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Response to letter regarding “Limited Scope for Latitudinal Extension of Reef Corals”

In their recent letter, Madin et al. (2016) dispute our findings in Muir et al. (2015a) that reduced levels of light during winter confine staghorn corals to shallower depths at higher latitudes and will ultimately limit their scope for latitudinal expansion as oceans warm. We based our conclusions on a rich global dataset analysed using two types of analyses: polynomial quantile regression models and species distribution models. Madin and colleagues’ reanalysis of our data focuses only on the quantile regression model, and in our view, provides no convincing quantitative evidence in support of their proposition that most species exhibit either no trend or a reverse trend to the one we described.

Madin et al. (2016) note that across the 122–171 species of staghorn corals (Wallace et al. 2012, Veron 2000) there is likely to be variation in the maximum depths at which these corals occur with respect to latitude, and claim we made an implicit assumption that all species exhibit the same depth-latitude response. To the contrary, we explicitly accounted for random variation in the regression parameters describing the relationship between maximum depths and latitude among species; and importantly, our model was a better fit to the data than the alternative models proposed (Table 1). Madin et al. (2016) were mistaken in which model we used and we accept some responsibility for this: the full details required to repeat the analyses properly were not given in our methods.

We limited our inferences to average effects of the group, rather than the fixed effects of particular species, to circumvent potentially spurious findings caused by data limitations. Our decision to focus on the group as a whole both defines our point of focus on the collective properties of Earth’s richest group of reef-building corals and acknowledges that the available data (<https://datadryad.org/resource/doi:10.5061/dryad.3b568>) are not adequate for the modelling of many individual species. By contrast, Madin et

al. (2016) modelled 50 individual species, highlighting four that appeared to have significantly deeper maximum depths with increasing latitude (model “C” documented at: https://github.com/jmadin/muir_comment). This analysis is flawed: it fails the goodness of fit test for fixed effects quantile regression models (Geraci 2016, Table 1) and in the current version of the `quantreg` R package produces fatal errors during the significance testing routine, terminating without output. Moreover, closer examination of the data indicates that the fitted values and associated regression parameters for species showing a convex pattern were highly leveraged by a few outlying points (Fig. 1). It is possible that some of these outlying points are the result of recorder error but more likely result from individuals dislodged downslope from the shallows during storm events (Muir et al. 2015b).

Madin et al. (2016) contend that the preferred light environments for all deep-water tropical species are present in temperate locations; they just occur at shallower depths. Though stated as a criticism of our work, this is in fact an affirmation of our basic model. We had already pointed out that conditions on wave-exposed shallow substrates would not be viable for the mostly fragile deep-water forms.

Madin et al. (2016) also suggest that, following our reasoning, a shallow water tropical fauna with very high seasonal light requirements should exist. This may be a fruitful avenue for further research, but the current data set shows no such thing. Of more interest in a global climate change context we believe, is the observation that other zooxanthellate scleractinian genera have been recorded at latitudes a few degrees beyond those of staghorn corals (Veron 2000).

Finally, Madin et al. (2016) cite the presence of fossil staghorn corals at higher latitudes than the current distribution as evidence that low winter light is unlikely to hinder range expansion as temperate seas warm. Our contention, sup-

Table 1. Specifications for the polynomial quantile regression models discussed. *Madin model C fails the goodness of fit test (GOFT) for quantile regression models ($GOFT = 2 \times 10^{-4}$, $p < 0.001$), is a poor fit to the data (Fig. 1) and terminates without producing an output in the current version of the quantreg R package (see text). GOFT is currently not available for mixed quantile regression models. Muir et al. (2015a) model is best fit compared to the remaining valid models Madin A and B ($\Delta AIC = 1442$ and $\Delta AIC = 725$ respectively). Note that ΔAIC cannot be used for comparison with Madin model C which uses a different dataset. The Muir et al. (2015a) model defined a symmetric positive-definite covariance structure for the random effects rather than the default positive-definite diagonal covariance structure. A symmetric positive-definite covariance structure allows for covariances among the intercepts, slopes and curvatures of the species random effects, rather than fixing them at zero as in Madin model B. Allowing for covariance among the regression parameters for each species significantly improves the fit of the model to the data and allows more nuanced interpretations of the data. The analysis also used orthogonal polynomials rather than raw polynomials, to avoid potential problems associated with multicollinearity, which can be extreme for raw polynomials, and is perhaps the source of the warning messages published when attempting Madin model B.

Source	Model Description	Fixed	Random	Covariance structure	LL	df	AIC	Comments
Muir et al. (2015a)	Random variation among species in depth-latitude relationships, symmetric covariance structure	$I + L + L^2$	$(I + L + L^2) S$	$\begin{matrix} \sigma^2_I & \sigma_{I,L} & \sigma_{I,L^2} \\ \sigma_{I,L} & \sigma^2_L & \sigma_{L,L^2} \\ \sigma_{I,L^2} & \sigma_{L,L^2} & \sigma^2_{L^2} \end{matrix}$	-54632	10	109283	Best Fit
Madin et al. (2016) Model A	Random variation among species in intercepts	$I + L + L^2$	$I S$	σ^2_I	-55357	5	110725	Poor Fit
Madin et al. (2016) Model B	Random variation among species in depth-latitude relationships, diagonal covariance structure	$I + L + L^2$	$(I + L + L^2) S$	$\begin{matrix} \sigma^2_I & 0 & 0 \\ 0 & \sigma^2_L & 0 \\ 0 & 0 & \sigma^2_{L^2} \end{matrix}$	-54997	7	110008	Warnings in quantreg
Madin et al. (2016) Model C	Fixed variation among species in depth-latitude relationships	$S + L S + L^2 S$	None	-	-46417	150	93133	Failed GOFT, failed to run*

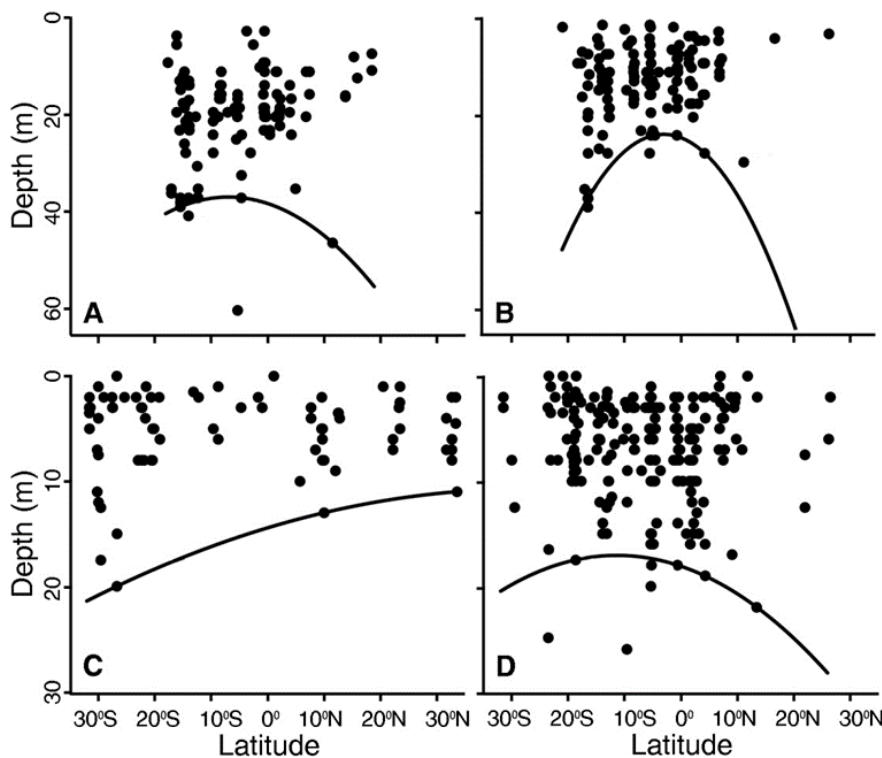


Figure 1. The Madin et al. (2016) analysis (fixed effects polynomial quantile regression, model C, Table 1) produced a poor fit for many individual species with the predicted maximum depth (0.975 quantile) highly leveraged by one or two points. The four “reverse trend” species noted by Madin et al. (2016) are shown here (A) *Acropora speciosa* (B) *A. paniculata* (C) *A. glauca* (D) *A. tenuis*.

ported by species distribution models in Muir et al. (2015a), is that the scope for latitudinal extension is limited (not non-existent), and that even when local temperature, salinity and aragonite saturation are otherwise suitable, the limiting factor will be insufficient light during winter. It is axiomatic that there is a latitude beyond which no amount of warming of temperate seas will sustain corals with a high reliance on photosynthate, such as the staghorn corals. Beyond that limit, they would need to supplement their meagre winter photosynthate supply by either stored energy reserves, heterotrophy (suspended sediments, dissolved organic matter, bacteria, protozoans, plankton), or both (Anthony and Fabricius 2000). Indeed deep reef-building Scleractinia on cold and dark sea mounts lack zooxanthellae and are entirely heterotrophic (Roberts et al. 2006).

In conclusion, we believe our paper documents a global phenomenon that is both interesting and important in the context of global climate change, and, along with this exchange of views, points to potentially fruitful lines of investigation regarding how corals might meet their nutritional requirements in warming seas and at depths and latitudes where sunlight becomes a limiting resource.

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