

A generalized light-driven model of community transitions along coral reef depth gradients

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Abstract

Aim: Coral reefs shift between distinct communities with depth throughout the world. Yet, despite over half a century of research on coral reef depth gradients, researchers have not addressed the driving force of these patterns. We present a theoretical, process-based model of light's influence on the shallow to mesophotic reef transition as a single quantitative framework. We also share an interactive web application. Moving beyond depth as an ecological proxy will enhance research conducted on deeper coral reefs.

Location: Global; subtropical and tropical coral reefs, oligotrophic and turbid coastal waters.

Time period: Present day (2020).

Major taxa: Scleractinia.

Methods: We constructed ordinary differential equations representing the preferred light environments of shallow and mesophotic Scleractinia. We projected these as depth bands using light attenuation coefficients from around the world, and performed a sensitivity analysis.

Results: We found light relationships alone are sufficient to capture major ecological features across coral reef depth gradients. Our model supports the depth limits currently used in coral reef ecology, predicting a global range for the shallow-upper mesophotic boundary at $36.1 \text{ m} \pm 5.6$ and the upper-lower mesophotic boundary at $61.9 \text{ m} \pm 9.6$. However, our model allows researchers to move past these fixed depth limits, and quantitatively predict the depths of reef zones in locations around the world.

Main conclusions: The use of depth as a proxy for changes in coral reef communities offers no guidance for environmental variation between sites. We have shown it is possible to use light to predict the depth boundaries of reef zones as a continuous variable, and to accommodate this variability. Predicting the depths of reef zones in unusual light environments suggests that shallow-water turbid reefs should be considered as mesophotic coral ecosystems. Nonetheless, the current depth-based heuristics are relatively accurate at a global level.

Jack H. Laverick and Raz Tamir contributed equally to this study.

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KEYWORDS

depth gradients, light, marine, mesophotic coral ecosystems, reef zonation, tropical reefs

1 | INTRODUCTION

Tropical coral reefs attract considerable research attention; however, studies have largely ignored their total depth range (Menza, Kendall, & Hile, 2008). The global depth record for photosynthetic hard corals currently stands at 165 m (Maragos & Jokiell, 1986; Pyle & Copus, 2019). Despite this, only about 800 studies (Bongaerts et al., 2019) have considered reefs deeper than 30 m. We refer to this understudied depth zone as the mesophotic, and define mesophotic coral ecosystems (MCEs) by the presence of light-dependent corals and associated communities (Hinderstein et al., 2010). MCEs are typically found at depths ranging from 30–40 to 150 m in tropical and subtropical regions (Kahng et al., 2010; Lesser, Slattery, & Leichter, 2009; Puglise, Hinderstein, Marr, Dowgiallo, & Martinez, 2009; Pyle & Copus, 2019). Though mesophotic research has increased over the past two decades, MCEs are still particularly understudied (Laverick et al., 2018; Loya, Eyal, Treibitz, Lesser, & Appeldoorn, 2016; Turner, Babcock, Hovey, & Kendrick, 2017).

Mesophotic reefs could be considered marginal habitat, because of their low light levels. However, these reefs thrive world-wide (Baker et al., 2016), and contain their own diversity (Muir, Wallace, Pichon, & Bongaerts, 2018). Though we must be careful when generalizing, a number of ecological patterns have been observed down coral reef depth gradients, from the shallows to MCEs. There is now broad agreement that the mesophotic zone is subdivided into the 'upper mesophotic' and 'lower mesophotic', with a transition at approximately 60 m, depending on water clarity and depth of the thermocline (Lesser, Slattery, & Mobley, 2018; Slattery, Lesser, Brazeau, Stokes, & Leichter, 2011). This '60 m rule' has been linked to reductions in shallow species richness with increasing depth, and holds across ocean basins (Fricke & Meischner, 1985; Kahng et al., 2010; Lesser, Slattery, Laverick, Macartney, & Bridge, 2019; Slattery & Lesser, 2012). The upper mesophotic zone is an area of overlap between shallow and mesophotic taxa, while the lower mesophotic is characterized by taxa adapted to low-light environments (Kahng et al., 2019). These changes are in parallel to zonation in *Symbiodinium* phylotypes in some places (Lesser et al., 2010). The lower depth limit of the mesophotic zone, meanwhile, is linked to the deepest occurrence of zooxanthellate corals (Kahng et al., 2010).

Yet, significant gaps remain in our knowledge. A lack of information on the functioning of these ecosystems has caused researchers to rely on a fixed depth limit of 30 m as a boundary between shallow and mesophotic reefs (Laverick et al., 2018). This 30-m limit is based on SCUBA regulations and difficulties of access (Pyle, 2019), and fails to explicitly accommodate environmental variation. Recently the boundary was updated to 30–40 m, and to be theoretically rooted in ecology (Baker et al., 2016), but still remains a largely untested assumption with little empirical support. In the Gulf of Eilat/Aqaba in the Red Sea, shifts in community structure were detected at 40 and 70 m (Tamir, Eyal, Kramer, Laverick,

& Loya, 2019). However, the same approach when applied to the reefs off Utila in the Caribbean returned boundaries at approximately 15 and 40 m (Laverick, Andradi-Brown, & Rogers, 2017). For more examples of varying boundary depths, see Pyle and Copus (2019). The underlying causes, and variability, in these faunal breaks requires more research.

The principal candidate driver of change along coral reef depth gradients is light. In their review, Lesser et al. (2018) recognized that optical properties of the water column are likely to have the strongest correlation with MCE community patterns. Muir et al. (2018) reported mesophotic species are more likely to be found in shaded microhabitats in the brighter portions of their depth range, with the same being true for juvenile corals (Kramer, Eyal, Tamir, & Loya, 2019). This can blur trends in physiology with depth for mesophotic corals (Laverick, Green, Burdett, Newton, & Rogers, 2019). Kahng et al. (2010) found notable correlations between light attenuation with depth (K_{dPAR}) and regional maximum depth records for zooxanthellate corals world-wide. This in turn could be linked to the small-scale optics of corals at the cellular level. Highly organized skeletal geometries have been observed in some mesophotic species, consisting of ridges and furrows, in contrast to typically shallow species (Kahng et al., 2012). The skeletal scattering of photons can increase path lengths and the potential for photons being absorbed (Wangpraseurt et al., 2014). This highlights how species physiology may need to be linked to community models through an understanding of the light field. Linking mesophotic taxa to abiotic conditions is, therefore, a research priority for the field (Costa et al., 2015; Turner et al., 2019). When doing this, it is important to remember that depth range alone is a poor descriptor of a species' niche. Individuals at maximum and minimum observed depths may exist at the limits of their physiology, inflating our sense of where species are likely to occur (Roberts, Bridge, Caley, Madin, & Baird, 2019). When assessing these physiological envelopes, we must look at the whole distribution of abundance with depth.

The number of studies that include community characterization through the mesophotic zone, combined with the optics of the water column, have increased (Lesser et al., 2018). While MCEs share species with shallow water reefs (Laverick et al., 2018; Muir et al., 2018), the dominant habitat forming species largely differ (Kahng et al., 2010). This means the relationships between different taxa and light across depth gradients need to be quantified (Edmunds, Tsounis, Boulon, & Bramanti, 2018; Kleypas, Mcmanus, & Meñez, 1999; Lesser et al., 2018; Muir et al., 2018). Recent studies in the Red Sea have shown this can be achieved at a community level by linking light data (Tamir et al., 2019) to cluster analyses of co-occurring coral taxa (Laverick et al., 2017; Lin & Denis, 2019). Similarly, in upper mesophotic sites throughout the central Indo-Pacific, light controls community structure in tandem with hydrodynamic effects (Turak & DeVantier, 2019). Substrate type, rugosity, and slope angle all alter the light environment and were found to lead to zoned communities when interacting with the habitat preferences of hard corals.

Modelling exercises are particularly powerful when they direct our current knowledge towards answering an overarching question. The last 10 years has seen the mesophotic literature increase threefold (Laverick et al., 2018; Pyle & Copus, 2019; Turner et al., 2017), allowing us to present a framework for thinking of mesophotic reefs as ecological entities (Baker et al., 2016). However, the empirical work in mesophotic ecology has rarely been supported by theoretical studies (see Roberts, Keith, et al., 2019 for an exception). With this in mind, Lesser et al. (2018) used an existing model (Mobley, Zhang, & Voss, 2003) to combine a simple 3D reef geometry with features that affect the underwater light field. In doing so, they created a quantitative representation of the current candidate structuring force across coral reef depth gradients. Lesser et al. (2018) suggested that by uniting a community approach to defining MCEs (Laverick et al., 2017) with optical data describing the underwater light field, it may be possible to provide a reef-to-reef definition of where community boundaries occur. Though they are right to call for more studies through the entire depth range of photosynthetic reefs linked to optical data, a working quantitative theory is valuable to compare against data as they become available. We believe it is already possible to theoretically link these approaches at a community level.

Here, we present a generalized, mechanistic, light-driven model of the shallow to mesophotic reef transition. In doing so we unify key ecological patterns from coral reef depth gradients into a single quantitative framework. Our model assumes community-level light relationships, and reproduces plausible patterns. We can express current ecological definitions as mathematical conditions, and can now predict how the boundaries between reef zones will shift under different light regimes.

2 | MATERIALS AND METHODS

We take a community level approach to create a theoretical, mechanistic, model of the shallow to mesophotic reef transition. Machine-learning algorithms have already been applied in the Caribbean (Laverick et al., 2017) and the Red Sea (Tamir et al., 2019) to show mesophotic and shallow reefs can be grouped as two assemblages of Scleractinia (Hartigan & Wong, 1979). By assessing the similarity of field observations to these two communities across light gradients, it is apparent that shallow taxa may be light-limited with depth, while mesophotic taxa occur in an optimal light envelope (Tamir et al., 2019). We now construct a light-driven model to predict community values (D) for reef patches down a generalized depth gradient. We refer to community values as D because the two studies previously mentioned co-opted the equations of Defrene and Legendre traditionally used for indicator species identification (Dufrene & Legendre, 1997). We highlight that the Caribbean and Red Sea studies only inspire this model, and that the machine-learning and calculation of D for indicator values are not required for the construction and use of this model.

To build our model, we begin by assuming shallow communities (D_{Shallow}) are light-limited beneath a threshold, and that community values (how similar a reef patch is to the typical shallow community)

increase asymptotically with increasing light (Figure 1 middle). Values will plateau as habitat heterogeneity and the size of reef patches considered will prevent all shallow taxa occurring in the same place, even under optimal light levels. We assume mesophotic communities ($D_{\text{Mesophotic}}$) centre on a preferred light value, between light limitation and light-induced stress (Figure 1 bottom). Finally we assume a trade-off, where an observed patch of reef can approach a mesophotic or shallow community. A patch of reef cannot simultaneously look like the exemplar mesophotic and shallow reef patch (D_{Reef}). The functions to represent these assumptions, and create the curves in Figure 1, are reported below (Equations 1–3). A detailed description of model parameters is available in Table 1. In brief, V_{max} is the ceiling of the relationship between shallow communities and light, $\%PAR_{\text{surface}}$ is the percentage of photosynthetically active radiation from the surface, K is the point of light limitation of shallow taxa, a is a scalar term and b is the shape term in the light relationship for the mesophotic community. The D_{Shallow} and $D_{\text{Mesophotic}}$ functions were recently validated on mesophotic reefs in the Red Sea (Tamir et al., 2019).

$$D_{\text{Shallow}} = V_{\text{max}} \times (\%PAR_{\text{surface}} / (K + \%PAR_{\text{surface}})) \quad (1)$$

$$D_{\text{Mesophotic}} = (a/b) \times (\%PAR_{\text{surface}}/b)^{(a-1)} \times e^{-(\%PAR_{\text{surface}}/b)a} \quad (2)$$

$$D_{\text{Reef}} = D_{\text{Mesophotic}} - D_{\text{Shallow}} \quad (3)$$

To transform the community–light relationships into depth ranges we use the Lambert–Beer law (Kirk, 2011). Light levels are often recorded from open water casts (500–1,000 m from the reef), and so the result of this equation is really a maximum depth for community values ($Depth_{\text{max}}$; Figure 1 top). To introduce the variation in the light field on the reef we incorporate an additional term for bathymetric shading ($Depth_{\text{Shade}}$), to estimate a shallow limit for community values. $Depth_{\text{max}}$ refers to the special case of the $Depth$ function when $Shade = 1$, $Depth_{\text{Shade}}$ refers to the result of the depth equation under user-defined maximum bathymetric shading. When K_{dPAR} (light attenuation with depth) and $Shade$ are bounded by 0 and 1:

$$Depth = \ln(\text{Proportion } PAR_{\text{surface}} / \text{Shade}) / -K_{\text{dPAR}} \quad (4)$$

We find the upper and lower depths of the upper mesophotic zone by finding the root of D_{Reef} . We do this numerically using the `[rootSolve]` package (Soetaert, 2016) in R (R core team, 2020). This light value is then passed to the $Depth$ function under maximum and minimum shading.

To test the performance of our model, we predicted where community boundaries occur for 11 different reefs and compared these to the depth limits currently used as proxies in the field. Kahng et al. (2010) collated light attenuation coefficients (K_{dPAR}) and photosynthetic coral depth records from around the world. We used these K_{dPAR} values to parameterize the underwater light field functions in our model. For this analysis the community relationships were parameterized to Tamir et al. (2019).

We explore the sensitivity of the model, to varying parameter values, in terms of the change in the predicted depths of the upper

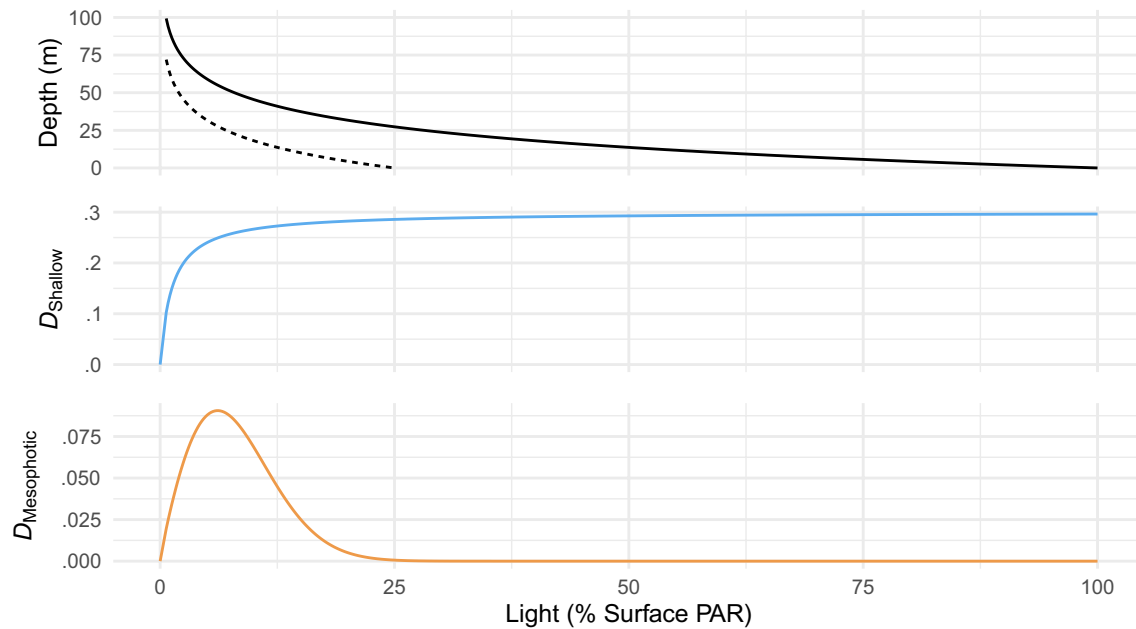


FIGURE 1 Underlying model distributions. Plots of the equations underpinning our model, helping visualize our assumptions. The abiotic equations are plotted in black in the top panel. $Depth_{max}$ is the solid line, and shows the depths we would expect a given light level to occur for an unshaded, horizontal plane. $Depth_{shade}$ is plotted as a dashed black line, and shows the same relationship, penalized by a shading value as estimated by Lesser et al. (2018) for a vertical reef wall. The shallow community–light relationship ($D_{Shallow}$) is plotted in blue, and assumes light limitation at low light levels. The mesophotic community–light relationship ($D_{Mesophotic}$) is plotted in orange, and assumes a preference for low-light environments

TABLE 1 A list of the parameters, with descriptions, from the three equations that create the model

Parameter	Description
<i>Depth</i>	
$PAR_{surface}$	Photosynthetically active radiation ($\mu\text{mol}/\text{m}^2/\text{s}$) just below the air–water interface. Also found in $D_{Shallow}$ and $D_{Mesophotic}$.
K_{dPAR}	A light attenuation coefficient, indicating water clarity. Bounded between 0 and 1. Lower numbers indicate clearer water, which allows the passage of more light.
<i>Shade</i>	A parameter to penalize the light available because of slope angle. Vertical walls are shaded in comparison to horizontal planes. Bounded between 0 and 1, Shade can be interpreted as the proportion of light available. A value of 1 means no shading, a value of 0 means no light reaches the shaded area.
<i>$D_{Shallow}$</i>	
V_{max}	The maximum similarity of a reef patch to the idealized shallow reef assemblage. Bounded by 0 and 1. Factors such as the size of the reef patch, and spatial heterogeneity of taxa will affect the maximum similarity a reef patch can achieve, that is, a small 1-m ² quadrat is unlikely to contain all shallow coral species.
K	The light value where $D_{Shallow} = V_{max}/2$. This can be interpreted as the light level at which shallow reef communities become light limited, on a percentage scale.
<i>$D_{Mesophotic}$</i>	
a	The scale parameter of a Weibull distribution. a describes the spread of the data, or ‘the peakyness’. Larger numbers create a flatter, wider, curve. Varying a will simultaneously change the width of the preferred light environment of mesophotic taxa, and the maximum similarity a reef patch is expected to achieve in comparison to the idealized mesophotic assemblage.
b	The shape parameter of a Weibull distribution. A value of 3 approximates a normal distribution. Values larger than 3 introduce a left-skew to the curve. This means mesophotic taxa can be light-limited, while keeping mesophotic communities in low-light environments. Varying b will therefore shift the preferred light environment of mesophotic communities.

mesophotic zone. For the proportion of light available after bathymetric shading we explore the range from 1 to .25 [no shading, to shading from a vertical wall (Lesser et al., 2018)]. For K_{dPAR} we investigate values between .045 and .3. These are the smallest light attenuation coefficients reviewed by Kahng et al. (2010) recorded off the Marshall

Islands, and the mean K_{dPAR} reported from a turbid reef by Chow, Chan, Jain, and Huang (2019). Little data currently exist to inform us of the variability in parameters of the community level light relationships for shallow and mesophotic reefs (V_{max} , K , a , b). We, therefore, use the parameter estimates reported for $PAR \sim D$ in June from Tamir

et al. (2019) $\pm 10\%$ of the parameter estimate. When a parameter value is changed, all others are held constant using parameter values from Tamir et al. (2019) as a reference only: $V_{\max} = .393$, $K = 13.5$, $a = 1.54$, $b = 8.92$ and $K_{dPAR} = .05$, $Shade = .250$ to three significant figures. The shading value represents the difference in light levels on a vertical wall in contrast to a horizontal plane, estimated by Lesser et al. (2018). The sensitivity of the model to these values is shown in Figure 4. The results of these sensitivity analyses are not site specific.

3 | RESULTS

Our model succeeds in returning key ecological features, such as a shallow to upper mesophotic and upper to lower mesophotic boundary (Figure 2). We can now predict the depths of these features at different sites (Figure 3), and find support for the heuristics used in mesophotic ecology. We can define these ecological features in a single unified, quantitative, framework. To achieve this, we characterized coral photo-physiology and the underwater light field with a series of equations. Combining these equations gives us a model of community transitions down a general coral reef gradient. Our model is comprised of two curves that represent coral communities at the two extremes of light variability for a given depth (Figure 2). We introduced this variability through bathymetry, varying slope angle from horizontal to vertical. A full explanation of the model parameters, and the values used, can be found in the methods and in Table 1.

The points on the two curves where $D = 0$ represent the shallow to upper mesophotic, and the upper to lower mesophotic boundaries.

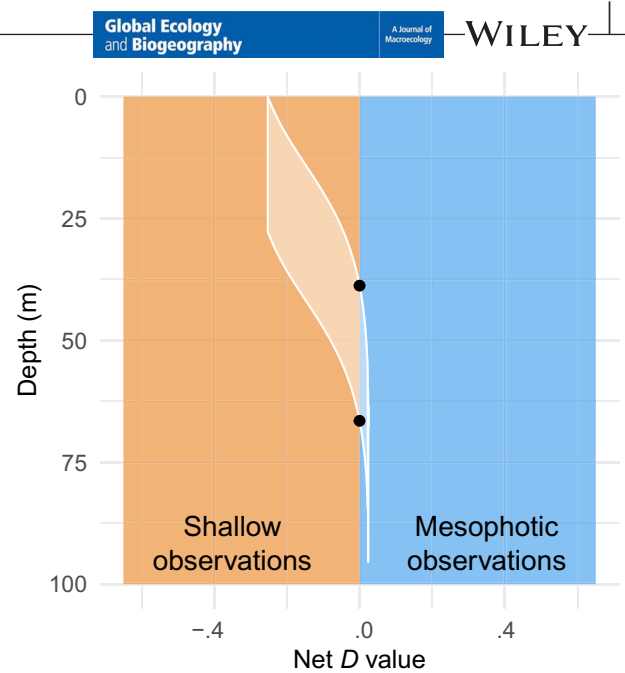


FIGURE 2 Predicted community identity along a theoretical depth gradient on a coral reef. The model output is shown as a pale ribbon. The range covers the predicted depths for particular community values following the shaded and non-shaded light-depth relationships. Positive net D values (orange) indicate a mesophotic community. Negative values (blue) indicate shallow communities. Black points show the depth boundaries of the upper mesophotic zone ($D = 0$). We provide an interactive version of Figure 2 in the Supporting Information. The predicted depths and community values will change as you change parameter values by moving sliders. This static version is parameterized for the Red Sea according to Tamir et al. (2019)

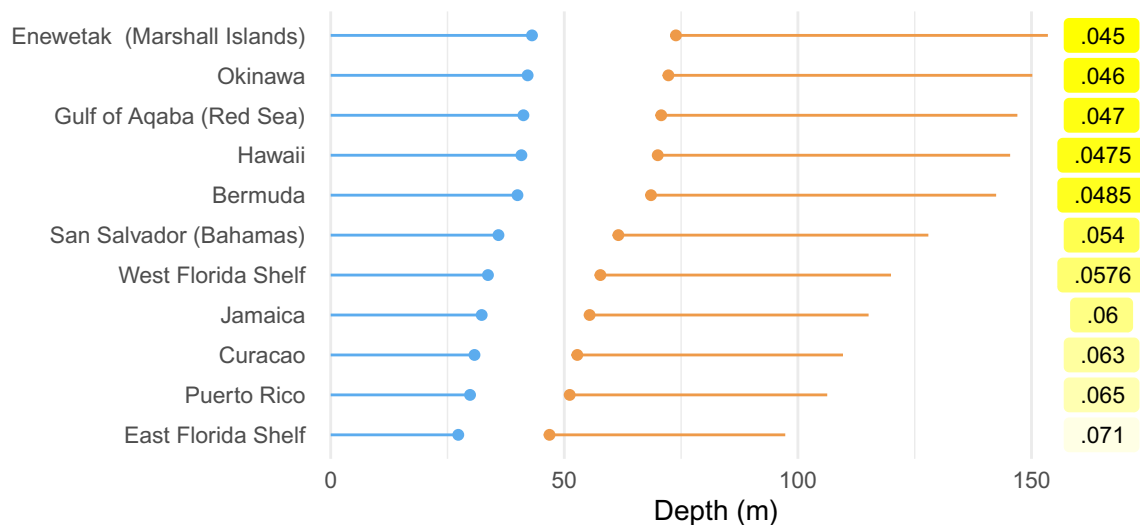


FIGURE 3 Predicted community boundaries from selected reefs around the world. K_{dPAR} values (light attenuation coefficients) and photosynthetic coral depth records were reported by Kahng et al. (2010). We use these values to predict the shallow-upper, and upper-lower, mesophotic boundaries for 11 locations. The blue line represents the depths of shallow reefs, the orange line represents the lower mesophotic. The maximum depth shown for lower mesophotic communities is the depth of 0.1% surface photosynthetically active radiation (PAR). The gap between blue and orange points for a location is the area of community overlap, the upper mesophotic zone. K_{dPAR} values for each site are shown to the right of the figure, with more yellow labels indicating greater light penetration

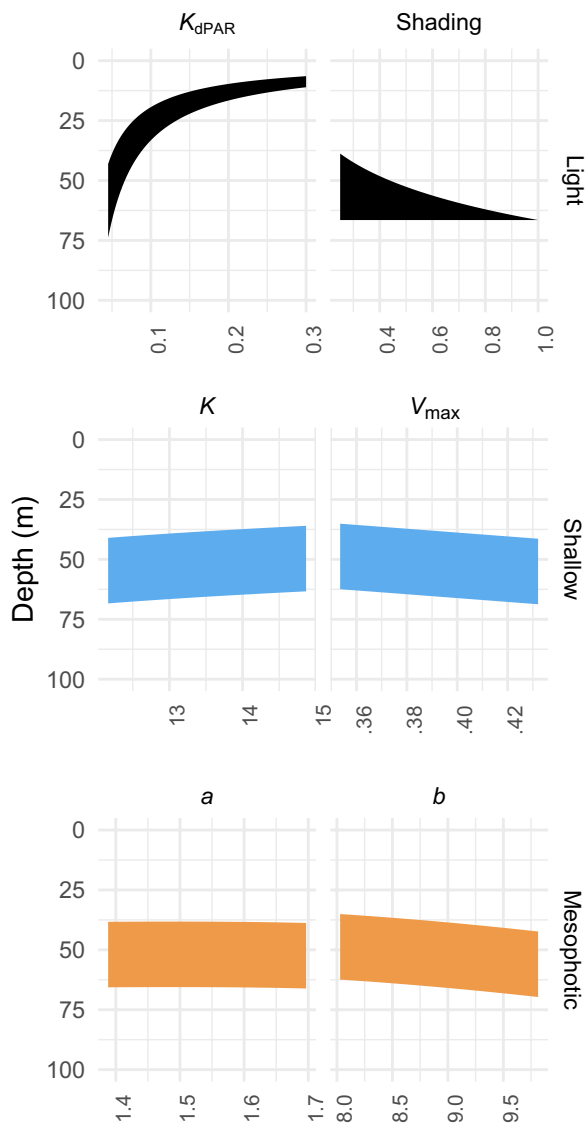


FIGURE 4 Sensitivity analyses. Each panel shows the variation in the estimated depths of the upper mesophotic zone, introduced by changing model parameters in each of the three functions (black = light function, orange = mesophotic function, blue = shallow function). Each panel is labelled by the parameter that is changed. The model parameters are defined in the Materials and methods section, but in brief: K_{dPAR} is light attenuation, Shading is the reduction of light by slope angle, V_{max} is the ceiling of the shallow community-light relationship, K is the point of light limitation of shallow taxa, a is a scalar term and b is the shape term in the mesophotic community - light relationship

This is as when $D = .0$, a reef patch is equally similar to a mesophotic or shallow community. Therefore, $D = .0$ in areas of community overlap. For the visualization of the model in Figure 2 we use parameter estimates from Tamir et al. (2019) for the site Katza (Gulf of Eilat/Aqaba, Red Sea) in June. Our estimate of the shallow to upper mesophotic boundary is 38.8 m. We estimate that the upper to lower mesophotic boundary occurs at 66.5 m. This agrees with broad patterns in dominant coral taxa identified by Tamir et al. (2019), who locate the upper mesophotic between depths of 40 and 70 m, verifying our

models performance. Larger, more varied, D values are returned for shallow reef patches than mesophotic patches, in keeping with existing ecological data (Laverick et al., 2017; Tamir et al., 2019).

In addition to the fixed representation of our model (Figure 2), an interactive web app can be accessed at https://laverick.shinyapps.io/a_light-driven_mesophotic_model/. We provide the R script (version: 1.2.1335) in Supporting Information Code S1 to safeguard against stability issues. By opening the app, the reader is able to vary parameter values by moving sliders, and see how this changes community transitions with depth. Figure 1 shows the distributions contributing to the model as community-level light relationships, and the underwater light field.

When parameterizing our model for the light conditions reported by Kahng et al. (2010; Figure 3) locations with higher water clarity are predicted to have deeper boundaries between reef zones. The estimated depths have been tabulated in Supporting Information Table S1. For these disparate reefs, our model predicts a mean depth for the shallow to upper mesophotic boundary of 36.1 m ($SD = 5.6$). The mean depth predicted for the upper to lower mesophotic boundary is 61.9 m ($SD = 9.6$). We arbitrarily end the lower mesophotic zone at 0.1% surface photosynthetically active radiation (PAR) in the figure. These results verify our model's performance, as they closely match the heuristics used for the limits to the upper mesophotic zone [a 30–40 m upper limit (Puglise et al., 2009), and a 60 m lower limit (Lesser et al., 2019)].

Our sensitivity analysis revealed that changes in the underwater light field may have a stronger influence on community structure than community level physiology. Changing the parameters controlling the preference of shallow and mesophotic taxa for different light levels can be thought of as changing their physiology (Table 1). Varying these parameters introduced only minor shifts in reef boundaries, and no change in the depth range of the upper mesophotic zone (Figure 4). Meanwhile, light parameters (i.e. light attenuation as K_{dPAR} and shading) can be changed to predict community transitions at sites with differing underwater light fields. These parameters produced the largest changes in community boundaries in our model. Changing K_{dPAR} from .3 [a turbid near shore reef (Chow et al., 2019)] to .045 [the clearest waters reviewed by Kahng et al. (2010)] caused the upper to lower mesophotic boundary to shift by 62 m vertically. For the shallow to upper mesophotic boundary the shift was 35.5 m. This relationship is asymptotic, indicating higher sensitivities to change in clearer waters. Reducing the maximum degree of shading (increasing the proportion of light available), related to the maximum slope angle in our model, increased the vertical distance between the shallow to upper/upper to lower mesophotic boundaries. It would be possible to change the minimum shading value in the same way, to move the upper to lower mesophotic boundary shallower when brighter, horizontal, planes are not present on a reef.

4 | DISCUSSION

Our model unifies the broad community patterns from coral reef depth gradients into a mathematical framework. By specifying

community-level light relationships, and combining these with an understanding of the underwater light field (Lesser et al., 2018), we are able to return the key features in community structure (Figure 2). Using only light, ecological features of interest such as the shallow-mesophotic boundary can now be objectively defined within a repeatable methodology. We have been able to attach a quantitative definition ($D = .0$) to the limits of mesophotic communities, and have further defined the upper mesophotic zone as the depths where $D = .0$ under variable light levels. This will help us make fair comparisons among geographically distant coral reefs, and aid us in identifying key processes that affect mesophotic communities globally. From here, we are able to predict how site-specific light environments may alter the vertical distributions of coral communities from the shallows to the lower mesophotic world-wide (Figure 3).

Not only does our model return expected ecological features, but it also accurately predicts their depths of occurrence when tested against heuristics. Multiple studies have considered the vertical zonation of coral reefs, identifying different depths for community boundaries (Baldwin, Tornabene, & Robertson, 2018; Fricke & Knauer, 1986; Kahng et al., 2019; Kinzie, 1973; Laverick et al., 2017; Lesser et al., 2019; Rocha et al., 2018; Semmler, Hoot, & Reaka, 2016). When the term mesophotic was adopted at a 2008 workshop (Puglise et al., 2009) – although the word had been published earlier (Ginsburg, 2008) – a working definition of the shallow to mesophotic boundary emerged (30–40 m). Using our model to predict for coral reefs with varied light environments (Figure 3) returned depth estimates for this boundary ranging by 16 m (Supporting Information Table S1). Despite this variability, the mean predicted depth for the boundary was 36.1 m ($SD = 5.6$). This is remarkably similar to the heuristic currently used in the field, given that our model is based on light alone and has no a priori information on the current mesophotic definition. Similarly, a 60-m rule has been used as the depth limit between the upper and lower mesophotic zones (Kahng, Copus, & Wagner, 2014; Lesser & Slaterry, 2018; Lesser et al., 2019). Once again, our model successfully captures this second rule of thumb using light values, predicting a mean boundary depth of 61.9 m ($SD = 9.6$).

Beyond vindicating the depth boundaries used as rules of thumb in mesophotic coral ecology, our model forces us to consider whether we should expand where we expect to find mesophotic reefs. Unusual observations exist in the literature that our model should also be able to accommodate. Muir and Wallace (2015) reported a 'deep-water' coral assemblage from a shallow lagoon in Micronesia. They stopped short of calling this a mesophotic reef as the assemblage was located between 10 and 20 m deep. However, they did note a high level of dissolved tannins had lowered light levels. In the central Indo-West Pacific, Turak and DeVantier (2019) found communities of mesophotic 'specialist' corals on reef slopes shallower than 10 m. Renema (2019) discussed the influence of light on light-dependent large benthic foraminifera, suggesting changes in water transparency with terrestrial runoff and seasonal variations were key drivers of community structure (Renema, 2018, 2019). Like corals, these foraminifera are unable to move vertically and are restricted to areas where sufficient light reaches the seafloor.

Similarly, Chow et al. (2019) studied the effect of light on the urbanized, sediment-stressed coral communities of Singapore, reporting plating species typical of the mesophotic zone such as *Pachyseris speciosa* and *Montipora* sp. These species were found in the top 10 m of Chow et al.'s two study sites, with mean K_{dPAR} values of .3 and .24. Inserting these values in our model returns predictions of a shallow to upper mesophotic boundary depth of 6.55 and 8.25 m, respectively. The upper to lower mesophotic boundaries were predicted at 11.23 and 14.15 m.

Our model shows we can expect to find mesophotic communities in relatively shallow waters when light attenuation is high. We should, therefore, embrace shallow-water turbid reefs as mesophotic coral ecosystems. This is not to say there will not be deviations between the predictions of our simplistic model and the observed communities on shallow-water turbid reefs. Additional variables can affect community structure beyond light quantity for example, sedimentation, nutrients and hydrodynamic conditions (Bridge et al., 2012; Colin & Lindfield, 2019; Erftemeijer, Riegl, Hoeksema, & Todd, 2012; Fabricius, 2005; Fabricius, De'ath, McCook, Turak, & Williams, 2005; Magris & Ban, 2019; Rowley et al., 2019; Sherman et al., 2016). A difference has been detected between 'blue-water' and 'brown water' mesophotic reefs, which is relevant to this discussion on shallow-water turbid reefs (Renema, 2019). However, the nuance of whether shallow turbid reefs fall into either the new blue or brown water categories can come after acknowledging they share characteristics with the low-light communities more generally found on mesophotic reefs.

Having established realistic behaviour, our model can open exciting research opportunities by providing candidate drivers of change across coral depth gradients. Our sensitivity analysis (Figure 4) indicates that the underwater light field has a larger influence over the vertical zonation of coral reefs than the intrinsic qualities of coral photo-physiology. However, we cannot be certain that this finding is not an artefact of our methodology. As community-level light relationships down the shallow to mesophotic gradient have only been characterized once (Tamir et al., 2019), we don't know the scale of global variability in these parameters. It is possible that the light preferences of corals in the Red Sea are not representative of those in the Indo-Pacific, for example. As our model has succeeded in capturing the global patterns in community recognized by the field using the Red Sea light relationships, it is our opinion that these values will be largely similar. We require studies from other locations, preferably different ocean basins, to help us understand how variation in scleractinian physiology could affect community transitions globally. When these studies are conducted, it is important to use the distribution of abundances instead of depth ranges to avoid extending the physiological niche of communities with depth (Roberts, Bridge, et al., 2019). We stress that this does not impact our model's ability to predict community boundaries, as discussed above. Knowing the range of values that mesophotic and shallow communities can exhibit, will open up exciting modelling opportunities regarding the evolution and competition of different coral groups under environmental change (Laverick et al., 2017).

We kept our model deliberately simple, as a demonstration that light data can unite patterns in mesophotic ecology. For over a decade the field has used 30–40 m as a strawman explanation of where MCEs begin. We now provide a new tool based on a contemporary understanding of shallow and mesophotic coral community structure and their relationships with light. It will be part of the iterative nature of science for this model to eventually be superseded by a more nuanced method for identifying MCEs, as we hope this tool allows the field to move on from fixed depth limits. There are clearly other processes that would provide valuable extensions, once characterized by future studies (Turner et al., 2019). Substrate availability, maximum depth of a site, temperatures, and other uncaptured processes could all contribute to deviations from model predictions in the field.

Despite successfully returning the global heuristics used in mesophotic ecology, there are differences between our predictions and empirical data. We currently predict a lower limit for the lower mesophotic zone deeper than 100 m for all but one location. For some this is accurate, such as the Gulf of Aqaba and Hawai'i (Baker et al., 2016). For other locations, such as Bermuda, we are likely predicting too deep. It is important to remember that, unlike the upper and lower mesophotic boundaries, our model's definition of the maximum depth for the lower mesophotic zone is arbitrarily set at 0.1% of surface irradiance. Research in the lower mesophotic is rarer than even in the upper mesophotic (Lesser et al., 2019). Collecting data on the minimum irradiance levels required to support photosynthesis in corals from the lower mesophotic zone would be valuable for our model. Additionally, our model is predicting maximum depths based on light alone. Other factors, for example sedimentation (as opposed to turbidity/optical water clarity), that may influence the occurrence of mesophotic communities (Appeldoorn et al., 2015; Sherman et al., 2016) are not yet in the model framework, and could reduce the depths reefs extend to. A missing factor important for Bermuda is the absence of seasonal changes in irradiance, which are greater at higher latitudes.

We have identified two major processes missing from our theoretical framework. As well as environmental seasonality, heterotrophy (Houlbrèque & Ferrier-Pagès, 2009; Lesser et al., 2010, 2018) could introduce error into model predictions. Some corals have been seen to increase their reliance on heterotrophy under low irradiance at depth (Lesser et al., 2010; Muscatine, Falkowski, Dubinsky, Cook, & McCloskey, 1989). Similarly, light levels are increasingly seasonal at higher latitudes. Corals may also vary their reliance on heterotrophy in response to this variation in irradiance throughout the year (Nir, Gruber, Shemesh, Glasser, & Tchernov, 2014). Heterotrophic subsidy may permit corals to exist on reef patches (Anthony & Fabricius, 2000), or to survive disturbance events (Grottoli et al., 2014), which a model based on light alone may fail to predict. Seasonal changes in irradiance could lead to shifts in the depths at which transitions between autotrophy and heterotrophy might occur (Brandtneris, Brandt, Glynn, Gyory, & Smith, 2016), while other taxa may be somewhat unaffected by seasonal variability in light levels (Alamaru, Loya, Brokovich, Yam, & Shemesh, 2009).

Rapid changes in K_{dPAR} are expected to change the energy flux on coral reefs, particularly for deep populations at the limits of photosynthetic performance. These changes in the underwater light field may occur seasonally, such as algal blooms, seasonal runoff, and flash flood events. The magnitude and duration of such events may constrain the depth distributions of coral communities, when annual mean values may otherwise seem favourable for coral communities (Tamir et al., 2019).

Incorporating heterotrophy and seasonality into our model would allow us to consider the annual energy budget of coral taxa. But to do this we require studies that capture temporal variability down coral reef depth gradients. Understandably, as accessing MCEs is logistically demanding, our knowledge of these ecosystems comes from a collection of snapshot studies. Observing temporal variability, and linking this to changes in local abiotic factors (e.g. light, temperature, and nutrients), will represent an important contribution to the field. Even short time series have the potential to reveal new processes on MCEs by capturing seasonal change. There is evidence that some mesophotic corals experience seasonal feast and famine, unlike their shallow reef counterparts (Brandtneris et al., 2016). Energy budgets must, therefore, balance across the course of a year, and could explain observations of seasonal coral bleaching on MCEs (Nir et al., 2014). Phenological investigations of MCEs are, therefore, necessary to identify which periods of the year for different sites are key to the persistence of MCEs. This will allow us to target research effort to key points in the year that lock in long-term trends, and will allow us to design effective management strategies.

A third missing factor worthy of mention, but less connected to the discussion of light so far, is hydrodynamics. Violent waters may keep some low-light specialist taxa at mesophotic depths (e.g. *Acropora pichoni* and *Acropora tenella*). These species may only be found in shallow low-light environments when sheltered, such as lagoons in Kimbe Bay (Micronesia; Rowley et al., 2019), and the Great Barrier Reef (Bridge et al., 2012). Similarly cyclones may impact on MCEs to varying degrees. Mesophotic coral communities in areas exposed to tropical storms such as the Great Barrier Reef (Bongaerts, Muir, Englebert, Bridge, & Hoegh-Guldberg, 2013) and Okinawa (White et al., 2013) differ from MCEs where storms are less frequent and weaker [e.g. Papua New Guinea: Smith, Holstein, & Ennis, 2019] despite minimal differences in water quality and, therefore, light quality.

Theoretical work has been largely neglected in mesophotic ecology. We have made a contribution to rectifying this, as theoretical work is needed to complement and direct empirical studies. Models such as ours are a valuable tool for generating questions and formulating hypotheses. Though a number of processes are not included in our framework, this model represents a much needed successor to the strawman argument of the 30-m depth boundary for mesophotic reefs. We have shown that we can get remarkably far in explaining ecological pattern using light as a single abiotic factor, but we require more empirical studies before we can include additional processes. Creating this model was a crucial step in the iterative process that allows us to better understand the structure of coral communities with depth.

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CONFLICT OF INTEREST

The authors declare that they have no conflicts of interest.

DATA AVAILABILITY STATEMENT

The authors declare there are no data to archive. However, the R code behind this model is provided in the Supporting Information, and an interactive version of the model framework can be found at https://laverick.shinyapps.io/a_light-driven_mesophotic_model/.

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BIOSKETCH

The authors have a collective interest in the ecology of mesophotic coral ecosystems. As a research team, they focus on modelling the processes that explain the shallow to mesophotic reef transition.

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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