	7.7±0.1
		High	89.1±6.3	8.0±1.7	9.4±0.1	1±0.1	0.4±0.1	22.0±1.3	1.6±0.4	0.7±0.1	0.8±0.1	7.6±0.1
	31	Low	84.8±3.5	3.9±2.4	0.7±0.1	0.6±0.1	0.1±0.1	9.8±1.0	0.9±0.5	0.1±0.1	0.3±0.1	7.6±0.1
		Medium	90.0±3.2	5.2±1.3	4.7±0.2	1±0.1	0.4±0.1	15.7±0.6	1.3±0.3	0.4±0.1	0.5±0.1	7.7±0.1
		High	93.8±6.8	8.3±2.8	9.6±0.3	1.1±0.1	0.4±0.1	21.9±0.5	1.9±0.5	0.7±0.1	0.9±0.1	7.6±0.1
	32	Low	90.7±2.5	4.3±3.1	0.7±0.1	0.8±0.1	0.1±0.1	10±0	1.1±1.1	0.2±0.1	0.3±0.1	7.7±0.1
		Medium	90.8±2.9	5.0±0.2	4.6±0.3	1.1±0.1	0.4±0.1	14.9±0.3	1.4±0.1	0.4±0.1	0.5±0.1	7.6±0.1
		High	95.7±1.8	8.2±2.7	9.7±0.2	1.0±0.1	0.3±0.1	22.2±1.0	1.7±0.4	0.5±0.1	0.9±0.1	7.5±0.1
1c, d, 2	27	Low	76.8±2.8	8.3±2.0	0.8±0.1	0.6±0.1	0.3±0.1	10.7±0.9	1.7±0.1	0.1±0.1	0.3±0.1	8.2±0.1
		Medium	85.9±2.4	19.7±3.5	4.5±0.2	0.6±0.1	0.3±0.1	16±0.5	5.0±0.7	0.3±0.1	0.5±0.1	7.7±0.1
		High	87.5±7.6	23.2±1.3	6.1±0.3	0.6±0.1	0.3±0.1	18.2±1.3	6.2±0.4	0.4±0.1	0.6±0.1	7.6±0.1
	29	Low	102.9±25.4	6.8±0.6	0.8±0.1	0.6±0.1	0.3±0.1	11.7±0.7	1.6±0.3	0.2±0.1	0.4±0.1	7.9±0.1
		Medium	111.9±32.7	25.7±1.7	5.0±0.1	0.6±0.1	0.3±0.1	17.2±0.3	4.3±0.1	0.3±0.1	0.5±0.2	7.7±0.1
		High	120.2±39.8	34.8±6.0	7.5±0.1	0.7±0.1	0.4±0.1	20.2±0.6	6.3±0.5	0.5±0.1	0.6±0.1	7.6±0.1
	30	Low	82.9±0.2	11.3±0.9	0.9±0.1	0.6±0.1	0.3±0.1	11.4±0	1.7±0.1	0.2±0.1	0.4±0.1	7.7±0.1
		Medium	83.1±4.1	21.3±6.4	4.8±0.3	0.6±0.1	0.2±0.1	16.4±1.9	5.4±1.5	0.4±0.1	0.5±0.1	7.6±0.1
		High	87.6±3.8	21.6±3.5	7.9±0.2	0.6±0.1	0.3±0.1	20.0±0.5	5.3±1.2	0.5±0.1	0.7±0.1	7.5±0.1
	31	Low	82.3±2.9	7.2±1.6	0.7±0.0	0.6±0.1	0.1±0.1	9.8±1.0	0.9±0.1	0.1±0.1	0.3±0.1	7.7±0.1
		Medium	86.4±5.9	17.9±1.7	5.1±0.1	0.5±0.1	0.2±0.1	16.8±0.3	3.8±0.3	0.4±0.1	0.4±0.1	7.7±0.1
		High	87.4±5.4	25.6±1.2	8.1±0.8	0.6±0.1	0.3±0.1	21.1±0.2	5.7±0	0.6±0.1	0.8±0.1	7.6±0.1
	32	Low	101.9±16.2	7.7±NA	0.9±0.1	0.6±0.1	0.3±0.1	11.0±0.3	1±NA	0.2±0.1	0.2±0.1	7.6±0.1
		Medium	102.7±23.3	20.3±2.2	5.0±0.0	0.6±0.1	0.2±0.1	16.6±0.1	3.9±0.1	0.4±0.1	0.5±0.1	7.6±0.1
		High	154.9±95.6	27.2±NA	8.7±0.8	0.6±0.1	0.3±0.1	22.5±2.2	6.3±NA	0.6±0.1	0.7±0.1	7.5±0.1
3	27	Low	152.1±25.5	45.2±28.5	4.3±9.3	0.2±0.1	0.1±0.1	32.1±39.2	7.1±4.3	0.1±0.1	0.2±0.1	8.0±0.2
		Medium	167.2±68.3	64.7±34.0	7.3±10.4	0.2±0.1	0.1±0.1	35.9±24.7	11.6±7.3	0.3±0.4	0.5±0.6	7.8±0.1
		High	173.9±36.6	74.6±51.8	15±23.3	0.3±0.4	0.1±0.1	44.8±41.8	14.5±12	0.7±0.9	0.9±1.1	7.6±0.2
	30	Low	160.3±50.1	35.7±30.5	0.6±0.4	0.1±0.1	0.1±0.1	14.5±2.8	5.6±3.5	0.1±0.1	0.2±0.1	7.7±0.1
		Medium	161.5±23.2	42.7±32.4	0.9±0.8	0.1±0.1	0.1±0.1	18.4±8.1	7.0±5.4	0.1±0.1	0.2±0.1	7.7±0.1
		High	187.3±31.8	50.8±23.5	1.2±1.6	0.1±0.1	0.1±0.1	39.5±38.8	7.6±3.3	0.1±0.1	0.2±0.1	7.6±0.1
	32	Low	159.3±37.7	44.5±24.0	1.7±2.1	0.1±0.1	0.1±0.1	22.5±8.8	8.0±4.0	0.1±0.1	0.2±0.1	7.6±0.1
		Medium	171±31.7	53±35.2	5.3±9.1	0.1±0.1	0.1±0.1	56.1±37.3	9.4±7.8	0.1±0.1	0.2±0.1	7.7±0.3
		High	178.3±39.4	63±37.4	6.4±7.8	0.2±0.1	0.1±0.1	80±76.4	10.3±8	0.1±0.1	0.3±0.1	7.6±0.1

Table 2.1: Water quality parameters for the different temperatures (°C) and nutrient enrichment treatments (low in white, medium in light grey and high in dark grey) at the start of each experiment. Values shown are means and standard deviations. Number of replicates: 2 per water quality factor and treatment for Experiments 2.1 and 2.2, 18 per treatment for Experiment 2.3 at 27°C, and 6 per treatment for Experiment 2.3 at 30 and 32°C temperature. Ranges from seawater values from the inshore of the Great Barrier Reef are added for comparison (Schaffelke et al. 2012).

Experiment	Nutrient enrichment	Temperature (°C)	Treatment volume (ml)	Replicates	Exposure time	Stage exposed	Number of individuals per replicate	Variable measured
1a	Low, medium, high	27, 29, 30, 31, 32	12	6	2.5 hours	Gametes	~170 eggs	% Fertilization
1b	Low, medium, high	27, 29, 30, 31, 32	12	6	2.5 hours	Gametes		% Abnormalities
1c	Low, medium, high	27, 29, 30, 31, 32	40	6	5 days	Larvae	20 larvae	% Larvae survivorship
1d	Low, medium, high	27, 29, 30, 31, 32	10	6	6 days	Larvae	10 larvae	% Larvae settlement
2	Low, medium, high	27, 29, 30, 31, 32	10	12	1 day	Larvae	10 larvae	% Larvae settlement
3	Low, medium, high	27, 30, 32	4000	2	59 days	Juveniles	19 juveniles	Growth, production of new polyps, final weight F_v/F_m, survivorship

Table 2.2: Experimental conditions used in each experiment performed at different temperatures and nutrient enrichment levels.

Duplicate plates (n = 12 wells) containing 6 ml of the nutrient enriched seawater, combined with either ~170 eggs or 1 ml stock sperm mixture, were prepared for each treatment in order to pre-expose gametes separately for 30 min before combining them to initiate fertilization. The final sperm concentration was $5x10^4$ sperm ml^{-1}, being slightly suboptimal for maximum fertilization (Willis et al. 1997), thereby increasing the sensitivity of the assay (Marshall 2006, Ricardo et al. 2015). When the third cleavage was observed (after 2.5 h), 2 ml of buffered zinc formalin fixative (Z-fix preservative, Anatech Limited) were added to terminate embryo development and preserve embryo integrity.

Early embryo development (Experiment 2.1b, Fig. 2.1, Table 2.2) was assessed using a stereomicroscope, and fertilization success (proportion of eggs fertilized) and embryo quality (proportion of normal versus abnormal embryos developing from the fertilized gametes) were recorded. Coral embryos were considered normal if they underwent radial holoblastic cleavage, with regular cleavage patterns until the eight-cell stage, which generally occurred within 3-8 h (Ball et al. 2002); abnormal embryos deviated from this division pattern, resulting in asymmetrical development and/or fragmentation.

Embryos (2.5 h old) that were developing normally in the same 15 treatments were selected to test larval survivorship (Experiment 2.1c, Fig. 2.1, Table 2.2). For each temperature-nutrient combination, 20 embryos were incubated at 60 µmol photons m^{-2} s^{-1} in 50 ml polypropylene jars containing 40 ml of treatment seawater (as above, n = 6 jars per treatment). Water changes with new enriched seawater were performed 48, 72, and 96 h after fertilization. Larval survivorship was assessed on day 5, when larvae show active swimming movements, display settlement behaviour by testing the substratum for settlement cues, and become competent to settle (Harrison and Wallace 1990). Larvae were counted and transferred to six-well plates with 10 ml of treatment seawater (n = 6 replicate wells per treatment; 1-10 larvae per well depending on larval survivorship). To induce larval settlement, 2 mm^2 chips of live *Porolithon onkodes, a* crustose coralline algae (CCA), were added to each well (Heyward and Negri 1999). Chips were prepared using bone cutters 1 h before adding larvae to the wells, and were obtained from a single 10 cm^2 fragment of CCA that had been maintained in a 400 l flow-through tank at 27°C with low light intensity (60-µmol photons m^{-2} s^{-1} over a 12:12 diurnal cycle). Special care was taken during the maintenance of CCA fragments (i.e. algae removed with a toothbrush when necessary), and their ability to induce settlement was tested 18 h before

using them in the experiment by offering chips of the same fragment to larvae fertilized and reared under control conditions (n = 6 replicate wells, 10 larvae per well, settlement success = 98%). After 24 h, the number of metamorphosed larvae in each well was recorded (Experiment 2.1d, Fig. 1).

2.2.5. Elevated temperature and nutrient enrichment effects on the settlement of 5-day-old larvae (no preceding stages exposed to treatment conditions; Experiment 2.2)

Larvae that had not previously been exposed to elevated temperatures or nutrients (i.e. raised under control conditions for 5-days) were used to assess the effects of nutrient enrichment (+0, +0.3, +0.6 mg OC l^{-1} FSW) and temperature (27, 29, 30, 31 and 32°C) on the process of larval settlement (Experiment 2.2, Fig. 2.1). Six-well plates were maintained in temperature incubators for 60 min before the start of each experiment to reach treatment temperatures (S2.1 Table) and during the experiment. Ten larvae were added to each well of two six-well polystyrene tissue culture plates (NuncTM, Denmark), for each of the three nutrient-enriched seawater treatments (n = 12 wells/treatment; seawater enriched as per Experiment 2.1). CCA chips (as above) were added to each well and settlement success was assessed after 24 h.

2.2.6. Elevated temperature and nutrient enrichment effects on the physiology and survivorship of 4-month-old coral juveniles (Experiment 2.3)

Four-month-old juveniles of *A. tenuis* (1-11 polyps) individually settled on manufactured aragonite substrata (~2 cm in diameter) commonly used by aquarists, were exposed to three levels of both nutrient enrichment (+0, +0.3, +0.6 mg OC l^{-1} FSW) and temperatures (27, 30 and 32°C, Fig. 2.1, Table 2.2). Prior to the experiment and during all their preceding life stages, juveniles were kept at 27°C and ambient nutrient conditions. Two replicate tanks (each 4 l) were set up for each of the nine treatments, and 19 juveniles were added to each of the 18 tanks. The juveniles were exposed to the three nutrient enrichment treatments at 27°C for 20 days before starting the temperature stress. For the heat stress, external sensor-controlled heat exchange units were used to warm the water in four water baths (two used for the incubation of the nutrient enrichment FSW, and two for the experimental tanks, S2.1 Table). Temperature was ramped up from 27 to 30 or 32ºC over a 2-day period. Water temperature was measured daily in all tanks, and temperature loggers were used in each experimental water bath housing the tanks. Once

established, juveniles were kept under treatment conditions for a further 37 days, by which time half of the juveniles in the highest temperature treatment (32ºC) had died and measurable differences had been detected among treatments for most of the variables.

2.2.7. Photochemical efficiency of the symbionts

Maximum quantum yield (F_v/F_m) of photosystem II (PSII), a measure of the proportion of available light that can be photochemically quenched, was measured for all surviving juveniles on day 54 of the experiment. A reduction of F_v/F_m is indicative of photooxidative stress and damage to PSII (Jones et al. 1999). Measurements of F_v/F_m were made using a Maxi Imaging Amplitude Modulation Fluorometer (I-PAM, Walz GmbH, Germany), which measures the fluorescence of a selected area of interest in an image (i.e., the juvenile). Measurements were performed by placing all surviving juveniles from each treatment tank into a 0.5 l container under the treatment conditions. Juveniles were dark-adapted for one hour prior to each saturation light pulse (gain = 1, intensity = 7, saturation pulse = 5) and F_v/F_m calculated using the formula $F_v/F_m = (F_m - F_0)/F_m$ with F_v = variable fluorescence, F_m = maximum fluorescence, and F_0 = minimum fluorescence (Ralph et al. 2007).

2.2.8. Survivorship, growth and weight

Survivorship of juveniles was assessed every two days by placing each recruit in a 60 ml chamber filled with the treatment water and observing it using a stereomicroscope. Death was defined as the time point when live tissue was no longer present. Survivorship was expressed as the proportion of colonies within each tank that survived to day 59 (20 days of nutrient exposure + 2 days of temperature ramping + 37 days nutrient and temperature exposure) in relation to the initial number of juveniles at the beginning of the experiment (19 juveniles per tank). The number of polyps per juvenile was counted on days 4 and 59. Images of each juvenile were taken on days 39 and 59, using a Leica MC170 stereomicroscope. The area of live tissue was measured with the program ToupView 3.7 and was used as an estimate of the colony size. At this age, juvenile morphology was typically 2-dimensional, enabling a good estimation of their planar surface areas (size). Growth ($\mu m^2\ day^{-1}$) was estimated as the change in area of each juvenile colony over 20 days (between day 39 and 59 of the experiment). On day 59, the juveniles were carefully detached from the substrate using a needle, and placed in 20 ml scintillation vials with chlorine 6% for 3 days. Skeletons were washed twice with

Milli-Q water and dried at 60°C for 48 hours in an oven before final weight measurements were taken with a microbalance.

2.2.9. Data analysis

Generalized linear models (GLM) were used to assess changes in fertilization success, embryo development, larval survivorship and settlement as a function of temperature (fixed numerical factor) and nutrient enrichment (fixed categorical factor). Quasi-binomial errors and the log link function were used when models had overdispersion. Linear mixed effects models (LME) were used to model changes in growth rates, the production of new polyps, the ratio of final weight to final size of coral juveniles, and photochemical efficiency of symbiotic *Symbiodinium* (F_v/F_m) with both temperature and nutrient enrichment as fixed factors (categorical) and tank as a random error term. Survivorship curves of coral juveniles were estimated using the Kaplan-Meier method, a non-parametric statistic that estimates survivorship conditional probabilities at each time point. Survivorship curves were compared using an accelerated failure time model with a Weibull distribution. The analyses were conducted with the lme4 and the survival packages in R (R Development Core Team, 2016). The functions glm (for the GLM), lme (for the LME) and drop1 were used to estimate p-values. A multiplicative model was used to determine the type of effects (additive, multiplicative synergistic or multiplicative antagonistic) in all analyses except for the response variable F_v/F_m for which an additive model was used since data were normally distributed and no transformation was required (Folt et al. 1999).

To determine the total effect size (SEF_{total}) of the simultaneous exposure to the two factors, the effect sizes (SEF) of all individual factors and their interactions were expressed as the proportion of change in the response variable evaluated (i.e., fertilization, larval survivorship and settlement, and juvenile survivorship) compared to that observed under control conditions (27 ºC, +0 mg l^{-1} OC). In order to estimate the total effect of exposing several early stages to combined temperature and nutrient enrichment, the following equation was used:

$$SEF_{total} = 100*[(1-SEF_i)*(1-SEF_{i+1})*(1-SEF_n)]$$

where SEF_{total} denotes the size (percentage) of the total effect on the final process considered (*i.e.* recruit success), SEF_i denotes the size of the effect of the stressors (proportion) on a particular process (*i.e.* fertilization), and n denotes the number of stages.

SEF_{total} values can vary between 0 and +∞. SEF_{total} = 0 indicates the maximum treatment effect (i.e. 0 recruit success), SEF_{total} = 100 indicate no treatment effect, and SEF_{total} < 100 and SEF_{total} > 100 indicate a negative and positive effect of the treatment, respectively (*i.e*. SEF_{total} = 80 represents a decrease of recruitment by 20%, and SEF_{total} = 150 indicates an increase of 50% in recruitment). The SEF_{total} was estimated for early life history stages that had been exposed to treatment conditions for gamete fertilization, embryo development, larval survivorship and settlement, and the survivorship of 4-month-old juveniles. This represents a minimum estimation of the total effect, because the stages between recently settled larvae and 4-month-old juveniles were not exposed to the temperature and nutrient treatments and are therefore considered to be constant.

2.3. Results

2.3.1. Elevated temperature and nutrient enrichment effects on gamete fertilization (Experiment 2.1a)

Fertilization success was high (83 ± 6%, mean ± sd) across all temperatures and nutrient enrichment treatment combinations up to 30°C (Fig. 2.2). There were significant detrimental main effects from both temperature elevation and nutrient enrichment on fertilization success ($p < 0.001$, Table 2.3; Fig. 2.2), while the interactions were non-significant, indicating additivity of effects on the log scale ($p_{Temperature*Nuttrients} = 0.389$ Fig. 2.2, Table 2.3). The reduction in fertilization success compared to that observed in the control treatment (nutrient enrichment = 'low', temperature = 27°C) was 5 ± 6% at nutrient enrichment = 'high' (temperature = 27°C), and 8 ± 7% at temperature = 32°C (nutrient enrichment = 'low'), while temperature = 32°C and nutrient enrichment = 'high' in combination resulted in a 14 ± 10% decline in fertilization.

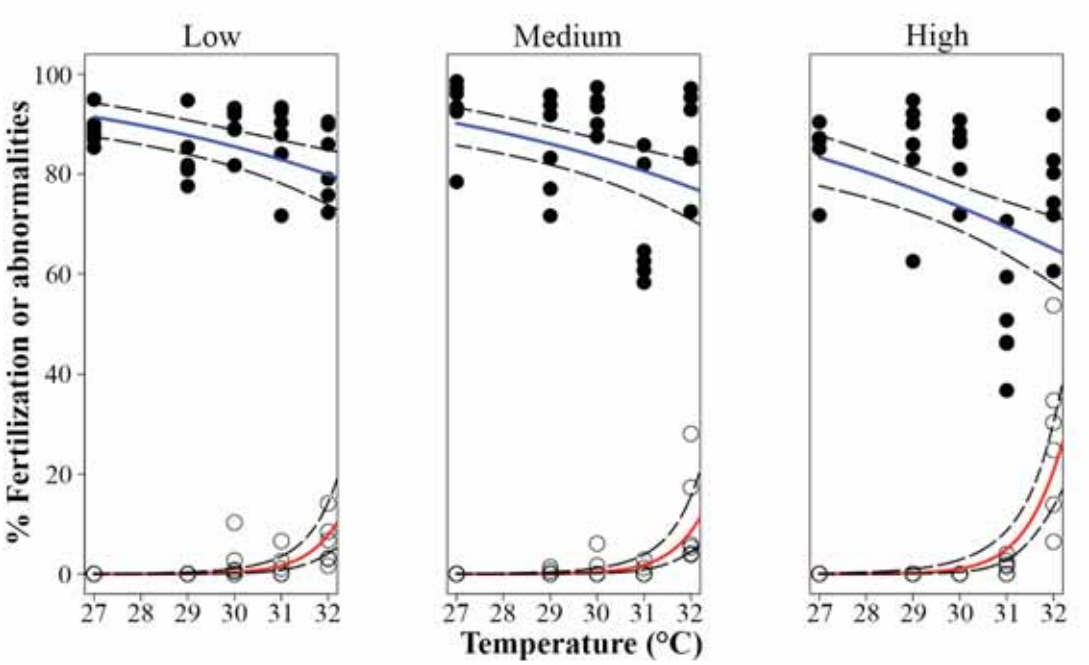


Figure 2.2: Effects of temperature and nutrient enrichment on the percentage of fertilized eggs (blue line, black circles; Experiment 2.1a) and abnormal embryos (red line, open circles; Experiment 2.1b) of *Acropora tenuis*. Control treatment: 'low' nutrient enrichment and at temperature = 27°C. Solid lines indicate fitted GLM trend lines, while dashed lines are 95% confidence intervals.

2.3.2. Elevated temperature and nutrient enrichment effects on embryo development and larval settlement (Experiment 2.1b)

Elevated temperature and nutrient enrichment together increased the proportions of abnormal embryos (Fig. 2) in an interactive fashion ($p_{Temperature*Nutrients} < 0.001$, Table 2.3). Between 27 and 29°C, 100% of embryos underwent normal development characterized by radial holoblastic cleavage, resulting in equally-sized blastomeres, regardless of nutrient enrichment. Abnormalities in the form of asymmetrical and irregular cleavage increased in the 'high' nutrient enrichment (6 ± 12%), while the individual effect of the highest temperature (32°C) was a pronounced increase (15 ± 14%). When the highest levels of both factors co-occurred, the proportion of abnormal embryos increased (27 ± 16%) to values higher than expected for the addition of the individual effects of temperature and nutrient enrichment (Fig. 2), indicating a multiplicative synergistic interaction of both stressors according to the GLM model with the log-link function.

Experiment	Dependent variable	Treatment effect	p values		
			Temp	Nut	Temp x Nut
2.1a	Fertilization	Temp and Nut decreased fertilization	**<0.001**	**<0.001**	0.389
2.1b	Abnormalities	Temp and Nut increased abnormalities	**<0.001**	**<0.001**	**<0.001**
2.1c	Larval survivorship	Temp decreased larval survivorship	**<0.001**	0.880	0.181
2.1d	Settlement	Temp decreased settlement	**<0.001**	0.951	0.895
2.2	Settlement	Temp increased settlement	**<0.001**	0.061	0.968
2.3	Growth	Temp increased growth	**0.010**	0.302	0.845
	Production of new polyps	No effect	0.793	0.204	0.825
	Final weight/Final size	No effect	0.255	0.251	0.229
	F_v/F_m on day 54	Nut increased F_v/F_m while Temp decreased it	**<0.001**	**0.013**	**0.017**
	Survivorship curves	Nut increased survivorship while Temp decreased it	**<0.001**	0.076	**0.001**

Table 2.3: Results of treatments effects on *Acropora tenuis* early life history stages based on generalized linear models (GLM) with log-link function temperature (Temp) and nutrient enrichment (Nut) as fixed factors and tank as random error term. Significance at $p<0.05$ is shown in **bold**. Refer to Table S2.2 for detailed information for the analyses.

2.3.3. Elevated temperature and nutrient enrichment effects on larval survivorship (all preceding stages exposed to stressors; Experiment 2.1c)

After exposure of all early life processes (fertilization and embryo development) to the different treatments, survivorship of larvae in their first few days was significantly affected by temperature ($p_{Temperature} < 0.001$, Table 2.3). Larvae had highest survivorship (95 ± 4%) in treatments between 27-30°C, and at higher temperatures larval mortality increased significantly from 12 ± 18 at 30°C to 60 ± 18% at 32°C (Fig. 2.3a). In contrast, nutrient enrichment and its interaction with temperature had no effect ($p_{Nutrients} = 0.880$, $p_{Temperature*Nutrients} = 0.181$, Table 2.3).

2.3.4. Elevated temperature and nutrient enrichment effects on larval settlement (all preceding stages were exposed to stressors; Experiment 2.1d)

Settlement success of larvae that had developed from gametes under the different temperature and nutrient enrichment treatments was significantly affected only by temperature ($p_{Temperature} < 0.001$, Table 2.3). The highest settlement success was observed at 27°C (68 ± 13%), and settlement declined to 0% at 32°C (Fig. 2.3b).

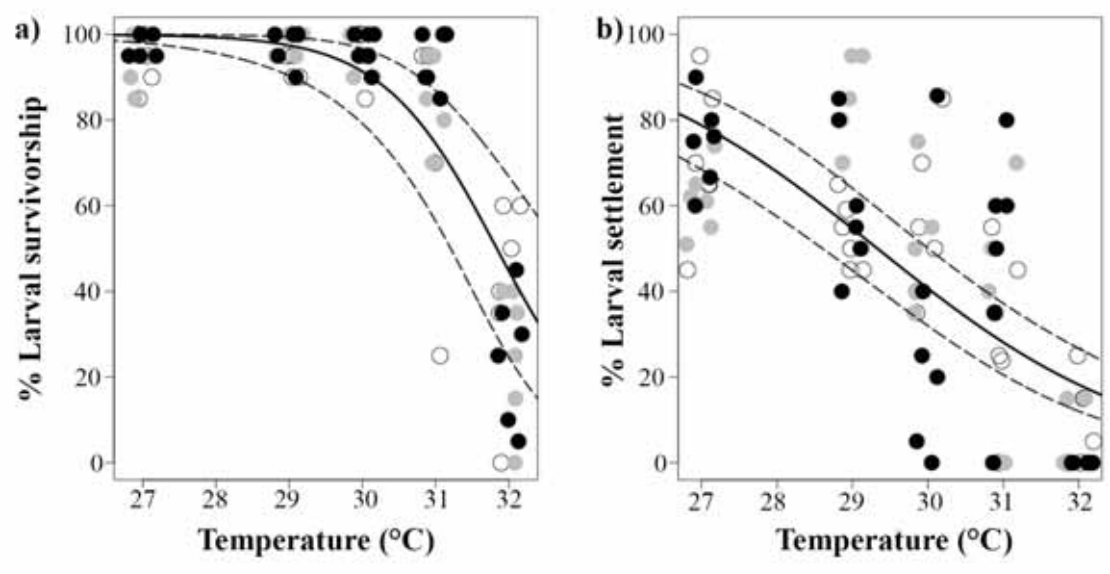


Figure 2.3: a) Percentage larval survivorship 5 days after fertilization for *Acropora tenuis* reared under different temperatures and nutrient enrichment [low (open circles), medium (grey circles), high (black circles); Experiment 2.1c]. b) Settlement rates for larvae of *A. tenuis* that had being fertilized, reared and settled under different temperatures and nutrient enrichment (Experiment 2.1d). Control treatment: 'low' nutrient enrichment and at temperature = 27°C. Solid lines indicate fitted GLM trends, while dashed lines are 95% confidence intervals. Individual points are jittered horizontally for clarity.

2.3.5. Elevated temperature and nutrient enrichment effects on the settlement of 5-day-old larvae (no preceding stages exposed to treatment conditions; Experiment 2.2)

Settlement success of larvae fertilized and reared under control conditions (27ºC and ambient nutrient levels) increased significantly with temperature ($p_{Temperature} < 0.001$, Table 3; Fig. 2.4) being lowest (81 ± 11%) in the temperature control treatment (27°C), and highest (95 ± 5%) at 32°C, while no effect was found in response to nutrient enrichment or its interaction with temperature ($p_{Nutrients} = 0.061$, $p_{Temperature*Nutrients} = 0.968$, Table 2.3, Fig. 2.4).

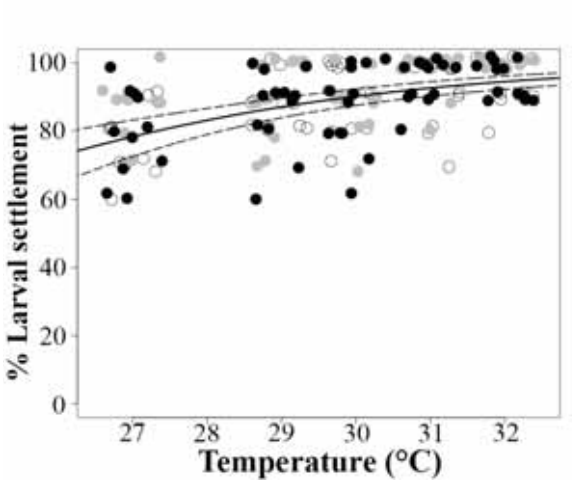


Figure 2.4: Proportion of 5 days old *Acropora tenuis* larvae, fertilized and reared under control conditions (27°C and FSW) but settled under different temperatures and nutrient enrichment [low (open circles), medium (grey circles), high (black circles); Experiment 2.2]. Control treatment: 'low' nutrient enrichment and at temperature = 27°C. Solid lines indicate fitted GLM trends, dashed lines are 95% confidence intervals. Individual points are jittered horizontally for clarity.

2.3.6. Elevated temperature and nutrient enrichment effects on physiology and survivorship of 4-month-old coral juveniles (no preceding stages exposed to treatment conditions; Experiment 2.3)

Growth rates (μm^2 day^{-1}) of coral juveniles changed significantly with temperature ($p_{Temperature} = 0.010$, Table 2.3, Fig. 2.5a, Fig. 2.6), but were unaffected by nutrient enrichment or a combination of the two factors ($p_{Nutrients} = 0.302$ and $p_{Temperature*Nutrients} = 0.845$, Table 2.3, Fig. 2.5a). Juveniles exposed to 32°C exhibited the highest growth rates, having a 1.6-fold increase in area when compared to juveniles at 27°C (Fig. 2.5a).

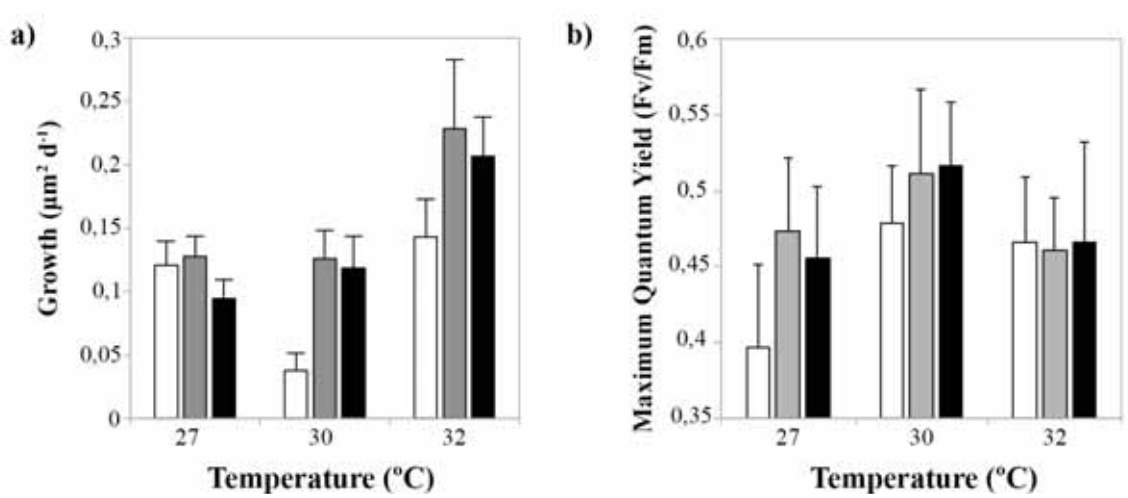


Figure 2.5: Four-month-old *Acropora tenuis* juveniles. a) Growth rates (mean ± sd) under different temperatures and nutrient enrichment [low (white bars), medium (grey bars), high (black bars)], b) maximum quantum yields (Fv/Fm, mean ± sd) under different temperatures and nutrient enrichment (Experiment 2.3). Control treatment: 'low' nutrient enrichment and at temperature = 27°C.

However, there was no effect of temperature or nutrient enrichment on the rate of budding of new polyps ($p_{Temperature}$ = 0.793 and $p_{Nutrients}$ =0.204, Table 2.3), or on the relationship between their final skeletal dry weights and final size ($p_{Temperature}$ = 0.255 and $p_{Nutrients}$ = 0.251 respectively, Table 2.3). Photochemical efficiency (F_v/F_m) of the symbiotic algae was significantly affected by the combination of elevated temperature and nutrient enrichment in an interactive fashion ($p_{Temperature*Nutrients}$ = 0.017, Table 2.3), and the combined effect of these factors was antagonistic (Fig. 2.5b). Nutrient enrichment had a positive effect on F_v/F_m until 30ºC, but at 32ºC (Fig. 2.5b) the effect of the enrichment was counteracted by the negative effects of high temperatures, dropping F_v/F_m values in the 'medium' and 'high' nutrient enrichment treatments to values similar to the 'low' nutrient enrichment treatment.

Juvenile survival was also affected in an interactive fashion by temperature and nutrient enrichment ($p_{Temperature*Nutrients}$ = 0.001, Table 2.3, Fig. 2.7) and their interaction was multiplicatively antagonistic (GLM model). Survivorship at 27ºC was slightly higher in the 'low' nutrient enrichment treatment (Fig. 2.7a), while an increase to 30 and 32ºC resulted in improved survivorship for juveniles exposed to 'high' nutrient enrichment (Fig. 2.7b and c).

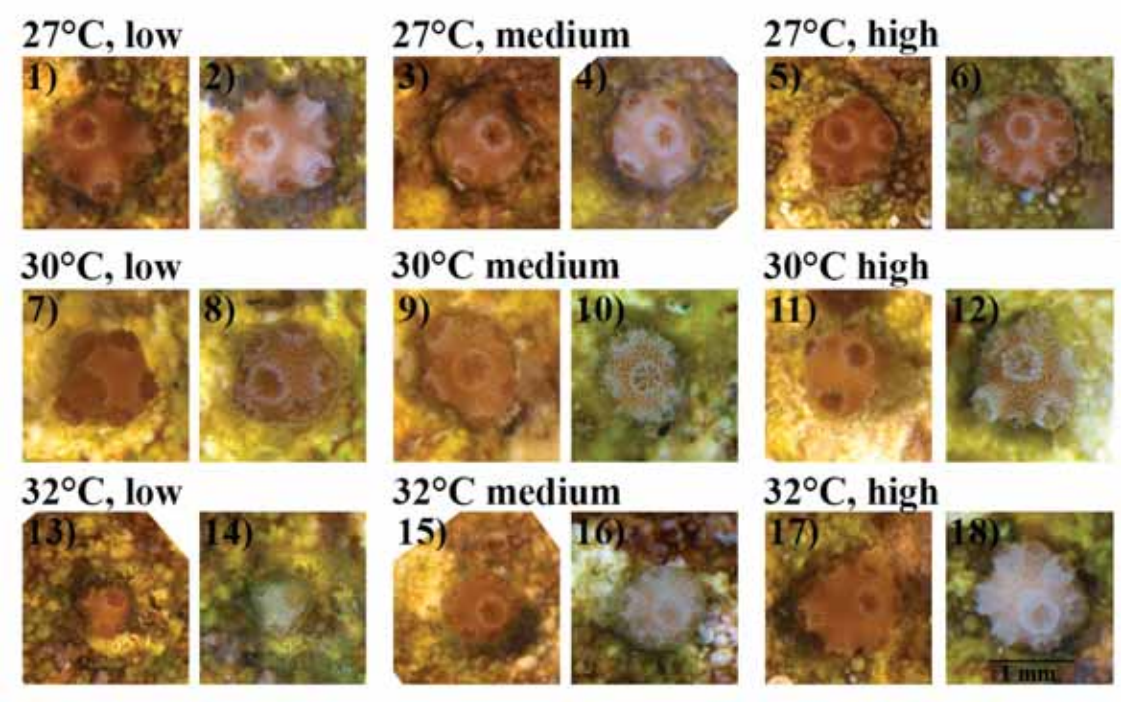


Figure 2.6: Images of juveniles on day 39 (odd numbers) and 59 (even numbers) of treatment exposure. Treatments consisted of three levels of nutrient enrichment (low, medium and high) and three temperatures (27, 30 and 32°C). Control treatment: 'low' nutrient enrichment and at temperature = 27°C.

2.3.7. Cumulative effects of elevated temperature and nutrient enrichment on total recruitment success

When modelled together, the total effect of temperature increases and nutrient enrichment on recruitment success of *A. tenuis* was deleterious: it was reduced under exposure to the higher levels of either of the treatments, and was further reduced when the treatments were combined (Fig. 2.8). Recruitment success declined compared with control values (normalised to 100%) to ≤ 50% at 30ºC and 'medium' nutrient enrichment (Fig. 2.8). Temperatures > 30ºC lead to a < 50% reduction in recruitment success in all nutrient enrichment treatments.

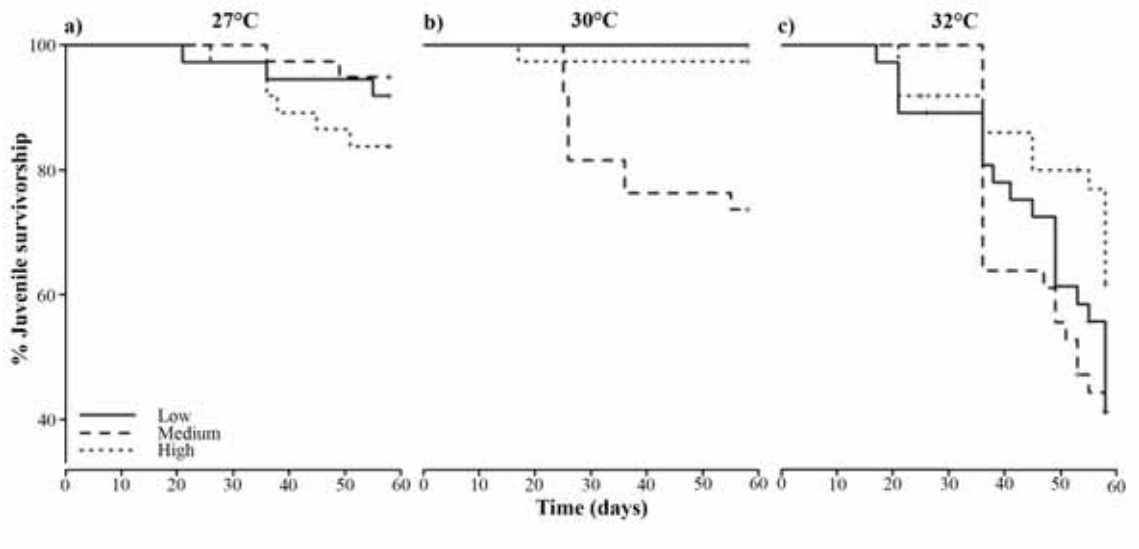


Figure 2.7: Survivorship curves of 4-month-old juveniles of *Acropora tenuis* that were exposed to nutrient enrichment [low (continuous line), medium (dashed line) and high (dotted line)] and temperature for 58 days. Control treatment: 'low' nutrient enrichment and at temperature = 27°C. Nutrient enrichment started on day one of the experiment, while heat stress started on day 21.

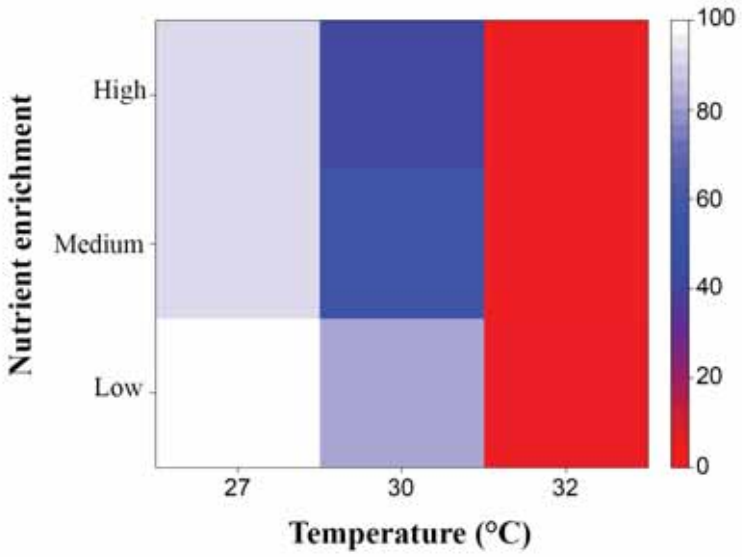


Figure 2.8: Total effect size of nutrient enrichment and temperature on recruitment success when the different stages (fertilization, embryo and larval development, settlement and 4-month-old juveniles) were equally exposed to contrasting temperatures and nutrient enrichment (low, medium and high). Control treatment: 'low' nutrient enrichment and at temperature = 27°C. Values between 0 and 100 indicate a negative effect of the treatment (*e.g.* 0 represents 0% survivorship), while a value of 100 indicates no effect of the treatment on the final stage considered (*i.e.* 100% survivorship).

2.4. Discussion

This study illustrates that early life history stages of *A. tenuis* have different sensitivities to increased temperatures and nutrient enriched waters. Temperature and nutrient enrichment both reduced fertilization success, with their combined effects being additive for fertilization and synergistic for abnormal early embryo development respectively. Larval survivorship and settlement, and the growth rates of juveniles were only affected by increased temperatures, while survivorship of 4-month-old juveniles decreased in an antagonistic fashion when simultaneously impacted by increased temperature and nutrient enrichment. Modelling the effects of nutrient enrichment and heat stress together illustrated how changes in both local (water quality) and global factors (ocean warming) may interact to jointly decrease the success of successive early life history stages in corals. These results also demonstrate serious consequences for overall recruitment if early life stages (from fertilization to recruit survival) are cumulatively exposed to elevated temperatures and/or nutrient enrichment.

This is the first study to test the effect of combined organic and inorganic nutrient enrichment on corals early life history stages, contrasting this work with previous studies which only tested the effects of elevated inorganic nutrients. This experimental approach realistically preserves the stoichiometric composition of nutrients and trace elements present in seawater on river-exposed inshore reefs. This method has inherently higher natural variability among nutrient treatments than additions of specific forms of dissolved organic and inorganic nutrients, and also may affect other variables not measured here (microbial and plankton successions, enrichment or depletion of trace elements, accumulation of metabolites or pathogenic interactions). Consequently, my experimental design cannot tease apart effects of other variables potentially affected by the co-occurrence of nutrient enrichment and warming temperatures, limiting my capacity to fully elucidate mechanism affecting early life history stages. However, all these variables will also vary under natural conditions of eutrophication (Fabricius 2011), and their impacts are likely to increase with increases of nutrient enrichment and temperature. These experiments therefore represent a valid first step to understand the interplay between nutrient enrichment and temperature and identify the most sensitive processes and stages to these stressors. Future research efforts should aim to understand the underlying mechanisms driving the observed impacts.

2.4.1. Fertilization and embryo development under heat and nutrient enrichment stress

Reduced fertilization was observed in treatments with either high temperatures or nutrient enrichment (organic and inorganics), and effects were additive once treatments were combined (Experiment 2.1a). Previous single stress studies experiments have also found reduced fertilization under elevated temperatures (Omori et al. 2001, Negri et al. 2007) or inorganic nutrients (Humphrey et al. 2008, Lam et al. 2015). Although my experimental design did not allow us to identify the individual mechanism(s) driving the impacts of combined stressors, results of previous single-factor studies suggest possible explanations. Elevated temperature is likely to impair coral fertilization through a reduction in the sperm flagella motility, reducing the number of sperm-egg interactions (Omori et al. 2001). In addition to possible molecular and biochemical impacts, nutrient enrichment is likely to foster the development of microbial communities that could be deleterious to gametes, a possibility that deserves further study. However, although other studies have also found elevated concentrations of dissolved inorganic nutrients reduce coral fertilization success (Harrison and Ward 2001, Humphrey et al. 2008, Lam et al. 2015); the underlying mechanisms of nutrient toxicity on fertilization remain unknown. The additive effect of increased temperatures and nutrients indicates that enrichment is likely to exacerbate impacts on fertilization when high temperatures and coastal runoff coincide with coral spawning.

Abnormalities in early embryos were higher following exposure to high temperatures and nutrient enrichment, and these stressors acted synergistically when they co-occurred (Experiment 2.1b). Abnormal embryo development in corals has been described previously in response to temperature increases (Bassim et al. 2002, Negri et al. 2007, Randall and Szmant 2009, Woolsey et al. 2015) or in the presence of inorganic nutrients (Harrison and Ward 2001, however see Humphrey et al. 2008, Lam et al. 2015). Abnormalities could result from disruption of processes such as gene expression, cell rearrangement and differentiation, signalling pathways, arrested mitotic divisions, or impairment of functional enzymes or structural proteins (Negri et al. 2007, Voolstra et al. 2009, Portune et al. 2010). The mechanism by which nutrients and elevated temperatures simultaneously affect embryo development at the ultrastructure level is unknown, although I hypothesize that it may be due to molecular, biochemical or microbial processes. Moreover, population-level implications of abnormal embryo development

also remain unclear, as no studies so far have examined the ultimate fate of aberrant embryos. However, studies with other marine invertebrates (Thiyagarajan et al. 2003, Caldwell et al. 2005, Bartolini et al. 2013) suggest that abnormalities result in energy depletion and higher mortality rates, which would clearly be deleterious for larval fitness and consequently for population maintenance.

2.4.2. Larval survivorship and settlement under heat and nutrient enrichment stress

Embryos resulting from fertilization at high temperatures (>30ºC) exhibited significantly reduced survivorship as they developed into planula larvae (Experiment 2.1c). The impacts of thermal stress on azooxanthellate larvae may be related to inhibition of their development or to sub-cellular damage, since decreases in larval cilia motility, pre-competency periods and survivorship have been observed after exposures to high temperatures (Edmunds et al. 2001, Randall and Szmant 2009, Heyward and Negri 2010, Negri and Hoogenboom 2011, Schnitzler et al. 2012). In this study, the sensitivity of developing larvae to thermal stress may have been exacerbated by prior exposure during fertilization and early embryogenesis. The present study represents the first report of exposure of developing coral larvae to enriched seawater (Experiment 2.1c) and my results indicate that for *A. tenuis,* this life history stage may not be sensitive to nutrient enrichment.

My results show that the effects of thermal stress on settlement success of *A. tenuis* depended on prior exposure during early development stages. Higher temperatures enhanced settlement success of larvae developed under control conditions (Experiment 2). Conversely, larvae developed from gametes and embryos that were also exposed to thermal stress exhibited reduced settlement and metamorphosis success (Experiment 2.1d). Larval settlement success has been observed to vary with intensity and frequency of temperature changes. Short-term (minutes to hours) exposure of larvae to higher temperatures have positive effects on settlement (Edmunds et al. 2001, Nozawa and Harrison 2007), while longer exposures (days to months) can have negative effects (Bassim and Sammarco 2003, Nozawa and Harrison 2007, Randall and Szmant 2009, however see 56). Results from this study demonstrate that exposures to thermal stress and nutrient enrichment over fertilization and early (<2 h) embryogenesis can have significant flow-on impacts on larval fitness and function.

Positive effects of high temperatures on settlement success have been related to acceleration of metabolic rates in coral larvae (Nozawa and Harrison 2000, Nozawa and Harrison 2007, Heyward and Negri 2010). However, increases in settlement success at elevated temperatures have also been accompanied by increases in post-settlement mortality (Edmunds et al. 2001, Nozawa and Harrison 2007). The consequences of accelerated settlement with increased temperature could be deleterious for population and metapopulation dynamics, since larval dispersal, connectivity and post-settlement survivorship have been observed to be compromised when larvae are exposed to thermal stress (Nozawa and Harrison 2000, Figueiredo et al. 2014). Consequently, thermal stress impacts on already competent larvae (Experiment 2.2) could have negative implications for coral reef resilience; however, they could also improve local settlement success.

2.4.3. Single exposure of nutrients and temperature on 4-month-old juveniles

Physiological responses of 4-month-old juveniles of *A. tenuis* differed depending on the temperature and level of nutrient enrichment. For example, elevated temperatures had positive effects on growth, while the combination of both stressors affected photochemical performance (F_v/F_m) and survivorship of the juveniles. While long-term impacts of thermal stress on adult corals are overwhelmingly negative (Hoegh-Guldberg 2011), the effects of elevated organic and inorganic nutrients on adult corals are varied and can be negative, neutral or positive (Anthony and Fabricius 2000, Ferrier-Pages et al. 2000, Bongiorni et al. 2003a, Sawall et al. 2011). These results confirm that stressors have different mechanisms of action on metabolic processes and suggest trade-offs between processes that might determine the corals' overall physiological performance under the co-occurrence of these stressors.

The maximum quantum yield of PSII in symbiotic zooxanthellae responded positively to nutrient enrichment at temperatures less than 32°C. This estimate is conservative since the most sensitive individuals died and were not included in the analysis. It has been proposed that enhancement of photosynthesis by dissolved and particulate organic nutrients occurs through the transfer of nitrogen from the host to the zooxanthellae and increases zooxanthellae division rates (Houlbrèque et al. 2003). However, the positive effect of nutrient enrichment on photosystem efficiency was counteracted when temperatures reached 32ºC, indicating that oxidative stress from high temperatures damaged PSII (Takahashi et al. 2004). The occurrence of optimal F_v/F_m

values at 30°C is similar to findings previously reported for *A. tenuis* juveniles (Ferrier-Pages et al. 2000) and in adult corals of other species (Sawall et al. 2011). Improved performance of PSII at warmer (30ºC) temperatures than at ambient (27ºC) temperatures in *A. tenuis* associations may be related to symbiont clades having different reaction norms (Bongiorni et al. 2003a), presenting as greater photochemical performance and tolerance at high temperatures due to local adaptations (Howells et al. 2012). However, values of F_v/F_m at 32°C were similar to values obtained at 27°C despite marked differences in mortality in these two treatments, suggesting that F_v/F_m was not a good predictor of the health status of coral juveniles in this experiment.

Among the physiological responses investigated for 4-month-old juveniles, growth and survivorship were affected to the greatest extent. Growth rates increased at the highest temperatures (32ºC), in contrast to previous reports for other species (Edmunds 2004, Jones and Berkelmans 2010, Cunning et al. 2015). Reduced growth rates in those studies were often linked to bleaching and the subsequent loss of energy derived from the zooxanthellae. While increasing temperatures had a clear negative effect on the survival of juveniles, the effects of nutrient enrichment varied, similar to a previous study with adult colonies of *A. millepora* (Fabricius et al. 2013a).

2.4.4. Cumulative effects of nutrient enrichment and temperature stress on early life history stages

There is mounting evidence that nutrients and heat stress produce adverse and long lasting effects on the reproductive output of corals. These stressors have induced reductions in the fecundity of colonies (Jones and Berkelmans 2011), fertilization and normal embryo developmental success (Harrison and Ward 2001, Bassim et al. 2002, Negri et al. 2007), larval respiration rates (Edmunds et al. 2011), the duration of the larval pre-competency period (Heyward and Negri 2010) and larval survivorship (Schnitzler et al. 2012). The present study demonstrates that although some of the variables evaluated (i.e., larval settlement when exposed to the nutrient enrichment and temperature only during settlement and juvenile growth) had positive effects, the final outcome of the exposure of early life-history stages of *A. tenuis* to nutrient enrichment and temperature increases was a significant reduction in survivorship. The type of effect (additive vs synergistic or antagonistic) of nutrient enrichment and high temperatures varied in direction and intensity between the different early life history stages of *A. tenuis*.

Nonetheless, I found temperature increase to be the main driver of detrimental impacts on recruitment success, with nutrient enrichment subtly increasing the impacts at the highest temperatures.

My results indicate that the early life history stages of corals can be sensitive to temperature and that this effect is more pronounced (i) in early development (gametes and early embryos) and (ii) in the presence of nutrient-enriched water. This study shows that nutrient enrichment increases the impact of thermal stress on *A. tenuis* by compromising their replenishment capacity through reductions in survivorship of sexually produced individuals. Even without heat stress, exposure to nutrient enrichment will have a strong detrimental effect on the earliest development processes of hard corals (fertilization and embryo development), compromising their later larval settlement and juvenile survivorship. Future research studies should be focused on understanding the possible mechanism of action of the individual and simultaneous occurrence of nutrient enrichment and temperature stress on corals early life history stages, including detailed analysis of structural and metabolic pathways changes during exposures. Management strategies focused on water quality improvements by reducing the input of fertilizers will not only prevent coral mortality and macroalgae blooms (Fabricius et al. 2005), but they will also enhance reef resilience by improving the thermal tolerance of early life history stages of some inshore coral species.

Chapter 3: Cumulative effects of suspended solids, organic nutrients and temperature stress on early life history stages of the coral *Acropora tenuis*

3.1. Introduction

Increasing levels of turbidity and sedimentation are contributing to coral reef degradation worldwide (Fabricius 2005, De'ath and Fabricius 2010, Brodie et al. 2012, Erftemeijer et al. 2012a) and are recognised as pressures of major concern for environmental managers (Great Barrier Reef Marine Park Authority 2014). The introduction, resuspension and deposition of sediments in coastal marine ecosystems can be caused by natural factors (*e.g.*, waves and currents, river discharges) or human activities (*e.g.*, dredging, or enhanced terrestrial runoff of sediments due to coastal development, deforestation or poor agricultural practices). Once reaching the ocean, the fate of newly imported sediments depends on their grain size and geochemical properties (Storlazzi et al. 2015). Large particles are frequently deposited near the river mouth, whereas fine particles (*i.e.*, silts and clays) either flocculate or are deposited, but can also easily be resuspended, traveling 10's of km from the source to reach inshore and mid-shelf coral reefs (Brodie et al. 2001, Devlin and Brodie 2005, Bainbridge et al. 2012).

Since European settlement in 1850, the development of Australia's North Queensland catchments adjacent to the Great Barrier Reef (GBR) has led to significant changes in the quantity and quality of water discharges into the GBR lagoon (McCulloch et al. 2003, Kroon et al. 2012). Expansion of agricultural activities, clearing of vegetation and grazing have led to widespread soil erosion in the region, and the application of fertilizers has increased river discharges of sediments together with dissolved and particulate organic and inorganic nutrients and trace elements (Furnas 2003, Devlin and Brodie 2005, Brodie et al. 2010, Kroon et al. 2012). Modelled estimates indicate that the mean annual loads of sediments delivered to the GBR lagoon have increased 2.9-fold since 1850 to 8,500 mty^{-1}. Correspondingly, mean annual total nitrogen loads have increased 5.7 times to 37,000 ty^{-1}, and mean annual phosphorus loads have increased 8.9 times to 6,300 ty^{-1} (Waters et al. 2014).

River discharges from catchments with significant cropping area are characterised by high concentrations of dissolved and particulate inorganic nutrients, especially nitrogen and phosphorus (Furnas 2003, Kroon et al. 2012). Inorganic nutrients from anthropogenic sources generally only persist in the GBR lagoon for periods of days to weeks (Brodie et al. 2010), as they are rapidly taken up by microbial and planktonic communities. They are then transformed into organic matter and undergo complex cycling between particulate and dissolved organic and inorganic forms, and undergo repeated deposition-resuspension cycling (Grossart and Ploug 2001, Brodie et al. 2010). Particulate organic nutrients reduce water clarity, stimulate microbial communities that exude mucopolysaccharides (Angly et al. 2016) and form aggregates with sediments contributing to biological oxygen demand (Murphy and Richmond 2016), causing increases in oxidative stress at the sediment/seawater interface and reducing the pH at this layer (Martinez et al. 2012). Organically-enriched sediments are known to increase the detrimental effects of turbidity and sedimentation on the physiology and survival of corals, as a consequence of decreased light availability for photosynthesis (Anthony et al. 2004) causing reductions of calcification rates (Marubini et al. 2001). Disruption of the *Symbiodinium*-coral symbiosis, decreases in productivity and growth rates, and increases in partial mortality (Fabricius 2005, Weber et al. 2006, Weber et al. 2012) are among the more serious effects that nutrient enriched sediments have on adult corals. Sediment particles can also be carriers of a variety of pollutants, including pesticides, polycyclic aromatic hydrocarbons and heavy metals, which have been related to reductions in coral cover (Jones 2011, Berry et al. 2013)

In addition to stress induced by elevated concentrations of sediments and nutrients, inshore coral reefs may be simultaneously exposed to high sea surface temperatures (SST) during the summer monsoonal periods (Lough 1992), compromising the health and replenishment of hard coral populations (Ban et al. 2014). Since the beginning of the 20th century, SST has risen by a global average of ~1°C (Brohan et al. 2006) and is projected to increase by a further 2 to 3°C by the end of the century under a moderate Representative Concentration Scenario of the Intergovernmental Panel on Climate Change (IPCC RCP 4.5, Meissner et al. 2012). Such increases in SST alone would endanger many coral species, which typically live close to their upper thermal tolerance limits (Berkelmans and Willis 1999). It has been hypothesized that the effects of high temperatures on adult corals are ameliorated when co-occurring with suspended sediments due to reductions in light irradiance levels through shading and the provision

of alterative food resources by suspended particles (Anthony et al. 2007, Cacciapaglia and van Woesik 2016).

The early life-history stages of corals are susceptible to a range of water quality and climate pressures (Hoegh-Guldberg et al. 2007a, Jones et al. 2015b) and this is critically important as reproduction and recruitment underpin the maintenance and resilience of reef communities (Harrison et al. 1984, Hughes et al. 2000). Despite the perception that early life history stages of corals are more sensitive to environmental change and pollution than adult stages (Fabricius 2005), few studies have empirically addressed their susceptibility to individual and multiple co-occurring multiple pressures (Harrison and Ward 2001, Bassim and Sammarco 2003, Humphrey et al. 2008, Negri and Hoogenboom 2011, Miin Chua et al. 2013). To improve our understanding of how the combined pressures of declining water quality and mounting temperature stress will affect the early life history stages of corals, I conducted controlled experiments to examine the effects of suspended sediments, with and without nutrient enrichment, and at different temperatures, on gamete fertilization, larval survival and larval settlement of the broadcast spawning coral *Acropora tenuis.* Experiments were designed to mimic the impact of environmentally-relevant concentrations of suspended sediments originating from runoff events, dredging or coastal activities under two different scenarios: i) elevated temperatures typical of those experienced during summer months, and ii) nutrients typical of those produced by agricultural or coastal development activities that promote plankton blooms (Kaltenböck and Herndl 1992, Grossart and Ploug 2001, Furnas 2003). Results enabled me the identification of differences in the sensitivity of processes that take place during the early life history stages of *A. tenuis* to single and combined effects of suspended sediments, nutrient enrichment and temperature, and to explore their implications for inshore coral reefs exposed to river floods, dredging and high temperatures.

3.2. Materials and methods

3.2.1. Obtaining coral gametes

Gravid colonies (> 20 cm diameter) of the broadcast spawning coral *A. tenuis* (Dana, 1846) were collected from 3–5 m depth from Davies Reefs (18.832°S, 147.633°E) on the 6th of November 2014, and from Esk Island (18.462° S, 146.311°E) on the 3rd of

November 2015 under the permit G12/35236.1 issued by the Great Barrier Reef Marine Park Authority. Colonies were transferred to outdoor flow-through, temperature-controlled aquaria with the temperature set to the one found at the reef on the day of collection (27°C) in the National Sea Simulator (SeaSim) at the Australian Institute of Marine Science (AIMS). Experiments 3.1 and 3.3 were performed in 2014, while experiments 3.2 and 3.4 were completed in 2015. Following spawning on night 5 after the November full moon (at 19:30), egg-sperm bundles from 7 colonies were gently scooped from the surface of the water and eggs were separated from sperm using a 100 µm mesh filter and washed five times in FSW (0.2 µm filtered sea water) as described by Negri and Heyward (2000). Concentrated sperm was diluted to achieve a working stock of ~1 x 10^7 sperm ml^{-1}. Gametes separated in this way were used in the fertilization experiment (Experiment 3.1), while the remainder of the gametes were fertilized and raised in bulk flow-through embryo and larval cultures (Negri and Heyward 2000) for the embryo development, larval survivorship and larval settlement experiments (Experiments 3.2, 3.3 and 3.4).

3.2.2. Preparation of sediments, temperature and nutrient enrichment treatments

Experiments investigated the combined effects of 1) suspended sediments and nutrient enrichment; and 2) suspended sediments and temperature on key processes (fertilization, larval survival and settlement) in the early life histories of *A. tenuis* (Fig. 3.1). Sediments and nutrient enrichment treatments were prepared as follows. Sediments had been collected at Orpheus Island (18° 36'S, 146° 29'E) at 2 m depth two weeks before spawning each year and transported to AIMS. Sediments were wet-sieved to obtain fine particles (mean ± std. particle size 7.3 ± 1.5 µm 95% <20 µm) and kept in 60 l tanks with flow-through seawater at 27°C until experiments commenced. The nutrients were collected with a plankton net (mesh size 100-µm), sieved to remove large fragments (>26 µm), blended and frozen until use. On the inshore of the GBR, suspended particulate matter mostly consists of decayed detritus resuspended from the seafloor, and zooplankton (Fabricius et al. 2014).

Suspended sediment concentrations used in all experiments (0, 5, 10, 30 and 100 mg l^{-1}) were prepared using a nephelometer (TPS 90FL-T, Fig. S3.1). Sediments were added to FSW, then agitated manually, and turbidity was estimated in Nephelometric

Turbidity Units (NTU). To prepare the suspended sediments and temperature treatments (Experiments 3.1 and 3.3), two replicate Schott bottles (2 l) per treatment combination, containing the appropriate concentration of sediments, were incubated for 3 h at the designated treatment temperatures (27, 30, and 32°C, Table S3.2), prior to the start of each experiment. Nutrient enrichment treatments for the suspended sediments and nutrient enrichment experiments were also prepared in two replicate Schott bottles (2 l) per treatment combination by adding the appropriate quantity of nutrients to bottles containing the different suspended sediment concentrations. Based on the total organic carbon (OC) present in the nutrient solution, three nutrient enrichment treatments were prepared by adding the required volume of the solution to FSW at a nominal concentration of +0, +0.3, or +0.6 mg OC l^{-1} FSW. In order to promote microbial communities to take up the bioavailable fraction of inorganic nutrients and transform it into organic nutrients (Arrigo 2005), incubations lasted 48 h at 200 µmol photons m^{-2} s^{-1} light intensity (12 h:12 h diurnal cycle) at 27°C. Incubations were done to allow the microbial community to take up the bioavailable fraction of the inorganic nutrients and transform it into organic nutrients. Nutrient enrichment treatments were performed using decaying natural plankton in order to maintain a realistic stoichiometric composition of nutrients and trace elements. Previous studies have used this method (Fabricius et al. 2003b, Weber et al. 2012) for studying the effects of nutrients on corals, and the incubation lasted the required time to allow the microbial community to take up the bioavailable fraction of the dissolved inorganic nutrients and convert it into organic matter (McCarren et al. 2010, Fabricius 2011, Bryson et al. 2016).

Experimental suspended sediment concentrations targeted are within the range of *in situ* water quality measured on inshore GBR reefs and in association with dredging projects. Concentrations up to 5 mg l^{-1} occur under calm conditions on inshore reefs (Macdonald et al. 2013), concentrations between 5 and 30 mg l^{-1} are typical after storms and river plumes, and concentrations up to 100 mg l^{-1} have been recorded close to dredging activities (Thomas et al. 2003, Stoddart and Anstee 2005, Jones et al. 2015a, Ricardo et al. 2015). Nutrient enrichment concentrations were based on *in situ* water quality measured in the GBR (Table S3.3; Kroon et al. 2012, Schaffelke et al. 2012, Waters et al. 2014). Control treatments were always 0 mg l^{-1} suspended sediments at 27°C, and with no addition of OC (+0 mg OC l^{-1} FSW).

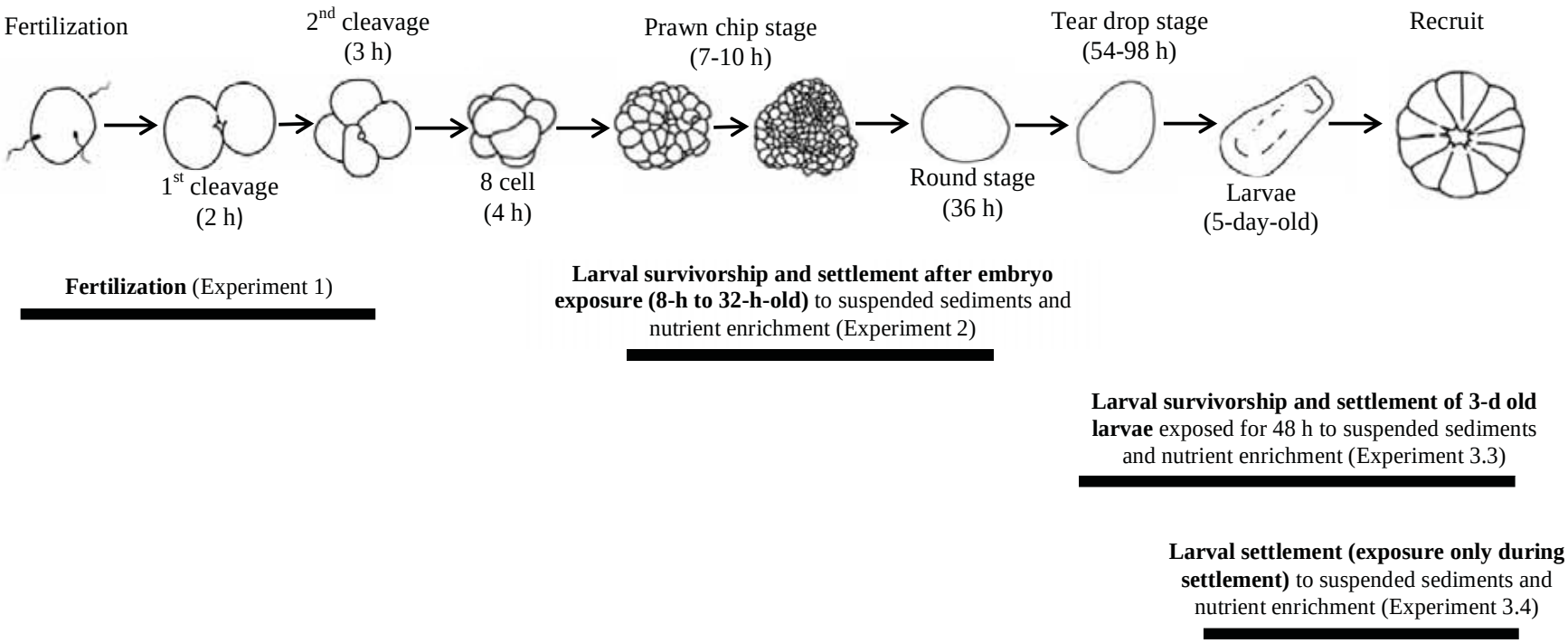


Figure 3.1: Experiments performed with early life history stages of *Acropora tenuis* exposed to different concentrations of suspended sediments (SS: 0, 5, 10, 30 and 100 mg l^{-1}) and a) different levels of nutrient enrichment (low, medium, high), or b) constrasting temperatures (27, 30 and 32°C) treatments. Black bars indicate the processes or stages involved in each experiment (modified from Jones et al. 2015).

To characterize water quality in the different treatment combinations, concentrations of suspended sediments, total organic carbon, dissolved organic carbon, particulate organic carbon, total dissolved phosphorus, dissolved organic nitrogen, total particulate nitrogen, ammonium, nitrate and nitrite, were measured once in duplicate subsamples at the end of each incubation in each replicate (Schott bottles). Water quality samples were analyzed by the analytical services laboratory at AIMS following Schaffelke et al. (2012).

3.2.3. Experiment 3.1: Gamete fertilization under treatment conditions

To test the impacts of suspended sediments, nutrient enrichment and temperature on gamete fertilization, 5 levels of suspended sediments (0, 5, 10, 30 and 100 mg l^{-1}) were combined with either 3 levels of nutrient enrichment (+0, +0.3, or +0.6 mg OC l^{-1} FSW), or 3 levels of temperature (27, 30, and 32°C) to produce 30 experimental treatment combinations (15 combinations for the suspended sediments and nutrient enrichment experiment; 15 combinations for the suspended sediments and temperature experiment). For each treatment combination, twelve replicate chambers were prepared, each containing 25 ml of appropriately modified seawater in 50 ml clear polypropylene chambers. Eggs were added to half of the chambers (~200 eggs per chamber), and aliquots of the stock sperm mixture were added to the other half of the chambers to pre-expose gametes separately for 30 min before combining them to initiate fertilization. Chambers (a total of 180 across the 30 treatments) were transferred into temperature incubators at the designated treatment temperature (27°C for the suspended sediments and nutrient enrichment treatments, and 27, 30 and 32°C for the suspended sediments and temperature treatments, Table S3.2). After 30 min, the contents of each of the sperm and egg chambers were combined to initiate fertilization (*i.e.* 6 replicate chambers per treatment combination) and chambers were kept in the incubators for the duration of the experiment. The final sperm concentration was $5x10^4$ sperm ml^{-1}, being slightly suboptimal for maximum fertilization (Willis et al. 1997), thereby increasing the sensitivity of the assay (Marshall 2006, Ricardo et al. 2015). Every 30 minutes, containers were gently shaken to maintain suspended sediments at treatment levels (Table S3.4). When the second cleavage was observed (1.5 h after fertilization), 2 ml of zinc formalin fixative (Z-fix preservative, Anatech Limited) were added to terminate embryo development and preserve embryo integrity. Eggs and embryos were transferred to counting trays, and

fertilization success (proportion of eggs fertilized, Table S3.5) was assessed under a stereomicroscope.

3.2.4. Experiment 3.2: Larval settlement after embryo and larval exposure to treatment conditions

Embryos fertilized under control conditions were exposed to the 30 treatment combinations (15 suspended sediment and nutrient enrichment combinations; 15 suspended sediment and temperature combinations) from the early gastrula stage (8-h old embryos; "prawn chip" shape, Gilmour 1999) until they were ciliated larvae (~36-h old; Fig. 3.1). In a temperature-controlled room, 6 water bath tanks (400 l) were used to maintain seawater temperatures in experimental systems (27°C for the suspended sediment and nutrient enrichment treatments; 27, 30 and 32°C for suspended sediment and temperature treatments, Table S3.2). Each experimental system consisted of two polyethylene containers: 1) a sump tank (4 l), which contained an air-stone to keep the sediments in suspension and a pump to transfer the modified seawater up into the experimental tank at 20 ml s^{-1}; and 2) an experimental tank (5 l), which was at a height greater than that of the sump tank, and had an outflow pipe that operated as a siphon (Fig. S3.5a). The outflow pipe was covered with 160 µm plankton mesh and had an air-stone positioned beneath it to prevent loss of embryos. For each of the 30 treatments (suspended sediments and nutrient enrichment or suspended sediments and temperature), four replicate experimental systems were set up and ~250 embryos added to each experimental tank. Suspended sediment concentrations were derived from turbidity readings taken every 6 h in each experimental tank (Table S3.7).

After 28 h treatment exposure, larvae from each replicate tank were transferred to six-well polystyrene tissue culture plates (NuncTM, Denmark). Each well replicate contained 10 ml of FSW at 27°C and 10 larvae (n = 12 replicate wells for each suspended sediment and nutrient enrichment combination, and n = 24 replicate wells for each suspended sediment and temperature combination). Six-well plates were maintained at 27°C in a temperature-controlled room for the duration of the experiment. When larvae where 5-d old, 2-mm^2 chips of live crustose coralline algae (CCA) *Porolithon onkodes* were used to induce larval settlement and attachment (Heyward and Negri 1999). Chips were prepared using bone cutters 1 h before adding the larvae to the wells, and were obtained from a single 10 cm^2 fragment of CCA that had been maintained in a 400 l flow-

through tank at 27°C with low light intensity (60 μmol photons m^{-2} s^{-1} over a 12 h:12 h diurnal cycle). Special care was taken during the maintenance of CCA fragments (i.e. algae removal with a toothbrush when necessary), and their ability to induce settlement was tested 18 h before using them in the experiment by offering chips of the same fragment to larvae fertilized and reared under control conditions (n = 6 replicate wells, 10 larvae per well, settlement success = 97%). After 24 h, the number of settled and metamorphosed larvae in each well was recorded (Table S3.5).

3.2.5. Experiment 3.3: Larval survivorship and settlement following exposure of 3-d old larval to treatment conditions

For each of the 30 treatment combinations (15 suspended sediment and nutrient enrichment combinations; 15 suspended sediment and temperature combinations), six replicate 100 ml clear polystyrene chambers were prepared containing 80 ml of the appropriately modified seawater and 3-d old larvae (n = 20 larvae per replicate). Mechanical rollers at 0.3 revolutions s^{-1} (Fig. S3.6b) were used to maintain a constant suspension of the sediments throughout the experiment (Table S3.8). Rollers were kept inside temperature incubators to maintain the treatment temperatures (27°C for suspended sediments and nutrient enrichment; 27, 30 and 32°C for suspended sediments and temperature; Table S3.3). Larvae were exposed to the treatment conditions for 48 h, with one water change after 24 h. After exposure, larvae from each replicate were counted and transferred to six-well polystyrene tissue culture plates (NuncTM, Denmark, n = 6 replicate wells per treatment, n = 10 larvae per well). CCA chips (as above) were added to each well and settlement success was assessed after 24 h (Table S3.5).

3.2.6. Experiment 3.4: Larval settlement under treatment conditions

The experimental setup from Experiment 3.2 was used to expose 5-d old larvae to each of the 30 treatment combinations (15 suspended sediment and nutrient enrichment combinations; 15 suspended sediment and temperature combinations; n = 4 replicate experimental tanks per treatment; Tables S3.3, S3.9). Larvae (n = 150) were added to each experimental tank, which also contained 15 manufactured aragonite substrata (~2 cm in diameter, commonly used by aquarists) previously conditioned with CCA (Fig. S3.6a). The aragonite plugs were hung using a plastic coated wire attached to a grid that rested over the experimental tank. The CCA-colonized surface of each plug faced

downwards to prevent the accumulation of sediments on the CCA. After 24 h, the number of settlers on plug were assessed under a stereomicroscope (Table S3.5).

3.2.7. Data analysis

Generalized linear models (GLM) were used to assess changes in fertilization success, larval survivorship and settlement as a function of the three fixed factors: suspended sediments (numerical factor: 0, 5, 10, 30 and 100 mg l^{-1}), nutrient enrichment (categorical factor: low, medium, high organic nutrients) or temperature (categorical factor: control, low stress, moderate stress). Quasi-binomial errors and the log-link function were used when the model had overdispersion. All calculations were conducted using the package lme4 in R (R Development Core Team, 2016).

Data were further analyzed when more than one factor was significant (GLM), using nonlinear regression curves (four-parameter logistic models) using GraphPad Pism (v.7), to derive effective concentration point intercepts (i.e. EC_{50} values) for the various treatment combinations (Motulsky and Christopoulos 2003, Warne et al. 2014). All curves were tested for normality of the residuals and a replicate test was applied to assess goodness-of-fit. Absolute EC_{50} values were determined by interpolating from 50% of the 'top' (EC_{50}) best-fit parameter in the control temperature (27°C) or control nutrient concentration (low) treatments. In Experiment 3.2, 95% confidence intervals could not be determined for larval settlement success in the medium nutrient enrichment treatment because of ambiguity in the estimation of parameters.

3.3. Results

3.3.1. Suspended sediments, temperature and nutrient enrichment monitoring

Sediments were maintained in suspension throughout the 4 experiments with only minor deviations from the expected concentrations (Tables S3.4, S3.7, S3.8 and S3.9). Similarly, seawater was maintained at treatment temperatures with only minor deviations during the 4 experiments (Table S3.3). Addition of the nutrients to FSW increased concentrations of the water quality variables measured in each of the four experiments (Table S3.2). Nutrient concentrations varied after the incubations between experiments,

therefore nutrient enrichment treatments were designated as 'low', 'medium' and 'high' nutrient enrichment, corresponding to the addition of +0, +0.3, and +0.6 mg OC l^{-1} FSW.

3.3.2. Experiment 3.1: Gamete fertilization under treatment conditions

When suspended sediment concentrations were less than 10 mg l^{-1}, mean fertilization success was high (70 ± 21%, mean ± sd) across all nutrient enrichment and temperature treatment combinations (Fig. 3.2). In the absence of nutrient enrichment, the highest suspended sediment concentration (100 mg l^{-1}) reduced fertilization by a maximum of 59% in comparison to controls ($p_{\text{Suspended sediments}}$ = <0.001, Table 3.1, Fig. 3.2a). The addition of nutrients and its interaction with suspended sediments had no significant effect on fertilization success ($p_{\text{Nutrient enrichment}}$ = 0.113, $p_{\text{Suspended sediments and nutrient enrichment}}$ = 0.335, Table 3.1, Fig. 3.2a). Increments in suspended sediments and temperature both had significant detrimental effects on fertilization success ($p_{\text{Suspended sediments}}$ = <0.001, $p_{\text{Temperature}}$ = 0.039, Table 3.1, Fig. 3.2b). No interactive effects were observed ($p_{\text{Suspended sediments and temperature}}$ = 0.588, Table 3.1, Fig. 3.2b), indicating that when eggs were simultaneously exposed to elevated suspended sediments and temperature, impacts on fertilization were additive on a log scale. Declines in fertilization success for independent factors in comparison to the controls ranged from ~ 24% in the high temperature treatment (32°C) to 80% in the high suspended sediments treatment (100 mg l^{-1} suspended sediments). Thus suspended sediments had a greater impact on fertilization success than temperature (Table S3.10). Suspended sediments and temperature in combination resulted in a ~89% decline in fertilization in comparison to control conditions. The concentration of suspended sediments that caused fertilization success to be reduced by 50% (IC_{50}) decreased ~2-fold (from 37 to 18 mg l^{-1} suspended sediments, Fig. S3.11, Table S3.12) with rising temperatures (from 27 to 32ºC).

Life history stage	Dependent variable	Summary of findings	p-values					
			SS	Nut	SS x Nut	SS	Temp	SS x Temp
Gametes	3.1. Fertilization	1. SS decreased fertilization	**<0.001**	0.113	0.329			
		2. SS, Temp both decreased fertilization				**<0.001**	**0.039**	0.588
Embryos	3.2.a. Survivorship	1. No effect of SS or Nut	0.659	0.938	0.523			
		2. No effect of SS or Temp				0.078	0.416	0.809
	3.2.b. Settlement	1. SS, Nut both decreased settlement	**<0.001**	**<0.001**	0.577			
		2. SS, Temp both decreased settlement				**<0.001**	**<0.001**	0.112
Larvae	3.3.a. Survivorship	1. No effect of SS or Nut	0.444	0.135	0.784			
		2. No effect of SS or Temp				0.869	0.356	0.140
	3.3.b. Settlement	1. No effect of SS or Nut	0.613	0.448	0.487			
		2. Temp decreased settlement				0.269	**0.028**	0.271
Settlement	3.4. Settlement	1. No effect of SS or Nut	0.302	0.456	0.280			
		2. Temp decreased settlement				0.054	**0.001**	0.121

Table 3.1: Results of treatment effects on *Acropora tenuis* processes during early life history stages. Analyses are based on generalised linear models with different concentrations of suspended sediments (SS: 0, 5, 10, 30 and 100 mg l^{-1}), different levels of nutrient enrichment (Nut: low, medium, high) and contrasting temperatures (Temp: 27, 30, and 32 °C) as fixed factors. Significant relationships (at $p<0.05$) are printed in **bold**. Refer to Table S10 for more detailed information for each GLM analysis.

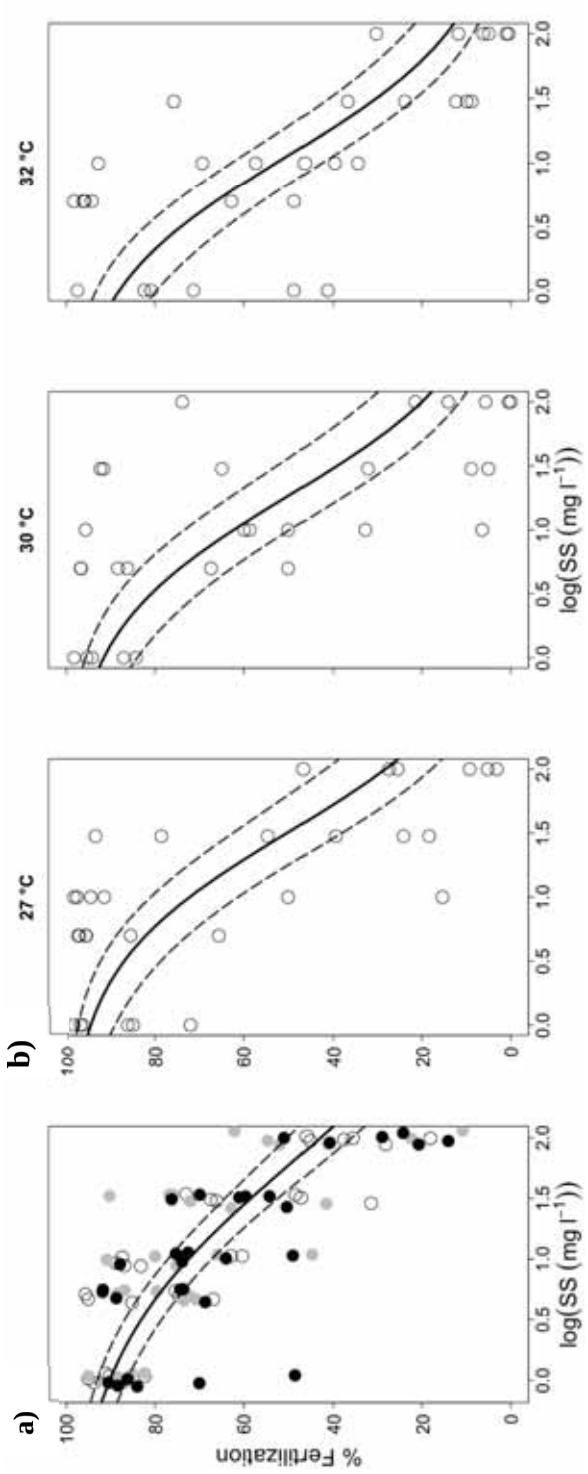


Figure 3.2: Percentage of fertilized eggs of *Acropora tenuis* exposed to different levels of suspended sediments (0, 5, 10, 30 and 100 mg l^{-1}) and a) nutrient enrichment [low (open circles), medium (grey circles), high (black circles)] at 27°C, or b) contrasting temperatures (27, 30, and 32°C) without organic nutrient enrichment. Solid lines indicate generalised linear model fits, while dashed lines are 95% confidence intervals. Points are jittered horizontally for clarity.

3.3.3. Experiment 3.2: Larval settlement after embryo and larval exposure to treatment conditions

Exposure of 8-h old embryos to both combinations of treatments for a period of 28 hours of embryological and larval development did not compromise their survivorship from the time they were 36-h old until settlement on day 5 ($p > 0.05$ for all factors and interactions, Table 3.1, Table S3.10). On average, 95 ± 6% of larvae survived across all treatments in the suspended sediment and nutrient enrichment treatments and 84 ± 15% in the suspended sediments and temperature treatments. Settlement was significantly reduced for embryos exposed to high suspended sediments, temperature or nutrient enrichment ($p < 0.001$ for all individual factors Table 3.1, Fig. 3.3, Table S3.10). None of the interactions were significant ($p > 0.05$ for both interactions, Table 3.1, Fig. 3.3, Table S3.10), indicating that the responses of larvae exposed as embryos simultaneously to elevated suspended sediments and nutrient enrichment or temperature were additive on a log scale. Suspended sediments reduced settlement by up to 43 and 55% (suspended sediments and nutrient enrichment and suspended sediments and temperature treatments respectively at 100 mg l^{-1}), nutrient enrichment by a maximum of 33% (Fig. 3.3a), while temperature reduced settlement by a maximum of 14% (Fig. 3.3b). Under both combinations of factors, suspended sediments had the greatest effect on larval settlement (Table S3.10). The concentration of suspended sediments that caused a reduction in larval settlement by 50% (IC_{50}) decreased with elevated nutrients and temperatures (Fig. S3.11, Table S3.12). A ~5-fold decrease in IC_{50} (from suspended sediments > 100 to 18 mg l^{-1}) was obtained when nutrient levels increased from low to high enrichment levels (S3.11 Fig., S3.12 Table), while temperature caused a ~1.5-fold decrease in IC_{50} (from suspended sediments 29 to 20 mg l^{-1}) with increasing temperature (from 27 to 32ºC, Fig. S3.11, Table S3.12).

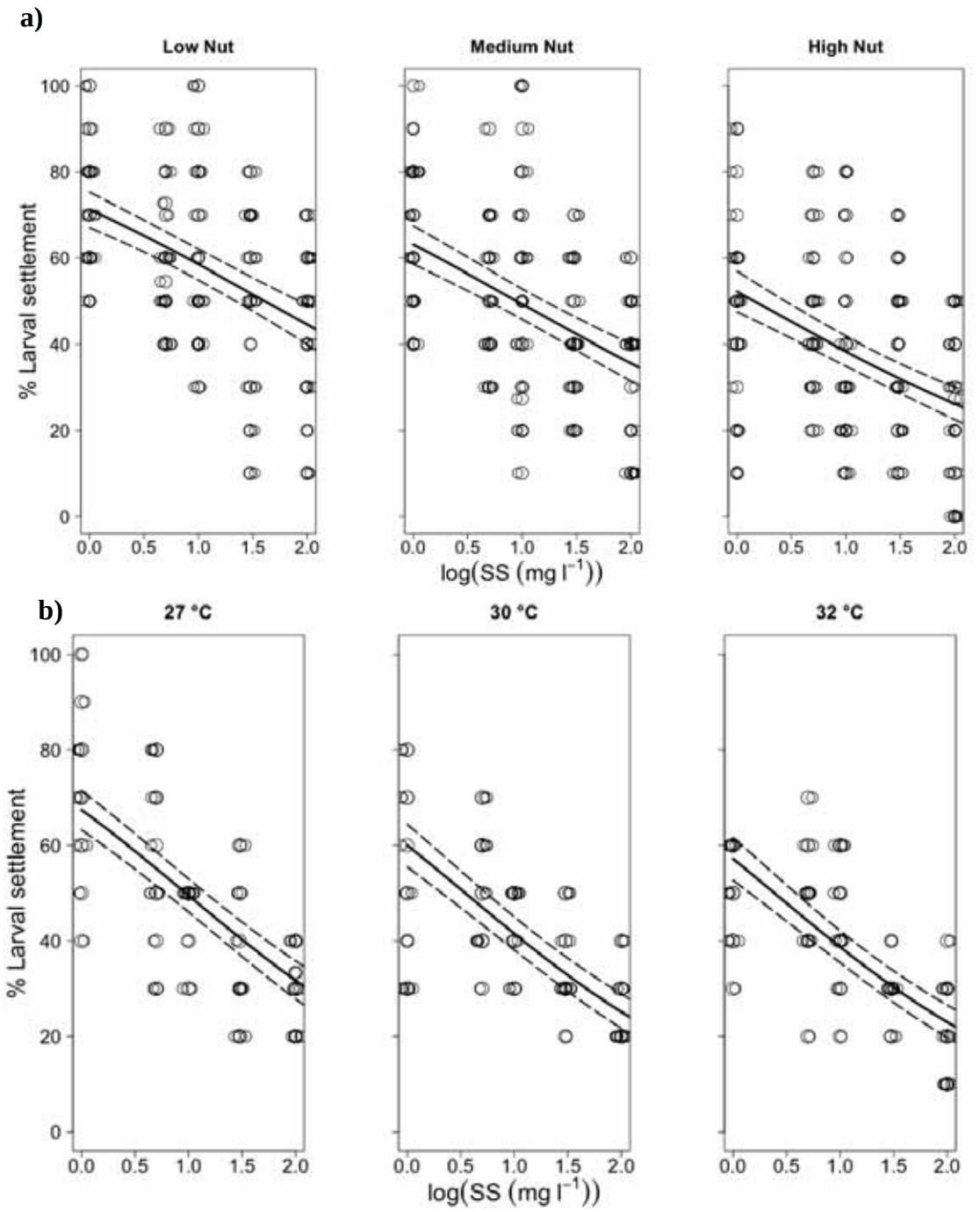


Figure 3.3: Experiment 3.2: percentage of *Acropora tenuis* larvae settlement success, after 8 h old embryos were reared for 28 h (until ciliated) under different concentrations of suspended sediments (0, 5, 10, 30 and 100 mg l^{-1}) and a) nutrient enrichment (low, medium, high) at 27°C, or b) contrasting temperatures (27, 30, and 32°C) without organic nutrient enrichment. After the 28 h exposure larvae were maintained and settled under control conditions (0 mg l^{-1} suspended sediements, low nutrient enrichment and 27°C). Solid lines indicate generalised linear model fits, while dashed lines are 95% confidence intervals.

3.3.4. Experiment 3.3: Larval survivorship and settlement following exposure of 3-d old larval to treatment conditions

On average, a high proportion of ciliated larvae (97 ± 4% in the suspended sediment and nutrient enrichment treatment; 84 ± 22% in the suspended sediment and temperature treatment) of the ciliated larvae (3-d old) survived the 48 h treatment exposures, and there were no significant effects of suspended sediments, nutrient enrichment or temperature on larvae survivorship ($p > 0.05$ for all individual factors and interactions, Table 3.1, Table S3.11). In contrast, their subsequent settlement success was affected by high temperatures ($p_{Temperature} = 0.003$, Table 3.1, Fig. 3.4a, Table S3.10), reducing it by 18% at 32°C in comparison to control conditions. Suspended sediments and nutrient enrichment, and combinations of these two pressures had no significant effect on larval settlement ($p > 0.05$ for both factors and their interaction, Table 3.1, Table S3.10).

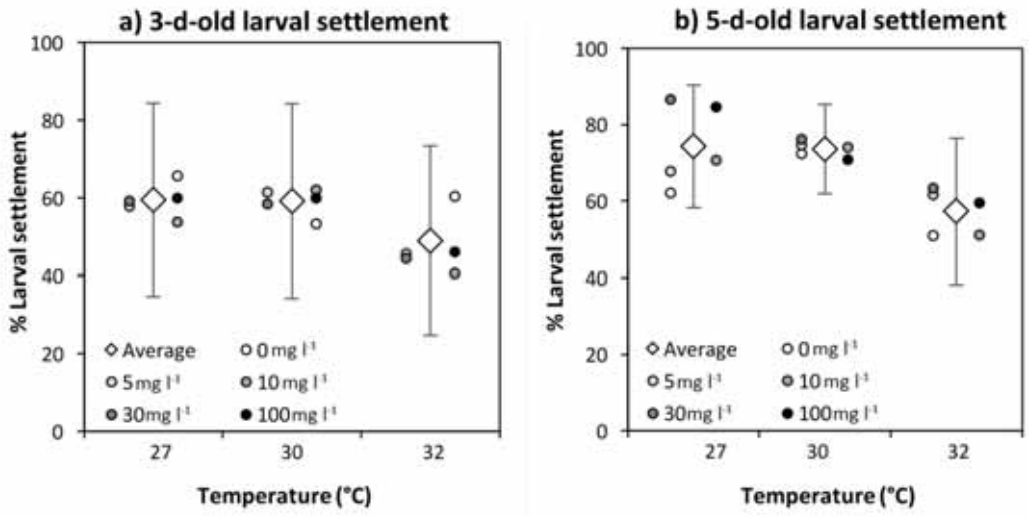


Figure 3.4: a) Experiment 3.3: settlement of 3-d old larvae previously exposed for 48 h to suspended sediments (0, 5, 10, 30 and 100 mg l^{-1}) and contrasting temperatures (27, 30, and 32°C). After the exposure larvae were settled under control conditions (0 mg l^{-1} suspended sediments, low nutrient enrichment and 27°C). b) Experiment 4: settlement of 5-d-old larvae exposed only during settlement to suspended sediments (0, 5, 10, 30 and 100 mg l^{-1}) and contrasting temperatures (27, 30, and 32°C). Diamonds indicate means at each temperature level (error bars are standard deviation), and circles indicate means for each suspended sediments treatment at the corresponding temperature treatment.

3.3.5. Experiment 3.4: Larval settlement under treatment conditions

Mean settlement success of larvae decreased significantly with temperature ($p_{Temperature} = 0.001$, Table 3.1, Fig. 3.4b, Table S3.10), whereas settlement success was not affected by suspended sediments or nutrient enrichment, nor by interactions of these factors ($p > 0.05$ for both factors and their interactions, Table 3.1, Table S3.10). The maximum settlement success (74 ± 16%) was obtained at 27°C, while the minimum success (57 ± 19%) was observed at 32°C, decreasing by 23% at the highest temperature in comparison to control conditions.

3.3.6. Comparison of the effects of suspended sediments, temperature and nutrient enrichment across processes occurring in early life stages of *A. tenuis*

The effects of suspended sediments, in combination with temperature or nutrient enrichment, on key processes in early life history stages of *A. tenuis* were additive (none of the interactions were significant) when more than one factor had a significant effect (Table 3.1). Fertilization success and settlement of embryos that were exposed to the treatments during part of their development were the processes most affected, with suspended solids being the factor causing the greatest impacts (Fig. 3.5a). Nutrient enrichment only affected the settlement of larvae exposed to treatment conditions during part of their embryo development (Fig. 3.5b) and the magnitudes of these effects were modest compared with those caused by suspended sediments. Temperature affected more processes (Fig. 3.5c: fertilization, settlement after embryo and larval exposure to temperature treatments and settlement under temperature treatments) than the other pressures, but the sizes of these effects were less than those caused by suspended sediments (Fig. 3.5a). Overall, the combination of suspended sediments aggravated by high temperatures poses the greatest risk to population replenishment of *A. tenuis*, since more processes were affected by these stressors, and when both stressors had a significant effect, their effects were additive.

Figure 3 5: Response of the different processes during the early stages of *Acropora tenuis* exposed to: a) suspended sediments (0, 5, 10, 30 and 100 mg l^{-1}), b) nutrient enrichment (low, medium, high), and c) contrasting temperatures (27, 30, and 32°C). Bars represent the size of the response of each level treatment (main effects) compared to control conditions (0 mg l^{-1} suspended sediements, low nutrient enrichment and 27°C). Stars indicate the effect of the factor was statistically significant ($p < 0.05$).

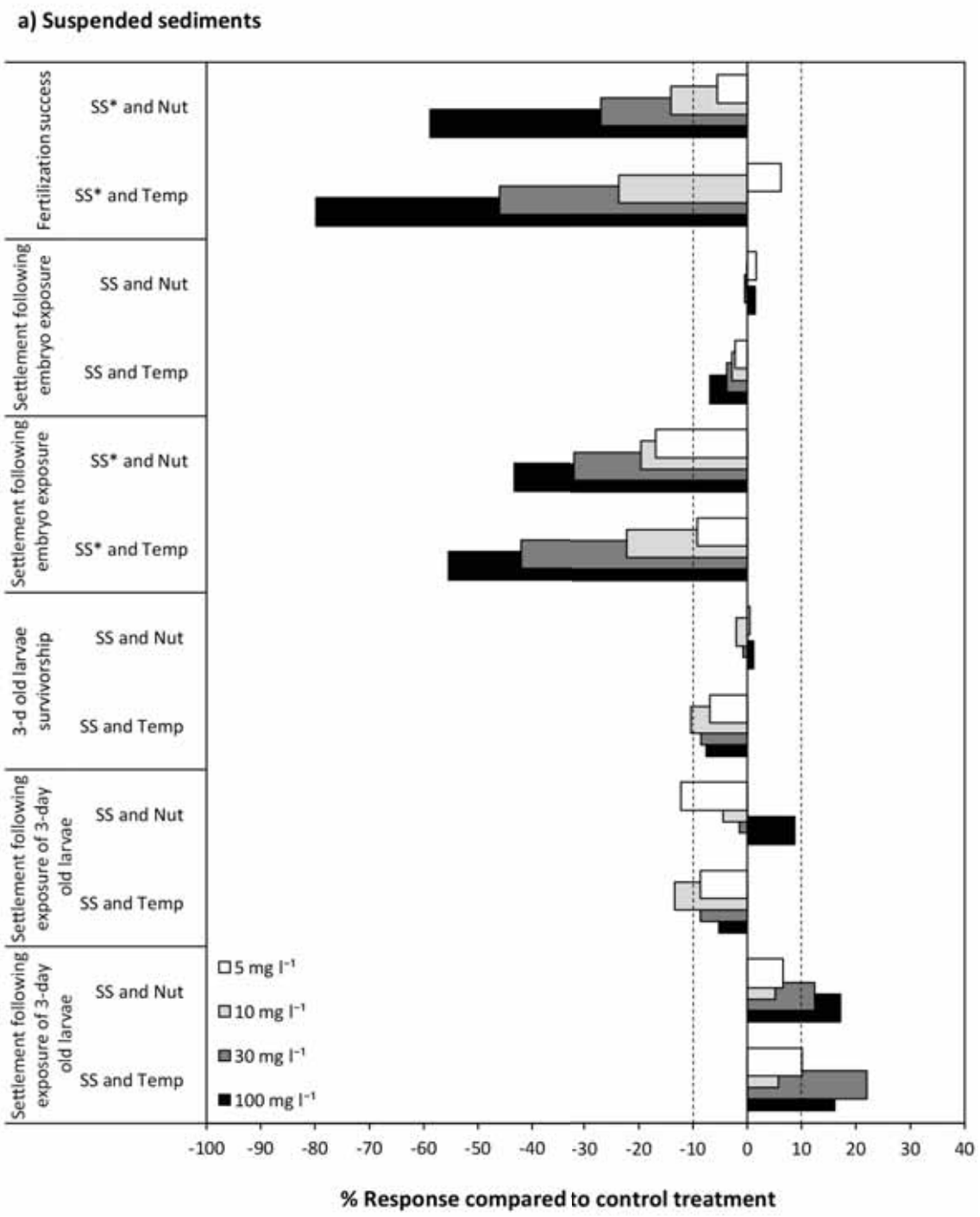
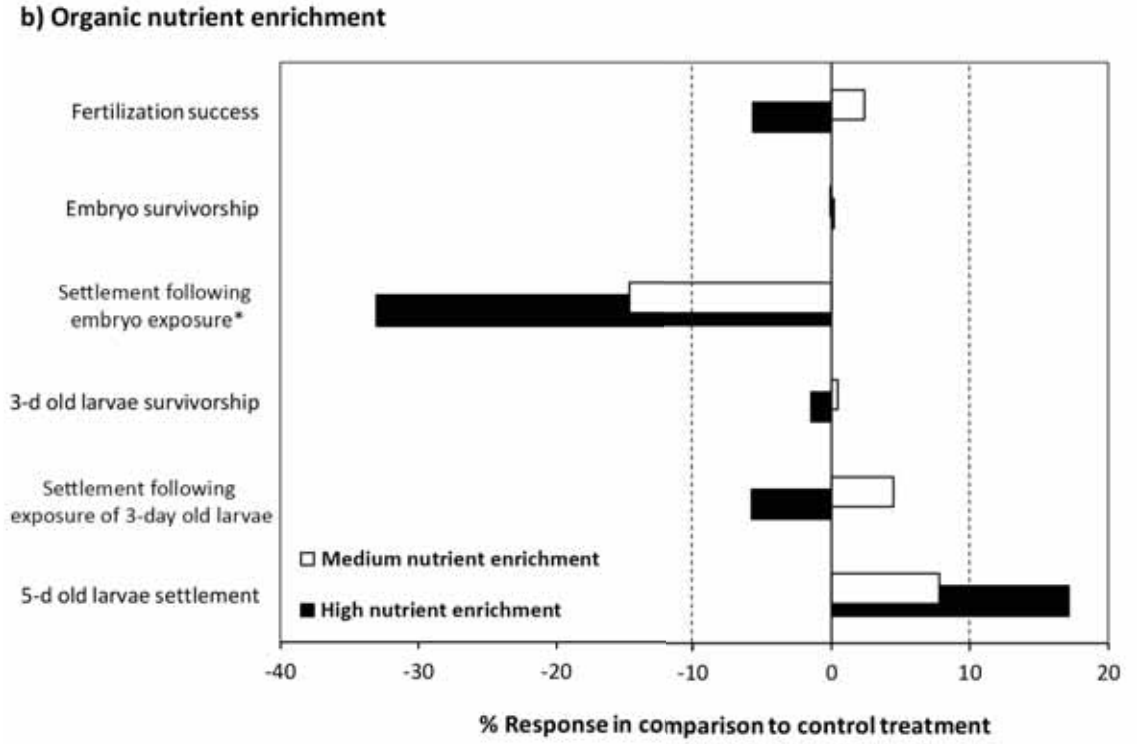
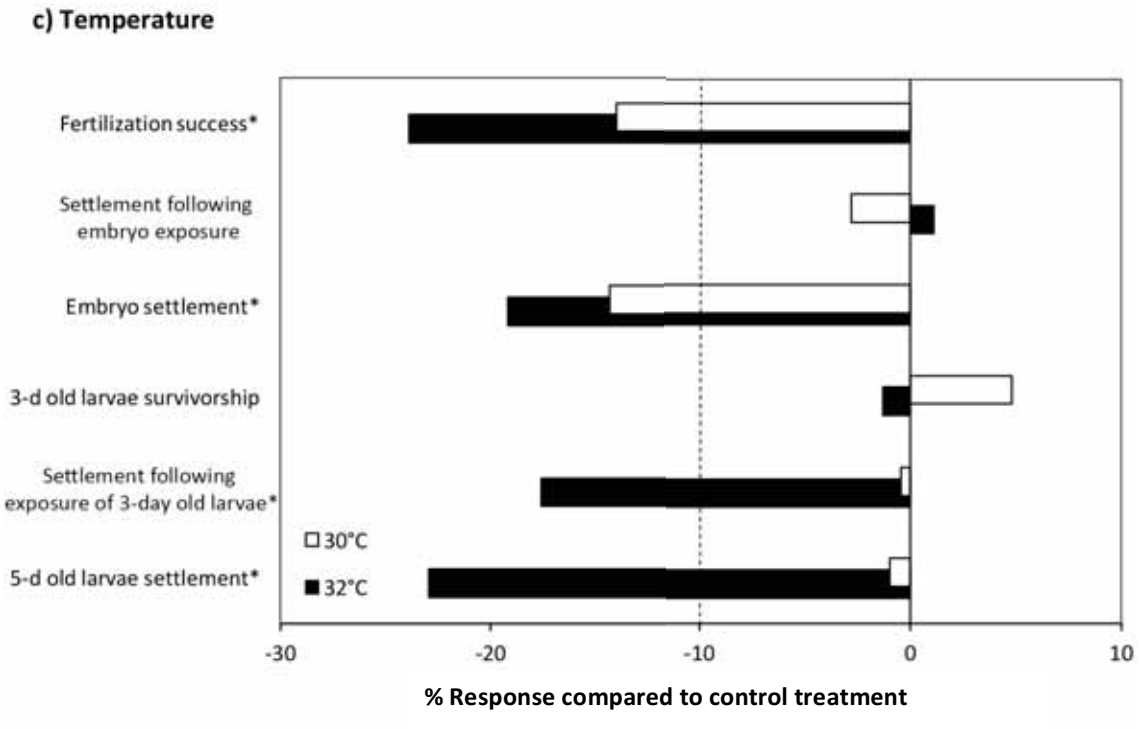


Figure 3.5 (continuation): Response of the different processes during the early stages of *Acropora tenuis* exposed to: a) suspended sediments (0, 5, 10, 30 and 100 mg l^{-1}), b) nutrient enrichment (low, medium, high), and c) contrasting temperatures (27, 30, and 32°C). Bars represent the size of the response of each level treatment (main effects) compared to control conditions (0 mg l^{-1} suspended sediements, low nutrient enrichment and 27°C). Stars indicate the effect of the factor was statistically significant ($p < 0.05$).





3.4. Discussion

This study illustrates that developmental processes occurring during the early life history stages of *Acropora tenuis* differ considerably in their sensitivity to increasing levels of suspended sediments, nutrient enrichment and temperature. Fertilization and embryo development were more sensitive to suspended sediments than to high temperatures and nutrient enrichment, while larval development (following cilia acquisition) and settlement were only affected by thermal stress. The combined pressures caused no interactive responses in any of the processes evaluated, indicating additivity of responses when more than one factor had a significant effect. The effects of suspended sediments, nutrient enrichment and temperature were most pronounced on processes occurring during (i) the earliest life history stages (fertilization and embryo development), when cell division, specialization and embryo development takes place (Harrison and Wallace 1990), and (ii) larval settlement and the metamorphosis of motile larvae to a sessile polyps, which involves extensive tissue remodeling (Grasso et al. 2011). These results suggest that environmentally realistic levels of suspended sediments or high temperatures during the nights of spawning can have considerable negative impacts on the reproductive success of *A. tenuis*. Unfavorable conditions due to local (*i.e.*, wind, waves, currents, flooding or dredging) or global (*i.e.*, ocean warming) factors that increase suspended sediments and temperatures during the narrow time window when gametes fertilization, embryo development and larval settlement occurs could result in reduced reproductive success of *A. tenuis* populations for that year.

Studies examining the effects of suspended sediments on coral gamete fertilization have reported decreases in fertilization success for several species (Gilmour 1999, Humphrey et al. 2008, Erftemeijer et al. 2012b, Ricardo et al. 2015). The primary mechanism by which suspended sediments affect gamete fertilization has recently been described as sperm limitation in *A. tenuis*, whereby sperm coagulates with suspended particles, lowering the sperm concentrations in the vicinity of the eggs, hence reducing the number of sperm-egg encounters and subsequently reducing fertilization success (Ricardo et al. 2015). The silt-sized sediments used in the present study are extremely cohesive and colloidal due to their physical and chemical characteristics (*e.g.* small grain sizes), readily forming flocs (Bainbridge et al. 2012, Bainbridge et al. 2015) that are likely to attract and capture coral sperm, explaining their observed impact on fertilization success.

The effects of high temperatures on fertilization success reported here are consistent with previous studies that documented reduced fertilization success under elevated temperatures (Omori et al. 2001, Negri et al. 2007). The mechanisms by which elevated temperatures affect fertilization may include a reduction in the sperm flagella motility, reducing the number of sperm-egg interactions (Omori et al. 2001), or impairment of biochemical processes involved in early cell division (Lam et al. 2015). Nutrient enrichment had no significant effect on fertilization success in this study, however, I previously reported detrimental effects of nutrient enrichment on fertilization success of *A. tenuis* after the exposure to combined nutrient enrichment and temperature stress (Humanes et al. 2016). However, the only common nutrient treatment that were common between studies (suspended sediments: 0 mg l^{-1}, temperature: 27°C, nutrient enrichment: low, medium and high) had no significant effects on fertilization success in either case (S13 Table).

This study is the first to examine the effects of suspended sediments during the last stages of embryo development (8 to 36-h old embryos) and their later effects on larval survivorship and settlement. Larvae survivorship was the only process that was not affected by the exposure to the treatments, even when exposure was performed before larvae developed cilia. However, embryo exposure to suspended sediments significantly reduced larval settlement success, revealing the latent effects that treatments can have on later developmental processes. The mechanism by which suspended sediments act on coral embryo development and their later impact on coral larvae settlement has not been studied previously; however, similar studies have been performed on other taxa. Changes in the gill structure of clownfish larvae were suggested to be the result of mucous discharge, growth of bacteria or the abrasive damage caused by the collision of suspended particles (Hess et al. 2015). Similarly, the production of mucus, enhancement of bacterial communities and the physical damage of regions involved in cue recognition and settlement of coral larvae could potentially affect their settlement success, aspects that merits further research.

Past studies of larval settlement under conditions of sediment deposition indicate that sedimentation can mask settlement cues, obstruct settlement substrata and smother recruits (see studies reviewed in Jones et al. 2015b). Therefore, most recruits are found on vertical and downward facing surfaces or on the walls of cracks in the substrata in sediment-rich environments (Babcock and Mundy 1996, Raimondi and Morse 2000, Mizrahi et al. 2014, Doropoulos et al. 2015). Since most field studies record coral

recruitment during different time frames (from several weeks up to 12 months after spawning, Humanes and Bastidas 2015), it has remained unresolved whether suspended sediments reduce settlement or decreases post-settlement survivorship (Te 1991, Fabricius 2005). My results show that under experimental conditions, high concentrations of suspended sediments (i.e. 100 mg l^{-1}) do not affect larval survival and settlement success if sediments are not allowed to accumulate on the available substrata. However, although there may be no direct effect of high turbidity on settlement, sediment deposition is likely to reduce the availability of suitable substrata and lower overall settlement and recruitment success (Hodgson 1990, Perez et al. 2014).

Suspended sediments together with temperature were the factors that affected the greatest number of reproductive processes for hard corals and had the greatest proportional impacts on most life stages. In addition, the co-occurrence of temperature with suspended sediments reduced thresholds of suspended sediments (IC_{50}). Conversely, elevated sediments are likely to affect thermal thresholds for early coral stages (unless these impacts are ameliorated by shading, which is uncertain for aposymbiotic gametes and larvae). Since ocean warming affects marine ecosystems at a global scale, management strategies should be directed towards minimizing dredging activities in coastal areas and improving water quality (i.e., suspended sediments) associated with river discharges during periods of coral spawning, in order to maintain population replenishment success in inshore reefs. Assessing the risks associated with the simultaneous effects of suspended sediments and high temperatures on inshore reefs of the GBR requires further studies to determine the impacts of more sediment types in combination with temperature stress on thresholds for sensitive early life stages of corals and other tropical species. These climate-adjusted thresholds can then be incorporated into improved spatial models in order to generate effective risk maps for identification of vulnerable habitats and opportunities for management intervention.

My results confirm that high levels of suspended sediments during periods of coral spawning affect the final reproductive success of *A. tenuis*, and indeed, are likely to affect the reproductive success of the majority of reef-building corals, which are broadcasters that release gametes synchronously during a few nights each year. I found that suspended sediments in the presence of high temperatures was the most detrimental combination of stressors. My results underscore the importance of managing local pressures, such as elevated sediments and nutrients inputs, to ameliorate the impacts of climate change on sensitive and ecologically important reproductive processes. The effects of suspended

sediments and high temperatures are likely to further increase in magnitude and change from additive to synergistic if co-occurring with additional stressors (e.g. organic nutrient enrichment, Crain et al. 2008). Complex interactions among cumulative stressors are becoming more common on inshore reefs affected by local and global stressors (Great Barrier Reef Marine Park Authority 2014), and pose a significant risk for maintaining successful reproductive output required for ongoing replenishment of hard coral populations.

Chapter 4: Experimental investigation into the effects of suspended sediments and nutrient enrichment on juvenile corals

4.1. Introduction

The scale of coral reef degradation resulting from anthropogenic impact is the subject of wide-ranging debate amongst scientists, advocates, managers and industry stakeholders. Nearly 25% of coral reefs globally are threatened by decreasing water quality, characterised by increasing loads of sediments, nutrients and pollutants from terrestrial runoff associated with coastal development, dredging, deforestation and agriculture (Burke et al. 2011). Declines in coastal water quality have been reported to cause: increases in macroalgal cover (Fabricius 2005), reductions in coral biodiversity (De'ath and Fabricius 2010); proliferation of macro-bioeroders that weaken the structural integrity of coral reefs (Le Grand and Fabricius 2011), increases in the frequency and severity of coral diseases (Bruno et al. 2003), and changes in the composition of biofilms that provide conditioned surfaces for larval settlement and metamorphosis of many sessile organisms (Wieczorek and Todd 1998, Webster et al. 2004, Sawall et al. 2012).

Field and laboratory studies have shown that, individually, sediments and nutrients can both have negative impacts on corals. Deleterious effects of high concentrations of suspended sediments on corals include reductions in gamete fertilization success and larval settlement (Gilmour 1999, Jones et al. 2015b, Ricardo et al. 2015, Chapter 3), shifts in the dominance of energy acquisition from phototrophy to heterotrophy (Anthony and Fabricius 2000), altered colony morphology, and decreases in growth and survivorship (Anthony and Fabricius 2000, Jones et al. 2016). High levels of nutrients also negatively affect all coral life history stages, including reducing gamete production (Ward and Harrison 2000, Loya et al. 2004), fertilization success (Humanes et al. 2016) and calcification rates, as well as increasing the ratio of symbiont to host cells, which can increase the vulnerability of this

symbiotic partnership to disruptions (bleaching) associated with high sea temperatures (Marubini and Davies 1996, Cunning and Baker 2012, Vega Thurber et al. 2014).

In combination, nutrient-enriched sediments in inshore areas influenced by river runoff (Brodie et al. 2012) can exacerbate the already detrimental effects of suspended and deposited sediments on corals, further reducing larval settlement success, and adult survivorship and growth rates (Fabricius 2005, Weber et al. 2006, Chapter 3). The introduction of high concentrations of dissolved and particulate inorganic nutrients, especially nitrogen and phosphorus (Furnas 2003, Kroon et al. 2012), also promotes the formation of phytoplankton blooms that rapidly take up dissolved inorganic nutrients and transform them into particulate organic nutrients (Grossart and Ploug 2001, Brodie et al. 2010). Particulate organic nutrients reduce water clarity and stimulate microbial communities that exude mucopolysaccharides (Angly et al. 2016) and form aggregates with sediments that compromise coral juveniles and adults survivorship when deposited over their tissues (Fabricius et al. 2003a, Weber et al. 2012).

The Great Barrier Reef (GBR), the World's largest coral reef system, is located adjacent to tropical catchments along the North Queensland coast of Australia that have been modified by extensive agricultural developments. At present, rivers discharge an estimated 17 million tonnes of suspended sediments, along with 80,000 tonnes of nitrogen and 16,000 tonnes of phosphorous annually, a 3-8-fold increase compared to pre-European settlement (McCulloch et al. 2003, Kroon et al. 2012). Over 30 major rivers discharge sediments and nutrients into the GBR lagoon during the wet season (December-March), simultaneously introducing dissolved and particulate organic and inorganic nutrients together with fine terrigenous sediments (Fabricius et al. 2014). Fine sediments then undergo repeated cycles of deposition and resuspension at bathymetry less than 20 m (Fabricius et al. 2013b), until they are eventually deposited either on the deeper seafloor below the reach of storm waves, or in north-facing coastal embayments (Larcombe et al. 1995, Wolanski et al. 2005). Consequently, high concentrations of suspended sediments are commonly found throughout the year in the shallow GBR lagoon, and their effects on the structure and function of these inshore marine ecosystems remains of great concern (Schaffelke et al. 2005, Brodie and Waterhouse 2012).

Although there has been a significant body of research on the impacts of enriched suspended or deposited sediments on fertilization, larval survivorship and settlement (Fabricius et al. 2003, Humphrey et al. 2008, Chapter 3), and on adult stages of scleractinian corals (Fabricius and Wolanski 2000, Weber et al. 2006, Weber et al. 2012, Liu et al. 2015), the effects on juvenile corals in the months following settlement remain unknown. This represents a significant knowledge gap, particularly as: i) sediment and nutrient discharges into coastal areas are recognized as a growing problem worldwide (Syvitski et al. 2005); ii) juvenile growth and survivorship rates play a key role in the maintenance and replenishment of coral populations (Ritson-Williams et al. 2010); iii) early life history stages of corals are typically considered more sensitive to environmental change and pollution than adult stages (Fabricius 2005); and iv) scleractinian corals are the main ecosystem engineers of coral reefs (Bellwood and Hughes 2001).

To improve current understanding of the effects of nutrient-enriched suspended sediments on juvenile corals, I performed a series of controlled laboratory exposures over 40 days. I compare the effects of non-enriched and enriched sediments on juveniles of three common coral species on inshore reefs of the GBR and throughout the tropical Indo-Pacific (*Acropora tenuis*, *Acropora millepora* and *Pocillopora acuta*). Comparison of the effects of treatments on juvenile survivorship and growth, respiration and photosynthesis, and on symbiont quantum yields provide insights into the vulnerability of coral juveniles to nutrient-enriched suspended sediments commonly associated with runoff events in inshore areas.

4.2 Materials and methods

4.2.1 Spawning, gamete collection and larval settlement

Gravid colonies (> 20 cm diameter) of the broadcast spawning corals *A. tenuis* (Dana 1846) and *Acropora millepora* (Ehrenberg, 1834) were collected from Davies Reef (19° 06’S, 146° 51’E) at ~6 m depth on the 6th of November 2014, and colonies of the brooding coral *Pocillopora acuta* (Lamarck, 1816) were collected from the same location on February 2015, under permit G12/35236.1 issued by the Great Barrier Reef Marine Park Authority. All three species have branching growth forms and are zooxanthellate corals, meeting much of their energy demands through photosynthesis by endosymbiotic *Symbiodinium* communities.

Colonies were transferred to outdoor flow-through, temperature-controlled aquaria, with temperature set to the reef conditions on the day of collection (27°C) in the National Sea Simulator (SeaSim) at the Australian Institute of Marine Science (AIMS). Following spawning of 11 colonies of *A. tenuis* and 13 colonies of *A. millepora* colonies (on days 5 and 8 after full moon, respectively), egg-sperm bundles were gently scooped from the surface of aquaria. Eggs were separated from sperm using a 100 µm mesh filter and washed five times in FSW (0.2 µm filtered sea water), and then cross-fertilized in bulk larval cultures, as described by Negri and Heyward (2000). Larvae were reared in 500 l flow-through tanks using 1 µm-filtered seawater at 27°C. To collect larvae from the brooding coral *P. acuta*, 15 colonies were isolated in 25 l flow-through tanks with 100 µm mesh collectors positioned at outflows, which collected larvae released between the 22nd and 25th of February 2015. Artificial aragonite substrata (~2 cm in diameter), commonly used by aquarists (Oceans Wonders LLC) and overgrown with crustose coralline algae (CCA), were offered to larvae of the three species as settlement substrata. The resulting recruits were reared in flow-through tanks at 27°C until the beginning of the experiment on 13th May 2015 (188 days for *A. tenuis*, 185 days for *A. millepora*, and 78 days for *P. acuta*).

4.2.2 Experimental design and treatment types

Juvenile colonies of all three species were exposed for 40 days to eight treatments, including four levels of suspended sediments (0, 10, 30 and 100 mg l^{-1}) and two levels of nutrient enrichment (+0, and +0.6 mg organic carbon l^{-1} FSW) in a fully crossed experimental design. Treatments mimicked the impact of terrestrial runoff events or dredging activities that simultaneously introduce nutrients and fine-sized particle sediments into inshore reef waters. Nutrients and sediments were collected at 2 m depth from Orpheus Island (18° 36'S, 146° 29'E) and transported to AIMS two weeks before starting treatment exposures.

Sediments were wet-sieved to obtain fine particles (mean ± sd. particle size: 7.3 ± 1.5 µm, 95% <20 µm), and kept in 60 l flow-through seawater tanks at 27°C until experiments commenced. Inshore organic and inorganic nutrients were collected with a plankton net (mesh size 100 µm), sieved to remove large fragments (> 26 µm), homogenized with a blender, and frozen in aliquots until use.

Suspended sediment concentrations (0, 10, 30 and 100 mg l^{-1}) were verified using a nephelometer calibrated with the same sediments (TPS 90FL-T, Fig. S4.1). Sediments were added to FSW, and then agitated manually to estimate turbidity in Nephelometric Turbidity Units (NTU). Experimental suspended sediment concentrations were chosen to represent the range of *in situ* water quality measurements recorded on inshore GBR reefs and in association with dredging projects. Concentrations up to 5 mg l^{-1} have been recorded under calm conditions on inshore reefs (Macdonald et al. 2013), between 5 and 30 mg l^{-1} after storms and river plumes, and up to 100 mg l^{-1} close to dredging activities (Thomas et al. 2003, Stoddart and Anstee 2005, Jones et al. 2015a, Ricardo et al. 2015).

The nutrient enrichment treatment was prepared by augmenting sediments with 0.6 mg l^{-1} FSW of organic carbon (OC) as plankton (as prepared above). Decaying natural plankton was used in order to maintain a realistic stoichiometric composition of organic and inorganic nutrients and trace elements present in inshore reefs, a method previously used for studying the effects of nutrient enrichment on hard corals (Fabricius et al. 2003a, Weber et al. 2012, Humanes et al. 2016, Chapter 3). Nutrient concentrations were based on *in situ* water quality measured in GBR lagoon waters (Kroon et al. 2012, Schaffelke et al. 2012, Waters et al. 2014).

4.2.3 Experimental setup

Eight custom-made 60 l stock tanks were used to prepare the modified seawater treatments, which were then mixed to produce four levels of suspended sediments (0, 10, 30 and 100 mg l^{-1}), each combined with two levels of nutrient enrichment (+0, or +0.6 mg OC l^{-1} FSW). Light intensities in stock treatments were 200 µmol photons m^{-2} s^{-1} over a 12 h:12 h diurnal cycle (Fig S4.2). Treatments were prepared on a daily basis by adding the corresponding amounts of sediments and nutrients to FSW. Air stones were used to maintain the sediments in suspension in the stock tanks, and an Eheim 1260 l h^{-1} pump (Eheim 1260: Eheim GmbH, Germany) was used to pulse the modified seawater (for 10 min every 90 min, approximately 2 l in total) into the treatment tanks (n = 3 tanks per treatment) via 4 mm hose (6 turnovers per day).

Exposures were conducted in 24 purpose-built, round-bottomed glass tanks (4 l) that were positioned below the stock tanks (Fig S4.2). A Vortech MP10 pump, positioned on the bottom in the center of each experimental tank, was used to keep sediments suspended. Aragonite substrata with attached juveniles were suspended vertically ~3 cm below the water surface to prevent sediment accumulation on juveniles. Lids of clear PVC helped stabilize temperatures and salinity. Light intensity was adjusted above each tank so all juveniles were exposed to 60 μmol photons m^{-2} s^{-1} over a 12 h:12 h diurnal cycle. The number of juveniles placed in each replicate tank depended on how many had survived the 3-6 month period post-settlement: 9-10 juveniles per tank for *A. tenuis*, 16-18 for *A. millepora,* and 20-22 for *P. acuta*.

Suspended sediment concentrations in each experimental tank were characterized daily based on turbidity readings (Table S4.3). Dissolved organic carbon, particulate organic carbon, total dissolved phosphorus, total particulate phosphorous, dissolved organic nitrogen, total particulate nitrogen, ammonium, nitrate, and nitrite were measured once per week in duplicate subsamples from the stock feeder tanks (Table S4.4). Water samples were analyzed by the analytical services laboratory at AIMS following Schaffelke et al. (2012). Nutrient treatments were designated as 'low' and 'high' nutrient enrichment, corresponding to the addition of +0, and +0.6 mg OC l-1 FSW. The treatment with 0 mg l^{-1} suspended sediments and low concentration of nutrients was designated the control.

4.2.4 Responses of juveniles to nutrient-enriched suspended sediments

Survivorship and growth: Juvenile survivorship was assessed every 3 to 4 days, with mortality defined as the point in time when live tissue was no longer present. Survivorship was expressed as the proportion of colonies within each tank that survived to the end of the experiment (day 40) in relation to the number of juveniles at the beginning of the experiment (day 1). Images of each juvenile were taken at the start of the experiment using a digital camera (Leica MC170) connected to a stereomicroscope. The area of live tissue on each juvenile colony was measured with the program ToupView 3.7. Initial size (S_{t1}) of juveniles varied between species; juveniles of *A. tenuis* and *A. millepora* had a similar size range (1.34 ± 0.84 and 1.49 ± 1.25 mm^2 respectively; average ± sd), whereas *P. acuta* juveniles were

considerably larger (18.5 ± 12.0 mm^2). Growth was estimated as the proportional change in size (ΔS) after the exposure (S_{t2}) using the formula $\Delta S = (S_{t2} - S_{t1})/ S_{t1}$.

Photochemical efficiency of symbionts: The quantum yields of *Symbiodinium* communities associated with juvenile corals were measured by pulse amplitude modulation (PAM) fluorometry. Maximum quantum yield of photosystem II (PSII) in dark-adapted samples represents the proportion of available light that can be photochemically quenched. Reductions in this parameter are indicative of photooxidative stress and damage to PSII (Jones et al. 1999). Effective quantum yield, as measured on illuminated samples, was used to estimate the efficiency of photochemical energy conversion within PSII under a given light intensity (Genty et al. 1989). Higher values of effective quantum yield represent more efficient use of incident radiation and, all other factors being equal, higher rates of photosynthesis (Finelli et al. 2005). Measurements of quantum yields were made using a Maxi Imaging PAM Fluorometer (I-PAM, Walz GmbH, Germany), which measures the fluorescence of a selected area of interest in the image (i.e., the juvenile). Measurements were performed on day 39, by placing all surviving juveniles from each treatment tank into a 0.5 l container filled with FSW. Juveniles were dark-adapted for one hour prior to each saturation light pulse (gain = 2, intensity = 1, saturation pulse = 8). Maximum quantum yield was calculated using the formula $F_v/F_m = (F_m - F_0)/F_m$, where F_v = variable fluorescence, F_m = maximum fluorescence under dark adaptions, and F_0 = minimum fluorescence. Effective quantum yields were measured while juveniles were illuminated with an actinic light 20 µmol photons m^{-1} s^{-1} and calculated using the formula $\Delta F/F_m' = (F_m' - F)/F_m'$, where F_m' = maximum fluorescence and F = fluorescence yield, both measured under light conditions (Ralph et al. 2007).

O_2 microelectrode characterization of respiration and net photosynthesis: O_2 microelectrodes were used to measure respiration and photosynthesis in *A. tenuis* juveniles exposed to two treatments: 1) 0 mg l^{-1} suspended sediments and 0 mg OC l^{-1} FSW of nutrient enrichment (control), and 2) 100 mg l^{-1} suspended sediments and +0 mg OC l^{-1} FSW of nutrient enrichment (high suspended sediments). Measurements were performed between days 16 and 18 for two individuals from the control treatment and two individuals from the high suspended sediment treatment. Each juvenile was placed in a custom-built flow chamber

(25 × 10 × 10 cm), through which seawater of each treatment was circulated at a flow velocity of ~1 cm s^{-1}. A light intensity of 60 µmol photons m^{-2} s^{-1} was used for homogeneous, vertical illumination of the coral juvenile in all treatments. O_2 microelectrodes (tip size: 10 µm in diameter; 90% response time (t90) <1 s) were built as described in (Revsbech 1989) and calibrated with air-saturated water (100% air-saturation) and N_2-bubbled water (0% air saturation) for salinity and temperature respectively. Microsensors were mounted on a motor-driven micromanipulator (MM3, Märzhäuser, Wetzlar, Germany) controlled by custom-written profiling software (µ-Profiler, http://www.microsen-wiki.net/), which also recorded signals amplified by a data acquisition device (DAQ-Pad 6009, National Instruments).

The micromanipulator was used to place microelectrodes in direct contact with coenosarc tissues (tissue connecting polyps) to minimize the influence of polyp movement. Positioning of the microelectrode on each juvenile was fine-tuned using the light-dark shift technique (Revsbech and Jorgensen 1983), i.e., position was adjusted until an instantaneous and clear response in the signal was obtained when the light was turned off. One hour after the microsensor was positioned, light and dark profiles were performed (n = 4-10 replicate profiles per colony) under the treatment conditions to which juveniles were exposed during the experiment (0 or 100 mg l^{-1} of suspended sediments). To evaluate the response of juveniles to changes in water quality, measurements were then repeated after changing treatment conditions (by adding sediments to the tank or adding water to wash the sediments resulting in concentrations of 100 or 0 mg l^{-1} of suspended sediments respectively). Methodological restrictions prevented measurements with nutrient-enriched sediments, because it is not possible to add previously incubated nutrient-enriched sediments to a volume of water with non-enriched sediments (i.e. to change treatment conditions from non-enriched sediments to enriched sediments) and maintain suspended sediment concentrations without diluting nutrients. O_2 concentration profiles were measured from the tissue surface upwards into the water column in vertical steps of 50 µm (Fig. S4.5). Net O_2 exchange fluxes were calculated from the measured steady-state concentration profiles using Fick's first law of diffusion, with a molecular diffusion coefficient for O_2 of 2.3535 x 10^{-5} cm^2 s^{-1} (27℃ and salinity 35 psu).

4.2.5 Data analysis

Effects of treatments on juvenile survivorship were estimated using the Cox's Proportional Hazard (CPH) model (Cox 1972), after statistical testing and fulfilling model assumptions (functions cox.zph. and coxph in the package 'survival' of the statistical software R; R Development Core Team, 2016). The CPH model is built on the premise that the hazard (i.e., mortality) rate is a log linear function of the factors, in this case suspended sediments and nutrient enrichment. Furthermore, it assumes that the effect of a covariate on survivorship does not vary over time, i.e., the effect of a covariate on the hazard rate is proportional to the baseline hazard. The effects of suspended sediments and nutrient enrichment on coral responses (growth, effective quantum yield and maximum quantum yield) were analyzed using linear mixed effects models (LME) with suspended sediments (numerical factor: 0, 10, 30 and 100 mg l^{-1}) and nutrient enrichment (categorical factor: low and high enrichment) as fixed factors and tank as a random factor. Effects of different water quality conditions (0 or 100 mg l^{-1}) on the respiration and net photosynthesis of previously exposed juveniles of *A. tenuis* were analyzed with general linear models (GLM) for each *A. tenuis* juvenile, with suspended sediments concentration (categorical factor) as fixed factor. A t-paired test was used to compare net photosynthesis estimates for each recruit between the 0 and 100 mg l^{-1} suspended sediment exposures. The functions glm (for the GLM), anova.lme with marginal sum of squares (for the LME) and drop1 were used to estimate p-values. All LME and GLM analysis were done using the package lme in R (R Development Core Team, 2016) .

4.3 Results

4.3.1 Survivorship and growth:

Survivorship of juveniles varied among species (Fig. 4.1). After 40 days of exposure, survivorship was high in all treatments for both *A. tenuis* (between 78.1 ± 0.1% and 90.6 ± 0.1%, average ± se per tank) and *P. acuta* (between 93.8 ± 3.3% and 100% per tank). Overall, survivorship of these two species was unaffected by the suspended sediment and nutrient enrichment treatments ($p > 0.05$ for all treatments and interactions, Table 4.1, Fig. 4.1). In contrast, survivorship of *A. millepora* juveniles was significantly reduced in high (100 mg l^{-}

^{1}) suspended sediment treatments, to 64 ± 0.06% when suspended sediments were combined with high nutrient enrichment, and to 82 ± 0.1% when combined with low nutrient enrichment ($p_{\text{Suspended sediments } A.\ millepora} = 0.002$). Neither nutrient enrichment on its own nor its interaction with sediments had a significant impact on juvenile survivorship ($p_{\text{Nutrient enrichment } A.\ millepora} = 0.325$, $p_{\text{Suspended sediments and nutrient enrichment } A.\ millepora} = 0.719$; Table 4.1, Fig. 4.1).

Table 4.1: Results of treatments effects on the survivorship of *Acropora tenuis*, *A. millepora* and *Pocillopora acuta* juveniels based on Cox hazard regression analysis with suspended sediments (SS) and nutrient enrichment (Nut) as fixed factors and tanks as random term error. Significance at $p<0.05$ is shown in **bold**.

Species	Factor	z-value	p-value
A. tenuis	SS	1.415	0.157
	Nut	0.318	0.750
	SS x Nut	-0.356	0.722
A. millepora	SS	3.002	**0.002**
	Nut	0.984	0.325
	SS x Nut	0.359	0.719
P. acuta	SS	-0.530	0.596
	Nut	0.419	0.675
	SS x Nut	0.768	0.442

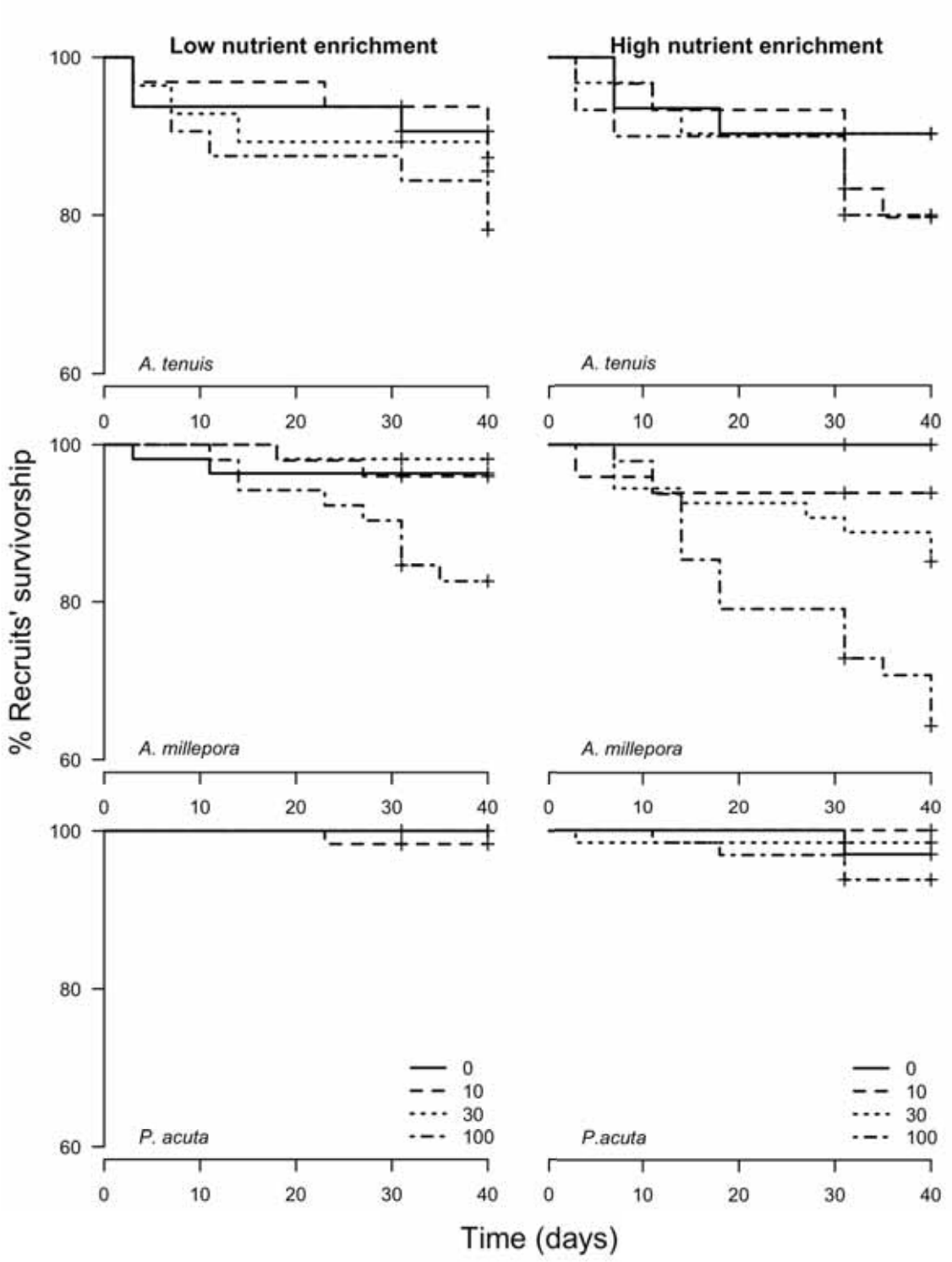


Figure 4.1: Survivorship rates of *Acropora tenuis*, *A. millepora* and *Pocillopora acuta* juveniles exposed to suspended solids (SS: 0, 10, 30 and 100 mg l^{-1}) and nutrient enrichment (low and high).

The effects of elevated levels of suspended sediments and nutrients on growth of juveniles were species-specific. Some juveniles of the three species declined in size (i.e., partial colony mortality) at high concentrations of suspended sediments (i.e., *A. tenuis* in the 30 and 100 mg l^{-1}/low nutrient enrichment Fig. 4.2a; *A. millepora* in the 30 mg l^{-1}/low nutrient enrichment and 100 mg l^{-1}/high nutrient enrichment treatments, Fig. 4.2b; *P. acuta* in 100 mg l^{-1} / high nutrient enrichment treatment, Fig. 4.2c). Growth was detrimentally affected by suspended sediments for both *A. tenuis* and *P. acuta* ($p_{\text{Suspended sediments } A. tenuis} = 0.043$, $p_{\text{Suspended sediments } P. acuta} = 0.001$, Table 4.2, Fig. 4.2), but overall growth of *A. millepora* was not affected significantly ($p_{\text{Suspended sediments } A. millepora} = 0.173$). Nutrient enrichment and its interaction with sediments did not affect growth in any of the three species (all $p > 0.05$; Table 4.2, Fig. 4.2.-4.3).

Table 4.2: Results of treatment effects on juveniles of *Acropora tenuis*, *A. millepora* and *Pocillopora acuta* based on linear mixed effects models (LME) with suspended sediments (SS) and nutrient enrichment (Nut) as fixed factors and tanks as random term error. Significance at $p<0.05$ is shown in **bold**. Refer to Table S3 for detailed information for the analyses.

Variable	Species	Factor	Df	F-value	p-value
Growth	*A. tenuis*	SS	1	9.089	**0.006**
		Nut	1	1.157	0.294
		SS x Nut	1	0.026	0.873
	A. millepora	SS	1	3.294	0.084
		Nut	1	1.325	0.263
		SS x Nut	1	1.343	0.260
	P. acuta	SS	1	15.913	**<0.001**
		Nut	1	1.190	0.288
		SS x Nut	1	0.028	0.867
Maximum quantum yield (F_v/F_m)	*A. tenuis*	SS	1	1.037	0.320
		Nut	1	1.060	0.315
		SS x Nut	1	1.288	0.269
	A. millepora	SS	1	2.026	0.171
		Nut	1	1.471	0.240
		SS x Nut	1	0.006	0.938
	P. acuta	SS	1	1.698	0207
		Nut	1	1.460	0.240
		SS x Nut	1	1.634	0.215
Effective quantum yield ($\Delta F/F_m'$)	*A. tenuis*	SS	1	5.940	**0.013**
		Nut	1	0.768	0.391
		SS x Nut	1	0.255	0.874
	A. millepora	SS	1	5.969	**0.024**
		Nut	1	0.314	0.581
		SS x Nut	1	0.004	0.946
	P. acuta	SS	1	1.650	0.213
		Nut	1	3.094	0.093
		SS x Nut	1	1.563	0.225

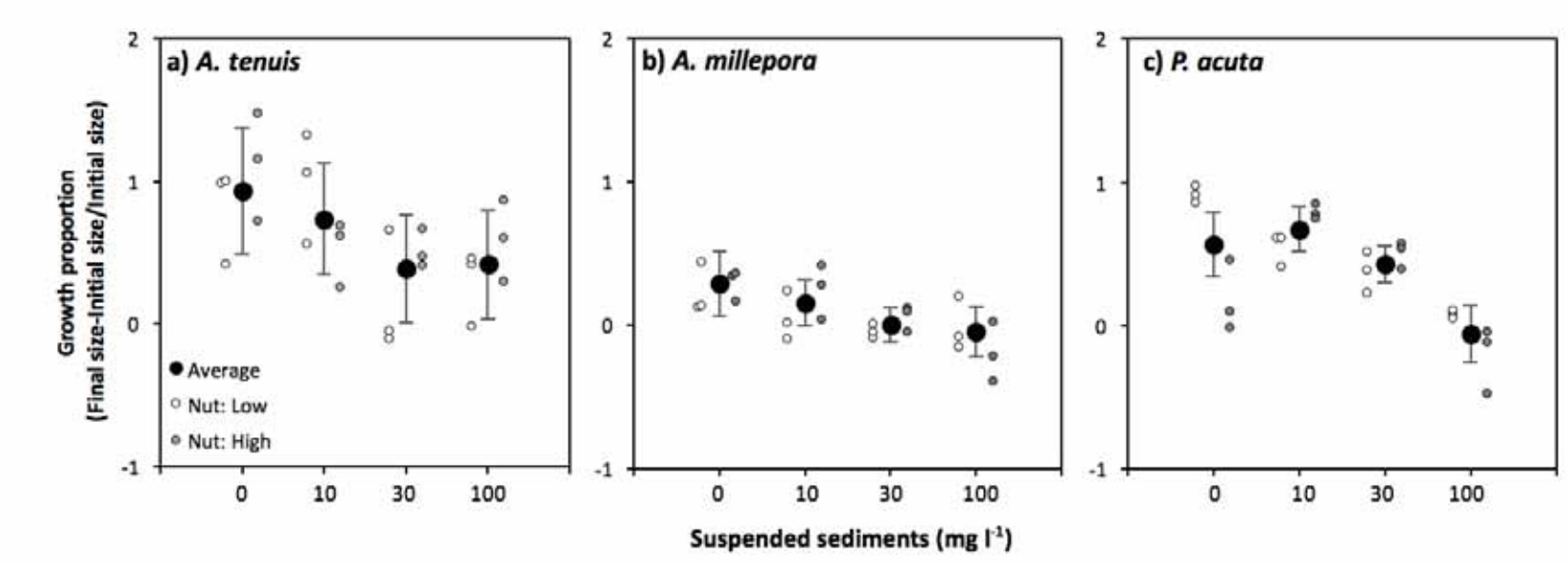


Figure 4.2: Growth proportion (average ± se) of *Acropora tenuis* (n = 9-10 per replicate tank), *A. millepora* (n = 16-18 per replicate tank) and *Pocillopora acuta* (n = 20-22 per replicate tank) juveniles exposed to suspended solids [SS: 0, 10, 30 and 100 mg l^{-1}(black circles)] and nutrient enrichment [Nut: low (empty circles) and high (grey circles), circles represent values of each tank replicate].

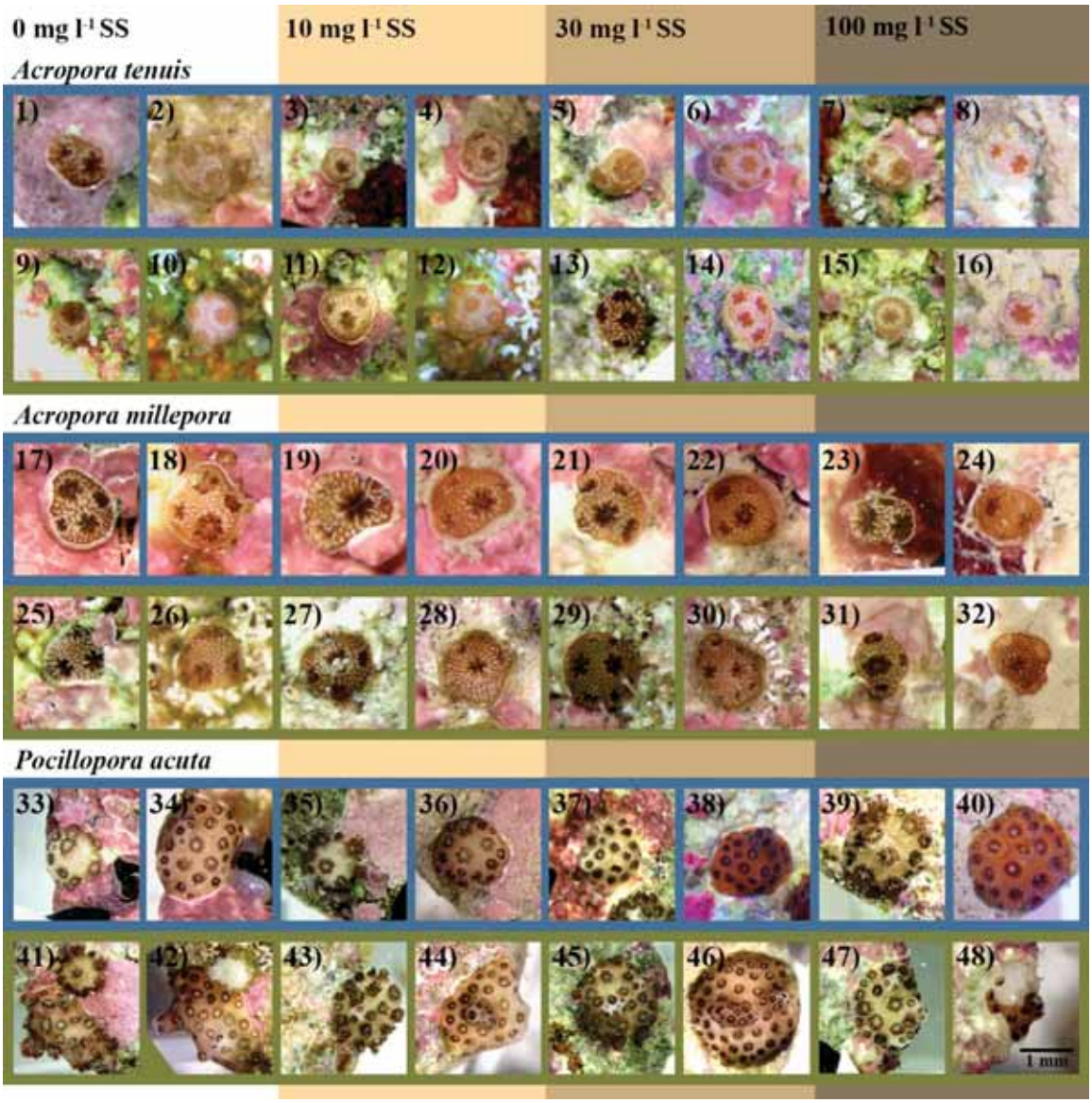


Figure 4.3: Images of juveniles of *Acropora tenuis*, *A. millepora* and *P. acuta* on day 1 (odd numbers) and day 40 (even numbers) of treatment exposure. Treatments consisted of two levels of nutrient enrichment (low [blue boxes], and high [green boxes]) and four suspended sediment concentrations (0, 10, 30 and 100 mg l^{-1}). Control treatment: 'low' nutrient enrichment and suspended sediments concentration = 0 mg l^{-1}.

4.3.2 Photochemical efficiency of the symbionts:

Maximum quantum yield (F_v/F_m) and effective quantum yield ($\Delta F/F_m$') were consistently greater for *P. acuta* (F_v/F_m = 0.59 ± 0.04 average ± sd, and $\Delta F/F_m$' = 0.48 ± 0.08, respectively) than for either *A. tenuis* (F_v/F_m = 0.50 ± 0.04, and $\Delta F/F_m$' = 0.33 ± 0.07, respectively) or *A. millepora* (F_v/F_m = 0.54 ± 0.04, and $\Delta F/F_m$' = 0.33 ± 0.07, respectively). After 40 days of exposure, maximum quantum yield was unaffected by any of the treatments in all three species (Table 4.2). In contrast, effective quantum yield

increased significantly as suspended sediment concentrations increased in both *A. tenuis* and *A. millepora* ($p_{\text{Suspended sediments } A.\ tenuis} = 0.013$, $p_{\text{Suspended sediments } A.\ millepora} = 0.024$, Table 4.2, Fig. 4.4). Effects of nutrients and their interaction with sediments were non-significant for both species (all $p > 0.05$; Table 4.2, Fig. 4.4). There were no significant effects of sediments, nutrients or their co-occurrence on the effective quantum yield of *P. acuta* (all $p > 0.05$, Table 4.2).

4.3.3 O_2 microelectrode characterization of respiration and net photosynthesis:

Respiration rates of the four replicate *A. tenuis* juveniles varied in response to exposure to suspended sediments (Fig. 4.5a). O_2 consumption rates were increased by ~1.6 to 7.9 fold in the high suspended sediment treatment (100 mg l^{-1}) and differed significantly from respiration rates in the control treatment (0 mg l^{-1} suspended sediments; $p < 0.05$ for all replicates, Table 4.3, Fig 4.5a). Net photosynthesis was significantly higher in one of the four juvenile replicates (replicate 2, which had not previously been exposed to high suspended sediments) and unaltered in the other three juveniles (Table 4.3, Fig. 4.5b). The ratio between net photosynthesis and dark respiration ($P_N : R_D$) was significantly lower when juveniles were exposed to high suspended sediments compared to the control treatment, declining by up 71% (paired t-test: $t = 3.9766$, $df = 3$, p-value = 0.028; Fig. 4.5c).

4.4 Discussion

Recently recruited coral juveniles (three to six months old) of three species common on Indo-Pacific inshore reefs responded to 40-day experimental exposures of elevated suspended sediments with contrasting patterns in survivorship, growth and photophysiology. High (100 mg l^{-1}) levels of suspended sediments significantly reduced survivorship but not the growth of *A. millepora* juveniles, whereas in *A. tenuis* and *P. acuta*, growth but not survivorship was affected. In contrast, nutrient enrichment had no effect on any of the physiological variables measured. The lack of an impact of nutrient enrichment when co-occurring with suspended sediments suggests that nutrient enrichment does not enhance the negative effects of suspended sediments on coral juveniles when sediments are maintained in suspension. My results contrast with observations of enriched sediments significantly reducing survivorship when deposited directly on four-week-old coral juveniles (Fabricius et al. 2003b).

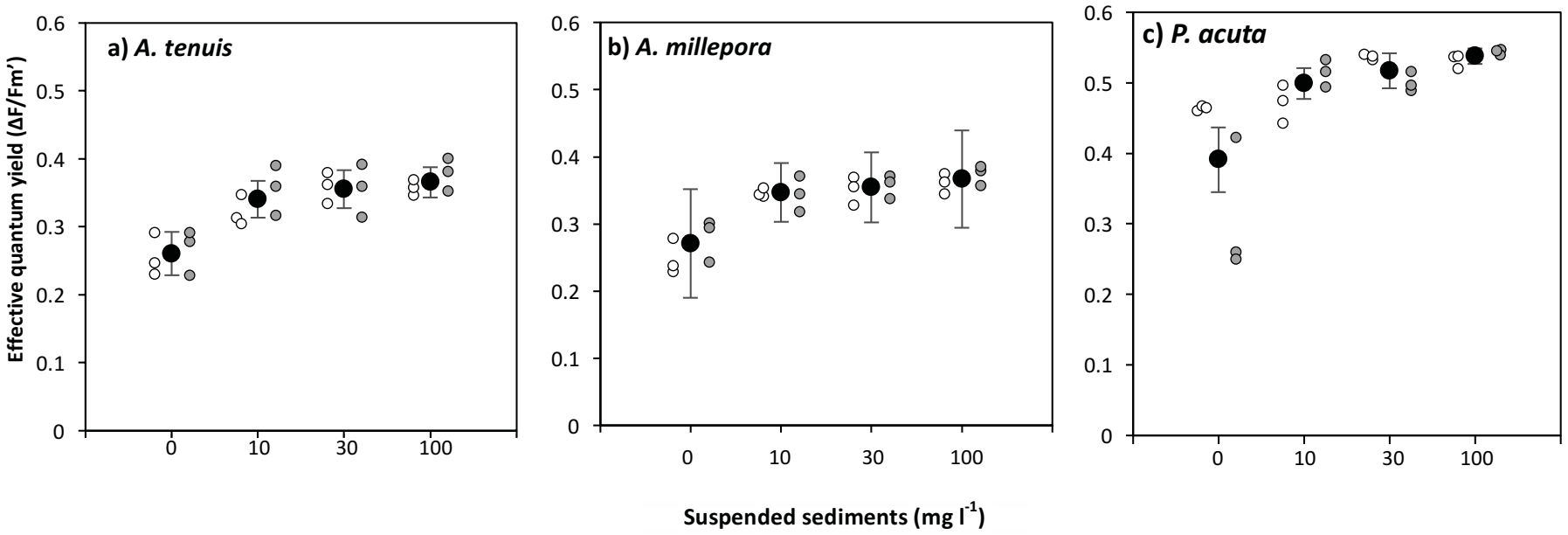


Figure 4.4: Effective quantum yield (ΔF/Fm', average ± se) of juvenile of Acropora tenuis (n = 9-10 per replicate tank), A. millepora (n = 16-18 per replicate tank) and Pocillopora acuta (n = 20-22 per replicate tank) exposed to suspended solids [SS: 0, 10, 30 and 100 mg l-1(black circles)] and nutrient enrichment [Nut: low (empty circles) and high (grey circles), circles represent values of each tank replicate].

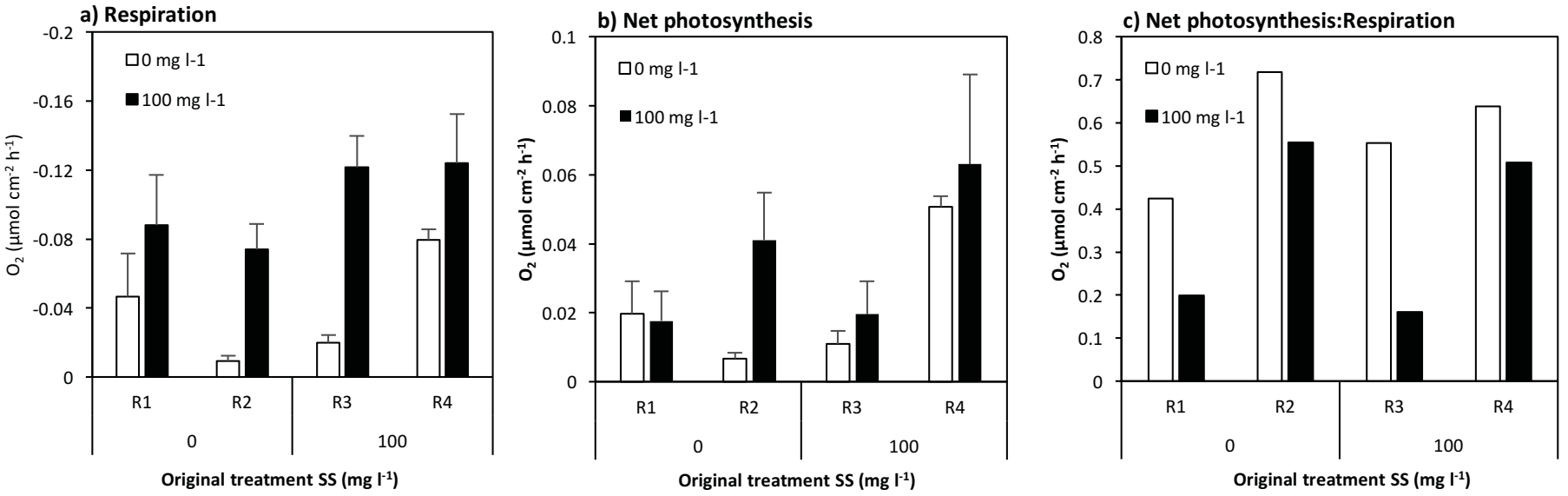


Figure 4.5: O_2 microelectrode measurements of *Acropora tenuis* juveniles of a) Dark respiration and b) Net photosynthesis, c) Net photosynthesis:respiration. Juveniles were previously exposed during 18 days to treatment conditions (SS: 0 mg l^{-1} or 100 mg l^{-1} SS in FSW, n= two replicate juveniles per treatment), and then exposed during O_2 measurements to different water quality conditions (white bars: 0 mg l^{-1} or black bars: 100 mg l^{-1} SS in FSW). Values are average ± sd (n = 4-6 replicate measurement per juvenile under each water quality condition). R = replicate.

Increasingly severe physiological impacts as sediment levels increased in experimental treatments were due to the presence of suspended particles rather than light attenuation associated with turbidity, given that juveniles in all treatments experienced the same light intensity. In studies of adult corals, decreases in survivorship and growth rates (linear extension) in response to suspended sediments (Dikou 2009, Flores et al. 2012, Browne et al. 2015b) have been attributed to depletion of available energy, as a consequence of high rates of energy consumption to support elevated respiration rates, sediment removal and repair of damaged tissues. My results indicate that juveniles of the three species differ in their sensitivity to suspended sediments and in their energy allocation strategies in response to this stressor; *A. millepora* preferentially allocates energy to maintain growth, whereas *A. tenuis* and *P. acuta* prioritise survivorship at the expense of growth as water quality declines.

The consistently high maximum quantum yields (F_v/F_m) I found across all treatments indicate that photosystem II of *Symbiodinium* symbionts is robust to levels of suspended sediments up to 100 mg l^{-1}. The absence of an effect of suspended sediments and nutrient enrichment on maximum quantum yields, either when the two stressors occurred singly simultaneously, is corroborated by results found for adult corals when sediments were maintained in suspension (Sofonia and Anthony 2008, Flores et al. 2012, Browne et al. 2015a, Liu et al. 2015). In contrast, reductions in F_v/F_m have been recorded when sediments accumulate on corals, causing tissue damage by smothering (Philipp and Fabricius 2003, Weber et al. 2006, Piniak 2007). In my study, sediments did not accumulate on coral tissues, thus symbionts had sufficient light to alleviate stress from potential shading and prevent damage to photosystem II.

Increases in effective quantum yield with increasing levels of suspended sediment suggest that symbionts associated with coral juveniles compensated for rising turbidity by increasing their photochemical efficiency, as has been found for adult corals in field studies (Piniak and Storlazzi 2008, Sawall et al. 2011). Although juveniles in all treatments were exposed to the same light intensity, light quality (spectral composition) might have varied subtly among treatments, a factor that was not considered in the experimental design of the present study. Light quality is fundamentally important in the physiology and ecology of coral-algal symbiosis, and changes in the light spectrum constitute another potential stressor for corals (Jones et al. 2016). A shift in light spectra resulting in poorer light quality (less red and blue) could have induced *Symbiodinium*

associated with juveniles of *A. tenuis* and *A. millepora* to increase their photochemical efficiency in an attempt to increase light capture. Alternatively, effective quantum yields have been reported to increase when food is abundant (i.e., high concentrations of sediments or nutrients) and heterotrophy favoured (Borell and Bischof 2008, Ferrier-Pagès et al. 2010). Under such circumstances, *Symbiodinium* can take up ammonium produced by host cells as a nitrogen source (Piniak et al. 2003), a process that would also be augmented in corals exposed to high concentrations of sediments and which could positively affect the photochemical efficiency of chlorophyll (Ferrier-Pagès et al. 2010).

Increased respiration rates of *A. tenuis* juveniles under high levels of suspended sediments suggest that processes having high oxygen demands and requiring significant energy expenditure were activated, as has been suggested from studies of adult corals (Telesnicki and Goldberg 1995, Browne et al. 2014). Corals are both autotrophs and heterotrophs, and many studies have demonstrated their ability to gain at least a portion of energy heterotrophically by tentacular suspension feeding (Houlbreque and Ferrier-Pages 2009). Ingestion of sediments has been observed in several coral species (Stafford-Smith 1993, Anthony 2000), occurring through entrapment of particles in surface mucus layers and subsequent transfer to the mouths of polyps via cilia and tentacle movements (Jones et al. 2016). Although capture of sediments and associated organic matter provides nutritional benefits to some coral species (Anthony 1999, Anthony and Fabricius 2000) it also represents an energetic cost to the colony as a consequence of their clearance activity to remove deposited sediments on their tissue.

Production of mucus and increased ciliary and tentacle activity that corals show under turbidity conditions are processes that demand oxygen (Abdel-Salam et al. 1988) and thus elevate respiration rates, which in turn, decreases energy available for processes like growth and survival. Such costs may potentially outweigh the benefits of heterotrophic feeding. Relative to zooplankton, suspended sediments represent a poor-quality food source (Anthony 1999), and energy costs associated with maintenance and repair of damaged tissues are higher when corals are exposed to this stressor. Decreases in the ratio of net photosynthesis to dark respiration (P_n:R_D) in reduced water quality treatments also suggest greater energy investment in maintenance and repair processes associated with metabolic costs incurred under suspended sediments conditions. Such energetic costs are likely to impact other important parameters, such as growth or survival of the colony, supporting my results and results from studies of adult colonies (Anthony

and Fabricius 2000, Anthony and Connolly 2004, Browne et al. 2015b). My results show that declines in water quality result in greater energy cost (i.e., higher respiration rates), which will have longer-term repercussions for coral health, population size structures and consequently for coral cover.

The energetics of corals and their ability to sustain growth and survivorship in differing turbidity regimes are functions of their capacity to tolerate and utilise sediments, and their strategies to cope with stress conditions. My study provides evidence that, although stress-related responses affecting growth and survivorship vary among juveniles of the three species, the final outcome for populations of each species is likely to be similar: a reduction in the numbers of new individuals reaching reproductive size classes due to increased mortality or reductions in growth rates of juveniles. Whereas morphological differences among species have been shown to be determinants of adult coral survival under sediment stress conditions (Stafford-Smith 1993, Huang et al. 2011, Flores et al. 2012, Junjie et al. 2014), physiological differences play a more important role in small-sized individuals that have not yet developed adult growth forms.

The lack of an effect of nutrient enrichment, either as a single stressor or when co-occurring with suspended sediments, on physiological variables measured for juveniles of the three common inshore species raises questions about the role of nutrient enrichment in coral reef declines. The view that nutrient enrichment is responsible for coral reef declines has also been challenged by evidence that some corals thrive in high-nutrient turbid waters, and by several experimental studies that did not find clear negative impacts on the physiology of adult corals (Bongiorni et al. 2003b, Rasher et al. 2012). However, my results should be interpreted with caution as the effects of sediment deposition were not assessed, a factor that when co-occurring with nutrient enrichment is known to have large impacts on juvenile survivorship (Fabricius et al. 2003b) and adult physiology (Weber et al. 2012). Also, the co-occurrence of many other factors (i.e., proliferation of competitors, predators) were not addressed in the present study, but are known to have negative effects on coral communities under scenarios of high turbidity and nutrient enrichment (Bruno et al. 2003, Le Grand and Fabricius 2011, Liu et al. 2015).

Ongoing development of coastal zones is likely to lead to further increases in suspended sediment and nutrient inputs into the marine system. Studies on how different early life history stages (i.e. gametes, larvae, recruits, juveniles and adult colonies) and processes (fecundity, fertilization, embryo development, colony growth and survival)

respond to these stressors will be critical to understand long-term effects of degraded water quality on the population dynamics of inshore coral reef species. Management strategies and plans need to take into account the different life history stages and thresholds for processes that are essential for the maintenance and replenishment of populations. Although adults of some coral species have moderately high tolerance to suspended sediments and nutrients, it is important to recognise that species thresholds might be determined by the susceptibility of early life history stages to these stressors.

Chapter 5: Effects of water quality and temperatures stress on the demography of corals

5.1 Introduction

To adequately manage coral reef ecosystems, it is necessary to know *how* and *why* coral cover changes through time. To comprehend the effects of disturbance in a population we first need a good understanding of its structure and dynamics; however, the development of population models has been limited to few reef taxa. Most marine population models have been developed for marine fishes (Kritzer and Sale 2004) due to their economic importance and the relative ease of parameterising their life history stages. For marine invertebrates, population studies have mostly focused on animals associated to rocky shores (i.e., mussels, barnacles, Becker et al. 2007, Carson et al. 2011), where marine ecological research began, or in high-value aquaculture species (i.e., crabs, urchins, oysters, Botsford et al. 1994, Wing et al. 1998, Kjelland et al. 2015).

Despite the substantial information that demographic analysis can provide on the health of a population and the effects of disturbances, development of these models for reef-building corals is not commonly used in monitoring programs, mostly due to the complexity of estimating their life history parameters (Jackson and Hughes 1985, Babcock 1991). Factors that complicate the use of population models for corals are: 1) their indeterminate growth and modular structure; 2) lack of senescence signs; 3) colony partial mortality, fragmentation and fusion; 4) contrasting reproductive modes (brooding or broadcast spawning); and 5) high larval dispersal potential which makes difficult measurements of their survivorship and settlement success in the field (Pineda et al. 2007, Jones et al. 2009, Kool et al. 2013, Burgess et al. 2014). Notwithstanding, advances in field and laboratory techniques have improved our understanding of coral population dynamics. For example, underwater photography can be used to estimate populations size structures and changes in coral cover through time (English et al. 1997, Ferrari et al. 2016, González-Rivero et al. 2016), genetic tools now exist to measure connectivity between populations (van Oppen and Gates 2006, Hellberg 2007), numerical modelling tools are used to estimate large-scale dispersion and connectivity (Andutta et al. 2012, Hock et al.

2014, Thomas et al. 2014, Wood et al. 2014), and our understanding of processes has improved through study of other colonial organisms (Tanner 2001, Linacre and Keough 2003, Hart and Keough 2009).

For colonial organisms like corals, most demographic parameters are related to colony size rather than age (Caswell 2000). Colony growth and mortality rates decrease with increasing sizes regardless of age (Loya 1976, Hughes and Jackson 1985, Hughes and Connell 1987), whereas fertility, fission, partial mortality and injury regeneration rates increase with colony size (Hughes 1984, Jackson and Hughes 1985, Meesters et al. 1996, Nozawa and Lin 2014). As a result, individuals from the same age cohort can have different demographic rates, making population age structure analysis extremely difficult. Thus, size-based models are a better method to study coral population dynamics and effect of disturbances on their demography (Hughes 1984, Edmunds and Elahi 2007, Hernández-Pacheco et al. 2011, Riegl and Purkis 2015).

The early life history stages of corals are considered one of the main drivers of population dynamics. However, no previous size-based population models (Hughes 1984, Done 1987, Hughes and Connell 1987, Done 1988, Babcock 1991, Smith 1992, Fong and Glynn 2000, Hughes and Tanner 2000, Meesters et al. 2001, Lirman and Miller 2003, Smith et al. 2005, Edmunds and Elahi 2007, Riegl and Purkis 2009, Hernández-Pacheco et al. 2011, Riegl and Purkis 2015) considered processes occurring during corals early life history stages (i.e., gamete fertilization, larval survivorship, larval settlement and recruit survivorship). Nor did they consider how disturbances during these stages could affect population structure and dynamics. Previous models oversimplified the contribution of early life history stages to the population, by assuming a constant number of individuals in the first size class (Hughes 1984). The exclusion of early life history stages in these models is justified by assuming that reefs are characterized by "open" populations, where larvae produced in a specific reef are dispersed to other reefs without contributing to the dynamics of source populations (Jones et al. 2009). However, field surveys and genetic studies suggest some degree of local retention and limited dispersal (Ayre and Hughes 2000, Hughes and Tanner 2000, Gilmour et al. 2009, Underwood et al. 2009, Figueiredo et al. 2013), therefore early life history stages should be considered in population dynamics analysis.

To improve our understanding of the effects of early life history stages on coral population dynamics, a size-based model considering all life history stages (i.e. from

gametes to adult colonies) was built for *Acropora tenuis*, a common species found across tropical Indo-Pacific and Red Sea waters (Veron 2000). Published empirical population demography data from juvenile and adult coral colonies (Smith et al. 2005), together with information on early life history stages (gamete fertilization, larval survivorship and settlement success) (Chapters 2 and 3) were used to construct the model. Contrasting water quality (i.e., nutrient enrichment and suspended sediments) and stress-inducing high temperatures were considered to occur during coral spawning, in order to examine their effects on annual population growth rates. This theoretical exercise provides a first insight into the effects of local (i.e. water quality) and global (i.e. temperature) stressors during the development of early life history stages on coral population dynamics. Results show the importance of considering early life history stages in monitoring and management plans in order to understand how coral cover changes when spawning events are affected by local and global stressors.

5.2 Materials and methods

5.2.1 Construction of the model:

A matrix model with density-independent structure (Caswell 2000) was used to incorporate demographic processes, namely decreasing in size, staying the same size class, growing to another size class, reproducing sexually, and dying (Fig. 5.1). In size-based models for corals, size represents the living area of the colony and determines rates of fecundity, survivorship, and growth, which are used to construct the population matrix $\overline{A}$. Demographic rates of each size class are the elements of $\overline{A}$ and will determine the population dynamic. This model predicts that in the long term, regardless of initial size structure (i.e. number of colonies per size class), the population will grow or decrease exponentially and reach a stable size distribution (Caswell 2000). A population growth rate is quantified by the dominant eigenvalue (λ) of matrix $\overline{A}$. When λ is>1, the population will grow exponentially, when λ is equal to 1 stability is reached, and when λ<1 the population will decrease exponentially.

Figure 5.1: a) Graphic representation of a size-based matrix model of a coral population. Size of circles represent sizes of the colonies, with recruits (R) being the smallest colonies, followed by juveniles (J) and adults (A). During each time interval surviving individuals may grow (g), stay the same size (loop, l), shrink (s) or reproduce (F). Sexual recruits are produced by adult sizes. Transitional probabilities are as follows: (growth) $0 \leq g \leq 1$, (loop) $0 \leq l \leq 1$, (shrink) $0 \leq s \leq 1$, (sexual reproduction) $0 \leq F$ (modified from Hughes, 1984). b) Graphic representation of migration of larvae which recruit locally in the same population, or emigrate to other populations. In this case larvae produced in population *n* can recruit locally, emigrate to population *i* (M_{ni}) or to other populations (M).

The model considers three life stages of a coral colony, which differ in size, survivorship and fecundity: recruits, juveniles and adults (Fig. 5.1a). Recruits originate from larvae sexually produced by adult colonies in the population (local retention), and by adult colonies in upstream source populations (Fig. 5.1b). Larvae are produced once per year during spawning events by reproductive individuals (adults) and become a recruit immediately after their settlement. Recruits turn into juveniles after 1 year and are infertile, an aspect that differentiates juveniles from adult colonies, which reproduce sexually (Hughes 1984). Juvenile and adult life stages can have various size classes which will be determined by their demographic rates (i.e., growth, survivorship, fecundity). The unit time of matrix $\overline{A}$ was set to be one year.

Population structure (size matrix): data from *Acropora* spp. populations of three nearshore Islands on the Great Barrier Reef (GBR) High Island, Franklin and Fitzroy Islands (Smith et al. 2005), were used to construct the matrices ($\overline{A}$) for each reef. Each population consisted of 3 juvenile size classes and one adult size (S1 Table). *Acropora* spp. colonies became fertile at diameters > 10 cm in the three studied reefs (Smith et al. 2005), characteristic used to separate juveniles from adult colonies.

Fecundity: maximum reproductive output (i.e., recruits) produced by an adult colony was estimated using empirical data from *A. tenuis* colonies in inshore reefs of the GBR. Pelagic larval duration of *A. tenuis* is ~32 days (Graham et al. 2008), and settlement competency is achieved within 4-5 days, while maximum settlement rates occur 7-10 days post-spawning (Nishikawa et al. 2003, Connolly and Baird 2010). Adult colony fecundity (F_i) was estimated using the following equation:

$$F_i = m_i * p_t$$

where F_i represents the average fecundity of individuals of size i, m is the number of eggs produced by an adult colony of size i (maternity) (Caswell 2000), and p_t is the recruitment success from gamete fertilization until recruit survival during the first year. Maternity was estimated using the following equation:

$$m_i = n * v * e * a_i$$

where n is the number of polyps per cm^2 of colony (13 polyps per cm^2, S1 Table), v is the proportion of polyps in a fertile colony that produce eggs (75%, Baird et al. 2009), e is the number of eggs produced per polyp (7 eggs per polyp, Cantin et al. 2007), a_i is the

area in cm^2 of a fertile colony of size i. Recruitment success (p_t) was estimated using data from previous chapters (Chapters 2 and 3) and empirical data (Maida et al. 2001, Arnold et al. 2010, Kuo and Soong 2010) using the following equation:

$$p_t = f * l * s * r$$

where f is gamete fertilization success, l is larval survivorship success, s is larval settlement success and r is recruit survivorship during the first year of life (Fig. S5.2).

Connectivity: Recruitment depends on the proportion of larvae locally produced and retained in a reef, plus larvae produced in other reefs that immigrate and settle on the reef of study. The percentage of local retention of *Acropora* species larvae has been estimated to vary between 13-60% (Figueiredo et al. 2013, Thomas et al. 2014) and is determined by: 1) the time for embryo development and for larvae to become competent to settle, and 2) the hydrodynamic particle retention around the reef of origin. Two recruitment scenarios were modelled in order to represent a reef with short water residency time resulting in 13% of local recruitment (open population), and a reef with a long water residency time resulting in 60% of local recruitment (closed population). To include these values in the model, the number of offspring produced in a population in one year was the result of the number of larvae produced by reproductive colonies in the population of study plus larvae produced by reproductive colonies from other source populations that immigrate to the population of interest, following equation:

$$R_{iT} = F_o * (1 - M_o) + F_u * M_u$$

where R_{iT} is the total replacement potential in the population of interest resulting from local retention and the immigration of larvae from upstream populations, F_o is the number of offspring produced by the population of interest (fecundity), M_o is the proportion of larvae that emigrate from the population of interest, F_u is the number of offspring produced by upstream populations (fecundity) and M_u is the proportion of larvae that immigrate from source populations to the population of interest. Dispersal models simulated for reefs with the size, shape and spacing typical of reefs in the GBR (Black 1993, Thomas et al. 2014) estimated that around ~10% of larvae produced in an upstream reef are intercepted when they are still competent by a downstream reefs. Considering this estimation, successful immigration of larvae produced in an upstream population was set to be 10%.

Size of reproductive colonies: Since production of gametes by a colony is size dependent, the influence of the size distributions of adult colonies in the population of study and in upstream populations was evaluated in the model. According to the size distribution of corals in the three studied reefs (Smith et al. 2005), reproductive adults ranged from 10 to 50 cm in diameter. In order to consider all possible adult sizes, the model was evaluated considering extreme scenarios where: i) either the population of interest and upstream populations had adult colonies with similar size distributions and were dominated by either the smallest or the biggest recorded size, respectively, or ii) adult colonies differed in size among populations. This resulted in 8 size-class combinations among populations. The first four scenarios considered that the population of study is comprised of adults of either the smallest reproductive size (10 cm) or the biggest reproductive size (50 cm), while the source populations consisted of one population of either small adult colonies (10 cm); or big adult colonies (50 cm Fig. 5.2a and b). Similarly, the same configuration of sizes in the population of study and in upstream populations were considered, but more than one upstream population was considered in the model (i.e., having 6 upstream populations, Fig. 5.2c and d).

5.2.2 Effects of water quality changes and warming temperatures:

Negative impacts on early life history stages of hard corals have been documented as the result of individual and combined effects of nutrient enrichment, suspended sediments and warming temperatures, causing a decrease or failure in coral reproduction (Chapters 2 and Chapter 3). Size effects of stressors varies with their duration, intensity and with their co-occurrence with other stressors. In order to estimate effects of the co-occurrence of local (water quality) and global stressors (warming temperatures) during early life history stages on the demography of a population, three different scenarios were considered that differed in stressor duration (short, medium and long) hence affecting different processes: i) gamete fertilization, ii) fertilization and larval development; iii) fertilization, larval development and larval settlement. Simulations were performed using combinations of two stressors: 1) nutrient enrichment and temperature stress (Chapter 2), 2) nutrient enrichment and suspended sediments (Chapter 3), 3) temperature stress and suspended sediments (Chapter 3).

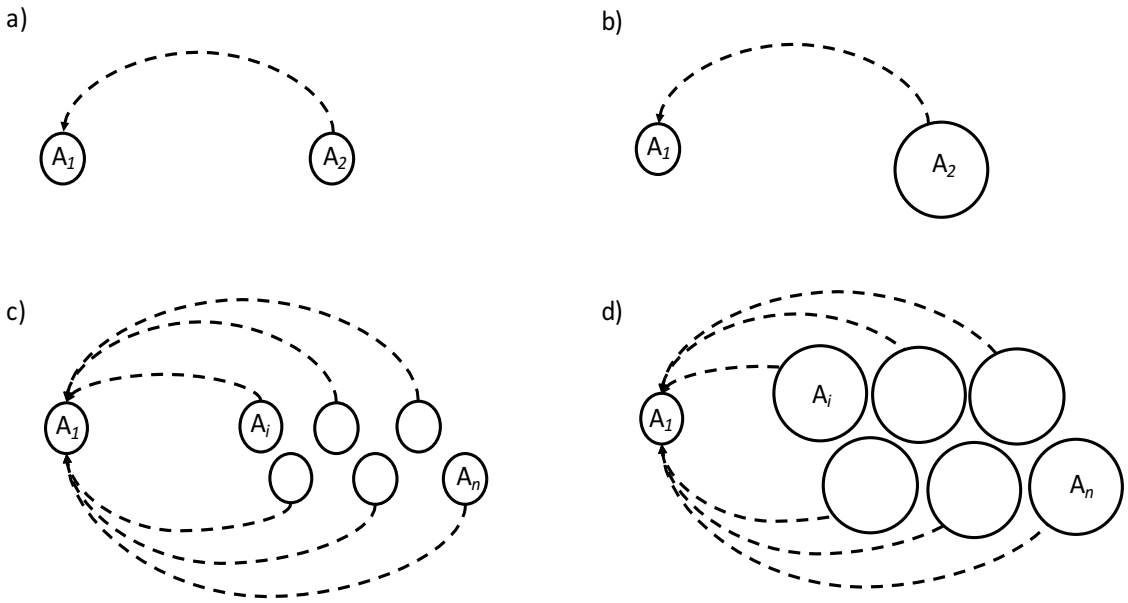


Figure 5.2: Representation of the different larvae immigration (dashed lines) scenarios considered from source populations to the population of study. A_1: adult colonies of population of study. A_{i-n}: Adult colonies from source populations. Sizes of adult colonies are represented with circles of different sizes (small diameter: small adult colonies of 10 cm, big diameter: big adult colonies of 50 cm).

The three reefs of study are reported to experience different water quality: Fitzroy has the highest water quality (considered here as "low" nutrient enrichment) followed by Frankland ("medium" nutrient enrichment) and High Island ("high" nutrient enrichment) has the lowest water quality (Thompson et al. 2014). To estimate the effects of nutrient enrichment and temperature stress comparisons were done between the three reefs considering their different water qualities. To estimate effects of suspended sediments with either nutrient enrichment or temperature, the model was evaluated only for the population of High Island, which is occasionally exposed to river plumes during the monsoonal wet season.

Effects of the co-occurrence of local and global stressors on population dynamics (target and source reefs) were evaluated by estimating the relative decrease in λ under combinations of stressors in comparison to: i) control conditions of local and global stressors (27ºC, low nutrient enrichment and/or 0 mg l^{-1} suspended sediments), and ii) control conditions only for local stressors (low nutrient enrichment and/or 0 mg l^{-1} suspended sediments) in order to estimate the effects of global stressors on the population of study and source populations. Results are presented only for the most important

outcomes of all studied scenarios, when decrease in annual population growth rate was >5%.

To evaluate the relative effects of stressors co-occurrence, elasticity analysis were performed for those scenarios with minimum and maximum decrease of λ. Elasticity is a prospective analysis that determines the proportional contribution of each model parameter to the population growth rate by assessing how that rate responds to proportional perturbations to individual elements (Caswell 2000). Because population growth rate is an indirect measure of fitness (McPeek and Peckarsky 1998), high elasticities can be used to indicate portions of the life cycle that are under the strongest selective pressure, and which might be best targeted by management efforts for population conservation purposes (Caswell 2000). Analyses were conducted with the package "popbio" in R (R Development Core Team, 2016).

5.3 Results:

5.3.1 Demographic analysis

Nutrient enrichment, suspended sediments and/or warming temperatures impacted population growth rates (λ), with effect sizes depending on the combination of stressors, their duration, intensity, and the extension of global stressors (i.e., whether upstream populations were also affected by thermal stress). Characteristics of the populations including size of reproductive colonies and percentage larval retention also determined population growth rates. The greatest decreases in annual population growth rates were obtained when: i) larval production depended mainly on local retention (closed populations); ii) population connectivity to upstream sources was minimum (i.e., one population), iii) big adult colonies comprised the population of study which had minimum connectivity to one source population constituted by small adult colonies, iv) global stressors (i.e., temperature) affected all populations simultaneously (the population of study and source populations). When the population of study was connected through larval migration to several source populations, λ was driven by the internal demography of the population (transition rates between size classes) under all stressors combinations, with early life history stages having a minor influence on population dynamics (relative percentage change in $\lambda < 5\%$, S5.4-6 Fig.).

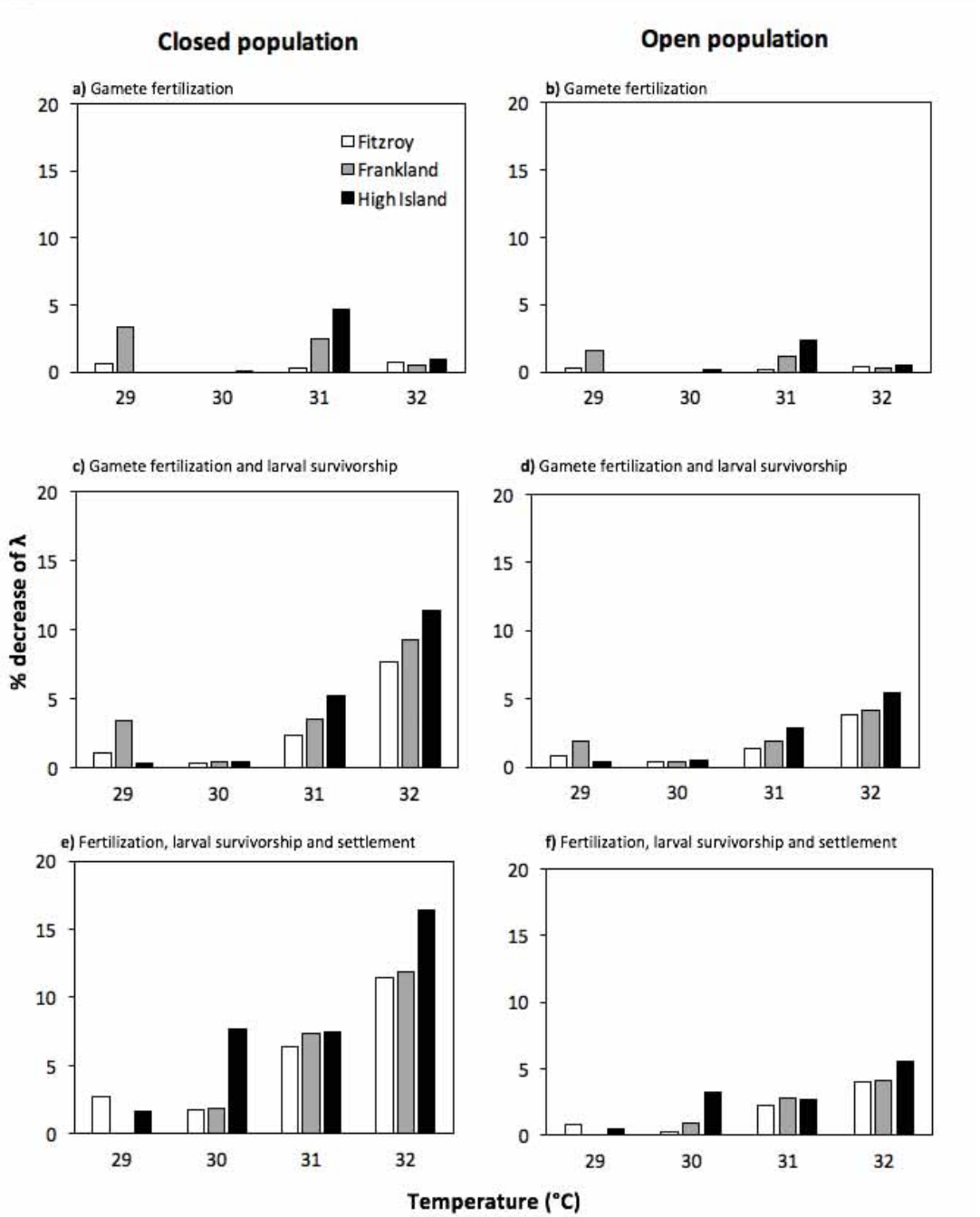


Figure 5.3: Effect of temperature on population growth rate in reefs with different water qualities (nutrient enrichment [Fitzroy: low nutrient enrichment, Frankland: medium nutrient enrichment, High Island: high nutrient enrichment]). Duration of temperature stress was simulated to occur during: **a-b)** gamete fertilization; **c-d)** gamete fertilization and larval development; **e-f)** gamete fertilization, larval development and larval settlement only in the population of study. Population of study consisted of small size (10 cm) adult colonies and larvae migration was from one upstream population with adult colonies of similar sizes (10 cm). Relative percentage change in growth rate (λ) was estimated in relation to control conditions (27°C) for each reef under different scenarios of local retention (open population: 13% of local retention, closed population: 60% of local retention).

Under all stressor combinations, the greatest decreases in λ were obtained under long-term exposures to stress conditions at the highest intensities (when gamete fertilization, larval development and settlement were exposed to the highest stress conditions, i.e., Fig. 5.3 e-f). As immigration of larvae from other populations augmented by increases in adult colony size of upstream populations not affected by global stressors (i.e., augmenting the input of non-affected larvae), the effects of stressors on the population dynamics were diluted (i.e., comparison between Fig. 5.3 a, c and e with 5.3 b, d and f). However, when global stressors affected the population of study and upstream populations, the positive effects of larval migration decreased considerably (S5.7 Fig.). Elasticity analysis showed that as duration of stressors on early life history stages increased, the importance of maintaining reproductive sizes increased while offspring elasticity declined (i.e., comparison between Fig. 5.4a and c). When λ decrease was greatest (Fig. 5.5c) maintenance of adult colonies was the transition with highest impact on population growth rates followed by transition probabilities between juvenile stages. When decrease in λ was negligible (S5.8 Fig.), elasticity analysis showed that the contribution of early life history stages on population growth rates increased and became similar to elasticities of transitions between juvenile sizes, while the importance of maintaining adult colonies declined.

5.3.2 Nutrient enrichment, warming temperatures and/or suspended sediments during early life history processes and their effect on population demography

At temperatures higher than 29ºC the high-nutrient reef High Island's population experienced the greatest decrease in λ under all scenarios (Fig. 5.3, S5.4 Fig.). When fertilization was the only process affected, the decrease in λ was minor (< 5%, i.e., Fig 5.3a), while successive exposures of gametes during fertilization and larval survivorship decreased growth rates up to ~15% at the highest temperature (32ºC) when population dynamics were driven by fecundity (i.e., Fig. 5.3e). The greatest effect (~50% decrease at 32°C under long term exposures) was observed for closed populations of big adult colonies receiving larvae from one population of small adult colonies (Fig. 5.4a).

The effects of short-term exposures (only fertilization) to suspended sediments and nutrient enrichment were similar to the effects of the co-occurrence of nutrient enrichment and warming temperatures (< 5 %). The greatest effect of nutrient enriched sediments (~30% decrease), was obtained under long term exposure to stressors, when

populations consisted of small adult colonies (Fig. 5.4 b-c) under both scenarios of larvae retention.

The effects of suspended sediments and warming temperatures were greater than the effects of nutrient enrichment and temperature stress, or nutrient enrichment and suspended sediments under short-term exposures (only fertilization), decreasing population growth rates by more than 5% in more scenarios than the two other combinations of stressors. Again, the greatest effect size (~30% decrease) of the co-occurrence of stressors was obtained with closed populations comprising big adult colonies, connected to one source population of small adult colonies (Fig. 5.4d).

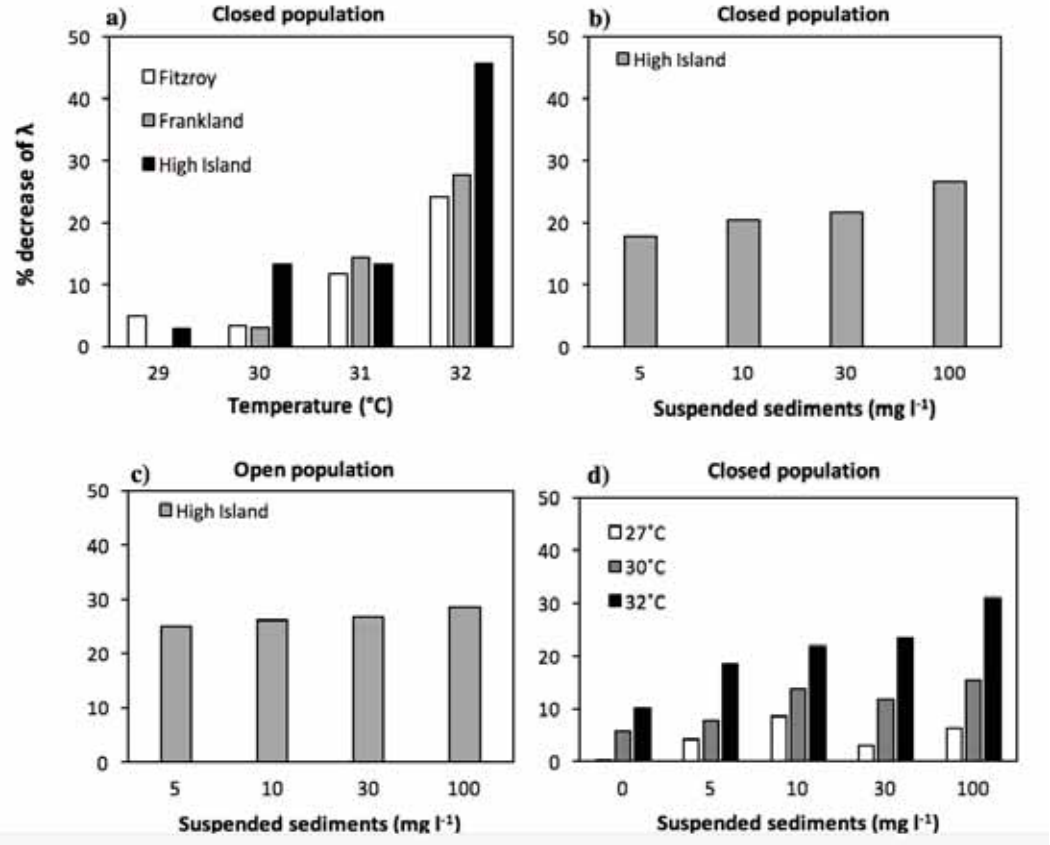


Figure 5.4: a) Effect of temperature on population growth rate in reefs with different water qualities (nutrient enrichment: Fitzroy: low nutrient enrichment, Frankland: medium nutrient enrichment, High Island: high nutrient enrichment). **b-c)** Effects of suspended sediments on population growth rates of corals in High Island reef. **d)** Effects of suspended sediments and temperature on population growth rates of corals in High Island reef. Population of study consisted of big size (50 cm) adult colonies and larvae migration came from one upstream population with adult colonies of small sizes (10 cm). The exposure to stressors was simulated to occur during gamete fertilization, larval development and larval settlement only in the population of study.

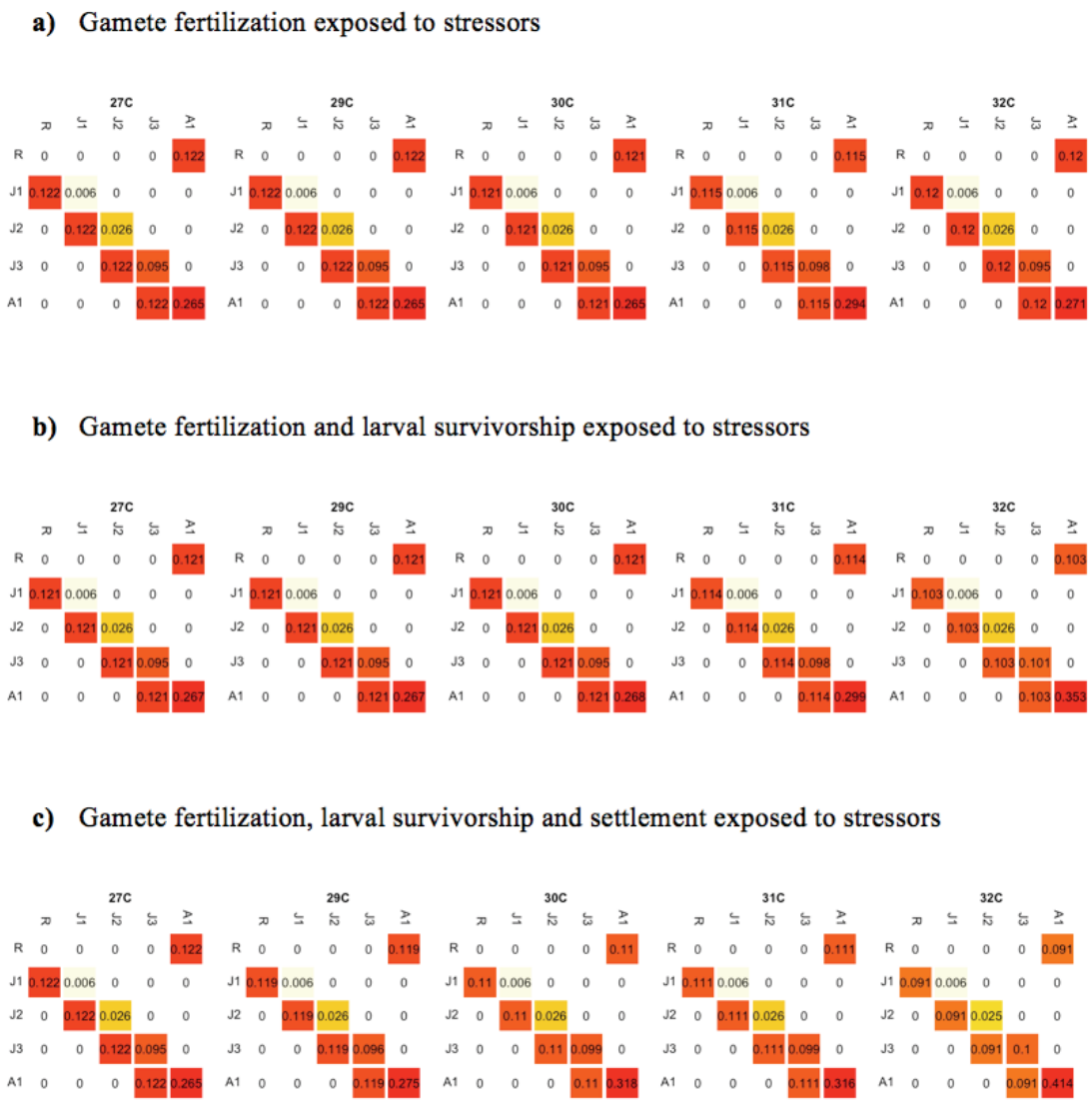


Figure 5.5: Elasticity analysis of High Island under a local retention scenario of 60% (closed population) when affected by temperature and nutrient enrichment. Population of study consisted of small size (10 cm) adult colonies, and larvae immigration came from one upstream population with adult colonies of small sizes (10 cm). Colors and numbers indicate proportional contribution of each model parameter to population growth rate (light yellow: lowest contribution, dark red: greatest contribution). For elasticity analysis of open populations see S5.9 Fig.

5.4 Discussion

This study provides an insight into the effects of water quality decline and warming temperatures on coral population demography when early life history processes are exposed to stress conditions. Water quality decline associated with river floods, costal developments and dredging activities increase concentrations of nutrients and suspended sediments to values similar to the ones applied in this study. Their co-occurrence with

warming temperatures during the months of coral spawning is likely under the projected climate change scenarios for the next century (Meissner et al. 2012). The results of the analyses presented here are not meant to be used as predictions of future population dynamics (i.e., absolute growth or population persistence) of the studied reefs under stress conditions, since they are based on simplified assumptions including constant dispersal and transitions rates, unlimited settlement substrata, density independent demographic parameters, and stressors effects are only on early life history stages (from gamete fertilization to larval settlement). However, the outcomes of the model provide a valuable insight into how local and global factors affecting early life demographic parameters can influence population growth rates, when all other parameters remain equal.

The greatest effects caused by all combinations of stressors for open populations were obtained when connectivity was low (i.e., only one source population existed), decreasing population growth rates by ~25% compared to control conditions. The effects were more pronounced for closed populations, with their population growth rates decreasing by up ~50%, supporting the idea that closed populations are less resilient to disturbances than open populations (Almany et al. 2009). Nonetheless, closed populations that show local adaptations to stressors are likely to benefit from genotypes that have already been selected for in the local environment, hence they may be more resilient to local disturbances than open populations (e.g., Moe et al. 2013, Kenkel and Matz 2016). Population connectivity was clearly important under strong long-term disturbances (on multiple early life processes), since the effects of stressors on a population's growth rate were diluted by the immigration of larvae from other populations, and dynamics were driven by colonies demographic parameters (recruit, juvenile and adult growth and survival rates). However, when connectivity was minimal or the effects of global stressors also affected source populations, early life history stage contributions to population growth rates increased, with similar influences as reported for coral reef fish (Figueira 2009) and rocky shores mytilid mussels (Carson et al. 2011). These results highlight the importance in designing marine protected areas to facilitate connectivity between reefs, since increases in the number of sexually produced individuals ameliorates the impacts of stressors during periods of coral spawning on population dynamics.

The analysis of population dynamics in this study were performed for extreme model conditions (i.e., populations with low local retention and low connectivity), and declines in growth rates represent the greatest effects that local and global stressors could have during coral spawning on population dynamics on these reefs. Although the natural

co-occurrence of all these conditions might be low, a great proportion of inshore reefs in the GBR are constantly exposed to stressful conditions at local scales (i.e., nutrient enrichment, suspended sediments, Great Barrier Reef Marine Park Authority 2014), increasing their vulnerability to disturbances that are becoming more frequent in time (i.e., massive coral bleaching, cyclones). For example, tropical storms (cyclones, hurricanes or typhoons) are the most severe form of mechanical disturbance in coral reefs, causing adult colony fragmentation in branching species and affecting size-class distributions, especially in inshore reefs (Fabricius et al. 2008). Several studies have shown that the proportion of intense tropical storms reaching categories 4 and 5 has increased significantly within the last 35 years in many geographic regions (Walsh et al. 2004, Klotzbach 2006), and the increase in their frequency is best explained by increases in sea surface temperatures (Hoyos et al. 2006). Consequently, storms will skew size-class distributions in branching corals towards small size classes, reducing fecundity at the population-level. Moreover, warming temperatures are also known to have long term negative effects on colony fecundity during successive reproductive periods, reducing gamete production and altering spawning synchrony (Michalek-Wagner and Willis 2001, Paxton et al. 2016). Accordingly, reefs in areas impacted by a storm will experience a reduction in the percentage of adult colonies and in the fecundity of reproductive colonies, decreasing offspring production and connectivity.

In the GBR reserve network, the distance separating neighboring reefs ranges from 4 m to 52 km (median = 1.8 km) and more than 99% reefs have a neighboring reef within 14 km (Almany et al. 2009). Based on current evidence, coral populations on most reefs are connected to populations on several, possibly many, other reefs (Jones et al. 2009). However, expected sea surface temperature increases due to climate change can affect reef connectivity considerably. Embryo development time and larval pelagic duration are known to decrease with warming temperatures, increasing local retention and compromising connectivity between reefs (Nozawa and Harrison 2000, Heyward and Negri 2010, Figueiredo et al. 2014). Furthermore, the influence of larval immigration on population dynamics means that the effects of water quality decline at local scales are not constrained to the impacted reefs but can rather be extended to connected reefs, having implications for management and conservation actions.

Population growth rates in this study were influenced by early life history stages under scenarios of intense chronic disturbances and specific local retention and connectivity conditions. Intense long-term exposure to stressors on successive early life

history stages increased the relevance of adult colonies on population growth rates for *A. tenuis.* If local disturbances are expected to occur regularly during the months of coral spawning, management efforts should be focused on maintaining adult populations given the high likelihood that global stressors could compromise connectivity and fecundity of reef networks. On the other hand, if connectivity and larvae supply are known to be high, and stressors are known to occur regularly during spawning periods, management plans should be directed to protect early life history stages and juveniles, and promote conditions that ensure juvenile colony growth rates that will translate into production of adult colonies and maintenance of coral cover.

The most frequently used tool for describing changes in coral community structure is live coral cover, a variable used as an estimate of reef condition (Hughes and Tanner 2000, Gardner et al. 2003, De'ath et al. 2012). However, coral cover provides little information regarding mechanistic basis of changes and consequences, being an ambiguous indicator of population dynamics (Edmunds and Elahi 2007). The impacts of disturbance events on the fecundity of colonies, early life history stages and size distributions are rarely addressed in monitoring programs, although these are essential variables for understanding population dynamics and the effects of stressors. The present analysis shows that impacts of local and global stressors on the early life history stages and processes of corals can influence coral cover and should therefore be considered along with population growth rates in future demographic studies. However, there are mismatches between the information needed to understand coral population dynamics and the empirical data required, which is difficult to gather as it relies on *in situ* monitoring of early life history stages to estimate transition rates. Quantifying the rate of exchange of small planktonic larvae between populations in the ocean is also challenging and there remains a paucity of quantitative life history data (fecundity, growth and survivorship) required to populate demographic models. However, recent technological advances in underwater photography are providing tools to estimate precise size distributions in a cost-effective manner (Turner et al. 2015, Ferrari et al. 2016, González-Rivero et al. 2016), providing powerful information if incorporated in monitoring programs.

Coral cover is declining globally even in pristine reefs, and the diversity of anthropogenic disturbances that contribute to this decline demand a better understanding of the ecological significance of coral death in a demographic context. This study provides insights into the way in which information on early life history stages obtained

under laboratory conditions could be used to project population dynamics under different stress scenarios and highlights the importance of including size distribution analysis in monitoring programs. It is evident that there is a pressing need for demographic studies to investigate the effects of simultaneous stressors on all stages of the life cycle of corals, in order to better understand how coral cover will change in the coming centuries under the influence of local and global stressors.

Chapter 6: General discussion

Effects of multiple stressors on the early life history stages of corals and implications for population maintenance

6.1 Introduction

Understanding the effects of local and global stressors on early life history stages in corals, and upscaling these effects to the demography of coral populations, underpins our capacity to predict and manage coral reefs. Results presented in this dissertation demonstrate that the effects of current and near-future stressors are likely to reduce the reproductive success and hence the long-term resilience and persistence of coral populations. Successive exposure of early life stages to multiple stressors will cause cumulative negative impacts on gamete fertilization success, embryo development, larval survivorship, larval settlement, juvenile physiology and fitness, such that by the recruitment stage, overall negative effects are greatly amplified. In this final chapter, I synthesize results presented in **Chapters 2** through **5** to offer an ecological perspective on the combined impacts of multiple stressors on early life history processes, and highlight the relevance of describing and quantifying their effects for coral reef ecologists and managers. The implications of water quality decline and warming temperatures on each of the early life history processes are discussed below.

6.1.1 Gamete fertilization

In the broadcast spawning coral *Acropora tenuis*, fertilization was affected by all stressors (nutrient enrichment, suspended sediments and temperature), although their effects in isolation were not always significant and, in combination, depended on the stressor that co-occurred (Fig. 6.1). For example, nutrient enrichment had a negative effect on fertilization success when co-occurred with temperature stress (Chapter 2), but not when combined with suspended sediments (Chapter 3). These results demonstrate that effects can vary depending on the co-occurrence of other stressors, making predictions about their ecological impacts extremely difficult, particularly given the great

variety of co-occurring stressors in marine ecosystems. Instead of identifying the outcome of every possible stressor combination, it may therefore be necessary to focus primarily on the underlying mechanisms of action of stressors in order to identify generalities (interactions, effect size and direction) that provide practical information for managers (Cote et al. 2016).

In all experiments testing the effects of stressors on fertilization, impacts were negative, and when stressors were combined, impacts were additive. It should be noted that effect types and sizes will vary with methodological and biological features. For example, fertilization success differs with gamete contact time (Nozawa et al. 2015) and sperm concentrations (Willis et al. 1997, Marshall 2006, Ricardo et al. 2015), and experiments should therefore employ a wide range of sperm concentrations to accurately assess effect sizes. In addition, gamete compatibility can greatly impact fertilization success (Levitan et al. 2004, Ritson-Williams et al. 2010), hence experiments conducted here were performed using gametes from multiple colonies. Other factors that affect outcomes are related to the methodologies and materials used to generate the different stress treatments. In the case of sediments, their geochemical characteristics, particle grain size and nutrient content can result in different outcomes, with some sediments (e.g., those with high organic carbon content) causing greater impacts than others (e.g. carbonate sediments, Humphrey et al. 2008, Jones et al. 2015b, Ricardo et al. 2015). The different methods employed to perform nutrient enrichment or re-suspend the sediments will also influence the response obtained, with some approaches using only constant concentrations of inorganic nutrients at non-ecologically relevant concentrations or methods unlikely to achieve a constant suspension of particles throughout the experiment (Jones et al. 2015b).

Suspended sediments had the greatest negative effects on fertilization of the three stressors tested (Fig. 6.1), decreasing fertilization success considerably (~50%) at concentrations (37 mg l^{-1}) that are frequently reported in inshore areas of the GBR during flood and resuspension events (Jones et al. 2015a). The magnitude of the effect of suspended sediments on fertilization success might be related to the underlying mechanism of action of this stressor; entanglement in suspended sediments would reduce sperm concentration near the water surface (Ricardo et al. 2015). In contrast, thermal stress reduces sperm motility rather than gamete concentrations (Omori et al. 2001). The much smaller effect size of nutrient enrichment and temperature stress compared with

suspended sediments suggests that local management strategies to reduce sediment inputs into coastal areas would be of considerable benefit for fertilization and subsequent recruitment success of hard corals in the face of climate change.

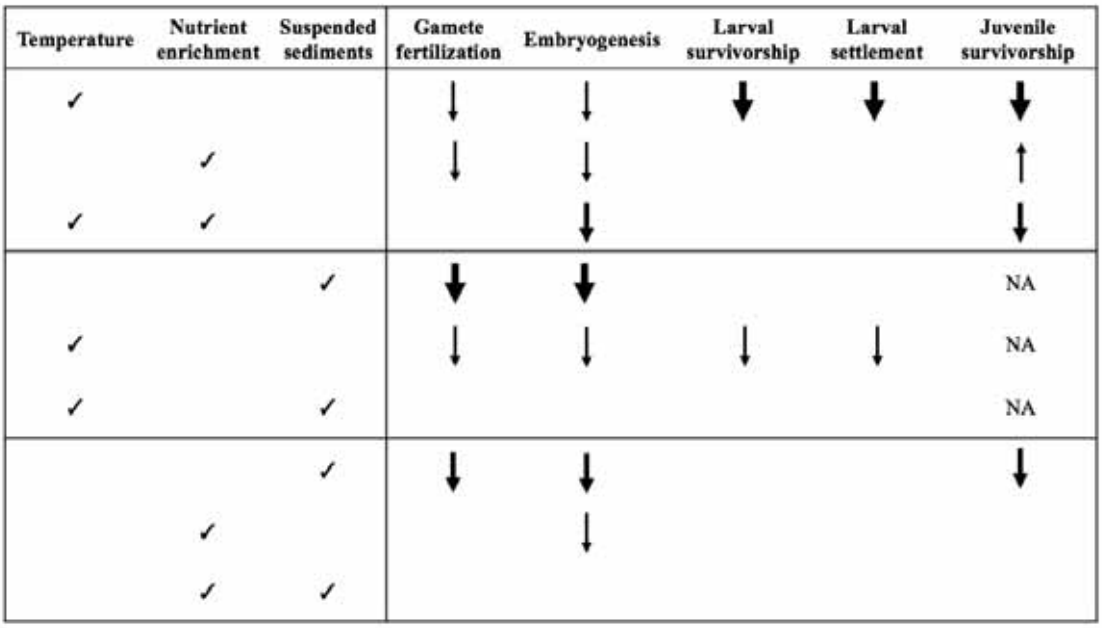


Figure 6.1: Summary of the effects of temperature stress, nutrient enrichment, and suspended sediments on early life history processes in *Acropora tenuis*, based on studies presented in this thesis. *Check symbols indicate* stressors that were present in individual experiments and *two checks represent* the interaction of both stressors. Directions (positive or negative) of the main effects of individual stressors and of interactions between stressors are indicated by arrows (up arrow: positive; down arrow: negative). Arrows also indicate relative strength and direction of the response (thick arrow = strong, medium = moderate, thin = weak effect); empty cells indicate that effects are not significant, and NA indicates data are not available.

Effects of water quality and thermal stress on gamete fertilization found for broadcast spawners may also apply to internal fertilization in brooding species. As with broadcast spawners, male gametes are released by brooding species into the water column, where they swim towards the egg, which in the case of brooders, are contained within another sexually mature colony. Nutrient enrichment and warming temperatures may impair sperm flagella motility and biochemical processes (Omori et al. 2001, Lam et al. 2015) in the same way in both brooding and broadcast spawning species, limiting their movement in the water column and decreasing fertilization success. These effects of suspended sediments might be equally severe for both reproductive modes, considering that sperm cells are likely to become entrapped with fine sediments, lose mobility and sink (Ricardo et al. 2015), reducing sperm available to the egg and decreasing fertilization

success. The effects of these stressors would only be ameliorated in brooders in comparison to broadcast spawners if egg viability was affected through metabolic or physical damage, considering that the polyp of brooding species confers protection to the eggs. Suspended sediments do not directly affect egg viability (Ricardo et al. 2015), however the effects of nutrient enrichment and temperature stress on female gametes is a topic that needs further research.

6.1.2 Embryo development

Embryogenesis was the most sensitive reproductive process to all three individual stressors (Fig. 6.1). Furthermore, exposure to stressors during embryo development had a carry-over effect on subsequent settlement success, and this effect occurred independently of previous (i.e., fertilization, Chapter 3) or subsequent exposures (i.e., larval development, Chapter 2). Embryo development commences within an hour or two of fertilization, and includes processes such as cell division, rearrangement and differentiation, finishing when the epidermis differentiates and cilia are formed, at which point the embryo becomes a larva (Harrison and Wallace 1990, Okubo and Motokawa 2007). During these processes, embryos are also vulnerable to physical disturbances that can fragment them, resulting in smaller but functional embryos (Heyward and Negri 2012). The high sensitivity of embryogenesis to nutrient enrichment, warming temperatures and suspended sediments (Chapters 2 and 3) might be related to impacts on one or more of the cellular developmental processes described above, which could have flow-on effects for embryo development, larval survivorship and larval settlement if metabolic functions are impaired (Portune et al. 2010).

This is the first study to report that the negative effects of nutrient enrichment, thermal stress and suspended sediments on embryogenesis are additive and have follow-on effects for subsequent settlement of coral larvae. Previous studies have reported that mucus is produced by early embryos (~6-24-hours-old) of *A. tenuis* and *A. millepora* exposed to suspended sediments, but no subsequent effects on larval survivorship nor ability to settle were detected (Ricardo et al. 2016). My results suggest that stressors that cause effects on cellular function, increase energy demands, or cause mechanical abrasion during embryo development can be negative for larval settlement. It should be noted that the sensitivity of embryos to stressors is likely to change with embryo age, thus comparisons between studies are only valid when similar embryo ages and exposure

times have been studied. In this thesis, the effects of suspended sediments with either nutrient enrichment or high temperatures on survival and function of abnormal embryos was not assessed. However, a previous study found no effects of sediment exposures (200 mg l^{-1}) on embryo development in very early stages (~four-cell stage) of *A. millepora* (Humphrey et al. 2008). Similarly, no clear trends in survival of 3-18 h-old embryos of *A. digitifera* were found following sediment exposures of 100 mg l^{-1} (Gilmour 1999).

The effects of temperature, nutrients and sediments on embryo development might vary considerably between broadcasting and brooding species, since embryo development occurs within the polyps of brooders. Internal development may confer physical protection to brooded embryos from the abrasive action of suspended sediments (Ricardo et al. 2016). However, if brooding colonies are exposed to thermal stress conditions for longer periods, effects on embryo development could be amplified, as embryogenesis can be a far more prolonged process (~weeks to months) in comparison with broadcasters (hours-days) (Harrison and Wallace 1990). Moreover, exposure of brooding adult colonies to individual and simultaneous stress conditions could affect embryogenesis as a consequence of resource reallocation of energy from embryo development to cleaning, repair and maintenance (Tomascik and Sander 1987b), or as a consequence of premature embryo abortion (Loya and Rinkevich 1979) or reabsorption (Cantin et al. 2007).

6.1.3 Larval survivorship

Larval survivorship was affected by temperature stress, but was relatively resilient to the effects of suspended sediments and nutrient enrichment, even when previous stages (e.g. fertilization and larval settlement) were co-exposed to nutrients and sediments (Fig. 6.1). Unlike embryos, larvae have differentiated tissue layers and developed cilia, show active swimming and phototaxic behaviors (Harrison and Wallace 1990), and contain substantial lipid reserves used as energy sources during their planktonic phase (Figueiredo et al. 2012). Coral larvae seem to be more resilient to stressors than previous stages, possibly due to the presence of differentiated cells and the energy resources they obtain from lipid storage, which could confer resistance to stress conditions.

Coral larvae can be either symbiotic or aposymbiotic (symbiont-free), depending on whether or not *Symbiodinium* spp. are transmitted from the parental colony into the egg or embryo prior to their release into the water column. If *Symbiodinium* are not

acquired in the water column, then aposymbiotic larvae depend exclusively on energy reserves provided by the egg, whereas symbiotic larvae can obtain energy from endosymbiotic *Symbiodinium* (Richmond 1987), enabling them to survive longer and possibly disperse further (Graham et al. 2008). The effect of thermal stress is likely to differ between symbiotic and aposymbiotic larvae, with bleaching reducing survivorship and settlement of symbiotic larvae dependent on symbiont-derived energy. In addition, thermal stress in symbiotic larvae is known to enhance the production of reactive oxygen species (ROS) by photosynthetic electron transport in the chloroplast of the *Symbiodinium*, which can damage cells of the host (Desalvo et al. 2008, Rodriguez-Lanetty et al. 2009).

Newly developed larvae of *A. tenuis* are aposymbiotic, acquiring *Symbiodinium* cells either from the water column while swimming or once settled and metamorphosed (Little et al. 2004, Cumbo et al. 2013, Yamashita et al. 2014). In all experiments conducted in this thesis, I used aposymbiotic larvae, hence any effects of thermal stress detected on the energy budget of larvae must have resulted from increased larval metabolic rates (Clarke and Fraser 2004, O'Connor et al. 2007). Moreover, observed effects of high temperatures on larval survivorship might be related to sub-cellular damage and disruption of biochemical steps affecting metabolic pathways or physiological properties of the larvae. For example, cilia motility and pre-competency periods have been observed to decrease in aposymbiotic larvae after exposures to high temperatures (Edmunds et al. 2001, Heyward and Negri 2010, Negri and Hoogenboom 2011, Schnitzler et al. 2012).

The effects of stressors might also vary between brooded and non-brooded larvae due to differences in development state when they are first exposed to the water column. Brooded larvae tend to be symbiotic, more advanced in development, have higher reserves of lipids and are often larger when released than larvae of broadcast spawning species (Harrison and Wallace 1990). These characteristics could confer brooded larvae higher resistance to stressors and greater survivorship in comparison to the smaller larvae of broadcast spawners. However, a great proportion of brooded larvae settle in the vicinity of parental colonies (Ayre and Hughes 2000, Warner et al. 2016), possibly compromising their post-settlement survivorship if stressors are frequent or if environmental conditions are declining in the area, a clear disadvantage in comparison to the long dispersal

distances reported for larvae of broadcast-spawning species (Lukoschek et al. 2016), which can disperse to low disturbance areas.

6.1.4 Larval settlement

Larval settlement was affected following the exposure of embryos to high levels of nutrients, suspended sediments and temperatures (see section 6.1.2, Chapter 3), and the combined effects of these stressors were additive (Fig 6.1). In contrast, developed larvae (≥ 3d old) were only affected by thermal stress if: i) previous stages were also exposed to thermal stress (Chapter 2), ii) developed larvae were exposed but settlement was performed under control conditions (Chapter 3), or iii) larvae were exposed to thermal stress during settlement (Chapters 2 and 3). The effects of thermal stress on the settlement success of aposymbiotic larvae of *A. tenuis* may be related to sub-cellular damage and disruption of biochemical steps involved in the detection of settlement cues, since larvae exposed to high temperatures were still actively swimming and searching for settlement substrata in all temperature treatments. Coral larvae of many species selectively choose their settlement sites using external chemical cues that induce settlement and metamorphosis (Morse et al. 1994, Morse et al. 1996, Heyward and Negri 1999). However, the mechanisms that determine larval responses to these cues remain poorly understood (Tebben et al. 2011), and effects of stressors on this potential mechanism were not specifically addressed in this study. Nonetheless, my results provide insights into the effects of simultaneous stressors on settlement, and suggest thermal stress can be an important driver of subsequent recruitment success for *A. tenuis*.

Nutrient effects varied with the duration of exposure and the process or life stage exposed. Effects on settlement success were significant only following short-term exposure of embryos (previously discussed in section 6.1.2), while no effects were observed when nutrients were high during larval development or during the settlement process. High nutrients may affect larval settlement as a result of complex biological (i.e. bacteria, zooplankton and phytoplankton communities) and physicochemical (dissolved and particulate organic and inorganics, trace elements) dynamics that may interact with early life history processes in different ways (see sections 2.4.2 and 3.4). The range of responses between life stages and exposure durations clearly highlights the need for further studies on the mechanism by which high levels of nutrients affect larval settlement.

Settlement success was also affected by suspended sediments but only in larvae that had been previously exposed during the embryo stage (see section 6.1.2), while suspended particles did not affect settlement success when substrata availability was not a limiting factor. Nonetheless, increases in suspended sediment concentrations will enhance sediment deposition, negatively affecting larval settlement success (Rogers 1990, Birrell et al. 2005) and post-settlement survivorship (Fabricius et al. 2003b), variables that were not evaluated in this study.

Potential differences in the effects of water quality and climate stressors on settlement processes for brooded larvae versus larvae developed from broadcast-spawned gametes are unknown. Any differences in effects may be related to larval size, as previously discussed (Section 6.1.3). Species with different reproductive strategies have been shown to prefer different settlement substrata (Golbuu and Richmond 2007) and their chemical cues and signaling process may respond in different ways to stress.

6.1.5 Juvenile physiology, growth and survivorship

Experimental studies described in this thesis provide evidence that juvenile corals are vulnerable to nutrient enrichment, suspended sediments and temperature stress, and have also shown that increased susceptibility following simultaneous exposures to these stressors further compromises juvenile growth and fitness (Chapters 2 and 4). It is widely recognized that coral juveniles have higher mortality rates than their adult counterparts; small colonies have increased mortality risk from disturbances in contrast to larger individuals that more typically experience partial mortality (Hughes and Jackson 1985, Babcock and Davies 1991, Babcock 1991, Vermeij and Sandin 2008). A prominent cause of mortality for coral juveniles is direct or incidental predation by grazers, and size-escape thresholds have been reported for several species (Raymundo and Maypa 2004, Box and Mumby 2007). Thus any process that reduces coral juvenile growth (i.e., suspended sediments) will prolong their exposure to sources of mortality (pre-size-escape) and elevate mortality rates (Doropoulos et al. 2012).

The present study demonstrates that, although juvenile responses to stressors are species-specific and effect sizes and types vary among physiological variables, the final outcome of exposures to multiple stressors (Chapters 2 and 4) is likely to be a significant reduction in the number of colonies that attain reproductive sizes, as a result of decreases

in juvenile growth or survivorship rates. Differences between reproductive modes will not greatly affect juvenile responses since colonies are infertile.

The impacts of suspended sediments on the physiology of coral juveniles of *A. tenuis* suggest that energetic demands associated with respiration increase, possibly as a result of sediment cleaning, mucus production, and cell maintenance and repair causing trade-offs in their energy budgets, compromising fitness. The effects of sediments deposited on juveniles will further compromise colony survival, but this aspect was not addressed in the present study. Coral colonies have different strategies to clear deposited sediments from their surfaces, which are related to their growth forms and corallite morphologies (Jones et al. 2016), however, once sediment clearance rates have been exceeded, sediments will inevitability build-up on a coral's surface. In the present study, nutrient enrichment did not enhance the negative effects of suspended sediments, in contrast to previous reports of negative effects of sediments deposited on adult colonies (Weber et al. 2012). The deposition of nutrient-enriched particles induces tissue mortality through microbial processes triggered by organic matter in sediments, namely respiration and presumably fermentation and desulfurylation of products from tissue degradation (Weber et al. 2012). Nutrient-enriched sediments deposited on juvenile colonies, might operate in a similar way as those on adult colonies, however their effects might be more pronounced since their sediment clearance rates will be exceeded more quickly due to their small size, compromising their survivorship after short-term exposures (~43 h, Fabricius et al. 2003a).

6.1.6 Effects on gametogenesis in adult colonies

The effect of stressors on gametogenesis was not addressed in this study, because of the long duration of this process (up to 11 months for many species, Babcock et al. 1986, Vargas-Ángel et al. 2006) and the technical difficulties of exposing adult coral colonies for a long period of time to multiple stressors under controlled laboratory conditions. These factors have also limited the successful study of simultaneous stressors on coral fecundity, with previous studies focusing on the effects of individual stressors (e.g., Michalek-Wagner and Willis 2001, Cantin et al. 2007).

The reproductive success of colonies has been reported to be negatively affected during and after thermal stress and bleaching events. Changes in sea surface temperatures may be a cue to initiate oogenesis, and temperatures over subsequent months affect oocyte

development duration (Babcock et al. 1986, Hayashibara et al. 1993, Nozawa 2012). Fewer gametes were found in bleached polyps of several species (Ward et al. 2000, Jones and Berkelmans 2011), and this effect has been observed to last for up two years after a bleaching event (Ward et al. 2000, Michalek-Wagner and Willis 2001, Baird and Marshall 2002, however see Cox 2007). Additionally, temperature stress has been reported to affect the pre-spawning lipid content and egg size of bleached and unbleached colonies, with potential flow-on effects for embryo survivorship and development (Jones and Berkelmans 2011). These observations indicate that temperature increases can produce adverse and long-lasting effects on the fecundity and gametogenesis of hard corals.

Information on the effects of nutrient enrichment on coral fecundity is limited and inconclusive, mainly due to modest experimental designs used in previous studies, with only two levels of nutrients limiting comparisons among studies. Moreover, the direction of effects on the response variable cannot be assessed if only two levels of a stressor are used, resulting in modal responses. For example, decreases in oocyte size (Cox and Ward 2002, Loya et al. 2004), lipid content (Bongiorni et al. 2003a, Loya et al. 2004), and larval production (Tomascik and Sander 1987b, Cox and Ward 2002, Loya et al. 2004) are among the negative effects observed in colonies exposed to high nutrients levels. However, in contrast, other studies report increases in gamete production (Meyer and Schultz 1985, Lieberman et al. 1995, Bongiorni et al. 2003a) and in oocyte and testes sizes (Bongiorni et al. 2003a, Bongiorni et al. 2003b) under eutrophication conditions.

As with nutrient enrichment, no studies have directly manipulated suspended sediment levels to test their effects on gametogenesis; however, correlations between turbidity and the reproductive output of colonies have been reported (Kojis and Quinn 1984, Tomascik and Sander 1987a). The mechanisms by which suspended sediments are proposed to affect gametogenesis are related to a shift in energy allocation from reproduction to self-cleaning. In addition, suspended sediments cause light attenuation (Jones et al. 2016), reducing the translocation of photosynthates from endosymbiotic *Symbiodinium* spp. to coral cells (Kojis and Quinn 1984, Tomascik and Sander 1987a, Rinkevich 1989). More research is clearly needed to understand cause-effect pathways and modes of action of suspended sediments on gametogenesis and also on the effects that this stressor can have when co-occurring with nutrient enrichment or warming temperatures.

6.2 Demographic implications of stressors during early life stages of corals

The occurrence of stressors during early life history stages can have severe effects on population growth rates, affecting colony size distributions and consequently coral cover. My research advances our understanding of the potential cumulative impacts of water quality declines and warming temperatures on the sensitive early stages and processes during the first month of life of hard corals, and highlights the importance of protecting early life history stages from co-occurring stressors. In addition, I show that laboratory experiments can be used to complement field data and develop theoretical models to understand the effects of local and global stressors on population dynamics (Chapter 5). Moreover, stressors will not only affect exposed populations, but can also have negative impacts on other populations connected through larval dispersal.

Understanding recruitment dynamics and the relative contributions of relevant stressor levels is essential to assess how coral population structures and dynamics will respond to accumulating stressors. High settlement rates are essential for the replenishment of coral populations since survivorship rates are low during the first month of life of a colony (Penin et al. 2010, Humanes and Bastidas 2015) representing a population bottleneck for corals. Nonetheless, reefs with different coral cover can have similar settlement rates (van Woesik et al. 2014, Edmunds et al. 2015, Humanes and Bastidas 2015), suggesting that other variables besides early life history stages can determine coral cover. Coral population structure depends on demographic rates of the different life history stages, species-specific sensitivity to stressors, connectivity to other populations, inter and intra-specific relationships (i.e., competency, predation, symbiosis, mutualism), which together with the disturbance regime in the area determine population size distributions and dynamics. Therefore, understanding the effects of disturbances on early life history stages is not enough to predict coral cover and the effects of stressors on population dynamics; instead, a complete study of population demographic rates is needed.

6.3 Concluding remarks

In addition to contributing biological knowledge on the effects of multiple stressors on early life history stages of corals, the outcomes of this thesis provide practical

information that can be applied to reef management, especially for the GBR, where declining water quality and increasing temperatures threaten reef health (Great Barrier Reef Marine Park Authority 2014). My results demonstrate that the responses of early life history stages to stressors will depend on the intensity, timing of onset and duration of the stress exposure, whether other stressors co-occur, and on species-specific characteristics. Effective management of local stressors during coral spawning events will be important because many stressor combinations cause additive negative effects across early life stages. Early life stages are considered to be a sensitive and important phase in the life history of hard corals, with phenotypic and genetic characters of some species conferring greater resilience to environmental changes and disturbances. My results suggest that nutrient enrichment and sediment discharges into coastal areas of the GBR can exacerbate the impacts of temperature stress on early life history stages. Furthermore, the resilience of inshore coral populations to thermal stress would likely be improved through improved management actions regulating agricultural practices in river catchments and dredging of coastal areas.

Currently, most of our understanding of the effects of disturbances on early life stages are gleaned from experiments performed under controlled laboratory conditions using exposures to single stressors with low numbers of treatment levels, limiting the application of these findings to the natural environment. More multiple-level studies on the effects of simultaneous stressors on early life history stages, such as those presented in Chapters 2-4, are needed to better understand the impacts of anthropogenic activities and climate change on coral reefs. Future environmental changes in coastal regions are likely to alter several chemical and physical properties of seawater simultaneously (Meissner et al. 2012, Jones et al. 2015a, Angly et al. 2016) and information on the mechanisms by which such changes affect the reproductive biology of corals is still scarce. My results show that the negative effects of particular stressors acting on one, or more than one, early life history stage can have critical impacts on population growth rates and structure. Successful recruitment will depend on the reproductive output of a population and the subsequent rates of fertilization, embryogenesis, larval survivorship and settlement. Thus, any stressor capable of affecting these processes will cause a major impact on the input of new individuals, essential for the maintenance of coral populations.

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Supporting information

	Expected Temperature	Fertilization (Experiment 2.1a and b)	Larvae development (Experiment 2.1c)	Settlement (Experiment 2.1d and 2)	Juveniles (Experiment 2.3)
Incubation of nutrients	27°C	27.23 ± 0.36°C	27.40 ± 0.17°C	27.45 ± 0.15°C	27.10 ± 0.10°C
	29°C	28.64 ± 0.65°C	28.49 ± 0.70°C	29.76 ± 0.081°C	
	30°C	30.32 ± 0.70°C	30.62 ± 0.61°C	30.28 ± 0.18°C	27.13 ± 0.25°C
	31°C	31.08 ± 0.18°C	30.88 ± 0.70°C	31.60 ± 0.36°C	
	32°C	32.32 ± 0.44°C	32.52 ± 0.35°C	32.77 ± 0.10°C	27.15 ± 0.43°C
Experiment	27°C	27.55 ± 0.13°C	27.48 ± 0.15°C	27.39 ± 0.15°C	27.07 ± 0.18°C
	29°C	29.35 ± 0.19°C	29.44 ± 0.31°C	29.05 ± 0.62°C	
	30°C	30.58 ± 0.10°C	30.54 ± 0.48°C	30.49 ± 0.06°C	29.98 ± 0.16°C
	31°C	30.99 ± 0.18°C	31.44 ± 0.49°C	31.25 ± 0.68°C	
	32°C	32.76 ± 0.05°C	32.76 ± 0.11°C	32.70 ± 0.05°C	31.94 ± 0.20°C

S2.1Table: Temperatures (°C) reached during the incubation of the modified FSW with organic nutrient enrichment and during Experiments 2.1 (a, b, c and d), 2.2 and 2.3 (incubation period in Experiment 2.3 corresponds to the exposure to nutrient enrichment during 20 days before starting the temperature stress). Values shown are means ± standard deviations.

S2.2 Table: Effects of temperature (Temp) and organic nutrient enrichment (Nut) on i) fertilization success (Experiment 2.1a), embryo development (Experiment 1b), larval development (Experiment 2.1c) and larval settlement (Experiment 2.1d), and ii) juvenile growth, production of new polyps, final weigh/final size, F_v/F_m, survivorship curves (Experiment 2.3) of *Acropora tenuis*. Temperatuture (Temp) and organic nutrient enrichment (Nut) were considered as fixed factors. Significance at $p<0.05$ is shown in **bold**. Df: degrees of freedom.

i)

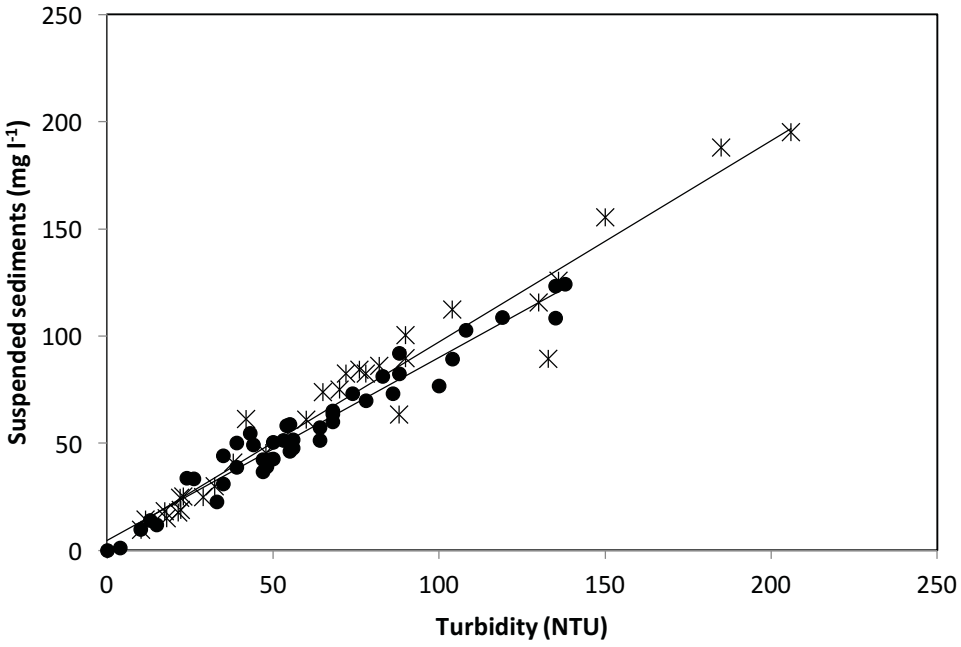
Experiment	Factor	Df	Deviance	F-value	p-value
Fertilization (1a)	Temp	1	1600.20	17.462	**<0.001**
	Nut	2	1616.20	9.245	**<0.001**
	Temp:Nut	2	1330.10	0.954	0.389
Embryo development (1b)	Temp	1	1207.73	173.532	**<0.001**
	Nut	2	494.46	10.128	**<0.001**
	Temp:Nut	2	512.75	12.975	**<0.001**
Larval survivorship (1c)	Temp	1	892.26	118.899	**<0.001**
	Nut	2	375.61	0.127	0.880
	Temp:Nut	2	374.50	1.739	0.181
Larval settlement (1d)	Temp	1	808.76	65.584	**<0.001**
	Nut	2	459.38	0.050	0.951
	Temp:Nut	2	458.84	0.111	0.895
Larval settlement (2)	Temp	1	241.53	43.052	**<0.001**
	Nut	2	200.11	2.828	0.061
	Temp:Nut	2	193.84	0.032	0.968

S2.3 Table (continuation): Effects of temperature (Temp) and organic nutrient enrichment (Nut) on i) fertilization success (Experiment 2.1a), embryo development (Experiment 1b), larval development (Experiment 2.1c) and larval settlement (Experiment 2.1d), and ii) juvenile growth, production of new polyps, final weigh/final size, F_v/F_m, survivorship curves (Experiment 2.3) of *Acropora tenuis*. Temperatuture (Temp) and organic nutrient enrichment (Nut) were considered as fixed factors. Significance at $p<0.05$ is shown in **bold**. Df: degrees of freedom.

ii)

Experiment	**Factor**	**Df**	**Likelihood ratio test**	**p-value**
Growth	Temp	2	9.175	**0.010**
	Nut	2	2.391	0.302
	Temp:Nut	4	3.447	0.485
Production of new polyps	Temp	2	0.463	0.793
	Nut	2	3.175	0.204
	Temp:Nut	4	1.504	0.825
Final weight/Final size	Temp	2	0.726	0.696
	Nut	2	2.259	0.323
	Temp:Nut	4	5.371	0.251
F_v/F_m	Temp	2	16.334	**<0.001**
	Nut	2	8.617	**0.013**
	Temp:Nut	4	11.931	**0.017**

S3.1 Figure: Suspended sediment treatments were prepared by adding sediments to FSW to reach the target levels. Each year a NTU-suspended sediments calibration curve was prepared based on i) 30 samples (crosses) ranging from 0 to 195 mg l^{-1} suspended sediments on 2014 (suspended sediments= 0.93NTU + 3.55) and, ii) 44 samples (circles) ranging from 0 to 130 mg l^{-1} suspended sediments on 2015 (suspended sediments= 0.85 NTU + 4.56). Turbidity was measured in each sample with a nephelometer (TPS 90FL-T). Samples were filtered onto 0.4 μm pre-weighted polycarbonate filters, dried overnight at 60°C and then weighted. The relationship between NTU and suspended sediments were linear and strong (R^2 = 0.95 for both years).



S3.2 Table: Temperatures (°C) during the performance of the Experiments 1, 2, 3 and 4 (mean ± sd). SS: suspended sediments, Nut: nutrient enrichment, Temp: temperature.

		Temperature obtained			
Factors combination	**Target temperature**	**Fertilization**	**Embryos**	**Larvae**	**Settlement**
SS x Nut	27°C	27.4±0.2	27.1±0.2	27.3±0.1	27.2±0.3
SS x Temp	27°C	27.3±0.4	27.2±0.1	27.3±0.2	27.4±0.1
	30°C	30±0.5	29.6±0.1	29.8±0.2	30.0±0.1
	32°C	32.1±0.4	31.1±0.1	31.9±0.4	31.5±0.3

Experiment	Suspended sediments	Nutrient enrichment	DOC (µM)	TOC (µM)	NH_4 (µM)	NO_3+NO_3 (µM)	NO_2 (µM)	TDN (µM)	TN (µM)	PO_4 (µM)	TDP (µM)
Schaffelke et al 2012			42.8-195.6	3.9-70.5	0-0.82	NA	NA	2.2-11.5	0.5-2.7	0.02-0.6	0-1.01
3.1	0	Low	88.4±1.7	16.6±3.0	0.6±0.1	0.7±0.1	0.2±0.1	9.6±0.6	3.1±0.9	0.1±0.1	0.2±0.1
		Medium	86.8±1.6	33.2±8.1	5.5±2.2	0.8±0.1	0.2±0.1	17.9±2.9	6.7±1.2	0.1±0.1	0.3±0.1
		High	103.1±27.2	33.7±3.3	6.0±1.5	0.8±0.1	0.2±0.1	18.7±1.9	6.3±0.2	0.2±0.1	0.4±0.2
	5	Low	81.1±2.9	36.1±3.5	0.8±0.1	0.8±0.1	0.2±0.1	12.2±0.1	4.8±0.4	0.1±0.1	0.2±0.1
		Medium	87.0±1.7	54.8±5.4	4.0±0.9	0.8±0.1	0.2±0.1	19.9±1.5	10.1±0.7	0.1±0.1	0.2±0.1
		High	105.4±18.3	65.4±5.5	6.2±0.2	0.8±0.1	0.2±0.1	21.6±1.2	10.8±1.9	0.1±0.1	0.3±0.1
	10	Low	79.1±3.8	46.2±4.1	0.7±0.0	0.6±0.1	0.2±0.1	11.4±0.9	7.1±1.2	0.1±0.1	0.4±0.3
		Medium	82.2±0.5	62.9±0.1	2.5±0.2	0.8±0.1	0.2±0.1	15.2±0.3	9.4±0.9	0.1±0.1	0.2±0.1
		High	100.4±4.1	66.2±1.5	5.9±0.1	0.8±0.1	0.2±0.1	19.1±0.8	11.4±1.3	0.1±0.1	0.3±0.1
	30	Low	88.6±2.2	108.8±42.1	0.7±0.1	0.5±0.1	0.2±0.1	12.0±0.2	15.0±4.0	0.1±0.1	0.2±0.1
		Medium	90.4±0.6	132.6±12.3	2.5±0.2	0.7±0.1	0.2±0.1	14.7±1.5	22.3±3.3	0.1±0.1	0.2±0.1
		High	108.4±18.7	201.2±30.9	5.2±0.5	0.8±0.1	0.2±0.1	19.5±0.4	33.4±6.1	0.1±0.1	0.3±0.1
	100	Low	91.4±0.2	NA	0.7±0.1	0.2±0.1	0.1±0.1	11.2±0.4	NA	0.1±0.1	0.2±0.1
		Medium	96.9±15.0	317.7±55.2	1.9±0.1	0.7±0.1	0.2±0.1	13.5±0.5	43.9±1.1	0.1±0.1	0.2±0.1
		High	97.9±11.3	313.1±17.2	4.1±0.6	0.8±0.1	0.2±0.1	17.6±0.5	45.2±3.3	0.1±0.1	0.2±0.1
3.2	0	Low	109.2±17.4	53.3±32.8	0.2±0.2	0.4±0.3	0.2±0.1	12.7±2.2	6.7±2.2	0.3±0.2	0.1±0.1
		Medium	115.7±8.7	101.2±56.5	0.2±0.2	0.4±0.3	0.2±0.1	14.7±4.0	10.3±3.3	0.3±0.1	0.1±0.1
		High	124.8±24.9	116.9±103.7	0.2±0.2	0.4±0.3	0.2±0.1	15.9±5.0	11.1±9.2	0.5±0.3	0.4±0.5
	5	Low	103.0±15.4	49.7±10.7	0.1±0.1	0.2±0.1	0.2±0.1	12.5±2.1	7.5±0.7	0.3±0.1	0.1±0.1
		Medium	114.2±3.6	161.6±17.3	0.2±0.2	0.3±0.3	0.2±0.1	16.8±2.1	20.7±1.0	0.4±0.3	0.1±0.1
		High	158.4±41.6	279.2±119.8	0.2±0.2	1.0±0.9	0.2±0.1	21.3±2.7	27.6±13.0	0.1±0.1	0.3±0.4
	10	Low	104.2±4.8	91.8±37.6	0.1±0.1	0.2±0.1	0.2±0.1	12.5±0.8	13.2±5.4	0.5±0.4	0.1±0.1
		Medium	111.3±13.5	114.9±7.6	0.1±0.1	0.4±0.3	0.2±0.1	13.7±2.3	17.3±3.0	0.2±0.1	0.1±0.1
		High	125.7±13.1	176.7±92.1	0.1±0.1	0.5±0.3	0.5±0.3	13.1±2.2	19.8±8.5	0.2±0.1	0.3±0.1
	30	Low	100.1±2.5	279.0±82.6	0.1±0.1	0.3±0.2	0.2±0.1	16.5±4.5	32.1±13.9	0.2±0.1	0.1±0.1
		Medium	104.5±8.9	296.3±104.6	0.2±0.2	0.3±0.3	0.2±0.1	17.8±6.8	41.2±8.2	0.3±0.1	0.2±0.1
		High	165.8±121.3	392.7±163.5	0.4±0.2	0.4±0.3	0.2±0.1	20.0±4.7	48.1±22.7	0.3±0.2	0.3±0.1
	100	Low	94.9±7.3	267.4±80.5	0.1±0.1	0.7±0.3	0.2±0.1	13.3±1.6	31.6±8.4	0.2±0.1	0.2±0.1
		Medium	106.4±26.4	295.8±29.4	0.1±0.1	0.7±0.2	0.2±0.1	14.2±3.3	36.9±8.8	0.3±0.1	0.2±0.1
		High	134.4±54.5	352.5±108.7	0.1±0.1	0.8±0.2	0.2±0.1	17.7±4.3	38.7±3.2	0.3±0.2	0.2±0.1

S3.3 Table: Water quality parameters for the different suspended sediments concentrations (mg l^{-1}) and nutrient enrichment (low in white, high in dark grey) at the start of each experiment. Values shown are means and standard deviations. Number of replicates: 2 per water quality factor and treatment.

Experiment	Suspended sediments	Nutrient enrichment	DOC (µM)	TOC (µM)	NH_4 (µM)	NO_2+NO_3 (µM)	NO_2 (µM)	TDN (µM)	TN (µM)	PO_4 (µM)	TDP (µM)
3.3	0	Low	84.8±14.0	16.9±1.5	0.9±0.1	1.3±0.1	0.3±0.1	17.2±1.4	1.6±0.1	0.1±0.1	0.5±0.1
		Medium	97.8±12.4	30.9±0.2	3.0±0.3	1.4±0.1	0.3±0.1	16.8±0.1	4.1±0.2	0.2±0.1	0.5±0.1
		High	103.9±2.4	36.2±1.5	5.6±0.1	1.4±0.1	0.3±0.1	19.2±0.7	5.9±0.4	0.4±0.1	0.7±0.1
	5	Low	104.6±10.7	39.8±12.9	0.8±0.1	1.2±0.1	0.3±0.1	13.3±2.3	4.1±0.9	0.1±0.1	0.3±0.1
		Medium	109.2±5.9	54.4±0.3	1.8±0.1	1.3±0.1	0.3±0.1	14.2±2.5	7.4±0.2	0.1±0.1	0.4±0.1
		High	129.4±5.7	83.1±6.1	4.7±0.6	1.3±0.1	0.3±0.1	20.5±0.1	14.6±0.4	0.2±0.1	0.5±0.1
	10	Low	90.5±0.6	49.0±7.4	0.8±0.1	1.2±0.1	0.3±0.1	12.2±0.1	4.9±0.5	0.1±0.1	0.3±0.1
		Medium	119.4±0.6	56.3±8.9	1.6±0.1	1.3±0.1	0.3±0.1	16.0±1.0	6.6±1.5	0.1±0.1	0.4±0.1
		High	125.7±24.0	85.3±2.7	4.2±0.2	1.4±0.1	0.3±0.1	23.2±0.6	14.0±1.2	0.1±0.1	0.5±0.1
	30	Low	123.4±6.7	120.2±2.3	0.9±0.1	1.0±0.1	0.3±0.1	13.1±0.5	14.5±5.6	0.1±0.1	0.3±0.1
		Medium	138.9±21.1	141.4±0.9	2.1±0.4	1.4±0.1	0.3±0.1	23.6±3.9	15.2±1.7	0.1±0.1	0.3±0.1
		High	241.5±133.4	173.2±115.2	6.2±0.3	1.4±0.1	0.3±0.1	25.5±0.7	19.7±2.4	0.1±0.1	0.5±0.1
	100	Low	131.8±14.6	243.6±16.2	0.8±0.1	0.7±0.2	0.3±0.1	13.1±0.1	25.9±1.4	0.1±0.1	0.3±0.1
		Medium	153.4±23.1	278.9±15.3	1.4±0.4	1.4±0.1	0.3±0.1	19.0±1.8	31.2±0.1	0.1±0.1	0.4±0.1
		High	154.8±27.3	298.2±26.8	5.7±0.3	1.5±0.1	0.3±0.1	26.4±2.4	33.8±1.5	0.2±0.1	0.5±0.1
3.4	0	Low	101.3±9.6	21.8±5.0	2.0±1.4	0.7±0.3	1.4±1.3	22.7±3.3	4.5±0.8	0.2±0.1	0.5±0.1
		Medium	112.0±3.8	25.7±1.3	4.6±3.4	0.7±0.2	1.7±0.1	24.7±0.6	5.3±0.2	0.2±0.1	0.6±0.1
		High	143.3±59.4	26.4±8.4	4.2±2.0	0.8±0.2	2.0±0.5	25.3±3.2	5.9±2.1	0.2±0.1	0.6±0.1
	5	Low	101.9±13.1	67.8±9.9	0.9±1.0	0.4±0.1	0.2±0.1	14.3±1.7	9.3±10.6	0.2±0.1	0.5±0.1
		Medium	109.2±4.2	77.3±3.4	1.4±1.1	0.4±0.1	0.2±0.1	18.9±0.9	10.6±2.4	0.2±0.1	0.5±0.1
		High	110.6±3.7	80.0±14.5	2.4±1.5	1.6±1.2	0.7±0.6	19.9±1.4	14.1±0.5	0.2±0.1	0.6±0.1
	10	Low	94.8±9.4	70.3±12.3	1.4±1.0	0.3±0.1	0.2±0.1	14.2±0.6	9.1±1.4	0.2±0.1	0.5±0.1
		Medium	110.5±5.8	81.4±5.7	1.3±0.9	1.7±1.5	0.7±0.5	13.9±2.3	11.8±0.8	0.2±0.1	0.6±0.1
		High	121.3±6.2	104.4±49.4	3.2±2.3	4.5±4.9	1.3±1.3	22.9±9.3	16.1±6.3	0.2±0.1	0.6±0.1
	30	Low	99.6±21.2	225.5±42.7	3.0±1.8	1.9±1.4	0.8±0.6	19.9±5.2	32.8±4.1	0.2±0.1	0.6±0.1
		Medium	110.6±18.2	343.3±34.8	3.2±1.4	3.1±2.1	1.0±0.6	19.1±2.3	48.1±9.2	0.2±0.1	0.7±0.2
		High	104.4±12.5	341.6±98.2	3.8±3.7	3.1±3.1	1.1±1.0	21.1±6.9	52.3±16.4	0.2±0.1	1.3±1.4
	100	Low	102.2±5.6	226.1±13.5	0.5±0.6	0.4±0.2	0.2±0.1	14.1±1.0	36.4±3.2	0.2±0.1	0.5±0.1
		Medium	112.5±16.7	236.1±16.9	0.9±0.8	0.3±0.3	0.2±0.1	15.3±3.9	39.3±8.1	0.2±0.1	0.6±0.1
		High	122.2±24.1	301.5±64.6	1.0±1.6	0.4±0.3	0.9±0.7	16.8±4.8	43.9±4.9	0.2±0.1	0.6±0.1

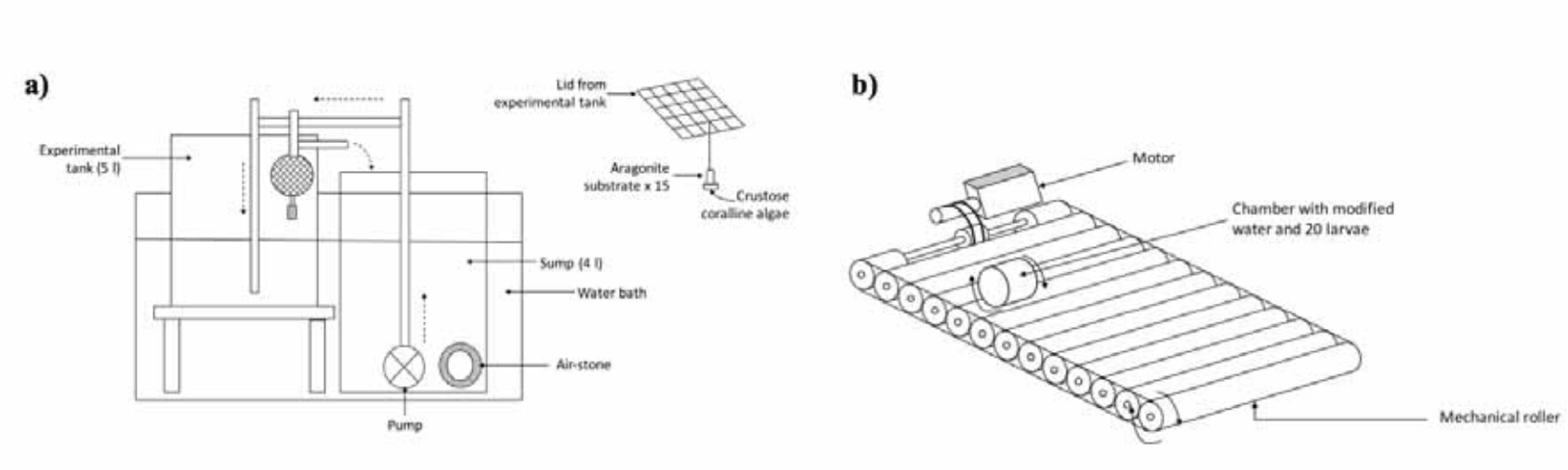
S3.3 Table (continuation): Water quality parameters for the different suspended sediments concentrations (mg l^{-1}) and nutrient enrichment (low in white, high in dark grey) at the start of each experiment. Values shown are means and standard deviations. Number of replicates: 2 per water quality factor and treatment

S3.4 Table: Concentration of suspended sediments (SS: 0, 5, 10, 30 and 100 mg l^{-1}) used in Experiment 1 (mean±sd). Measurements were performed before agitation of 3 additional replicates per treatment (containing SS and gametes) that were not used for the estimation of fertilization success.

SS (mg l^{-1})	Initial	30 min	60 min	90 min	120 min	150 min
0	1.1±0.1	1.2±0.6	1.2±0.4	0.9±0.3	0.8±0.2	0.8±0.1
5	5.6±0.5	4.4±0.5	4.8±0.9	4.8±0.1	4.4±0.5	5.1±1.0
10	10.8±0.5	10.4±0.5	9.4±0.5	8.3±1.0	7.2±0.5	7.6±1.0
30	30.4±0.9	29.6±1.3	29.7±0.5	27.9±0.5	27.2±1.5	25.7±1.1
100	103.6±1.0	101.5±0.5	95.4±2.3	96.9±6.3	94.0±1.8	93.3±2.3

Experiment	Suspended sediments (mg l^{-1})	Nutrient enrichment			Temperature		
		Low	Medium	High	27°C	30°C	32°C
Fertilization (Experiment 3.1)	0	90±5	89±4	78±16	89±10	92±6	70±21
	5	82±12	79±8	81±10	89±12	81±19	83±21
	10	78±13	72±16	70±13	75±34	51±30	57±22
	30	56±16	70±16	62±10	51±20	49±39	28±26
	100	35±11	40±20	30±14	20±17	19±28	9±11
Larvae survivorship (Experiment 3.2)	0	93±9	97±5	95±7	93±10	83±21	87±12
	5	98±4	94±8	97±6	83±21	85±14	89±14
	10	96±5	95±7	94±9	76±16	91±9	88±11
	30	94±8	94±8	95±7	93±10	74±13	86±13
	100	97±5	96±6	96±6	83±12	81±14	81±23
Larvae settlement (Experiment 3.2)	0	73±14	66±17	47±22	71±17	52±20	50±10
	5	59±16	50±16	46±17	58±19	51±13	48±13
	10	60±21	52±26	37±22	46±8	43±9	45±14
	30	49±21	42±16	35±19	37±15	34±9	29±5
	100	45±18	34±17	26±19	29±8	26±8	22±10
Larvae survivorship (Experiment 3.3)	0	80±18	67±22	84±10	84±15	93±21	86±23
	5	53±28	45±17	44±27	81±23	87±19	84±17
	10	37±25	58±30	72±23	74±32	86±19	81±31
	30	59±35	61±28	70±20	88±18	87±18	68±32
	100	85±31	89±7	66±32	88±16	83±31	88±21
Larvae settlement (Experiment 3.3)	0	30±23	35±21	36±25	66±22	53±29	60±20
	5	7±11	8±14	20±15	58±27	61±22	46±26
	10	27±32	15±16	27±13	54±33	62±21	41±28
	30	20±23	15±13	15±11	59±24	58±25	44±19
	100	6±7	32±19	26±16	60±21	60±31	46±26
Larvae settlement (Experiment 3.4)	0	46±14	48±6	26±16	62±19	72±13	51±23
	5	43±27	35±18	50±17	68±15	75±17	62±17
	10	38±21	43±24	45±7	71±19	74±16	51±12
	30	34±9	44±5	56±4	87±6	76±7	63±21
	100	39±10	44±4	57±27	85±7	71±8	60±27

S3.5 Table: Gamete fertilization success, larval survival and larval settlement (mean ± sd) per treatment level for each experiment performed (see Fig 3.1 for experiment details).



S3.6 Figure: a) Experimental tank set-up used for maintaining sediments in suspensions and expose a) 8-h old embryos for 28 h (Experiment 2), and b) 5-d-old larvae for 24 h (Experiment 4). The grids were used only during Experiment 4 to suspend settlement substrata (2 cm aragonite plugs covered with crustose coralline algae) in the larval tanks. Dashed lines indicate water flow. b) Mechanical rollers used to expose 3-d-old *Acropora tenuis* larvae to suspended sediments (0, 5, 10, 30 and 100 mg l^{-1}) under different nutrient enrichment (low, medium, high) or contrasting temperatures (27, 30, and 32°C). Three rollers sets were maintained within incubators set to reach each treatment temperatures.

S3.7 Table: Concentration of suspended sediments (0, 5, 10, 30 and 100 mg l^{-1}) used in Experiment 2 (mean ± sd). Measurements were performed before starting the experiment (initial) and every 6 h until the end of the experiment.

Suspended sediments (mg l^{-1})	Initial	6 h	12 h	18 h
0	1.1±0.2	1.2±0.3	1.8±0.6	1.4±0.5
5	5.5±1.0	4.0±0.8	3.4±1.0	4.3±1.0
10	10.6±2.3	10.5±1.3	8.7±0.8	7.2±1.0
30	29.5±1.7	27.8±3.4	25.7±1.3	20.7±1.7
100	102.3±2.3	94.4±1.7	89.6±1.4	87.4±2.6

S3.8 Table: Concentration of suspended sediments (0, 5, 10, 30 and 100 mg l^{-1}) used in Experiment 3 (mean ± sd). Measurements were performed before starting the experiment (initial), before the water change (24 h) and before finishing the experiment (48 h).

Suspended sediments (mg l^{-1})	Initial	24 h	48 h
0	1.2±0.6	1.5±0.9	1.8±0.9
5	7.6±1.0	1.9±0.5	1.2±1.0
10	12.6±0.5	5.5±0.5	4.0±1.3
30	34.6±0.9	21.8±0.9	19.7±1.7
100	110.7±1.3	83.0±1.3	86.2±2.9

S3.9 Table: Concentration of suspended sediments (0, 5, 10, 30 and 100 mg l^{-1}) used in Experiment 4 (mean ± sd). Measurements were performed before starting the experiment (initial) and every 6 hours until the end of the experiment.

Suspended sediments (mg l^{-1})	**Initial**	**6 h**	**12 h**	**18 h**
0	1.5±0.5	1.5±0.6	1.9±0.9	1.5±0.8
5	7.2±1.0	4.9±1.0	3.1±1.0	2.3±0.6
10	13.1±1.8	10.5±1.3	7.5±1.4	4.6±0.6
30	33.2±0.9	30.3±1.0	28.0±1.3	23.3±1.3
100	107.9±1.0	105.9±0.9	102.9±2.1	86.8±2.3

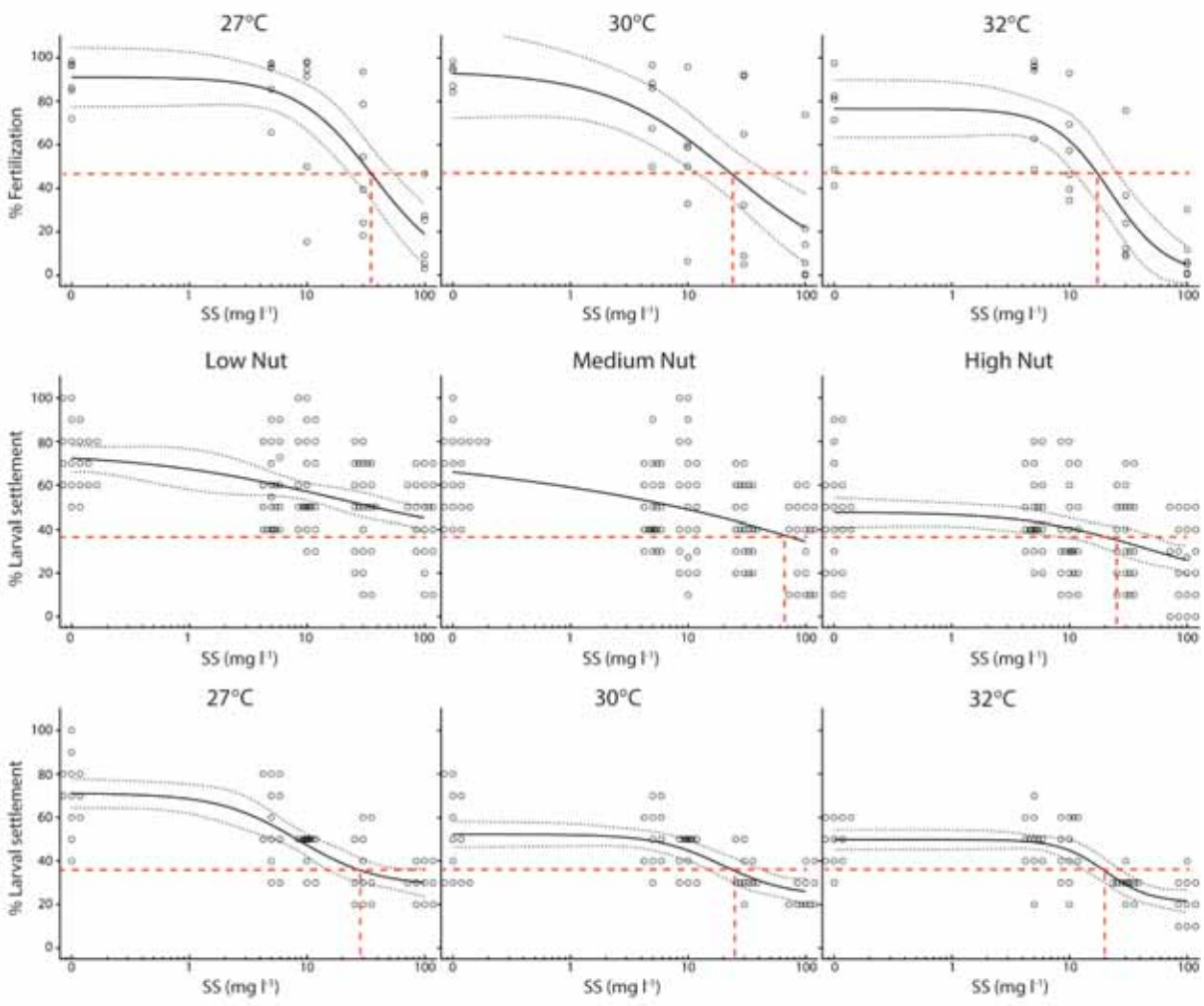
S3.10 Table: Results of generalized linear models (GLM) of the effects of suspended sediments (SS: 0, 5, 10, 30 and 100 mg l^{-1}) and a) nutrient enrichment (Nut: low, medium, high), or b) contrasting temperatures (Temp: 27, 30, and 32°C) on processes during the early life history stages (gamete fertilization, larvae survivorship and settlement) of *Acropora tenuis*. Suspended sediments, nutrient enrichment and temperature were considered as fixed factors, significance at $p<0.05$ (in **bold**). Df: degrees of freedom.

Experiment	Factor	Df	Deviance	F-value	p-value
Fertilization (Experiment 3.1)	SS	1	5864.2	139.92	**<0.001**
	Nut	2	2348.0	2.22	0.113
	SS x Nut	2	2232	1.12	0.329
	SS	1	9270.9	88.07	**<0.001**
	Temp	2	4912.3	3.35	**0.039**
	SS x Temp	2	4553.0	0.55	0.588
Larvae survivorship (Experiment 3.2)	SS	1	332.6	0.19	0.659
	Nut	2	332.6	0.06	0.938
	SS x Nut	2	332.4	0.64	0.523
	SS	1	261.1	3.14	0.077
	Temp	2	259.1	0.88	0.416
	SS x Temp	2	256.5	0.21	0.951
Larvae settlement (Experiment 3.2)	SS	1	696.1	72.75	**<0.001**
	Nut	2	666.6	27.36	**<0.001**
	SS x Nut	2	576.9	0.55	0.577
	SS	1	202.5	143.87	**<0.001**
	Temp	2	123.7	9.69	**<0.001**
	SS x Temp	2	111.4	2.21	0.112

S3.10 Table (continuation): Results of generalized linear models (GLM) of the effects of suspended sediments (SS: 0, 5, 10, 30 and 100 mg l^{-1}) and a) nutrient enrichment (Nut: low, medium, high), or b) contrasting temperatures (Temp: 27, 30, and 32°C) on processes during the early life history stages (gamete fertilization, larvae survivorship and settlement) of *Acropora tenuis*. Suspended sediments, nutrient enrichment and temperature were considered as fixed factors, significance at $p<0.05$ (in **bold**). Df: degrees of freedom.

Experiment	Factor	Df	Deviance	F-value	p-value
Larvae survivorship (Experiment 3.3)	SS	1	119.1	0.58	0.444
	Nut	2	123.2	2.03	0.135
	SS x Nut	2	118.4	0.24	0.784
	SS	1	428.0	0.02	0.869
	Temp	2	432.6	1.03	0.356
	SS x Temp	2	428.0	1.98	0.140
Larvae settlement (Experiment 3.3)	SS	1	335.0	0.25	0.613
	Nut	2	339.5	0.80	0.448
	SS x Nut	2	334.2	0.72	0.487
	SS	1	553.7	1.22	0.269
	Temp	2	570.7	3.60	**0.028**
	SS x Temp	2	550.2	1.31	0.271
Larvae settlement (Experiment 3.4)	SS	1	6.8	1.08	0.302
	Nut	2	6.9	0.79	0.456
	SS x Nut	2	6.7	1.30	0.280
	SS	1	6.8	3.86	0.054
	Temp	2	8.0	7.42	**0.001**
	SS x Temp	2	6.3	2.18	0.121

S3.11 Figure: *Acropora tenuis* inhibition of a) gamete fertilization and b-c) settlement of embryos exposed to treatment conditions during embryo development. Curves fitted to four-parameter logistic models plotted over a range of suspended sediments (SS: 0, 5, 10, 30 and 100 mg l^{-1}) and a-b) contrasting temperatures (Temp: 27, 30, and 32°C) or c) nutrient enrichment (Nut: low, medium, high).



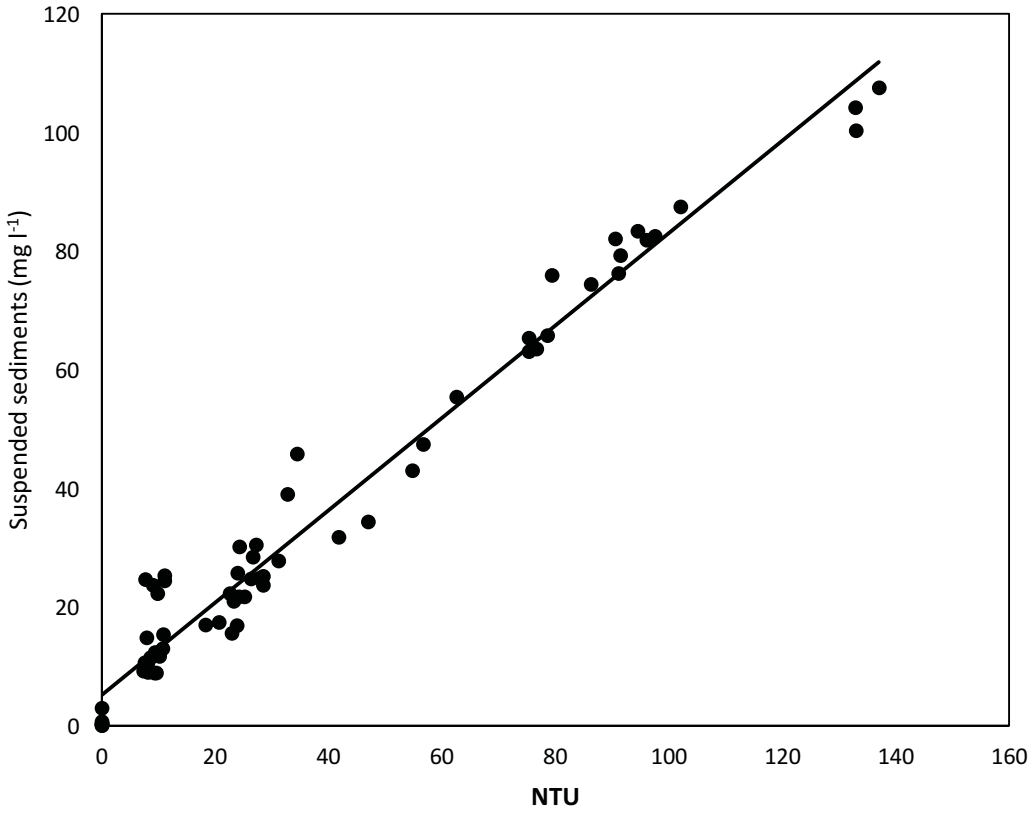
	Factor level	SS Best-fit parameters (95% CI)				N	R	H
		IC_{50} (mg l^{-1})	Top (%)	Bottom (%)	Slope			
Fertilization (Experiment 3.1)	**27°C**	36.61 (19.91–68.50)	91.05 (76.56–100.00)	0.00 (0.00)	-1.33 (-3.05–-0.69)	P	P	P
	30°C	25.00 (11.22–69.02)	93.83 (69.06–100.00)	0.00 (0.00)	-0.89 (-2.083–-0.23)	P	P	P
	32°C	17.99 (10.57–28.84)	76.57(63.03–91.98)	0.00 (0.00)	-1.79 (-∞–-0.93)	P	P	P
Larvae settlement (Experiment 3.2)	**Low**	>100	75.13 (N/A)	32.22 (N/A–100.00)	-0.51 (-2.65–2.65)	P	P	P
	Med	63.97 (N/A)	72.22 (N/A)	~0.00(N/A)	-0.35 (N/A)	N/A	N/A	N/A
	High	17.49 (3.88–54.20)	47.72 (40.42–81.57)	15.40 (N/A–35.06)	-0.86 (-∞–-0.14)	F	P	P
Larvae settlement (Experiment 3.2)	**27°C**	29.11(14.26–∞)	71.13 (63.08–N/A)	28.36 (0.00–37.59)	-1.28 (-3.93–N/A)	P	P	P
	30°C	24.66 (14.16–48.98)	52.28 (46.07–N/A)	23.90 (0.00–33.44)	-1.53 (-∞–N/A)	P	P	P
	32°C	19.82 (12.74–29.72)	49.82 (44.83–55.84)	20.90 (0.00–27.84)	-2.26 (N/A–0.71)	P	P	P

S3.12 Table: Concentration of suspended sediments which inhibit fertilization or settlement of coral embryos or larvae respectively by 50% (IC_{50}). Absolute EC_{50} values were calculated using a four-parameter logistic model (S11 Fig). All models were interpolated to half (50%) of the Top of the control temperature (27°C) or nutrient concentration (Low). N: Normality of residuals test, R: Replicates test, H: Homogeneity of variance. P: passed, F: failed.

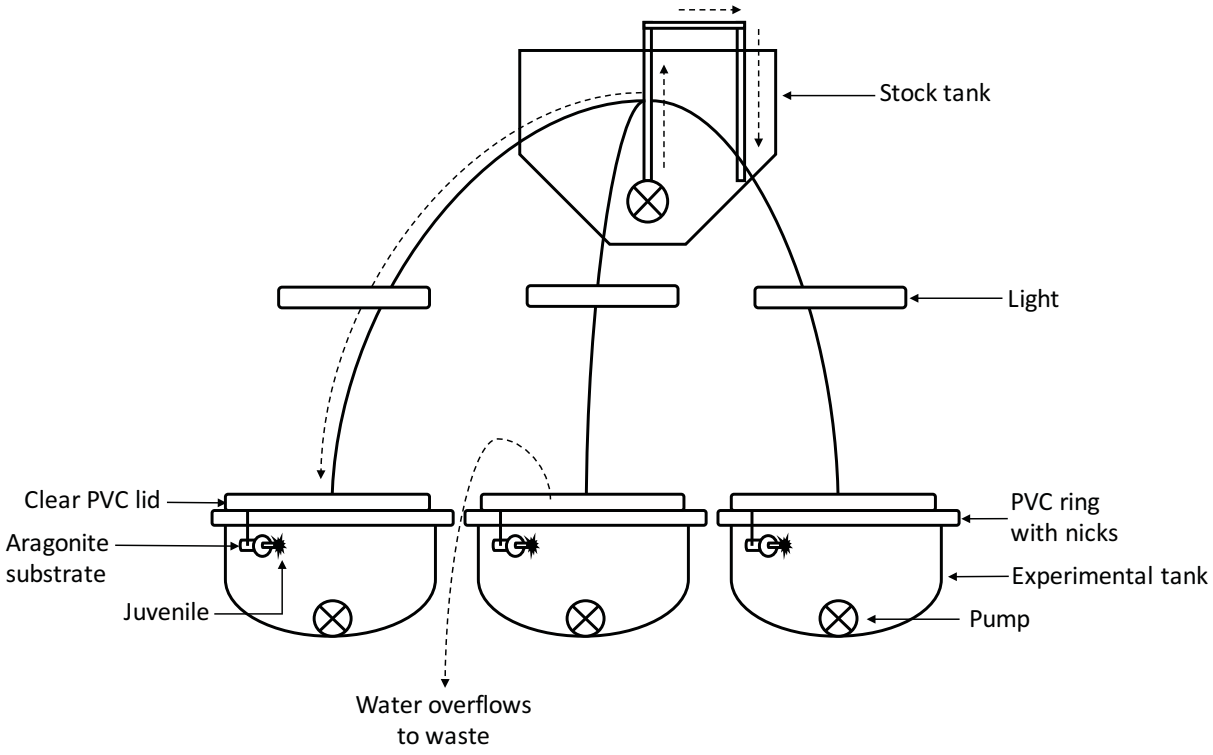
S3.13 Table: Results of generalized linear models (GLM) of the effects of organic nutrient enrichment (Nut: low, medium, high) during gamete fertilization of *Acropora tenuis* comparing common treatments (SS: 0 mg l^{-1} and Temp: 27 °C) of Chapter 2 and with Chapter 2. Suspended sediments, nutrient enrichment and temperature were considered as fixed factors, significance at $p<0.05$ (in **bold**). Df: degrees of freedom.

Factor	Df	Deviance	F-value	p-value
Experiment	1	308.1	1.90	0.117
Nut x Experiment	2	290.8	0.52	0.598

S4.1 Figure: Suspended sediment treatments were prepared by adding sediments at the required amount of sediments to FSW to reach the target levels. Each year a NTU-suspended sediments calibration curve was prepared based on 66 samples ranging from 0 to 108 mg l^{-1} suspended sediments (y= 0.77 NTU + 5.22). The relationship between NTU and suspended sediments was linear and strong (R^2 = 0.96). Turbidity was measured in each sample with a nephelometer (TPS 90FL-T). Samples were filtered onto 0.4 μm pre-weighted polycarbonate filters, dried overnight at 60 °C and then weighted.



S4.2 Figure: Experimental tank set-up used for maintaining sediments in suspensions (0, 10, 30 and 100 mg l^{-1}) and nutrient enrichment (Nut: low, high) in a flowthrough system. Dashed lines indicate water flow.



S4.3 Table: Concentration of suspended sediments (0, 10, 30 and 100 mg l^{-1}) during the 40 days of exposure (average ± sd). Averages were obtained from measurements performed on 3 replicate tanks of each treatment each day.

Suspended sediments (mg l^{-1})	Low nutrients	High nutrients
0	1.0±0.3	1.5±0.6
10	11.5±1.1	11.5±0.7
30	30.4±1.3	29.9±1.1
100	96.1±3.3	97.3±4.2

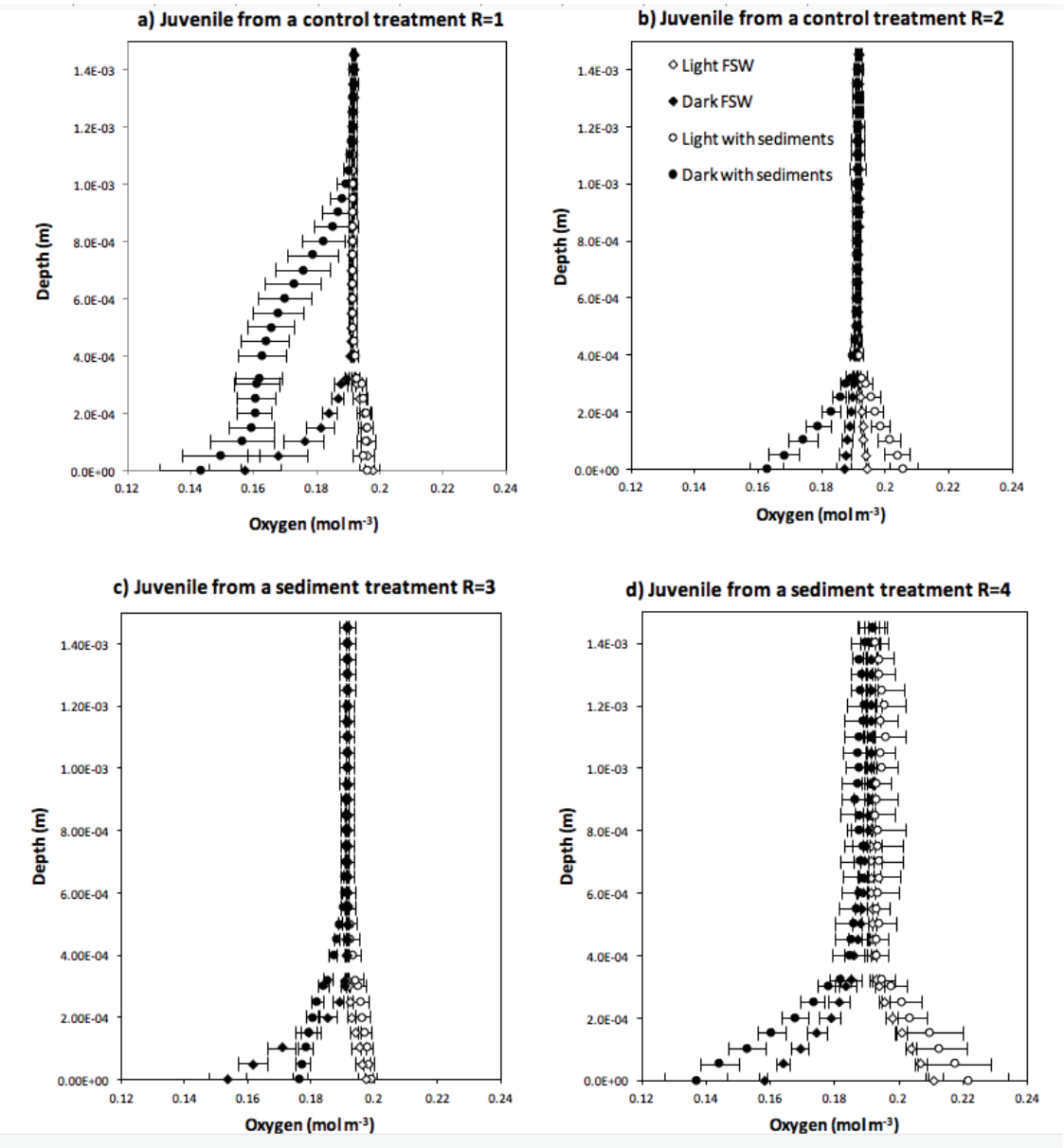
Week	Suspended sediments (mg l^{-1})	Nut	DOC (µM)	TOC (µM)	NH_4 (µM)	NO_2+NO_3 (µM)	NO_2 (µM)	TDN (µM)	TN (µM)	PO_4 (µM)	TDP (µM)
1	0	Low	109.0±3.4	21.2±1.7	1.0±0.1	0.1±0.1	0.1±0.1	2.9±0.1	10.3±1.2	0.1±0.1	0.4±0.2
		High	136.1±11.1	27.1±7.3	0.8±0.5	0.3±0.4	0.1±0.1	4.2±0.7	16.8±2.1	0.1±0.1	0.2±0.1
	10	Low	119.9±24.1	42.1±1.1	0.5±0.1	0.1±0.1	0.1±0.1	5.2±0.9	14.1±4.0	0.1±0.1	0.2±0.1
		High	150.2±9.9	50.0±6.0	0.8±0.4	0.3±0.3	0.1±0.1	6.3±0.2	10.7±0.9	0.1±0.1	0.5±0.4
	30	Low	105.9±7.5	99.8±1.3	0.8±0.4	0.2±0.3	0.1±0.1	11.6±0.6	12.9±1.0	0.1±0.1	0.2±0.1
		High	124.8±2.2	117.5±21.9	0.8±0.5	0.1±0.1	0.1±0.1	14.5±0.1	10.3±4.1	0.1±0.1	0.2±0.1
	100	Low	152.5±5.5	240.1±19.8	1.0±0.1	0.3±0.3	0.1±0.1	33.8±13.2	18.1±7.5	0.1±0.1	0.3±0.1
		High	221.9±36.4	285.0±93.0	0.6±0.3	0.1±0.1	0.1±0.1	31.5±1.5	16.9±6.0	0.1±0.1	0.2±0.1
2	0	Low	92.2±3.7	15.9±2.5	1.2±0.7	0.4±0.1	0.2±0.1	1.9±0.5	12.6±0.9	0.2±0.1	0.3±0.1
		High	112.3±19.3	34.9±6.0	1.5±0.3	0.6±0.1	0.2±0.1	6.2±0.9	14.8±8.4	0.2±0.1	0.3±0.1
	10	Low	86.6±6.3	49.8±1.0	1.1±0.5	0.5±0.1	0.2±0.1	5.1±0.4	13.2±2.5	0.2±0.1	0.7±0.7
		High	87.0±0.1	67.5±2.8	1.2±0.9	0.6±0.1	0.2±0.1	8.5±0.8	12.3±6.9	0.2±0.1	0.3±0.1
	30	Low	83.7±11.1	89.5±1.0	1.6±0.5	0.6±0.1	0.2±0.1	10.1±0.3	23.0±5.6	0.2±0.1	0.4±0.2
		High	112.8±12.3	107.1±2.4	2.0±0.4	0.7±0.1	0.2±0.1	14.1±1.5	16.3±8.1	0.2±0.2	0.4±0.2
	100	Low	113.1±2.8	236.6±2.8	1.0±0.6	0.5±0.1	0.2±0.1	29.7±4.0	13.7±1.2	0.3±0.1	0.3±0.1
		High	143.4±23.2	242.2±5.1	1.1±0.7	0.6±0.1	0.2±0.1	29.9±0.3	11.5±2.6	0.3±0.2	0.4±0.1
3	0	Low	97.2±16.3	25.4±0.0	0.7±0.1	0.1±0.1	0.1±0.1	2.5±0.1	21.1±11.1	0.1±0.1	0.3±0.1
		High	102.4±3.9	38.3±4.7	0.8±0.4	0.1±0.1	0.1±0.1	6.1±0.4	13.8±2.1	0.1±0.1	0.3±0.1
	10	Low	105.2±5.2	40.9±0.2	0.5±0.1	0.1±0.1	0.1±0.1	5.4±0.4	15.5±1.3	0.1±0.1	0.3±0.1
		High	118.6±17.6	57.6±8.9	0.6±0.1	0.1±0.1	0.1±0.1	8.1±0.1	13.9±3.2	0.1±0.1	0.5±0.3
	30	Low	121.6±3.0	80.3±3.8	1.1±0.8	0.1±0.1	0.1±0.1	4.6±0.3	21.5±5.9	0.1±0.1	0.3±0.1
		High	156.8±45.5	128.2±24.4	0.5±0.1	0.1±0.1	0.1±0.1	18.6±1.0	15.8±1.1	0.1±0.1	1.0±1.1
	100	Low	157.0±52.6	187.6±7.1	1.1±0.8	0.1±0.1	0.1±0.1	19.7±5.3	20.5±5.9	0.1±0.1	0.2±0.1
		High	249.4±53.7	221.4±1.4	1.2±0.1	0.1±0.1	0.2±0.1	24.5±1.7	18.8±4.7	0.1±0.1	0.3±0.1
4	0	Low	74.8±1.9	14.5±0.8	0.8±0.4	0.2±0.2	0.1±0.1	1.5±0.1	15.1±2.4	0.1±0.1	0.2±0.1
		High	89.4±15.7	29.9±0.6	1.1±0.5	0.3±0.1	0.1±0.1	4.9±0.4	11.6±2.0	0.1±0.1	0.3±0.1
	10	Low	89.7±15.2	47.7±4.1	0.9±0.5	0.2±0.2	0.1±0.1	4.5±0.3	17.0±1.8	0.1±0.1	0.2±0.1
		High	92.6±21.2	74.3±2.1	1.2±0.1	0.3±0.1	0.1±0.1	10.3±0.4	17.0±3.3	0.1±0.1	0.3±0.1
	30	Low	108.2±2.2	94.3±2.0	1.1±0.1	0.3±0.1	0.1±0.1	8.4±0.2	16.7±0.1	0.1±0.1	0.2±0.1
		High	122.7±40.0	122.9±0.5	1.6±0.6	0.3±0.2	0.1±0.1	13.4±0.7	16.7±3.1	0.1±0.1	0.3±0.1
	100	Low	180.2±54.4	258.3±20.6	0.9±0.3	0.5±0.4	0.1±0.1	25.9±3.4	14.8±1.6	0.2±0.1	0.2±0.1
		High	186.5±51.0	266.6±24.9	1.5±1.3	0.1±0.1	0.2±0.1	28.0±1.0	18.9±4.2	0.2±0.1	0.3±0.1

S4.4 Table: Water quality parameters for the different suspended sediments concentrations (mg l^{-1}) and nutrient enrichment (low in white, high in dark grey) at the start of each experiment. Values shown are means and standard deviations. Number of replicates: 2 per water quality factor and treatment.

Week	Suspended sediments (mg l^{-1})	Nut	DOC (µM)	TOC (µM)	NH_4 (µM)	NO_2+NO_3 (µM)	NO_2 (µM)	TDN (µM)	TN (µM)	PO_4 (µM)	TDP (µM)
5	0	Low	97.3±7.5	20.8±0.9	0.8±0.3	0.1±0.1	0.1±0.1	2.8±0.1	17.4±11.1	0.1±0.1	0.2±0.1
		High	100.5±2.9	29.6±0.1	0.9±0.3	0.1±0.1	0.1±0.1	4.4±0.1	16.4±5.8	0.1±0.1	0.3±0.1
	10	Low	108.0±10.0	52.8±2.2	0.8±0.2	0.1±0.1	0.1±0.1	5.7±0.8	33.1±24.1	0.1±0.1	0.3±0.1
		High	109.0±26.0	66.9±8.4	0.9±0.3	0.1±0.1	0.1±0.1	8.8±0.5	16.0±5.2	0.1±0.1	0.2±0.1
	30	Low	117.9±4.4	87.0±0.2	0.8±0.1	0.4±0.5	0.1±0.1	8.6±0.2	15.4±7.7	0.1±0.1	0.3±0.1
		High	131.1±11.3	100.0±8.3	1.1±0.2	0.1±0.1	0.1±0.1	13.0±1.4	12.8±0.4	0.1±0.1	0.8±0.7
	100	Low	134.0±7.3	161.8±8.5	1.2±0.2	0.2±0.3	0.1±0.1	17.7±1.7	24.8±8.3	0.2±0.1	0.3±0.1
		High	154.9±8.2	235.7±93.6	0.9±0.6	0.1±0.1	0.1±0.1	104.6±24.5	12.8±0.7	0.2±0.1	1.0±1.0
6	0	Low	87.0±1.8	17.9±0.6	0.8±0.4	0.1±0.1	0.1±0.1	2.2±0.2	9.7±0.8	0.1±0.1	0.2±0.1
		High	90.9±11.6	35.4±3.5	0.8±0.4	0.1±0.1	0.1±0.1	5.3±0.4	11.2±4.8	0.1±0.1	0.2±0.1
	10	Low	99.9±8.1	47.8±3.0	0.5±0.1	0.1±0.1	0.1±0.1	4.8±0.4	9.2±0.1	0.1±0.1	0.1±0.1
		High	101.3±0.9	51.6±3.8	0.7±0.2	0.1±0.1	0.1±0.1	6.8±0.7	14.3±0.3	0.1±0.1	0.3±0.1
	30	Low	102.1±0.1	77.3±1.1	0.8±0.4	0.1±0.1	0.1±0.1	8.6±0.1	7.1±0.6	0.1±0.1	0.2±0.1
		High	103.1±2.3	88.5±4.9	1.2±0.2	0.5±0.5	0.1±0.1	11.9±1.9	11.4±1.0	0.1±0.1	0.1±0.2
	100	Low	109.0±2.9	206.4±2.9	0.6±0.1	0.1±0.1	0.2±0.1	24.0±1.9	9.1±0.9	0.2±0.1	0.3±0.1
		High	114.0±4.4	262.8±94.1	1.1±0.7	0.4±0.5	0.2±0.1	24.3±1.1	11.0±0.3	0.2±0.1	0.3±0.1

S4.4 Table (continuation): Water quality parameters for the different suspended sediments concentrations (mg l^{-1}) and nutrient enrichment (low in white, high in dark grey) at the start of each experiment. Values shown are means and standard deviations. Number of replicates: 2 per water quality factor and treatment.

S4.5 Figure: O_2 profiles of a *A. tenuis* juvenile previously maintained for 25 days in four juveniles a-b) control conditions (diamond) (0 mg l^{-1} of suspended sediments, 0 mg OC l^{-1} FSW nutrient enrichment) and then exposed for microsensor measurements to suspended sediments (circle) (100 mg l^{-1} suspended sediments, 0 mg OC l^{-1} FSW nutrient enrichment), c-d) suspended sediments (circle) (100 mg l^{-1} nutrient enrichment, 0 mg OC l^{-1} FSW nutrient enrichment) and then exposed for microsensor measurements to control conditions (diamond) (0 mg l^{-1} suspended sediments, 0 mg OC l^{-1} FSW nutrient enrichment).



S5.1Table: Population matrices of *Acropora* spp at reefs in Fitzroy, Frankland, High Island. Data obtained from Smith et al. (2005), provided by James Gilmour.

Fitzroy Reef	**Recruit**	**Juvenile 1**	**Juvenile 2**	**Juvenile 3**	**Adult**
Recruit	0	0	0	0	f
Juvenile 1	0.03	0.09	0	0	0
Juvenile 2	0	0.43	0.43	0	0
Juvenile 3	0	0	0.18	0.51	0
Adult	0	0	0	0.17	0.90

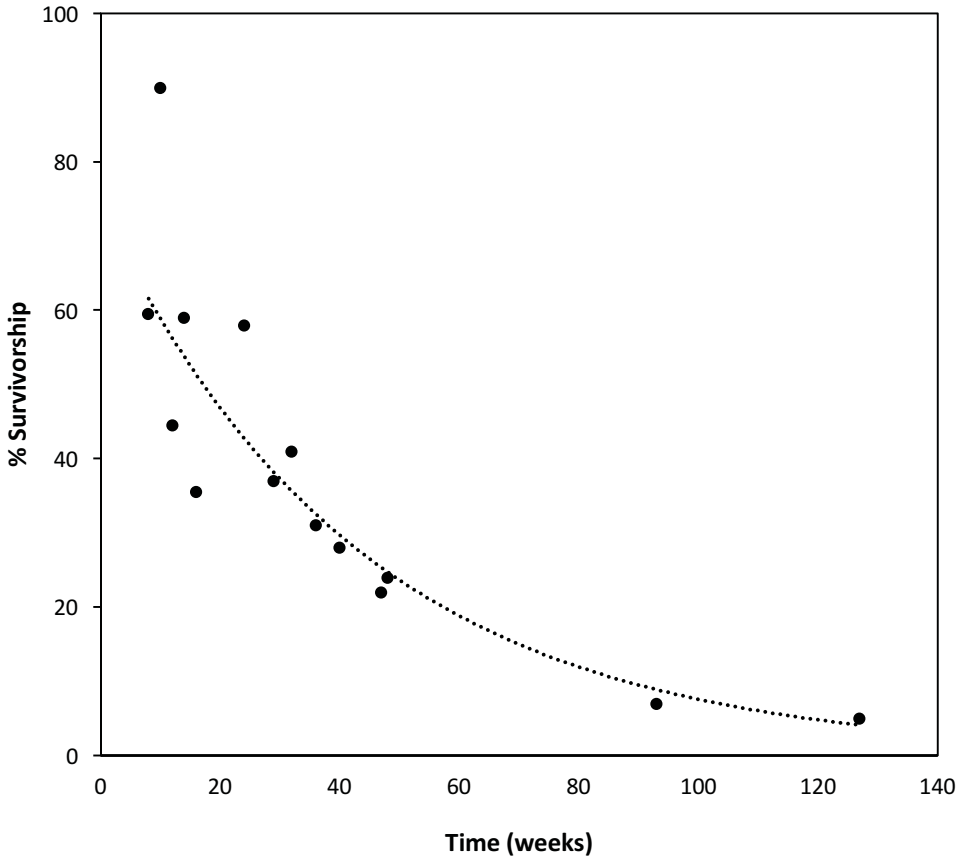
Frankland Reef	**Recruit**	**Juvenile 1**	**Juvenile 2**	**Juvenile 3**	**Adult**
Recruit	0	0	0	0	f
Juvenile 1	0.03	0.40	0	0	0
Juvenile 2	0	0.24	0.50	0	0
Juvenile 3	0	0	0.35	0.65	0
Adult	0	0	0	0.26	0.90

High Island Reef	**Recruit**	**Juvenile 1**	**Juvenile 2**	**Juvenile 3**	**Adult**
Recruit	0	0	0	0	f
Juvenile 1	0.03	0.06	0	0	0
Juvenile 2	0	0.51	0.23	0	0
Juvenile 3	0	0	0.61	0.67	0
Adult	0	0	0	0.26	0.90

# polyps 1 cm²	Colony 1	Colony 2	Colony 3	Colony 4	Colony 5	Colony 6	Colony 7	Colony 8	Colony 9	Colony 10
1	17	11	8	10	13	15	10	10	11	15
2	19	10	9	11	12	16	12	11	13	16
3	26	11	12	10	15	11	15	10	15	18
4	20	15	9	11	10	15	10	12	12	15
5	17	10	11	7	11	10	16	10	11	14
6	24	9	12	11	12	15	10	15	10	15
7	15	12	9	10	10	16	10	10	11	16
8	16	11	8	11	15	17	10	11	15	17
9	21	11	13	10	18	10	14	10	12	18
10	19	13	11	6	17	15	15	12	10	16
11	23	11	10	12	10	16	11	10	11	17
12	19	11	11	9	15	18	10	9	10	19
13	22	17	8	12	13	17	11	10	12	18
14	24	12	12	9	14	16	12	1	15	20
15	22	13	9	10	12	17	10	10	11	19
Average	20	12	10	10	13	15	12	10	12	17

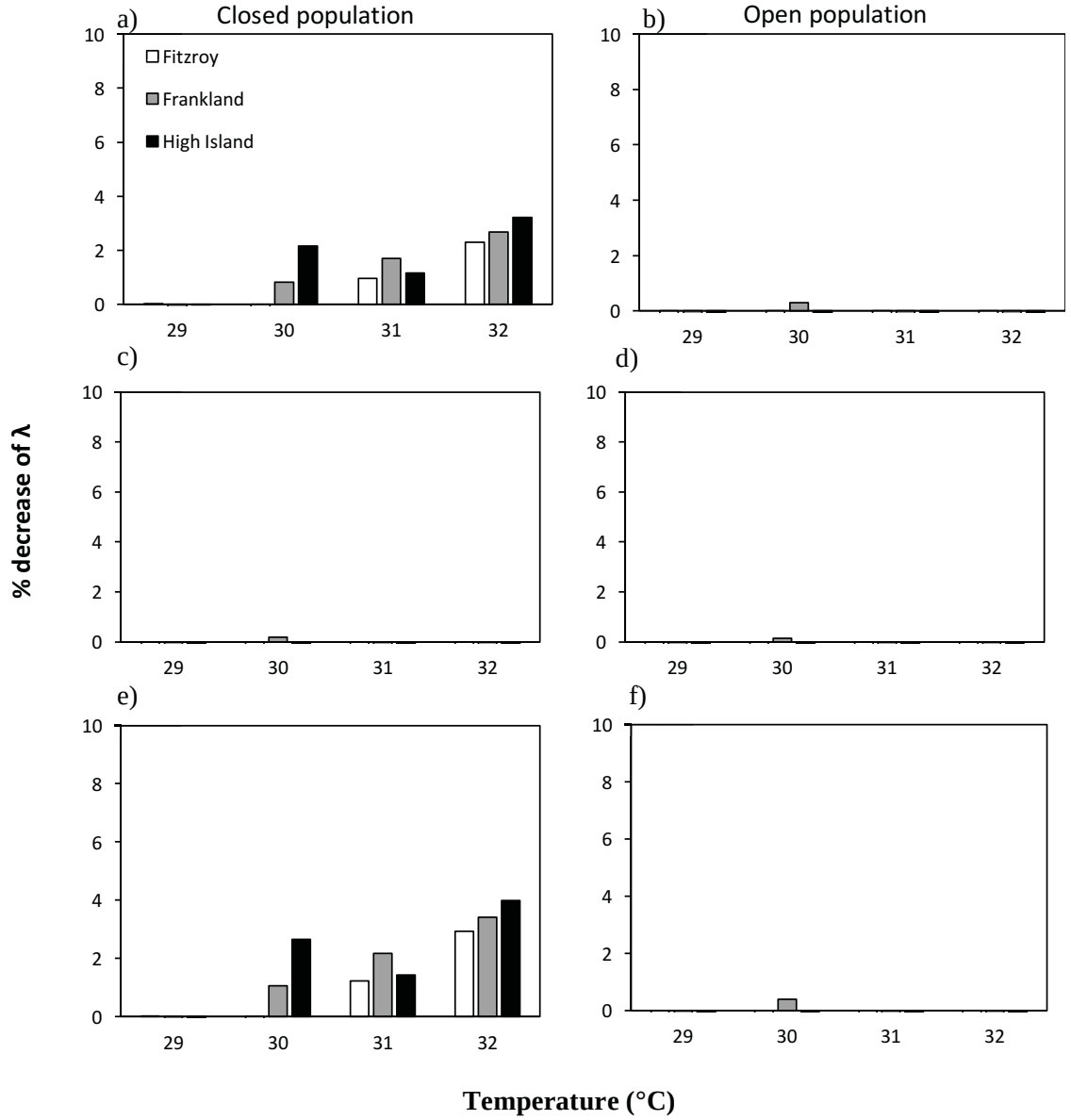
S5.2 Table: Number of polyps per cm^2 in 10 branches of 10 colonies. Colonies 1-5 where collected in Davies Reefs, 5-10 in Magnetic Island. All colonies were used for obtaining gametes used in experiments from Chapters 2 and 3. Colony sizes varied between 30 and 40 cm in diameter. Polyps where counted in an area of 1 cm^2 in 10 branches of each colony (5 from the centre of the colony and 5 from the margins of the colony).

S5.3 Figure: Estimation of recruit survivorship through time based on published data (Maida et al. 2001, Arnold et al. 2010, Kuo and Soong 2010). $y = 77.436e^{-0.024x}$, $R^2 = 0.92613$.



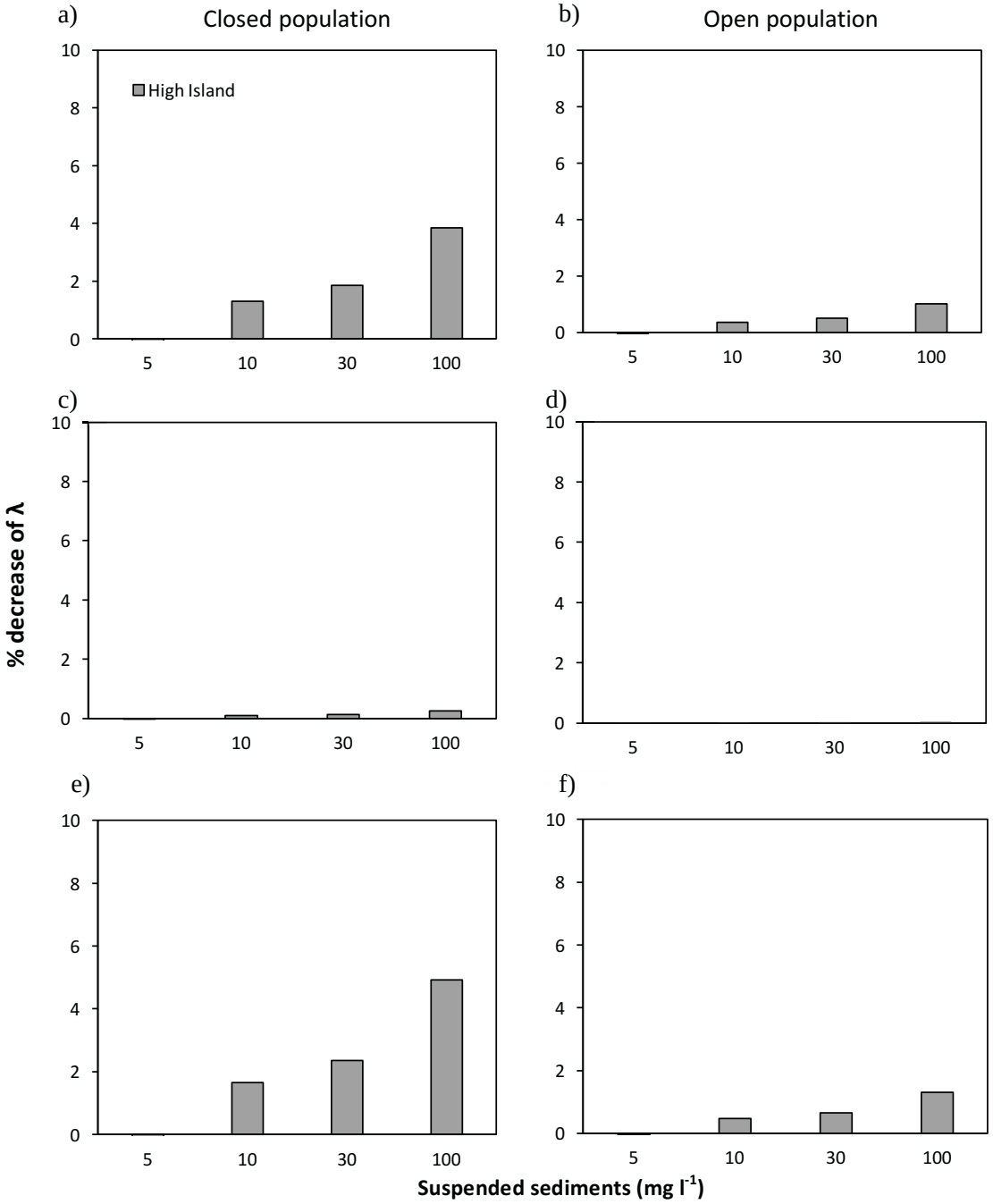
S5.4 Figure: Effect of temperature on population growth rate in reefs with different water qualities (nutrient enrichment [Fitzroy: low nutrient enrichment, Frankland: medium nutrient enrichment, High Island: high nutrient enrichment]). The exposure to temperature stress was simulated to occur during gamete fertilization, larval development

and larval settlement only in the population of study, which consisted of: **a-b)** small size (10 cm) adult colonies and larvae immigration came from 10 upstream population with adult colonies of similar sizes (10 cm); **c-d)** small size (10 cm) adult colonies and larvae imigration came from 10 upstream population with adult colonies of big sizes (50 cm); **e-f)** big size (50 cm) adult colonies and larvae immirations came from 10 upstream population with adult colonies of similar sizes (50 cm).



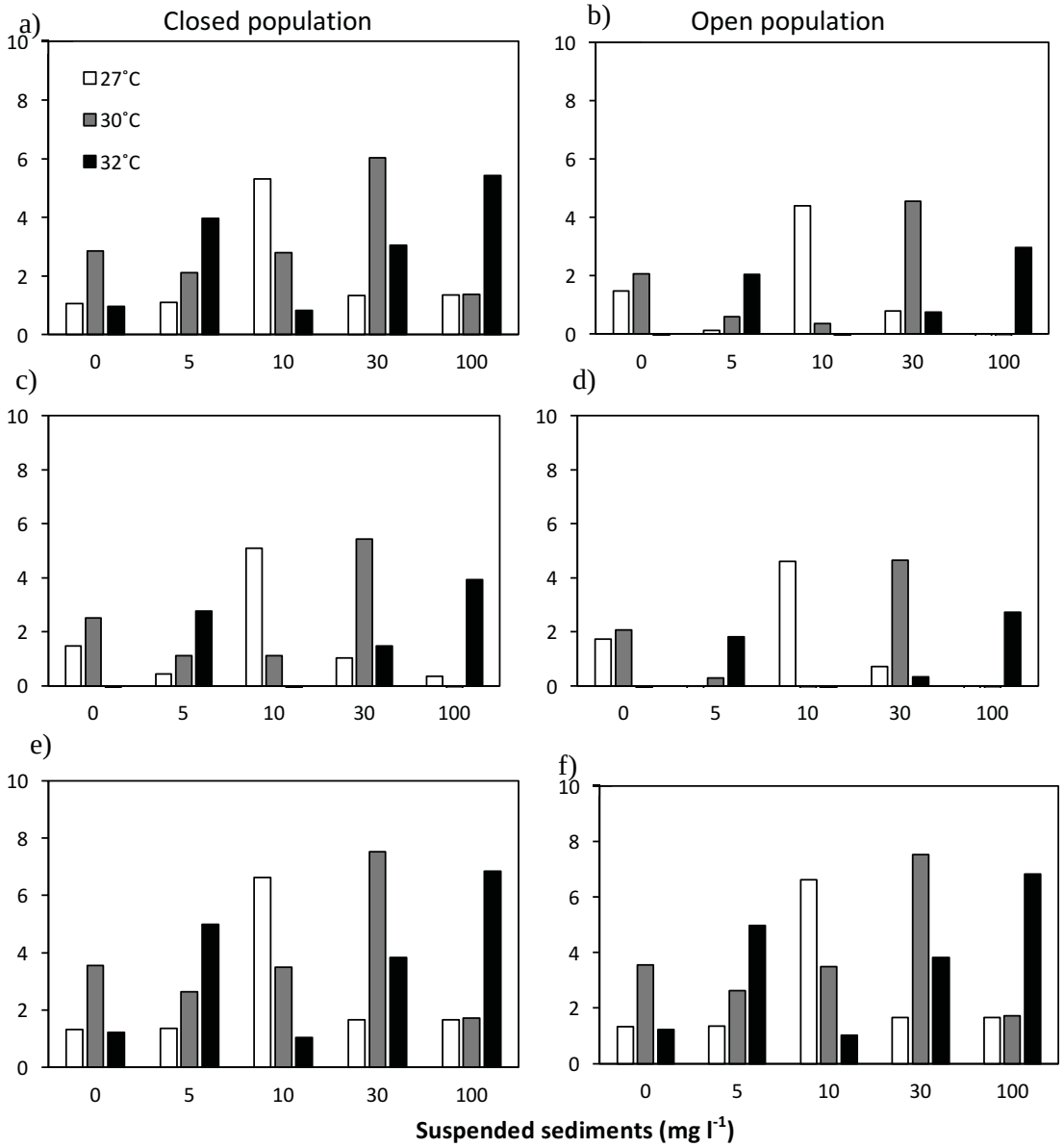
S5.5 Figure: Effects of suspended sediments on population growth rates of corals in High Island reef. The exposure to temperature stress was simulated to occur during gamete fertilization, larval development and larval settlement only in the population of study, which consisted of: **a-b)** small size (10 cm) adult colonies and larvae immigration came from 10 upstream populations with adult colonies of similar sizes (10 cm); **c-d)** small size

(10 cm) adult colonies and larvae immigration came from 10 upstream populations with adult colonies of big sizes (50 cm). **e-f)** big size (50 cm) adult colonies and larvae immigration came from 10 upstream populations with adult colonies of similar sizes (50 cm).



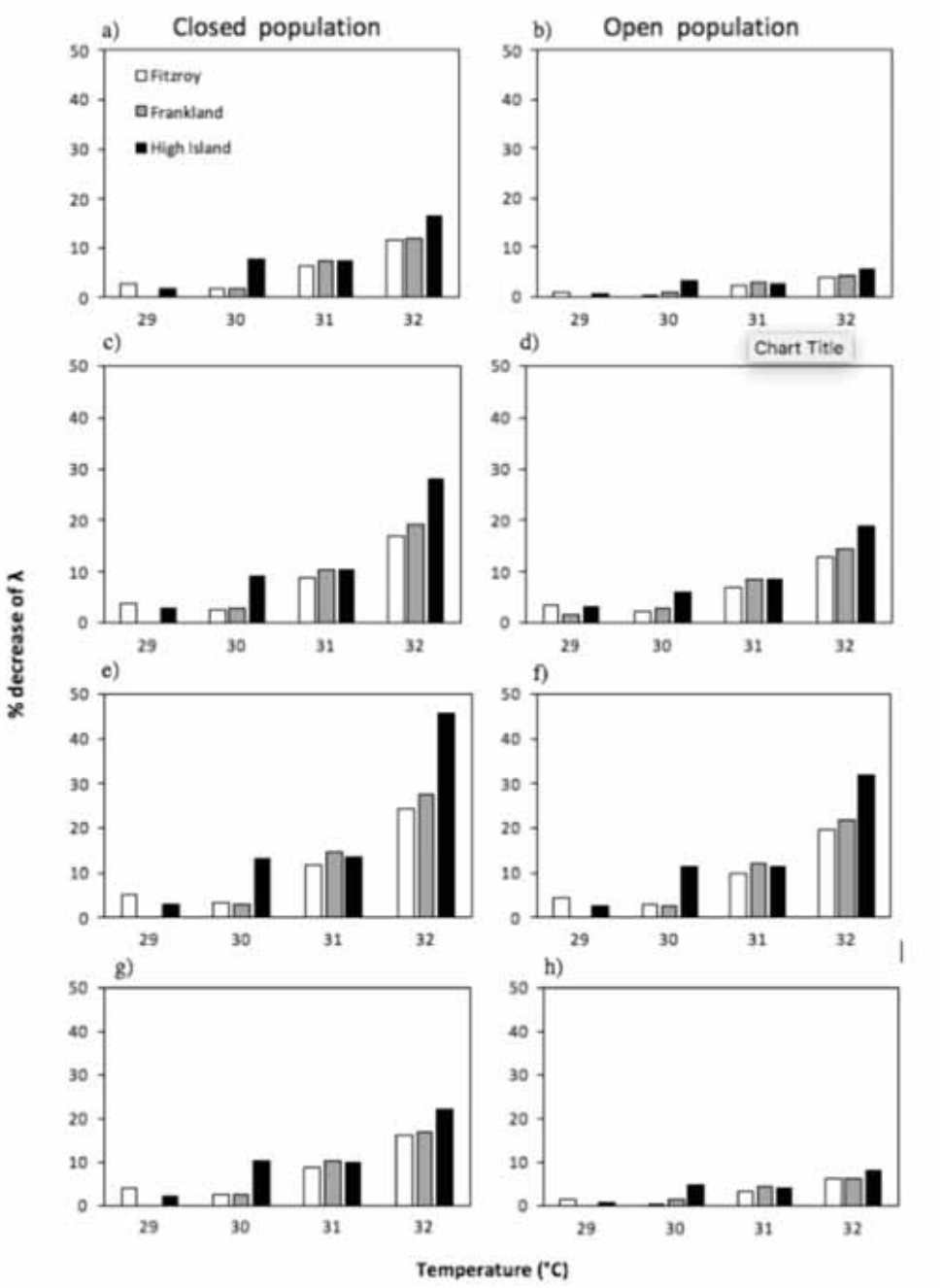
S5.6 Figure: Effects of suspended sediments and temperature on population growth rates of corals in High Island reef. The exposure to temperature stress was simulated to occur during gamete fertilization, larval development and larval settlement only in the population of study, which consisted of: **a-b)** small size (10 cm) adult colonies and larvae immigration came from 10 upstream populations with adult colonies of similar sizes (10

cm); **c-d)** small size (10 cm) adult colonies and larvae immigration came from 10 upstream population with adult colonies of big sizes (50 cm); **e-f)** big size (50 cm) adult colonies and larvae immigration came from 10 upstream population with adult colonies of similar sizes (50 cm). Duration of stressors were simulated to occur during gamete fertilization, larval development and larval settlement.



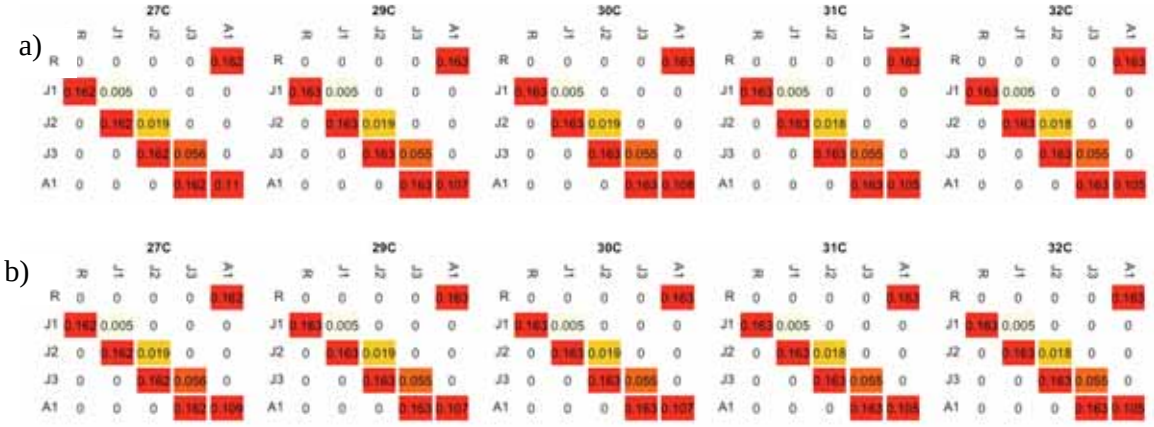
S5.7 Figure: Effects of suspended sediments and temperature on population growth rates of corals in High Island reef. The exposure to temperature stress was simulated to occur during gamete fertilization, larval development and larval settlement in the population of study and in upstream populations. The population of study consisted of: **a-b)** small size (10 cm) adult colonies and larvae immigration came from 10 upstream populations with adult colonies of similar sizes (10 cm); **c-d)** small size (10 cm) adult colonies and larvae

immigration came from 10 upstream population with adult colonies of big sizes (50 cm); **e-f)** big size (50 cm) adult colonies and larvae immigration came from 10 upstream population with adult colonies of similar sizes (50 cm). **g-h)** big size (50 cm) adult colonies and larvae immigration came from one upstream population with adult colonies of similar sizes (50 cm)



S5.8 Figure: Elasticity analysis of High Island under a local retention scenario of 13% (open population) when affected by temperature and nutrient enrichment. Population of study consisted of: **a)** small size (10 cm) adult colonies and larvae immigration came from 10 upstream population with adult colonies of big sizes (50 cm); **b)** small size (10 cm) adult colonies and larvae immigration came from 10 upstream population with adult colonies of big sizes (50 cm). The exposure to stressors were simulated to occur during gamete fertilization, larval development and larval settlement on the population of study.

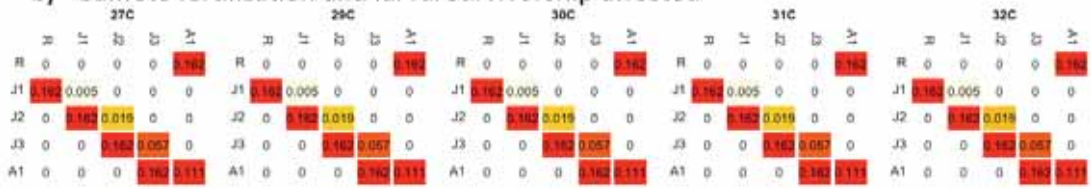
Colors and numbers indicate proportional contribution of each model parameter to population growth rate (light yellow: lowest contribution, dark red: greatest contribution).



S5.9 Figure: Elasticity analysis of High Island under a local retention scenario of 13% (open population) when affected by temperature and nutrient enrichment. Population of study consisted of by small size (10 cm) adult colonies and larvae from other populations were originated in 10 upstream population with adult colonies of big sizes (50 cm). Colors and numbers indicate proportional contribution of each model parameter to population growth rate (light yellow: lowest contribution, dark red: greatest contribution).

a) Gamete fertilization affected

b) Gamete fertilization and larval survivorship affected



c) Gamete fertilization, larval survivorship and settlement affected