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 and 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 to various degrees. In this study, we combined published experimental data in order to determine the relative importance of seawater properties for coral fertilisation and larval survivorship probabilities. Fertilisation success was most 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. We demonstrated the combined model using water samples from Sydney and Lizard Island in Australia, to estimate the likelihood of larvae surviving through both stages of development to settlement competency. Our 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 can, when accompanied by decreases in herbivory, lead to changes in ecosystem functioning, such as phase shifts that affect entire food webs (McCook 1999). Meanwhile, alterations in water chemistry and temperature are already having an effect in tropical ecosystems. Increased sea surface temperatures present an increasing threat to reef building corals associated with large scale bleaching events (Hoegh-Guldberg 1999; Hughes et al 2003). Ocean acidification reduces the ability of scleractinian corals to accrete and grow (Anthony 2008; Chua et al. 2013). How these environmental changes will influence the ecological distributions of species will depend in large part on the sensitivity of early life history stages.

The success of early life history stages of plants and animals are fundamental determinants to species’ abundances and distributions. These stages are especially important 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 such is the case in hydroids, bryozoans, ascidians as well as corals ([Jackson 1986](#_ENREF_36" \o "Jackson, 1986 #47); [Cowen and Sponaugle 2009](#_ENREF_16" \o "Cowen, 2009 #29)). Dispersal in the larval stage however, 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 their success ([Erwin and Szmant 2010](#_ENREF_20" \o "Erwin, 2010 #32)). These cues are highly species specific and can range from the presence of coral rubble (Baird and Morse, 2004) to bacteria found within a biofilm (Slattery et al., 1999; Tebben et al., 2011) and encourage larvae to develop as well as eventually settle onto the reef. 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 in seawater, have increased in concentrations as a result of mining and manufacturing ([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 resulted from 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 abnormal 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 ([Kurihara 2008](#_ENREF_38" \o "Kurihara, 2008 #12)). 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). 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)).

Studies quantifying the influence of environmental factors on the early life stages in corals tend to focus on one or two factors at a time. However, the success of these stages depends on numerous variables, and the relative importance of these variables needs to be quantified if we are to understand and predict success in different environments. Therefore, in this study, we quantified the relative importance of multiple 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 relationships between a range of nutrient, heavy metal and other seawater properties on fertilisation and larval success. Finally, we develop and demonstrate a combined model to estimate the joint probability of transitioning both early life history stages.

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 in 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 1). 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 generally focused on one or two environmental factors, and tended not to report non-manipulated factors, we filled data gaps in two different ways. For linear relationships (e.g., such as between copper and success probability), we used values corresponding to one percent of the maximum pollutant treatment level reported across all studies. For hump-shaped relationship (e.g., such as between salinity and success probability), we fit quadratic models and identified the peak probability (e.g., the salinity-success relationship for fertilisation peaked at approximately 34 psu). Because experimental treatments tended to be large for a given factor (e.g., cadmium ranged from 0 to 1000 µg/L), variation in the filled-in 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). The final data set is available in the supplementary material (Table S1).

In order to demonstrate usage of the different models (explained in the next section), we collected water samples from three locations: (1) Chowder Bay, which is inside Sydney Harbour and was expected to have higher levels of heavy metals, nutrients and sediment and lower salinity; (2) Mona Vale, which is an ocean beach outside Sydney Harbour and was expected to be less polluted than inside the harbour; and (3) Lizard Island, northern Great Barrier Reef, to represent a tropical location where larvae supposedly do well. Water samples were analysed for all of the seawater properties that we modelled by Envirolab Services, Sydney.

Data analysis

We were able to combine 20 research papers that quantified fertilisation success and larval survival of scleractinian corals for our analyses (Table 1). For fertilisation success, there were a total of 110,330 replicate trials across 11 environmental factors, nine studies and seven species. For larval survivorship, there were a total of 11,100 replicate trials across 7 environmental factors, 12 studies and 14 species. We were constrained to only include studies that reported the number of individual eggs or larvae in experiments, so that we were able to convert the published proportions into numbers of successes and failures. Because each experiment tended to manipulate one factor at a time, levels of collinearity were low or unquantifiable. 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 (Fig S1 and S2). To reduce the final number of fixed effects in the GLMMs, we first ran single factor models and removed highly non-significant factors and factors with too few replicates. Because studies experimental conditions and focal species differed among studies, we included study as a random effect. Hump-shape relationships were expected for temperature, salinity and pH. Therefore, both linear and quadratic effects 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’ ([Bates et al. 2012](#_ENREF_7" \o "Bates, 2012 #25)).

We used the final best model to predict both fertilisation success and larval survivorship based on levels of the environmental variables in the three water samples. We used hierarchical partitioning of variance (the function ‘hier.part’) (Walsh and MacNally 2013) 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 each given location. This probability is the product of probabilities for the two models. We calculated 95% confidence intervals for the joint model using bootstrapping; ie., by sampling 1000 times from normal distributions defined by the model predicted estimates and variance. These random samples were multiplied, sorted, and the median (5,000th value) and 95% confidence intervals (250th and 9750th values) calculated.

Results

Copper, sediment, ammonium, phosphate and salinity explained the majority of variation in fertilisation probability and were retained in the final model (Table 2, Fig 1). Nitrate, zinc, cadmium, tributyltin, pH and temperature did not have significant influences on fertilisation probability and were excluded. Salinity and copper explained the most variance accounting for 42.513% and 35.905% respectively in the fertilisation model, while sediment, ammonium and phosphate accounted for the remaining 21.581% of all variance (Table 4).

For survivorship success, copper, lead, and temperature explained the majority of variation and were retained in the final model (Table 3, Fig 2), whereas, ammonium, mercury, pH and salinity were dropped. Copper accounted for the highest levels of variance at 92.0.16% for the survivorship model, with salinity and lead accounting for just 7.984% (Fig 4).

Based on the water samples collected to demonstrate the models, the two early life history stages were predicted to do poorly in Chowder Bay (within Sydney Harbour) water compared with Mona Vale (outside Sydney Harbour) and tropical Lizard Island (Fig 3). The combined model demonstrates the overall probability of both fertilisation success and larval survivorship (i.e., the success of a single egg making it through development to settlement competency; Fig 3) with Lizard Island having the most success at 42% success, Mona Vale at 35% success and Chowder Bay with the lowest success at 10%.

Discussion

Our analysis 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)), copper had significant negative impacts on both fertilisation and larval survivorship. Copper occurs naturally at low levels in the marine environment; however, localised levels can be high in areas where it is used in anti-fouling agents on vessels and other structures ([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 is likely to lead to a reduction in the fertilisation 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 (Fig 1). Anthropogenic impacts, including climate change, greatly affect the marine environment and have led to changes in ocean temperatures, pH and salinity. Salinity affected both coral early life history stages, with increasing and decreasing levels reducing fertilisation success and larval survivorship. Episodic increases in freshwater influxes, decreasing salinity as a result of increased storms and runoff from urban areas, is a significant threat to coral development (Knutson et al. 2010; Scott et al., 2013). While 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 early stages of development (fertilisation and larval survivorship). To demonstrate, 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 highest estimated probability of success for both fertilisation and larval survivorship (70% and 60% on average, respectively). The water sample from a Sydney beach (Mona Vale) also showed a high level of success with an average fertilisation rate and larval survivorship of 60%. In contrast, the Sydney Harbour sample (Chowder Bay), where water was expected to be most polluted, the probability of success was lowest for both early life stages with 20% for fertilisation success and 50% for larval survivorship; however, reduced success was driven by lower salinity levels and higher sedimentation, rather than heavy metals, which were not significantly different to the oceanic locations. The joint probability of success, which reflects the probability of a single egg surviving through fertilisation as well as up to 14 days within the plankton, was subsequently lowest in Sydney Harbour and similarly higher at the other two locations. Even though the joint analysis is based on single water samples, it demonstrates how to integrate multiple water quality factors to predict success in early life history stages, and that these successes can then be combined to give an overall estimate of developmental success.

Our study is important because it estimates the relative importance of multiple environmental factors on the early life history stages of corals. However, there were several issues that are likely to influence the predictive capacity of the models. While we likely isolated the important environmental factors reducing fertilisation and larvae success, our analyses 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 also unable to check for interactions among factors, because studies tended to focus one variable at a time. This limitation also required us to estimate background levels of unmeasured variables, which could be particularly problematic for factors with quadratic response curves. Due to the variation in experimental protocol in each study certain factors including the presence of microbes as well as the level of water filtration used in each study was not included in the models, as these were rarely if ever stated. Finally, in order to demonstrate the applications of our models, we utilised water chemistry data collected from a single sample at each location, and so these samples obviously do not reflect the daily and longer-term fluctuations of some variables (e.g., salinity). Despite these limitations, we believe our analysis to be a good first step for improving our understanding of early life history responses to multiple environmental variables.

The ability to predict the success of organisms in their environment, and particularly in the early life history stages of sessile adult species, is an important step for understanding the effect of environmental change on species distributions. Our approach could be extended by including subsequent life history stages (e.g., settlement and metamorphosis), which would allow for the identification of bottlenecks to population persistence and also to develop guidelines for threshold levels of pollutions 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, our approach might be used to better understand and predict the success of coral species in novel environments, such as high-latitude habitats ([Yamano et al. 2011](#_ENREF_68" \o "Yamano, 2011 #61)).

Acknowledgements

We would like to thank the Quantitative Ecology and Evolution group at Macquarie University for helpful comments and suggestions. JSM and AHB were supported by the Australian Research Council.

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Figure Legends

Figure 1. Fertilisation success as a function of seawater properties: (a) copper, (b) sediment, (c) ammonium, (d) phosphate, and (e) salinity. The points are the raw proportions from the published studies. The black curves are model fits with grey shading representing 95% confidence intervals.

Figure 2. Larval survivorship as a function of seawater properties: (a) copper, (b) lead, and (c) salinity. The points are the raw proportions from the published studies. The black curves are model fits with grey shading representing 95% confidence intervals.

Figure 3. Predicted probability of (a) fertilisation success and (b) larval survivorship based on seawater sampled from three locations (Chowder Bay, Mona Vale and Lizard Island). (c) The joint probability of both early life stages. Error bars represent 95% confidence intervals.