Environmental factors limiting fertilisation and larval success in corals

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Abstract

Events in the early life history of reef-building corals, including fertilisation and larval survival, are susceptible to changes in the chemical and physical properties of seawater. Quantifying how changes in water quality affects these events is therefore important for understanding and predicting population establishment in novel or changing environments. A review of the literature identified that levels of salinity, temperature, pH, suspended sediment, nutrients, and heavy metals affect coral early life history stages. Using published experimental data, this study quantified the influence of seawater properties on coral fertilisation and larval survivorship probabilities. Fertilisation success was highly sensitive to suspended sediment, copper, salinity, phosphate and ammonium. Larval survivorship was sensitive to copper, lead and salinity. A combined model was developed that estimated the joint probability of both fertilisation and larval survivorship in seawater with different chemical and physical properties. This model was able to determine the likelihood of larvae surviving through each stage of development to settlement competency, as well as incorporating real life data from Sydney and Lizard Island in Australia. This combined model could therefore be used to recommend targets for water quality in coastal waterways as well as aid in predicting the potential for species to expand their geographical range in response to climate change.

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](#_ENREF_64); [Harley et al. 2006](#_ENREF_30); [Halpern et al. 2008](#_ENREF_28)). Run-off from agricultural activities increases eutrophication in the form of nitrogen and phosphate ([De-Bashan and Bashan 2004](#_ENREF_17)), while increased heavy metal contamination from industry leads to the bioaccumulation of pollutants in higher trophic level species (e.g., oysters and tuna), and therefore poses a direct threat to human food safety ([Howarth and Marino 2006](#_ENREF_34); [Copat et al. 2012](#_ENREF_14)). In nutrient poor systems, such as coral reefs, increases in nutrients, when accompanied by decreases in herbivory, can cause changes to ecosystem functioning, such as changes to alternative stable states that greatly affect the entire food web (McCook 1999). Meanwhile, alterations in water chemistry and temperature are already having an effect in the tropics. Increased sea surface temperatures (Hughes et al 2003) present an increasing threat to reef building corals associated with large scale bleaching events (Hoegh-Guldberg 1999). Ocean acidification also poses a threat to scleractinian corals (Chua et al. 2013), reducing their ability accrete and grow (Anthony 2008). How these environmental changes will influence the ecological distributions of species will depend in part on the sensitivity 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 most gamete fertilisation and larval dispersal occur in the plankton ([Grantham et al. 2003](#_ENREF_27)). Adult marine species often lack the ability to travel large distances once mature or are sedentary in their adult form ([Jackson 1986](#_ENREF_36); [Cowen and Sponaugle 2009](#_ENREF_16)). Larval dispersal ensures the connectivity of existing populations, including buffering from local extinction, and establishment of new or less populated locations ([Gaylord et al. 2013](#_ENREF_23)). Reef building corals disperse via pelagic larvae, potentially over vast distances (Jackson 1986; Richmond 1997; Graham et al. 2008). However, it is these early stages that are often vulnerable to slight changes in environmental conditions ([Hédouin and Gates 2013](#_ENREF_32)).

Pre-settlement stages of corals (embryos and larvae) are usually influenced by specific environmental and chemical cues, which dictate the success of these stages ([Erwin and Szmant 2010](#_ENREF_20)). Approximately 85% of scleractinian coral species broadcast spawn gametes that rise to the surface waters where fertilisation occurs (Baird et al. 2009). Following fertilisation, larvae of some species can survive for up to several months in the plankton (Graham et al. 2008), however most are competent to settle onto the reef after approximately four days (Connolly & Baird 2010; Figueiredo et al 2013). Subtle changes in nutrient concentrations, heavy metal toxicity and ocean chemistry severely reduce fertilisation success ([Victor and Richmond 2005](#_ENREF_65); [Humphrey et al. 2008](#_ENREF_35)). Heavy metals including copper and lead have been found within the ocean as a result of the mining and manufacturing sectors ([Howarth and Marino 2006](#_ENREF_39); [Copat et al. 2012](#_ENREF_16)). Pollutants in the form of increased nutrients including ammonium, phosphate and nitrates enter waterways and the ocean as run-off from agriculture, with their use in fertilisers and as a product of untreated organic matter and manure ([De-Bashan and Bashan 2004](#_ENREF_17)). Increased run-off has also been linked to human-induced climate change, where an increase in the occurrence of storms has resulted in freshwater influxes from the land, not only carrying pollutants, but also altering ocean salinity (Solomon 2007). Other factors associated with climate change include changes in sea surface temperature and pH, as a result of increased atmospheric carbon dioxide (Solomon, 2007). These environmental factors generally affect the growth and survival of marine organisms, but have been specifically shown to negatively affect early life history stages. Examples include polychaete worms ([Gopalakrishnan et al. 2008](#_ENREF_25)), echinoderms ([Heslinga 1976](#_ENREF_33); [Schlegel et al. 2012](#_ENREF_57)) and bivalves ([Calabrese et al. 1977](#_ENREF_11); [Kurihara 2008](#_ENREF_38)). Negative effects on survival have also been observed broadly for scleractinian coral species ([Reichelt-Brushett and Harrison 2005](#_ENREF_52); [Victor and Richmond 2005](#_ENREF_65); [Randall and Szmant 2009](#_ENREF_48)).

In this study, we quantify the relative importance of a number of factors known to affect the early life stages of reef building corals. To do so, we 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.

Materials and Methods

Data collection

Data were collected from experimental studies that observed the effect of seawater properties on the probability of fertilisation or larval survivorship for scleractinian corals. Literature searches for published articles using search terms “coral larvae”, “fertilisation”, “survivorship”, “success”, “water chemistry” and “nutrients and heavy metals” were conducted up until the 1st of July 2014. For fertilisation success, we selected studies that reported the proportion of eggs fertilised within a 1 to 36 hour period in seawater. In these studies, levels of ammonium, phosphate, nitrate, copper, zinc, cadmium, tributyltin, suspended sediment, salinity, pH or temperature had been experimentally manipulated (Table S1). For larval survivorship, we selected studies that reported the proportion of larvae that survived for 4 to 14 days in seawater. In these studies, levels of ammonium, copper, mercury, lead, salinity, acidification or temperature had been manipulated (Table S1). Studies that did not report the number of eggs or larvae used to calculate proportions were excluded, as they could not be converted into binomial trials. Studies that reported the effect of factors associated with petroleum pollution were also excluded, because they are not commonly found within the marine environment and tended to kill gametes and larvae outright. For salinity, the practical salinity unit (psu) was used instead of ppt, as psu is the most modern usage and both were assumed to be equal.

Because studies focusing on a given environmental factor did not report all other factors, we assumed they were at levels characteristic of typical seawater (Table 1). As experimental treatments tended to be large for a given factor, variation in typical water properties tended to have negligible effects on the final model, with the exception of factors expected to cause hump-shaped responses in fertilisation and larvae survivorship (i.e., temperature, pH and salinity). Typically salinity, temperature and pH levels for tropical seawater were therefore sourced from peer-reviewed articles ([Graham and Barnett 1987](#_ENREF_26); [Orr et al. 2005](#_ENREF_44); [Lee et al. 2006](#_ENREF_39)). For our analysis, salinity was set at 35psu, temperature at 28°C, and pH at 8.1. The final data set is available in the supplementary material (Appendix S1).

Data analysis

We utilised 18 scientific research papers FIG ?? (Table with number of papers per parameter) that quantified the fertilisation success and larval survival of scleractinian corals. Within our fertilisation success analysis we had 110300 replicates, across 11 factors and nine studies utilising seven species. For larval survivorship we had 9860 replicates, across 7 factors and 10 studies utilising 12 species. 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 successes and failures. Because each experiment tended to manipulate one factor at a time, levels of collinearity were low. Fertilisation and larval survivorship were analysed separately using generalised linear mixed-effects models (GLMM) with a binomial response and a logit link function ([Zuur et al. 2009](#_ENREF_69)) 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 (i.e., some of the 14 species were not tested for some seawater properties, Table S1). Because studies focused on single species, we included study as a random variable to account for variation that occurred among experiments, which also captured the effect of species. Hump-shape relationships were expected for temperature, salinity and pH. Therefore, both quadratic and linear terms were included for these factors. A drop-analysis was conducted to remove non-significant terms using the ‘drop1’ function in the statistical software package ‘R’ (R Development Core Team 2012). GLMMs were conducted using the ‘glmer’ function in the package ‘lme4’ ([Bates et al. 2012](#_ENREF_7)).

Following model selection, hierarchical partitioning of variance (the function ‘hier.part’) (Walsh and MacNally 2013) was used to determine the relative amount of variance explained by the remaining factors for each life stage.

Finally, we calculated the mean joint probability of progressing through both fertilisation and larval stages for a given set of water properties by multiplying model estimates. Uncertainty estimates were estimated using a Monte Carlo approach, 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

Copper, salinity, phosphate and sediment were retained in the final best model for fertilisation probability (Table 2, Fig. 1). Salinity had a significant quadratic effect, where fertilisation probability peaked at the imposed salinity of seawater (35 psu) and declined at higher and lower levels (Fig. 1b). Nitrate, ammonium, zinc, cadmium, tributyltin, pH and temperature did not have significant influences on fertilisation probability and were excluded from the final model.

Copper, lead, temperature and salinity were retained in the final best model for survivorship success (Table 3, Figure 2). Temperature had a significant quadratic effect, where survivorship probability peaked at the imposed tropical seawater temperatures (29°C) and declined at higher and 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.

Salinity and copper accounted for the highest levels of variance for the fertilisation model, with sediment and phosphate accounting for only 10% of all variance (Table 4). Copper and temperature accounted for the highest levels of variance for the survivorship model, with salinity and lead accounting for a minimal amount (Table 4).

By way of example, we ran a combined model of survival to assess the joint probability of success for the range of salinity used in the experimental data (Fig 3). This analysis showed that the probability of larvae surviving through both stages of development is much lower in this case when compared to each individual stage.

Discussion

Coral fertilisation success and larval survivorship were affected by multiple water quality factors and significantly, our approach allowed us to estimate the relative importance of these factors (Table 2 and 3). Suspended sediment, phosphate, copper and salinity significantly reduced fertilisation success, illustrating the sensitivity of larvae to their environment. Larval survivorship was most affected by the presence of the heavy metals copper and lead, but was also affected by temperate and salinity. Copper, which is related to industrial activity ([Negri and Heyward 2001](#_ENREF_43)), and salinity, which is related to changes in global climate as well as seasonal variability ([Solomon et al. 2007](#_ENREF_60)), were the two factors that had significant negative effects on both life history stages of corals.

Copper is known to have widespread negative impacts on marine invertebrates ([Calabrese et al. 1977](#_ENREF_11); [Ahsanullah and Arnott 1978](#_ENREF_1); [Rivera-Duarte et al. 2005](#_ENREF_55); [Fitzpatrick et al. 2008](#_ENREF_22); [Caldwell et al. 2011](#_ENREF_12)), including reef corals ([Reichelt-Brushett and Harrison 1999](#_ENREF_50); [Negri and Heyward 2001](#_ENREF_43); [Reichelt-Brushett and Harrison 2004](#_ENREF_51); [Reichelt-Brushett and Harrison 2005](#_ENREF_52)). However, copper does not occur at high concentrations in most coral reef environments ([Li et al. 2001](#_ENREF_40)). Nonetheless, the large effects observed at relatively low concentrations (in the order of 10µg/L) suggest that reducing the presence of copper in seawater is important for avoiding recruitment failure ([Reichelt-Brushett and Harrison 2004](#_ENREF_51)) especially in the vicinity of ports and shipping channels, given that most copper in marine environments originate from anti-fouling paints on older vessels and ship groundings ([Negri and Heyward 2001](#_ENREF_43)).

The other heavy metals analysed were generally not important predictors of fertilisation or larval success. One exception was lead, which significantly reduced larval survivorship and is of much greater concern than copper because it may occur at high levels in nearshore reef environments ([Li et al. 2001](#_ENREF_40); [Polkowska et al. 2001](#_ENREF_47)). Lead enters the marine environment through run-off from its use in leaded-petrol and as a by-product in the creation of industrial materials ([Polkowska et al. 2001](#_ENREF_47)).The negative effects of lead on the survival of marine invertebrate larvae have been shown with both molluscs and corals experiencing higher mortality rates ([Reichelt-Brushett and Harrison 2004](#_ENREF_51); [Wang et al. 2009](#_ENREF_66)).

The amount of suspended sediment significantly reduced coral fertilisation, a factor that is commonplace following both natural and anthropogenic disturbances, especially in shallower or nearshore habitats ([Styan and Rosser 2012](#_ENREF_62)). Suspended sediment severely reduces the success of fertilisation in a wide variety of marine organisms that reproduce via spawning of gametes, including most of the fishes ([Bilotta and Brazier 2008](#_ENREF_8)), sea urchins ([Pagano et al. 1993](#_ENREF_45)) and corals ([Humphrey et al. 2008](#_ENREF_35)). Low levels of sediment (less than 100mg/L) reduced fertilisation rates in scleractinian corals by up to 50% ([Humphrey et al. 2008](#_ENREF_35); [Erftemeijer et al. 2012](#_ENREF_19)). Natural and anthropogenic disturbances ranging from storms to seafloor dredging increase the amount of suspended sediment within marine environments. Recognising the negative impact of suspended sediment and particularly that induced by human activity, the Western Australian government has implemented a moratorium on dredging during spawning events limiting the effect of suspended sediments on coral reef ecosystems ([Styan and Rosser 2012](#_ENREF_62)).

Similarly to the suspended sediment response, increased phosphate levels reduced fertilisation success. Phosphate is common in run-off from agricultural land uses and excessive fertilisation in agriculture has been shown to severely diminish water quality and in some cases lead to anoxic surface waters ([Correll 1998](#_ENREF_15); [Harrison and Ward 2001](#_ENREF_31)). The fertilisation success of corals is highly sensitive to phosphate with just 1µM reducing success by up to 75% ([Harrison and Ward 2001](#_ENREF_31)). However, the implementation of nutrient removal techniques (metal precipitation, use of wetland systems to fix-nitrogen, and the adsorption by microorganisms) is effective in reducing phosphate within marine environments and therefore its effect on coral fertilisation ([De-Bashan and Bashan 2004](#_ENREF_17)).

Water temperature and salinity both reduced fertilisation success and larval survivorship and are strongly linked to global climate change. Increased water temperatures have been shown to reduce the survival of planular larvae ([Bassim and Sammarco 2003](#_ENREF_6); [Baird et al. 2006](#_ENREF_5); Woolsey et al. 2013). Increasing sea surface temperatures continue to threaten marine environments, especially in tropical waters, as a result of global climate change ([Solomon et al. 2007](#_ENREF_60)). Changes in salinity were found to significantly affect both early life history stages, with decreased salinity expected in the future as freshwater influxes are predicted to increase (Knutson et al. 2010). In agreement with our model estimates, such increases have been shown to reduce fertilisation in corals by up to 50%, with just slight declines in salinity ([Richmond 1996](#_ENREF_53); [Scott et al. 2013](#_ENREF_58)).

While both temperature and salinity reduced coral larval success, changes in seawater pH had little influence on either fertilisation or survivorship. The lack of a significant effect of pH contradicts much of the earlier work on the effect of ocean acidification (Albright et al 2010) on the early life history stages of corals, but is in strong agreement with more recent experimental work demonstrating that temperature has a much greater effect than pH (Chua et al. 2013).

To be successful, an individual needs to survive both stages of development (fertilisation and larval survivorship). As an example we conducted a joint probability analysis for salinity, which was found to be significant across both life history stages. This model determined the likelihood of a single egg 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](#_ENREF_54); [Connolly and Baird 2010](#_ENREF_13)). This analysis determined that in the case of salinity the probability of a single larvae surviving through both stages of development was lower compared to the probability of each life stage individually. This combined model can incorporate more than a single factor and can be based on actual water quality at different sites, to determine the effect of pollutants on larval development.

Our study is significant because it estimates the relative importance of various environmental factors on the early life history stages of corals. However, there were several issues that might have influenced the predictive capacity of the models. While the models likely isolated the important environmental factors reducing fertilisation and larvae success, they were based on only 18 experimental studies. The low number of studies forced us to group data for all species. Because studies mainly focused on one species at a time, we accounted for variation among species by including study as a random factor. However, species would be expected to respond differently to one another under more rigorous experimentation. Finally, we were unable to check for interactions among factors, because studies tended to focus one variable at a time. This limitation also forced us to select background levels of non-focal variables, which could be particularly problematic for factors with non-zero quadratic response curves. Despite these limitations, we believe our analysis to be a good first step for improving our understanding of early life history responses to environmental variables. The study highlights the importance of specific factors that reduce the success of coral development. While a number of previous studies have identified factors none have been able to determine which of these factors would be most effective for mitigating negative effects on corals.

Future studies should focus on later life history stages (e.g., settlement and metamorphosis). Once this is done, our approach can be used to identify bottlenecks to population persistent and also to develop guidelines for threshold levels of pollution in coral reef environments. Such models can also be used to determine dispersal and recruitment success under given water quality data scenarios and identify sensitive locations for protection. Finally, such models can help understand and predict the success of coral species in novel environments, such as might occur following observations and predictions of poleward range shifts associated with increasing sea surface temperatures ([Yamano et al. 2011](#_ENREF_68)). The application of this research to identify more optimal and novel environmental locations for the survival of corals will enable the persistence of these very important organisms into the future, along with coral reef ecosystems and the high diversity of organisms that inhabit them.

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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) Phosphate.

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 salinity on the probability of both fertilisation and survivorship with changing units of salinity.