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" \o "Tilman, 2001 #59); [Harley et al. 2006](#_ENREF_30" \o "Harley, 2006 #41); [Halpern et al. 2008](#_ENREF_28" \o "Halpern, 2008 #40)). Run-off from agricultural activities increases pollution in the form of nitrogen and phosphate ([De-Bashan and Bashan 2004](#_ENREF_17" \o "De-Bashan, 2004 #16)), while increased heavy metal contamination from industry leads to the bioaccumulation of contaminants in higher order trophic level species (e.g., tuna), and therefore poses a direct threat to human food safety ([Howarth and Marino 2006](#_ENREF_34" \o "Howarth, 2006 #45); [Copat et al. 2012](#_ENREF_14" \o "Copat, 2012 #28)). In nutrient poor systems, such as coral reefs, increases in nutrients, for example, when accompanied by decreases in herbivory, can lead to changes in ecosystem functioning, such as fluctuations in the current 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" \o "Grantham, 2003 #37)). Adult marine species often lack the ability to travel large distances once mature or are sedentary in their adult form ([Jackson 1986](#_ENREF_36" \o "Jackson, 1986 #47); [Cowen and Sponaugle 2009](#_ENREF_16" \o "Cowen, 2009 #29)). 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" \o "Gaylord, 2013 #35)). 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" \o "Hédouin, 2013 #81)).

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" \o "Erwin, 2010 #32)). 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" \o "Victor, 2005 #60); [Humphrey et al. 2008](#_ENREF_35" \o "Humphrey, 2008 #46)). Heavy metals including copper and lead which are naturally found within the oceans have increased in concentrations as a result of the mining and manufacturing sectors ([Howarth and Marino 2006](#_ENREF_39" \o "Howarth, 2006 #45); [Copat et al. 2012](#_ENREF_16" \o "Copat, 2012 #28)). Pollutants in the form of increased nutrients including ammonium, phosphate and nitrates can enter waterways and the ocean as run-off from agriculture, ([De-Bashan and Bashan 2004](#_ENREF_17" \o "De-Bashan, 2004 #16)). Increased run-off has also been linked to human-induced climate change, where an increase in the occurrence of storms has resulted in greater freshwater flows 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" \o "Gopalakrishnan, 2008 #36)), echinoderms ([Heslinga 1976](#_ENREF_33" \o "Heslinga, 1976 #44); [Schlegel et al. 2012](#_ENREF_57" \o "Schlegel, 2012 #78)) and bivalves ([Calabrese et al. 1977](#_ENREF_11" \o "Calabrese, 1977 #9); [Kurihara 2008](#_ENREF_38" \o "Kurihara, 2008 #12)). Negative effects on survival have also been observed broadly for scleractinian coral species ([Reichelt-Brushett and Harrison 2005](#_ENREF_52" \o "Reichelt-Brushett, 2005 #56); [Victor and Richmond 2005](#_ENREF_65" \o "Victor, 2005 #60); [Randall and Szmant 2009](#_ENREF_48" \o "Randall, 2009 #82)).

A broad range of factors including heavy metals, nutrients and changes in ocean chemistry are known to affect early life stages in corals, however mitigating these factors is difficult as they are diverse in origin. In recent years the use of meta-analysis techniques has become increasingly common to review the current state of a field and incorporate data from multiple published papers. These techniques including the use of generalised linear mixed effect models, allow for the use of response variables with different distributions (Stram, 1996). Within ecology and the marine fields these techniques are often used to understand large topics and answer broad scale questions (Collie et al., 2000; Claudet et al, 2008).

In this study, we quantify the relative importance of a number of factors known to affect the early life stages of reef building corals using generalised linear mixed effects models. 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 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, pH 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 naturally 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 calculated the level of each factor to be one percent of the maximum pollutant level reported within each study included in the model as papers tended to justified their maximum level. As experimental treatments tended to be large for a given factor (e.g., cadmium ranged from 0 to 1000 µg/L), variation in standard 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). Standardised salinity, temperature and pH levels for tropical seawater were therefore sourced from peer-reviewed articles ([Graham and Barnett 1987](#_ENREF_26" \o "Graham, 1987 #91); [Orr et al. 2005](#_ENREF_44" \o "Orr, 2005 #90); [Lee et al. 2006](#_ENREF_39" \o "Lee, 2006 #92)). For our analysis, salinity was set at 34psu, temperature at 28°C, and pH at 8.1. The final data set is available in the supplementary material (Appendix S1).

In order to test the applications of our models, real-world water samples were collect from inside and outside Sydney Harbour (Chowder Bay and Mona Vale, respectively) to highlight the difference between water qualities within the harbour compared to water collected outside the heads as well as from Lizard Island on the Great Barrier Reef. These samples were tested for each of the factors used within both the fertisliation and larval survivorship analyses by an external laboratory, Envirolab Services, Sydney.

Data analysis

We utilised 20 scientific research papers (Table 1) that quantified the fertilisation success and larval survival of scleractinian corals. Within our fertilisation success analysis we had 110330 replicates, across 11 factors and nine studies utilising seven species. For larval survivorship we had 11100 replicates, across 7 factors and 12 studies utilising 14 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" \o "Zuur, 2009 #62)) to determine the relative effect of each seawater property on fertilisation and larval survivorship probability. Prior to analysis each factor was checked for normality (Figure S1 and S2). As each GLMM included a large number of environmental factors individual models were first conducted to determine which factors were significant and should therefore be utilised in the larger model, these factors were also rescaled to ensure the final model would converge. Within the final models there were not enough combinations of species or reproductive mode (spawn or brood) in the treatments to include these factors as predictor variables. 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’ with the model optimiser ‘bobyqa’ to limit problems of over dispersion and convergence ([Bates et al. 2012](#_ENREF_7" \o "Bates, 2012 #25)).

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 utilised real-world water samples to show the applications of our created models for both fertilisation and larval survivorship. For each life history stage we calculated the percent likelihood of success for both fertilisation and larval survival individually, using each water sample as well as the standard error. We were then able to compare the likelihood of success at each location.

Finally, we calculated the mean joint probability of progressing through both fertilisation and larval stages for each given locations. The standard error of each water sample was also calculated to determine the variation for each location.

Results

Copper, sediment, ammonium, phosphate and salinity were retained in the final 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, zinc, cadmium, tributyltin, pH and temperature did not have significant influences on fertilisation probability and were excluded from the final model.

Copper, lead, and temperature were retained in the final model for survivorship success (Table 3, Figure 2). Ammonium, mercury, pH and salinity did not result in a significant effect on survivorship probability and were dropped from the final model.

Ammonium accounted for the highest levels of variance for the fertilisation model, with sediment, copper phosphate and salinity accounting for less than 20% of all variance (Table 4). Lead accounted for the highest levels of variance for the survivorship model, with salinity and copper accounting for a minimal amount.

By way of example we used real-world water samples collected from Chowder Bay, Mona Vale and Lizard Island to assess the probability of success under varying water quality. Chowder bay within Sydney showed a consistently lower level of success for both fertilisation and larval survivorship with Lizard Island and Mona Vale showing a high level of success across both life history stages (Figure 3). We then ran a model combining both life history stages (fertilisation and larval survivorship) to determine the success of a single egg through development to settlement competency (Figure 4). when combinedWithin this analysis Lizard Island and Mona Vale again had a great proportion of successful larvae compared to Chowder Bay.

Discussion

Our research demonstrates the relative importance of a range of environmental factors in estimating the success of early life history stages in corals. Coral fertilisation success and larval survivorship were affected by multiple water quality factors. Consistent with earlier studies ([Negri and Heyward 2001](#_ENREF_43" \o "Negri, 2001 #3)), the heavy metal copper had significant negative impacts on fertilisation and larval survivorship. Copper, which significantly affects both life history stages, occurs naturally at low levels within the marine environment. However, the levels at which copper significantly impacts coral development are not widespread, but are instead limited to localised pollution caused by anti-fouling agents on vessels ([Reichelt-Brushett and Harrison 2004](#_ENREF_51" \o "Reichelt-Brushett, 2004 #13); [Negri and Heyward 2001](#_ENREF_43" \o "Negri, 2001 #3)). Lead, which was also found to significantly reduce larval survivorship, can be found at high levels more broadly in nearshore reef environments, as a result of industrial activities ([Li et al. 2001](#_ENREF_40" \o "Li, 2001 #80); [Polkowska et al. 2001](#_ENREF_47" \o "Polkowska, 2001 #76)). The introduction of nutrients into marine environments, including phosphate and ammonium, severely diminishes water quality, which we show, will lead to a reduction in fertisliation success of corals. These nutrients are common in run-off from agricultural land uses including the use of fertilisers ([Correll 1998](#_ENREF_15" \o "Correll, 1998 #17); [Harrison and Ward 2001](#_ENREF_31" \o "Harrison, 2001 #43)). Natural and anthropogenic disturbances ranging from storms to seafloor dredging increase the amount of suspended sediment within marine environments, especially in shallower or nearshore habitats ([Humphrey et al. 2008](#_ENREF_35" \o "Humphrey, 2008 #46); [Erftemeijer et al. 2012](#_ENREF_19" \o "Erftemeijer, 2012 #69); [Styan and Rosser 2012](#_ENREF_62" \o "Styan, 2012 #63)). While suspended sediment significantly reduces fertilisation success in corals, it did not appear to have a major influence on larval survivorship (Figure 1). Anthropogenic impacts, including those linked to climate change, greatly affect the marine environment and often lead to changes in ocean temperatures, pH and salinity. Water temperature and salinity both affected coral early life history stages, with temperature changes decreasing fertilisation and changes in salinity decreasing larval survivorship. Increased water temperatures as a result of climate change threaten marine environments and therefore coral reefs ([Solomon et al. 2007](#_ENREF_60" \o "Solomon, 2007 #83)). Episodic increases in freshwater influxes, decreasing salinity as a result of increase storms and runoff from urban areas is also a significant threat to coral larval survival (Knutson et al. 2010; Scott et al., 2013). While both temperature and salinity reduced coral larval success, changes in seawater pH had little influence on either fertilisation or survivorship (Chua et al. 2013).

To be successful, an individual needs to survive both stages of development (fertilisation and larval survivorship). As an illustration, we collected water samples from three locations that were expected to differ dramatically in water properties. As expected the properties from the Lizard Island water sample, resulted in the greatest estimated success for both fertilisation success and larval survivorship, with 70% and 60% success, respectively. The beach water sample from Sydney (Mona Vale) as had a high level of success especially when compared to the Sydney Harbour sample (Chowder Bay), where water was expected to be most polluted and indeed it was, with the lowest estimated level of success for both early life stages. The joint probability of succeeding through both stages showed the same pattern (Figure 5). These probabilities are reflective 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 parameterised with larvae survivorship observations within their peak competency period ([Richmond 1997](#_ENREF_54" \o "Richmond, 1997 #58); [Connolly and Baird 2010](#_ENREF_13" \o "Connolly, 2010 #85)). ([Richmond 1997](#_ENREF_54" \o "Richmond, 1997 #58); [Connolly and Baird 2010](#_ENREF_13" \o "Connolly, 2010 #85)). This model shows that, at each location, the probability of a single egg surviving through both stages of development was lower, compared to the probability of each life stage individually. While this analysis is just an example (based on one-off water samples), it demonstrates how to integrate multiple water quality factors for early life history stages, and then combining success at each stage to give an overall estimate of developmental success. In doing so, the modelling framework can make predictions of success based on actual water quality data from different locations, to determine the effect of environmental changes 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 20 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. 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. Finally, in order to demonstrate the applications of our models we utilised water chemistry data collected from a single sample at each location, which does not reflect the daily fluctuations of some variables including salinity. 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, as well as allow real-world data to be analysed for success.

While this analysis is small in scale, it does highlight the practical applications of generalised linear models for understanding and predicting success in different environments. The ability to predict success, and particularly in the early life history stages of sensitive, sessile adult species, is imperative for understanding the effect of environmental change on species distributions. 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, with use of the combined model developed within this analysis, we can better 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" \o "Yamano, 2011 #61)). 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) Sediment, (c) Ammonium, (d) Phosphate, (e) Salinity.

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) Salinity.

Figure 3. Effect of water sampled from three locations (Chowder Bay, Mona Vale and Lizard Island) on the percent likelihood of success with standard error for - (a) Fertilisation and (b) Larval Survivorship.

Figure 4. Combined model using real-world water samples from Chowder Bay, Mona Vale and Lizard Island showing the likelihood of success through both life history stages (fertilisation and larval survivorship).