Environmental factors limiting fertilisation and larval success in corals

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Formatted for submission to Coral Reefs - ***Journal of the International Society for Reef Studies***

Note to Examiners

The following thesis contains a meta-analysis that quantifies coral fertilisation and larval survivorship rates, in response to numerous water quality factors taken from existing studies. However, I initially set out to explore the factors limiting the dispersal of tropical coral species into temperate environments, using tropical to temperate larval transplant experiments. The aim of my initial investigation was to determine if coral larvae are more flexible in their cues and temperatures for settlement and metamorphosis than previously thought.

I conducted this experiment at the Sydney Institute of Marine Science, on four species of fertilised coral larvae, collected at the annual mass spawning on Lizard Island, located on the northern Great Barrier Reef. Larvae were washed and stored in 0.2 micron filtered seawater and separated into two temperature treatments (28°C – tropical and 24°C – temperate) using two different settlement cues (tropical and temperate crustose coralline algae). Control treatments were also set up and larvae were monitored and washed on a 12-hour basis to determine their settlement success. After one day in Sydney seawater all larvae were dead or dying and the experiment could not be continued.

While this experiment was unsuccessful, it did lead me to examine which water quality factors might have caused my initial experiment to fail, and hence the following meta-analysis focusing on the success of coral development stages in response to chemical and physical water conditions. Through this very different approach, I was able to learn a different suite of skills, such as combining large datasets and statistical modelling in 'R'. The failure of the tropical larvae to survive within a temperate urban location is the foundation upon which my current thesis rests. The following thesis supports the result of my initial experiment by showing that factors associated with urban living such as heavy metal and nutrient run-off, along with factors associated with climate change (e.g., temperature) greatly impact the survival and development of coral larvae.

Abstract

Early life history stages of corals, including fertilisation and larval stages, are susceptible to changes in the chemical and physical properties of seawater, which can severely diminish pre-settlement success. Understanding these limiting factors is therefore important for understanding and predicting population establishment and persistence in novel or changing environments. A review of the literature identified numerous, often-overlapping properties of seawater that have the potential to impact fertilisation and larval survivorship, including salinity, temperature, pH, suspended sediment, nutrients, and heavy metals. Using published experimental data, this study aimed to quantify the influence of seawater properties on fertilisation and larval survivorship probabilities. I found that fertilisation success was most impacted by salinity, copper, phosphorous and sediment, and that larval survivorship was most affected by copper, lead and temperature. I evaluated success through both fertilisation and larval survivorship in order to identify the joint probability of survival in seawater with different chemical and physical properties. This combined model would be suitable for identifying locations that are environmentally compatible with coral larval survival and growth both presently and under future water quality scenarios. This model could therefore be used as a monitoring tool for assessing the potential for the early development of corals as well as recommending targets for water quality in coastal waterways.

KEYWORDS. Meta-analysis, early life history stage, coral reef, coral larvae

Introduction

Anthropogenic environmental impacts such as waterway pollution and the indirect effects of climate change are negatively affecting marine organisms (Tilman and Lehman 2001; Harley et al. 2006; Halpern et al. 2008). Run-off from agricultural activities increases eutrophication in the form of nitrogen and phosphorous (De-Bashan and Bashan 2004), while increased heavy metal contamination leads to the bioaccumulation of pollutants in higher trophic level species and poses a direct threat to human food safety (Howarth and Marino 2006; Copat et al. 2012). On reefs, pollutants can cause changes in ecosystem functioning, particularly a phase-shift from traditional coral reefs to algae dominated reefs, greatly affecting the entire food web (Diaz-Pulido et al. 2011). Moreover, alterations in water chemistry and temperature are most notable in the tropics where ocean acidification and increased sea surface temperatures present an increasing threat to the reef building corals (Kleypas et al. 1999; Harrington et al. 2004; Albright et al.

2010; Meyer et al. 2011; Doney et al. 2012). How these environmental changes will influence the ecological distributions of species will depend largely on the tolerances of their early life history stages.

The success of early life history stages of plants and animals is a fundamental determinant of species' abundances and distributions. This is especially the case in marine environments where gamete fertilisation and larval dispersal largely occur in the plankton (Grantham et al. 2003). Adult marine species often lack the ability to travel large distances once mature or are sedentary in their adult form (Jackson 1986; Cowen and Sponaugle 2009). Larval dispersal enables these organisms to travel kilometres to novel environments within reef systems, dependant on hydrological processes (Fletcher et al. 2013). While some species are not sedentary in their adult form they may be unable to move large distances on a short temporal scale, therefore the capacity for larvae to disperse ensures the connectivity of existing populations, including buffering from local extinction, and establishment of new or less populated locations (Gaylord et al. 2013). Similarly, the reef building corals utilise the larval pelagic stage to disperse. While locomotion of larvae themselves is ineffective for travelling large distances, time spent within the plankton of ocean currents can assist in the remarkably swift transport of larvae to hospitable habitats (Jackson 1986; Palmer et al. 1996; Baird et al. 2009). However, it is these early stages that are also vulnerable to slight changes in environmental conditions (Hédouin and Gates 2013).

Pre-settlement stages of corals (fertilisation and larval survivorship) are usually influenced by specific environmental and chemical cues, which dictate the timing and duration of these events (Erwin and Szmant 2010). In approximately 85% of scleractinian coral species, fertilisation is preceded by an annual mass-spawning event that is hypothesised to coincide with optimal environmental conditions (Richmond 1997). Once eggs and sperm are released, fertilisation is more likely under constant conditions, and subtle changes in nutrient load, heavy metal toxicity and ocean chemistry have been shown to severely reduce fertilisation success (Victor and Richmond 2005; Humphrey et al. 2008). Following fertilisation, larval survivorship is also highest in constant environmental conditions, where larvae can survive for up to several weeks in the plankton (Baird et al. 2009). Ocean acidification, increased sea surface temperatures and heavy metals (e.g. copper, zinc and lead) have been shown to negatively affect fertilisation, gamete development and larval survivorship in a number of polychaete worm, echinoderm, bivalve and crustacean species (Heslinga 1976; Calabrese et al. 1977; Bassim and Sammarco 2003; Reichelt-Brushett and Harrison 2005; Baird et al. 2006; Gopalakrishnan et al. 2008; Kurihara 2008; Byrne et al. 2009; Nakamura et al. 2011; Schlegel et al. 2012). This reduction in larval survival has also been observed within a number of scleractinian coral species (Reichelt-Brushett and Harrison 2005; Victor and Richmond 2005; Randall and Szmant 2009).

Here, I quantify the relative importance of factors that limit the pre-settlement, early life stages of reef building corals. To do so, I compiled data from the literature from coral fertilisation and larval survival experiments, and then used multiple regression and model selection to determine the relative importance of nutrients, heavy metals and water chemistry in surviving to settlement competency. Models for the two early life stages were then combined in order to make predictions about the suitability of seawater at different locations for coral development.

Materials and Methods

Data collection

Data were collected from experimental studies that observed the impact of seawater properties on the probability of egg fertilisation or larval survivorship within scleractinian corals. To find research articles, I used the Web of Science and Google Scholar, with the keywords: “coral larvae”, “fertilisation success”, “larval survivorship”, “water chemistry”, “nutrients” and “heavy metals”. Searches were conducted up until the 1st of July 2014. For fertilisation success the published articles reported the proportion of eggs fertilised within a 1 to 36 hour period in seawater where levels of ammonium, phosphorous, nitrate, copper, zinc, cadmium, tributyltin, suspended sediment, salinity, acidification or temperature had been experimentally manipulated (Table S1). For larval survivorship, the studies reported the proportion of larvae that survived for 4 to 14 days in seawater where levels of ammonium, copper, mercury, lead, salinity, acidification or temperature had been manipulated. Only 2 of the 18 papers manipulated more than one property within the same experiment (Table S1). Most ambient properties were close to zero, using measurements reported for typical seawater, and had negligible effects on the final model. For factors for which a hump-shaped response was expected, including salinity, temperature and pH the model would be expected to be more sensitive to the choice of ambient levels and so these were sources from peer-reviewed articles for tropical seawater where possible (Graham and Barnett 1987; Orr et al. 2005; Lee et al. 2006). The final data set is available in the supplementary material (Appendix S1). Studies that did not report the exact number of eggs or larvae used in each trial, as well as those that reported the effect of factors associated with petroleum pollution were excluded.

Data analysis

All studies selected reported the number of individual eggs or larvae used in experiments and these values were converted from proportions into the number of success and failures. As each experiment tended to manipulate one factor at a time there were low levels of collinearity among variables. Fertilisation and larval survivorship were analysed separately using a generalised linear mixed-effects model (GLMM) with a binomial response and a logit link function (Zuur et al. 2009) to determine the relative effect of each seawater property on fertilisation and larval survivorship probability. There were not enough combinations of species and treatments to include species as a predictor variable (14 species in total, Table S1). Instead, a unique identifier for experiment was included as a random variable to account for variation that occurred among experiments, which captured the effect of species. I expected hump-shape relationships for temperature, salinity and pH, and therefore included a quadratic term as well as a linear term for these factors. For the model selection, a drop-analysis was conducted to remove non-significant terms ($P>0.05$) using the ‘drop1’ function in the statistical software package ‘R’ (R Development Core Team 2012). GLMM’s were conducted using the ‘glmer’ function in the package ‘lme4’ (Bates et al. 2012).

A variance analysis was performed, to determine the impact of each factor within the two GLMM’s conducted. This analysis was performed on the significant factors of each of the life stages and was performed using Hierarchical Partitioning with a goodness of fit measure in the package ‘hier.part’ (R Development Core Team 2012).

The mean joint probability of progressing through both fertilisation and larval stages for a given set of water properties was calculated by multiplying model estimates. Errors for these estimates were calculated using a Monte Carlo randomization, where 10,000 random variates from the fixed effects component of the model distribution were multiplied. The 95% confidence intervals from this final distribution were reported (i.e., the 250th and 9750th ranked probability).

Results

This study utilised 18 scientific research papers that quantified the fertilisation success and larval survival of 14 scleractinian coral species. These studies were separated into 53 unique experiments spread across the two life stages. The meta-analyses conducted through two separate GLMM’s resulted in a number of significant factors for each life stage across all areas of nutrients, heavy metals and water chemistry. The negative effect of water quality was most noticeable with the addition of copper and changes in salinity which were significant across both life stages.

Fertilisation analysis

Copper, salinity, phosphorous and sediment had significant effects on fertilisation probability (Table 2, Figure 1). In addition, salinity had a significant quadratic effect, where fertilisation probability peaked at approximately 35psu and declined at higher or lower levels (Figure 1b). Nitrate, ammonium, zinc, cadmium, tributyltin, pH and temperature did not have significant effects on fertilisation probability and were excluded from the final model.

Larval survivorship analysis

Copper, lead, temperature and salinity each had a significant effect on survivorship success (Table 3, Figure 2). Furthermore, temperature had a significant quadratic effect, where survivorship probability peaked at approximately 29°C and declined at higher or lower levels (Figure 2c). Ammonium, mercury and pH did not result in a significant effect on survivorship probability and were dropped from the final model.

Variance analysis

Salinity and copper accounted for the highest levels of variance within the fertilisation GLMM, with sediment and phosphorus accounting for only 10% of all variance. Copper and temperature were observed to account for the most variance within the survivorship model with salinity and lead accounting for a minimal amount (Table 4).

Discussion

Coral fertilisation success and larval survivorship are known to be affected by multiple water quality factor; however, these factors have never been compared in the same analysis to determine their relative importance. Factors that reduced fertilisation success were spread across water chemistry, nutrients and heavy metals, with the presence of suspended sediment, phosphorous, copper and salinity significantly reducing success. Larval survivorship was significantly affected by the presence of heavy metals with both copper and lead resulting in the most significant effect on survival along with temperature and salinity, which are strongly related to changes in global climate (Solomon et al. 2007).

The most significant factor across both dispersal stages of fertilisation and larval survivorship was copper, identifying it as the largest threat to the success of dispersing early life stages in corals. These results have been similarly observed in a number of other marine invertebrates suggesting the wide spread impact of copper within marine environments (Calabrese et al. 1977; Ahsanullah and Arnott 1978; Rivera-Duarte et al. 2005; Fitzpatrick et al. 2008; Caldwell et al. 2011). Coral species are greatly affected by the presence of copper where a number of species within the *Acropora* and *Goniastrea* families were observed to be negatively impacted by relatively low levels within surface waters (Reichelt-Brushett and Harrison 1999; Negri and Heyward 2001; Reichelt-Brushett and Harrison 2004; Reichelt-Brushett and Harrison 2005). While copper has been shown to be a highly important factor inhibiting both fertilisation and larval survivorship, its presence in marine environments is limited as it does not dominate heavy metal pollution unlike both lead and zinc (Li et al. 2001). However, copper is used in anti-fouling paints on vessels and can be released into the environment through natural wear and tear as well as when boats collide with reefs (Negri and Heyward 2001). While this is a possibility it is not of major concern for marine environments and therefore does not impose any immediate threat to long-term, global coral persistence.

Another heavy metal affecting the development of coral larvae and also of high significance within this study, was the presence of lead. Lead has been shown to significantly reduce larval survivorship and is of a greater concern when compared to copper, as it is a much larger component of run-off from urban and industrial areas (Li et al. 2001; Polkowska et al. 2001). Lead toxins are released into the marine environment as run-off, through the use of leaded-petrol and as a by-product in the creation of industrial materials (Polkowska et al. 2001). The impact of lead on marine invertebrate larval survivorship has been much less studied with research in this area focusing on coral and clam species (Reichelt-Brushett and Harrison 2004; Wang et al. 2009). This meta-analysis has determined that the presence of lead is an important limiting factor to the survival of coral larvae and should be a focused area for future study.

Similarly to lead, the impact of suspended sediment is predominately a result of anthropogenic activities, sourced from both coastal areas as well as at sea (Fabricius 2005; McLaughlin et al. 2013). Sediment had the most significant impact on fertisliation success within this study, with an increase in particulate matter within the water column and surface waters observed to be a significant factor in reducing the fertilisation success of coral species. This form of environmental degradation greatly affects early life stages of marine organisms and not just corals, with a variety of organisms affected from fish (Bilotta and Brazier 2008) to sea urchins (Pagano et al. 1993). Scleractinian corals are highly susceptible to increased suspended sediment with fertilisation success reduced by 50% under low levels of suspension (Humphrey et al. 2008; Erftemeijer et al. 2012). As coral reef communities are open systems the effects of suspended sediment disturbances are likely to be wide spread (Gilmour 1999). While pulse events are limited temporally, increased development and the occurrence of industrial activities, most significantly dredging, during annual spawning and fertilisation events has been observed to significantly affect coral populations, reducing recruitment and larval success (Erftemeijer et al. 2012; Styan and Rosser 2012). To reduce this impact the role of Government has been imperative, prohibiting dredging during these spawning events, limiting anthropogenic impacts and the influence of suspended sediments on coral reef ecosystems (Styan and Rosser 2012).

Phosphorous, like sediment, was observed to be a highly significant factor in the reduction of fertisliation success in coral species. Coastal run-off from agriculture and urban areas can lead to eutrophication through heightened levels of nutrients in the form of phosphorous. Increased phosphorous as a result of the excessive fertilisation of soils in agriculture, can severely diminish water quality and in some cases lead to anoxic surface waters (Correll 1998; Harrison and Ward 2001). Coral fertilisation has been shown to be highly susceptible to the presence of phosphorous with levels of just 1 micromole and above resulting in up to a 75% reduction in fertilisation (Harrison and Ward 2001). The increased monitoring of phosphorus within run-off, as well as the removal of nutrients through the use of techniques (metal precipitation, use of wetland systems to fix-nitrogen and the adsorption by microorganisms) can result in a beneficial reduction in the amount of phosphorous within marine environments and a reduction in its effect on coral fertilisation (De-Bashan and Bashan 2004).

While direct anthropogenic impacts can severally diminish water quality affecting coral development, indirect impacts associated with climate change can be just as harmful to the persistence of coral reef ecosystems. The impact of climate change on marine environments is evident, with changes in both temperature and salinity found to be important factors, reducing the fertilisation and survivorship of coral larvae. Increased or decreased water temperatures have been shown to reduce the survival of planular larvae (Bassim and Sammarco 2003; Baird et al. 2006). Temperature change is of particular concern as increasing sea surface temperatures (Solomon et al. 2007) continue to threaten marine environments and especially tropical waters (Solomon et al. 2007). This increase is a result of the burning of fossil fuels leading to increased carbon dioxide within the atmosphere, resulting in global warming (Solomon et al. 2007). The impact of changing temperatures is not limited to coral species with clams, oysters and scallops all experiencing a reduction in larval survivorship (Talmage and Gobler 2011). Conversely, sea urchin development has been observed to increase up to a threshold of 3°C with a heightened growth rate observed. However, after this threshold mortality increased demonstrating the negative impact of temperature changes on marine invertebrates (Sheppard et al. 2010; Wangensteen et al. 2013).

Changes to naturally occurring salinity (35psu) within marine environments has also been shown to reduce larval survivorship as well as fertilisation success in corals (Richmond 1996; Humphrey et al. 2008; Scott et al. 2013). This analysis revealed that salinity was a significant factor affecting both stages of coral development with a greater significance observed in fertisliation success. Salinity of the earth's oceans are expected to change globally due to an increase in storm occurrences as well as freshwater influxes from terrestrial run-off in urbanised areas and can severely deteriorate marine environments (Pechenik et al. 2007; Solomon et al. 2007). These increases in freshwater can result in a halocline or the formation of a freshwater layer on the surface of the ocean negatively impacting coral larvae survival (Sprintall and Tomczak 1992). Similarly, other marine species such as sea urchins, starfish, sea cumbers and oysters are affected by changes in salinity, particularly where a planular larval stage occurs (Rao 1951; Roller and Stickle 1985; Hamel and Mercier 1996; Pechenik et al. 2007). The importance of constant, natural salinity for marine invertebrate development is clear and of high significance for the early life stages of corals, with up to a 50% reduction in fertilisation and survivorship observed with just a slight decline in salinity (Richmond 1996; Scott et al. 2013).

The effect of climate change related ocean acidification (pH) on coral larval development was not significant within this model. Previous studies have supported the importance of a neutral pH on the development of marine invertebrates including echinoderms, bivalves and crustaceans, with corals also shown to be highly susceptible to acidification through a number of key developmental stages, including fertilisation and larval survival (Kurihara 2008; Kroeker et al. 2010). The models conducted within this analysis did not support these findings, which may be the result of not capturing settlement and metamorphosis, the recruitment stages of coral development where larvae begin to calcify (Kurihara 2008).

While each of the significant factors discussed are important for the successful fertilisation and survival of coral larvae individually, the survival of coral offspring through both fertilisation and larval survival is of the greatest importance. For this reason the development of a combined model for both fertilisation and larval survivorship was created in order to calculate the percentage likelihood of larvae surviving through fertilisation as well as up to 14 days within the plankton. While larvae can survive for longer than this within the surface waters, this model was created to include larvae within their peak competency period who are most likely to settle within their natal reef (Richmond 1997; Connolly and Baird 2010). By way of demonstration, I calculated how the heavy metal copper (significant for both stages of development, Tables 2 and 3), is expected to influence the joint probability of progressing through both fertilisation and the larval stage. This model shows that when evaluating survival across both stages of development, the mean success rate declines along with an increase in the level of uncertainty surrounding each value (Figure 3).

This analysis has covered a broad range of factors, with the use of only a few studies documenting coral fertilisation and survivorship through these two early life history stages. While a small number of papers were available, I have been able to accurately evaluate these studies within two models and account for the weighting of research based on the number of trials as well as eggs or larvae tested within each study. Although this research area is limited, it is important to develop these modelling techniques as well as explore these important stages of development in the hope of mitigating these significant factors within the marine environment. However, the models developed within this analysis could be improved with the addition of a greater number of scientific studies, from both the laboratory environment as well as in the field. A more precise estimate of the effect of significant factors could be determined with an increase in studies, particularly where significant factors were not supported with a high number of papers. It is important to note that each of the models created are sensitive to changes in the trace values, particularly associated with pH, salinity and temperature where a quadratic affect was added. While all other trace values are almost zero within the natural open ocean, these values do vary with latitude.

The next stage forward within this meta-analysis would be to determine the water quality factors limiting the recruitment stage of larval development, specifically settlement and metamorphosis. As these stages are strongly linked with chemical and physical cues, water quality is likely to play a large role in the success of larvae through these phases. Settlement or the movement of planular larvae from the plankton towards the substrate is strongly stimulated by chemical cues with the dilution or alteration of chemical properties shown to inhibit or alter this phase (Baird and Morse 2004; Webster et al. 2013). Once in contact with the substrate the presence of minimal sediment and algae as well as a positive photo-taxis define the success of this early life history stage (Baird et al. 2003; Birrell et al. 2005). The final stage of metamorphosis also relies on constant ocean chemistry, light availability as well as a neutral pH which enables the secretion of a calcium carbonate skeleton (Albright et al. 2010; Albright and Langdon 2011). For these reasons I suggest that significant factors for the recruitment stage of development should be increased sediment (reducing settlement location as well as light availability), increased ocean acidification (affecting skeletal development), as well as increased nutrients (increasing algae growth competing with coral recruits). The use of this meta-analysis technique to determine which factors affect the growth and development of coral larvae, through both the dispersal and recruitment stages of development can allow for the mitigation of significant factors. As marine ecosystems are set to continue to change as a result of direct and indirect anthropogenic impacts, the ability to determine suitable current and novel habitats will ensure their survival. The use of the combined model developed within this study will allow scientists to determine areas based on water quality where coral larvae survival is the highest and which areas will be most suitable for survival. To ensure these locations remain suitable, increased protection of marine areas should occur through the creation of sanctuaries or marine protected areas ensuring coral survival. Finally, coral species have been observed to alter their range, moving in a poleward direction to combat changing conditions, such as increased sea surface temperatures (Yamano et al. 2011). The application of this research to identify future locations of corals will enable the survival of these very important organism into the future, along with coral reef ecosystems and the high diversity of organism that inhabit them.

This paper has enabled the ranking of water quality factors as to their significance on the fertilisation success and larval survivorship of coral larvae. By analysing a broad spectrum of data, this study confirms the importance of water quality for overall ecosystem health and how poor quality can be used to indicate present or future ecosystem breakdown. Individual factors leading to poor water quality threatens the health of marine environments and will be further exacerbated by the synergistic impact of factors resulting in marine degradation (Humphrey et al. 2008; Sheppard et al. 2010).

Many of the significant factors discussed within this paper can be directly related to human land usage in the form of urbanisation, leading to increased suspended sediment (McLaughlin et al. 2013), agriculture, resulting in increased phosphorous (Correll 1998), as well as the presence of heavy metals in the form of copper and lead (Polkowska et al. 2001). The other significant factors of temperature and salinity can be indirectly related to human activities through climate change. In order to ensure larval development and a consistent coral reef environment, it is imperative that anthropogenic impacts within the marine sphere are mitigated through the implementation of successful management techniques. These techniques include the filtration of run-off and waste water, sequestration of heavy metals from industry as well as a reduction in the use of fossil fuels in order to combat climate change (De-Bashan and Bashan 2004; Solomon et al. 2007). The implementation of these techniques as well as the use of clean energy will provide a stable and healthier environment for coral early life history stages and the proliferation of coral reef environments into the future.

Acknowledgements

I would like to acknowledge and thank Dr Joshua Madin for his advice, guidance and notes throughout this study. I would also like to thank all members of the Quantitative Ecology and Evolution Laboratory at Macquarie University for all their guidance and support with a special mention to Toni Mizerek for all her help throughout this experience.

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Figure Legends

FIGURE 1. Effect of the significant factors from the GLMM conducted on the probability of fertilisation with a 95% confidence interval – (a) Copper, (b) Salinity, (c) Sediment, (d) Phosphorous.

FIGURE 2. Effect of the significant factors from the GLMM conducted on the probability of survivorship with a 95% confidence interval – (a) Copper, (b) Lead, (c) Temperature, (d) Salinity.

FIGURE 3. Combined model of the effect of copper on the probability of both fertilisation and survivorship with increasing concentrations of copper.

TABLE 1. Mean trace levels of factors in seawater.
(Salinity – (Lee et al. 2006), pH – (Orr et al. 2005), Temperature - (Graham and Barnett 1987), Heavy metals, sediment, phosphorous - http://www.seafriends.org.nz/oceano/seawater.htm, Nitrates - http://www.advancedaquarist.com/2003/8/chemistry, Ammonium - http://reefkeeping.com/issues/2007-02/rhf/, Tributyltin - http://water.epa.gov/scitech/swguidance/standards/criteria/aqlife/tributyltin/fs-final.cfm)

TABLE 2. Results of the final GLMM for fertilisation success incorporating five factors - sediment, phosphorous, copper, salinity and salinity squared.

TABLE 3. Results of the final GLMM for survivorship success incorporating five factors - copper, lead, salinity, temperature and temperature squared.

TABLE 4. Variance analysis conducted on the results of both GLMM's investigating fertilisation success and larval survivorship on each of the significant factors observed.

Figures and Tables

FIGURE 1.

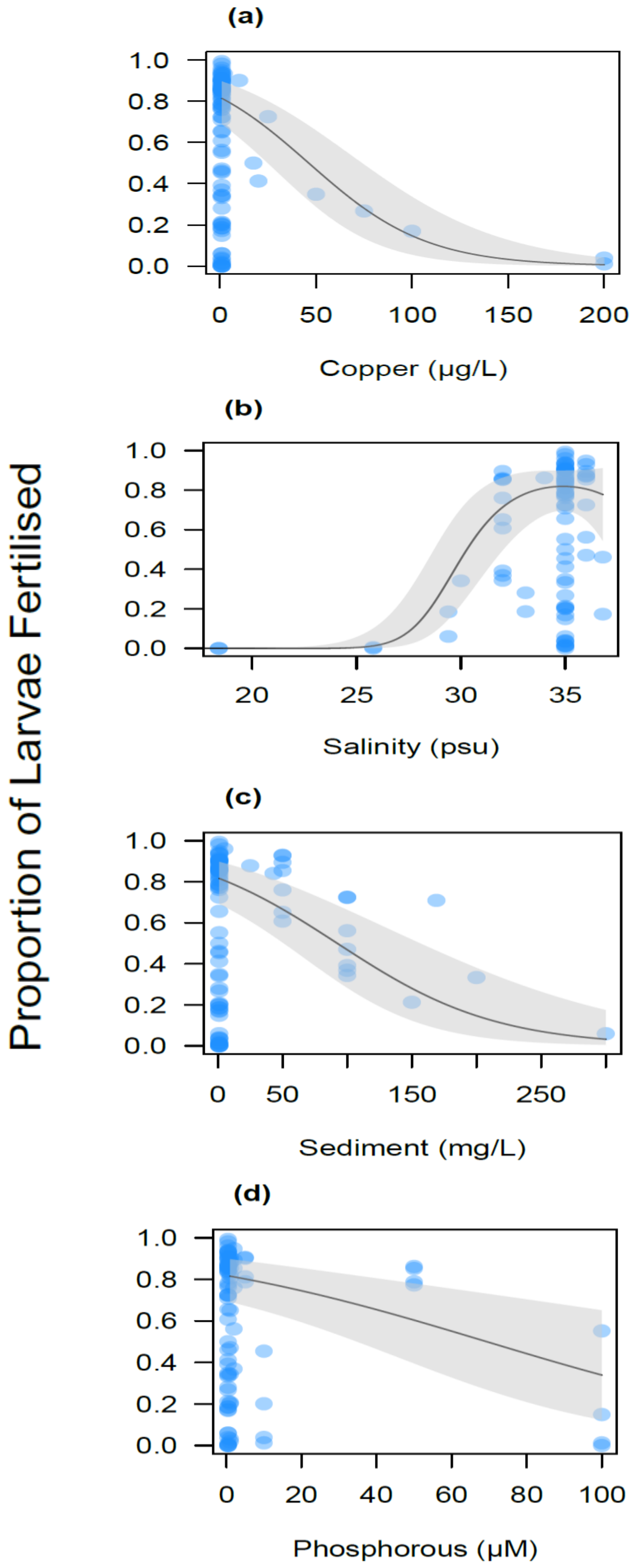
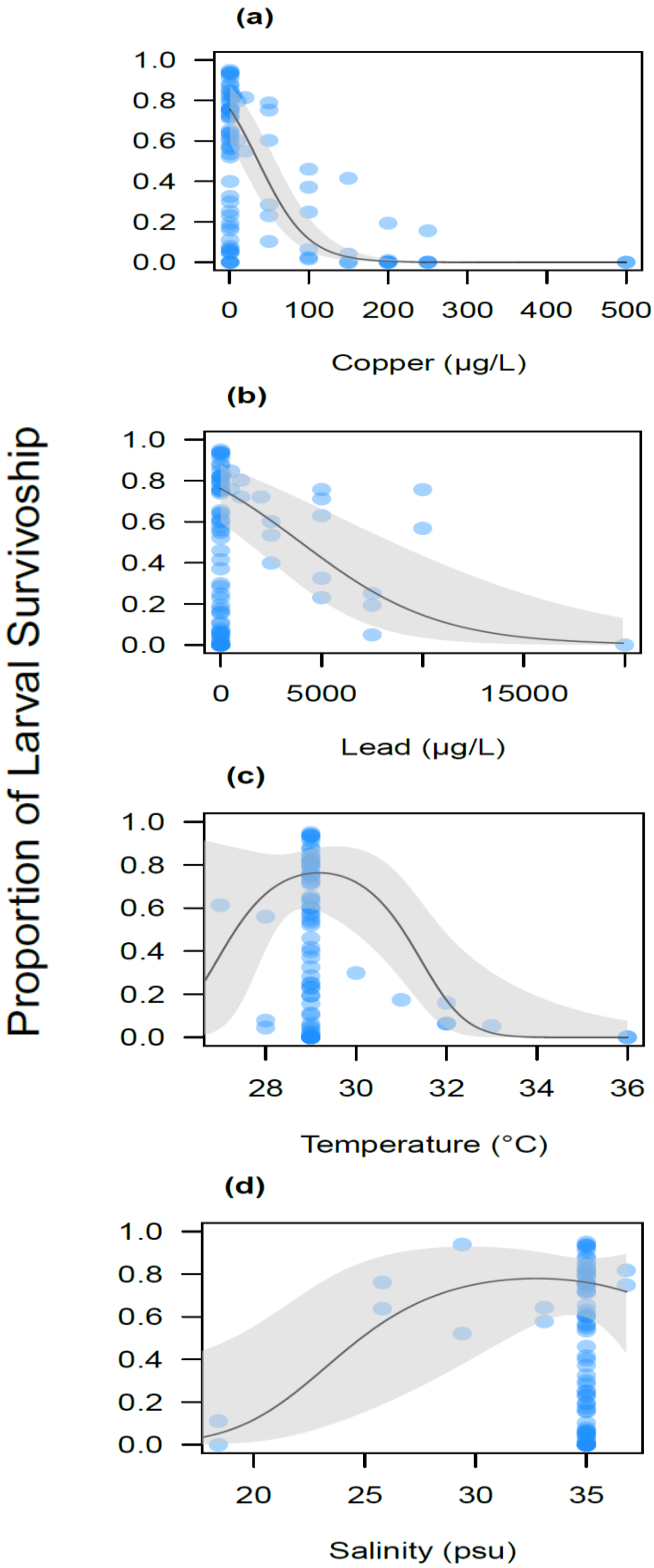
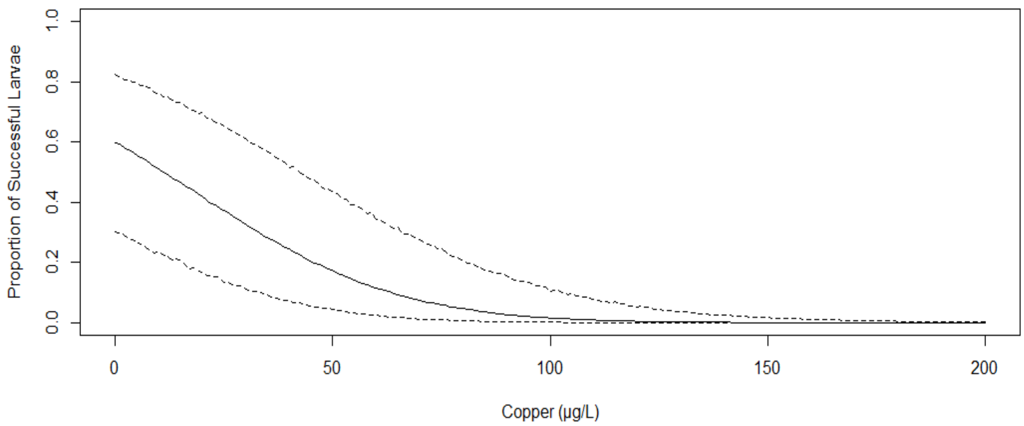


FIGURE 2.



(a)
1.0
0.8
0.6
0.4
0.2
0.0
0
100
200
300
400
500
Copper (µg/L)
(b)
1.0
0.8
0.6
0.4
0.2
0.0
0
5000
15000
Lead (µg/L)
(c)
1.0
0.8
0.6
0.4
0.2
0.0
28
30
32
34
36
Temperature (°C)
(d)
1.0
0.8
0.6
0.4
0.2
0.0
20
25
30
35
Salinity (psu)
Proportion of Larval Survivoship

FIGURE 3.



Proportion of Successful Larvae
0.0
0.2
0.4
0.6
0.8
1.0
0
50
100
150
200
Copper (µg/L)

TABLE 1.

Category	Factor	Trace Level	Units
Nutrients	Ammonium	0.01391	µM
	Phosphorous	0.446	µM
	Nitrate	0.254	µM
Heavy Metals	Copper	0.9	µg/L
	Cadmium	0.11	µg/L
	Lead	0.03	µg/L
	Mercury	0.15	µg/L
	Nickel	6.6	µg/L
	Tributyltin	0	µg/L
	Zinc	5	µg/L
Ocean Chemistry	Acidification	8.1	pH
	Salinity	35	psu
	Sediment	0	mg/L
	Temperature	29	°C

TABLE 2.

Random Effects

Group	Variance	Standard Deviation
Treatment	1.122	1.059
Experiment	1.944	1.394

Fixed Effects

Factors	Estimate	Standard Error	z value	Pr (>|z|)	Significance Code
Sediment	-0.016331	0.003152	-5.181	0.0009	***
Phosphorous	-0.021737	0.005929	-3.666	0.0002	***
Copper	-0.032662	0.004536	-7.200	0.0000	**
Salinity	4.9655077	1.626386	3.053	0.0022	**
Salinity^2	-0.071147	0.025435	-2.797	0.0051	*
Significance codes: 0 ***, 0.001 **, 0.01 *, 0.1 ., 1 -					

Correlation of Fixed Effects

Factor	Intercept	Sediment	Phosphorous	Copper	Salinity
Sediment	-0.011				
Phosphorous	0.013	-0.021			
Copper	-0.004	0.034	0.002		
Salinity	-0.998	0.007	-0.013	0.003	
Salinity^2	0.993	-0.006	0.011	-0.004	-0.999

TABLE 3.

Random Effects

Group	Variance	Standard Deviation
Treatment	2.099	1.449
Experiment	0.242	0.492

Fixed Effects

Factors	Estimate	Standard Error	z value	Pr (>|z|)	Significance Code
Copper	-0.0319	0.0032	-9.842	0.0000	***
Lead	-0.0002	0.0001	-4.222	0.0000	***
Temperature	20.0160	10.0510	1.918	0.0552	*
Temperature ^{2}	-0.3455	0.1754	-1.970	0.0489	.
Salinity	1.3220	0.7904	1.673	0.0944	.
Significance codes: 0 ***, 0.001 **, 0.01 *, 0.1 ., 1 -					

Correlation of Fixed Effects

Factor	Intercept	Copper	Lead	Temperature	Temperature^2
Copper	0.239				
Lead	-0.067	0.060			
Temperature	-0.997	-0.243	0.067		
Temperature ^{2}	0.997	0.245	-0.068	-1.000	
Salinity	-0.055	0.016	0.012	-0.012	0.013

TABLE 4.

Life Stage	Factor	Model variance explained (%)
Fertilisation	Salinity	49.537
	Copper	40.352
	Sediment	5.726
	Phosphorous	4.385
Survivorship	Copper	74.404
	Temperature	23.923
	Salinity	1.673
	Lead	0.000

Appendices

R Script - Fertilisation Analysis

GLMM - Sediment, ammonium, phosphorous, copper, tributyltin, zinc, cadmium, salinity, salinity sq, nitrate

```
data2 <- with(dat2, data.frame(life.stage, sediment_mg_per_l, ammonium_microM,
phosphorous_microM, copper_ug_per_l, tributyltin_ug_per_l, zinc_ug_per_l,
cadmium_ug_per_l, salinity_psu, nitrate_microM, acidification_pH,
tempertaure_degrees_celcius))

#Subset main dataset
data = dat[apply(!is.na(data2[, -1]), 1, sum) > 0 & data2$life.stage == "fertilisation",]
# Add random observation variable for overdispersion
data$rep <- 1:dim(data)[1]

# Full Model
mod_fert_full <- glmer(cbind(success, failure) ~ sediment_mg_per_l +
ammonium_microM + phosphorous_microM + copper_ug_per_l + tributyltin_ug_per_l +
zinc_ug_per_l + cadmium_ug_per_l + salinity_psu + salinity_psu_sq + nitrate_microM +
acidification_pH + acidification_pH_sq + tempertaure_degrees_celcius + (1 | experiment)
+ (1 | rep), family=binomial, data)

data = dat[apply(!is.na(data2[, -1]), 1, sum) > 0 & data2$life.stage == "fertilisation",]
data$rep <- 1:dim(data)[1]

drop1(mod_fert_full, test="Chisq")

# Final Model based on drop analsyis
data2 <- with(dat2, data.frame(life.stage, sediment_mg_per_l, phosphorous_microM,
copper_ug_per_l, salinity_psu))
data = dat[apply(!is.na(data2[, -1]), 1, sum) > 0 & data2$life.stage == "fertilisation",]
data$rep <- 1:dim(data)[1]

mod_fert_final <- glmer(cbind(success, failure) ~ sediment_mg_per_l +
phosphorous_microM + copper_ug_per_l + salinity_psu + salinity_psu_sq + (1 |
experiment) + (1 | rep), family=binomial, data,
control=glmerControl(optimizer="bobyqa"))
```

Note "rep" is needed to remove overdispersion;

```
sum(residuals(mod_fert_final, type="pearson")^2)/df.residual(mod_fert_final)

drop1(mod_fert_final, test="Chisq")
summary(mod_fert_final)
```

R Script – Larval Survivorship Analysis

GLMM - Ammonium, copper, mercury, lead, salinity, sediment, acidification, temperature

```
data2 <- with(dat2, data.frame(life.stage, ammonium_microM, copper_ug_per_l,
mercury_ug._per_l, lead_ug_per_l, salinity_psu, acidification_pH,
tempertaure_degrees_celcius))

# Subset main dataset
data = dat[apply(!is.na(data2[, -1]), 1, sum) > 0 & data2$life.stage == "survivorship",]
# Add random observation variable for overdispersion
data$rep <- 1:dim(data)[1]

#Full Model
mod_surv_full <- glmer(cbind(success, failure) ~ ammonium_microM +
copper_ug_per_l + mercury_ug._per_l + lead_ug_per_l + salinity_psu + salinity_psu_sq
+ acidification_pH + acidification_pH_sq + tempertaure_degrees_celcius +
tempertaure_degrees_celcius_sq + (1 | experiment) + (1 | rep), family=binomial, data)

data = dat[apply(!is.na(data2[, -1]), 1, sum) > 0 & data2$life.stage == "survivorship",]
data$rep <- 1:dim(data)[1]

drop1(mod_surv_full, test="Chisq")

# Final Model based on drop analsyis
data2 <- with(dat2, data.frame(life.stage, copper_ug_per_l, lead_ug_per_l, salinity_psu,
tempertaure_degrees_celcius))
data = dat[apply(!is.na(data2[, -1]), 1, sum) > 0 & data2$life.stage == "survivorship",]
data$rep <- 1:dim(data)[1]

mod_surv_final <- glmer(cbind(success, failure) ~ copper_ug_per_l + lead_ug_per_l +
salinity_psu + salinity_psu_sq + tempertaure_degrees_celcius +
tempertaure_degrees_celcius_sq + (1 | experiment) + (1 | rep), family=binomial, data,
control=glmerControl(optimizer="bobyqa"))
        Note "rep" is needed to remove overdispersion

sum(residuals(mod_surv_final, type="pearson")^2)/df.residual(mod_surv_final)

drop1(mod_surv_final, test="Chisq")
summary(mod_surv_final)
```

R-Script - Combined Model – Example - Copper

```
copper_store <- c()

for (cc in seq(0, 200, 1)) {

newdat <- expand.grid(sediment_mg_per_l=0, phosphorous_microM=0,
copper_ug_per_l = cc, salinity_psu = 35, salinity_psu_sq = 35^2, success=0,
failure=0)
  mm <- model.matrix(terms(mod_fert_final),newdat)
  success_fert <- mm %*% fixef(mod_fert_final)
  pvar1_fert <- 2*sqrt(diag(mm %*% tcrossprod(vcov(mod_fert_final), mm)))

newdat <- expand.grid(copper_ug_per_l=cc, lead_ug_per_l=0, salinity_psu=35,
salinity_psu_sq=35^2, tempertaure_degrees_celcius=29,
tempertaure_degrees_celcius_sq=29^2, success=0, failure=0)
  mm <- model.matrix(terms(mod_surv_final),newdat)
  success_surv <- mm %*% fixef(mod_surv_final)
  pvar1_surv <- 2*sqrt(diag(mm %*% tcrossprod(vcov(mod_surv_final),mm)))

vars <- sort(inv.logit(rnorm(10000, success_fert, pvar1_fert)) *
inv.logit(rnorm(10000, success_surv, pvar1_surv)))

copper_store <- rbind(copper_store, c(cc, vars[5000], vars[250], vars[9750]))

}
```

Table S1. Papers used in fertilisation and survivorship analysis

Author	**Year**	**Paper Title**	**Species**	**Factor**	**Life History Stage**
Baird, A. H., Gilmour, J. P., Kamiki, T. M., Nnaka, M., Pratchett, M. S., Yamamoto, H. H. and Yamasaki, H.	2006	Temperature tolerance of symbiotic and non-symbiotic coral larvae	*Acropora muricata*	Temperature	Survivorship
Bassim, K. M. and Sammarco, P. W	2003	Effects of temperature and ammonium on larval development and survivorship in a scleractinian coral (*Diploria strigosa*)	*Diploria strigosa*	Temperature and ammonium	Survivorship
Chua, CM., Leggat, W., Moya, A. and Baird, A. H.	2013	Near-future reduction in pH will have no consistent ecological effects on the early life-history stages of reef corals	*Acropora tenuis, Acropora millepora*	Acidification	Survivorship
Chua, CM., Leggat, W., Moya, A. and Baird, A. H.	2013	Temperature affects the early life history stages of corals more than near future ocean acidification	*Acropora tenuis, Acropora millepora*	Acidification	Fertilisation
Cox, E. F. and Ward, S.	2002	Impact of elevated ammonium on reproduction in two Hawaiian	*Pocillopora damicornis*	Ammonium	Survivorship

Erftemeijer, P. L. A., Hagedorn, M., Laterveer, M., Craggs, J. and Guest, J. R.	2012	Effects of suspended sediment on fertilisation success in the scleractinian coral *Pectinia lactuca*	*Pectnia lactuca*	Sediment	Fertilisation
Farina, O., Ramos, R., Bastidas, C. and Garcia, E.	2008	Biohemical reposne of cnidarian larvae to mercury and benzo(a)pyrene exposure	*Porites astreoides*	Mercury	Survivorship
Gilmour, J.	1999	Experimental investigation into the effects of suspended sediment on fertilisation, larval survival and settlement in a scleractinian coral	*Acropora digitfera*	Sediment	Fertilisation
Harrison, P. L. and Ward, S.	2001	Elevated levels of nitrogen and phosphorus reduce fertilisation success of gametes from scleractinian reef corals	*Acropora longicyathus* *Goniastrea aspera*	Ammonium, phosphorous, ammonium and phosphorous	Fertilisation
Humphrey C., Weber, M., Lott, C., Cooper, T., Fabricius, K.	2008	Effects of suspended sediments, dissolved inorganic nutrients and salinity on fertilisation and embryo development in the coral *Acropora millepora*	*Acropora millepora*	Sediment, salinity, nitrate and ammonium	Fertilisation
Nakamura, M., Ohki, S., Suzuki, A. and Sakai, K.	2011	Coral Larvae under Ocean Acidification- Survival, Metabolism, and Metamorphosis	*Acropora digitfera*	Acidification	Survivorship

Negri, A. P. and Heyward, A. J.	2001	Inhibition of coral fertilisation and larval metamorphosis by tributyltin and copper	*Acropora millepora*	Copper and tributyltin	Fertilisation
Randall, C. J. and Szmant, A. M.	2009	Elevated temperature reduces survivorship and settlement of the larvae of the Caribbean scleractinian coral, *Favia fragum (Esper)*	*Favia fragum*	Temperature	Survivorship
Reichelt-Brushett, A. J.and Harrison, P. L.	1999	The Effect of Copper, Zinc and Cadmium on Fertilisation Success of Gametes from Scleractinian Reef Corals	*Goniastrea aspera*	Copper, zinc and cadmium	Fertilisation
Reichelt-Brushett, A. J. and Harrison, P. L.	2004	Development of a Sublethal Test to Determine the Effects of Copper and Lead on Scleractinian Coral Larvae	*Goniastrea aspera*	Copper and lead	Survivorship
Reichelt-Brushett, A. J. and Harrison, P. L.	2005	The effect of selected trace metals on the fertilisation success of several scleractinian coral species	*Goniastrea retiformis, Goniastrea aspera, Acropora tenius, Acropora longicyathus*	Copper, cadmium, nickel, zinc	Survivorship

Scott, A., Harrison, P. L. and Brooks, L. O.	2013	Reduced salinity decreases the fertilisation success and larval survival of two scleractinian coral species	*Acropora millepora, Platygyra daedalea*	Salinity	Fertilisation and survivorship
Victor, S. and Richmond, R. H.	2005	Effect of copper on fertilisation success in the reef coral *Acropora surculosa*	*Acropora surcolosa*	Copper	Fertilisation