

# Responses to Reviewers

## *Exploring coral reef responses to millennial scale climatic forcings: insights from a 1-D numerical tool pyReef-Core*

### Editor's comments to the authors

**Comment 1:** *Our manuscript preparation guidelines require that all papers must include a model name and version number (or some other unique identifier) in their title. In the submitted version, the version number is missing. Could you please include the version number of the model actually described here, the more since the Zenodo repository already includes two versions.*

**Response:** Following Editor's comment and GMD guidelines, we have added the version number attached to the model described in our manuscript in the title. The version is v.1.0 and relates to the Zenodo repository ([doi:10.5281/zenodo.1080115](https://doi.org/10.5281/zenodo.1080115)) included in the code code availability section of the manuscript.

**Comment 2:** *I have furthermore come across one minor thing, that I would like to ask you to correct as well at this stage. Again, in our manuscript preparation guidelines, under "English guidelines and house standards" - "Abbreviations", you will see that the standard abbreviation used in our journal for "years" depends on the meaning (time/date or duration). Throughout the manuscript, I have found "ky" for both duration and dates:*

- *for durations, these should be corrected to "kyr"*
- *for dates (e.g., when sea-level stand high, etc.), they should read "ka".*

**Response:** Following Editor's comment, we have corrected the abbreviations for time/date and duration throughout the manuscript.

**Comment 3:** *Finally, and most important, on p. 9, lines 9-10, I read that "The equation requires an initial population for each assemblage  $N_i^0$ , which is assumed zero for all populations as the basement substrate is unpopulated at the beginning of reef initiation simulations." Although I agree that this translates the fact that the basement substrate is unpopulated initially, it has an unrealistic consequence: it actually means that all the  $dN_i/dt$ 's from equation (1) are zero initially, so that no populations can develop. Even a single assemblage  $i$  that has a zero initial population will be unable to develop according to equation 1. Since pyReef-Core obviously yields non-zero population evolutions as one can see in the results, there must be a special treatment to overcome this barrier.*

*I know that the "all populations are zero" state represents an unstable equilibrium, so I am wondering whether the model relies on some random procedure to start (initial negligibly small populations are sufficient to trigger population growth) or some other solution. The paper needs to provide an accurate description of the actually used procedures adopted in the model. With respect to the starting procedure, it is currently incomplete.*

**Response:** Any population growth from an initial state where no assemblages is present is triggered by the environmental conditions and is set using a 'turn-on' criterion presented in section 4.7. Following Editor's comment, we have added at the end of section 4.2 further explanations regarding the initialisation of coral assemblage population to make it clearer to the readers. In addition, we are now explicitly referring to the 'turn-on' criterion section (section 4.7) in the manuscript where the reasoning behind the procedure is explained in more details.

### First reviewer's comments to the authors

**General Comment:** *This manuscript is well organized and clearly presented. I thought the introductory materials on carbonate systems and environmental controls of reef development (accommodation, hydrodynamic energy, and sediment input) were very concise and adequately thorough. I believe it is essentially ready for publication. My suggestions are for making it more practical and relevant for present and near future coral-reef responses to environmental changes. I also have a few minor editorial suggestions.*

*The models in this manuscript are for a special circumstance where "populations number. . . is a proxy for carbonate*

production with larger assemblage population corresponding to faster rate of vertical accretion" (Caption for Figure 6 and elsewhere in the text). The first sentence of "3 Environmental controls on reef development" (bottom of page 3) states "Coral framework production is strongly linked to biological activity". Actually, there is a general "lack of congruence" between a reef's biological performance (rates of CaCO<sub>3</sub> accretion, provision of topographic complexity for shelter and substrata for fish and invertebrates, abundance and diversity of corals) and geological performance (Kleyvas et al. 2001). This is because of nearly ubiquitous bioerosion and export of carbonate materials. The authors do acknowledge that their". . . model does not consider the destructional processes that occur on the reef due to physical, chemical and biological erosion but does account for erosional process during phases of subaerial exposure. . ." It is generally true, especially in the Pleistocene and Holocene, that population abundance or living surface cover of corals is associated with overall rate of carbonate production, but because of varying rates of erosion and other destructive forces, rate of carbonate production is only sometimes associated with net rate of vertical growth. I feel the paper does not need to be changed, but I feel the model is limited to particular circumstances.

In the Introduction (line 14), the pyReef-Core model incorporates "coral community dynamics into reef growth modeling at reef-scale resolution". A recent dynamic of reef growth is the combination of disturbances and stressors as the frequencies of disturbances and the duration of stressors both increase. When they both increase, they consistently do not allow the processes of recovery to materialize. Although there are still a number of local coral-reef communities that display remarkably rapid recovery, numerous surveys have indicated that average living coral cover is decreasing circumtropically. This is partly because disturbance is nearly always faster than recovery, damaged or stressed corals generally produce fewer larvae, reef community recovery times become longer when fast-growing branching corals are more vulnerable to stresses and disturbances and are replaced by more tolerant slow-growing corals, combinations of local and global disturbances and stresses result in positive feedbacks that accelerate reef degradation, and degraded reefs decrease the proportion of habitat acceptable to recruiting larvae. In the Holocene, many reefs had time to largely recover before the next disturbance; otherwise the reefs at the sites would not have developed as well as they had. As more reefs are disturbed and become less favorable for survival of recruits, connectivity is reduced by fewer larvae produced, more areas become unattractive to larvae for settlement, distances between fewer favorable sites become longer, and larval pelagic duration sometimes becomes shorter with increasing temperature. As disturbances become more frequent and do not allow sufficient time for recovery, events become trends and feedback creates ratchets, perpetually inhibiting recovery. Without taking the frequency of disturbances and length of periods of stress, including their overlap, in relation to potential periods of successful recruitment, it does not serve an applied use for the present and near future. However, this is going beyond the scope of this manuscript. I realize that the model in this paper is to reproduce the details of stratigraphic sequences in the past, and it serves this purpose well, so the manuscript should be published.

**Response:** We would like to thank the reviewer for raising these 2 comments one on carbonate framework production vs biological performance or growth and the other about disturbance. We acknowledge and value the review comments about the general "lack of congruence" between a reef's biological performance and geological performance, but agree with the review that it is out of scope of the current MS. However in future iterations of the model, we plan to implement a modified version of the coral production framework so as to better investigate the case where vertical accretion rate do not reflect the growth rate of corals.

In regards to the second comment, we agree that accounting for the frequency of disturbances and length of periods of stress, is critical if one wants to investigate present and near future reef evolution processes. Adding this in our modelling framework might be possible by incorporating some sort of recruitments function as suggested by the referee.

**Comment 1:** Bottom line, page 4 – "acidity" is used to name an environmental factor in oceans. Although the ocean pH may have gotten as low as 7.4 – 7.6 during the Cretaceous and early Paleogene, I don't think the oceans have ever been actually acidic. The term "acidification" is being used to refer to a lowering of pH towards acidity, but it will never actually reach acidity.

**Response:** Following reviewer's comment, we have modified the text to prevent any confusion and we are now referring to pH instead of acidity throughout the manuscript.

**Comment 2:** Second line, page 6 – Change "have a negatively effect" to "have a negative effect".

**Response:** we have changed the corresponding line as suggested by the reviewer.

**Comment 3:** *Figure 2 caption – "GLVE equations" is redundant because the E in the initialization is for "equations".*

**Response:** We have delete "equations" to avoid redundancy.

**Comment 4:** *First line of text below Table 2 on page 15 – change "data implies" to "data imply" or "data suggest".*

**Response:** We have changed the text to "data suggest" as proposed by the reviewer.

**Comment 5:** *Top line, page 22 – change "data is scarce" to "data are scarce".*

**Response:** We have changed the text to "data are scarce".

**Comment 6:** *Figures 6 and 7 — I have a hard time distinguishing the shades of blue representing different depths. I suspect many readers will have the same problem. Please make the colors more distinct or use different colors for the different depths.*

**Response:** Following reviewer's comment, we have modified the colours to make them easier to read. To keep consistent over the manuscript we have modified the colours in figures 2, 5, 6, 7 and 8.

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## Second reviewer's comments to the authors

**General Comment:** *The paper is well written and easy to understand. My only criticism is that the paper contains perhaps too much detail on the controls on carbonate growth which have been well established in the literature for decades (sec 3.1 to 3.3). However, these sections then seem to come to the conclusion we don't know that much, but they are going to be in the model anyway. Perhaps shorter, more succinct summaries with a clear reason for inclusion in the model would clarify this? Another suggestion would be to move the discussion part of these intro sections to the discussion part of the manuscript? I'll leave this to the authors to decide here.*

**Response:** We would like to thank Jon Hill for his insightful comments on the paper, as these comments led us to an improvement of the work. Our revisions reflect all reviewer' suggestions and comments. Detailed responses to reviewers are given below. An update version of the manuscript is available as a pdf as a supplement.

Following reviewer's comment we have shorten by half (from 3 to 1.5 pages) the literature part on environmental controls (subsections 3.1 to 3.3). We believe these 3 sections are more useful before the part describing pyReef-Core (section 4) than in the discussion as they put in perspective the different parameters that the model intents to simulate and also highlight the main forcing conditions that drive coral assemblages evolution in our 1D framework. We have modified the last section (3.3) so that we acknowledge more the work done in respect to the control of sediment input on coral communities evolution. The fact that some of the effects of these environmental conditions are still unknown is the main reason why we should aim to try to simulate them in order to gain some insights from numerical models and potentially improve our general understanding of the complex interactions between corals and their environments.

**Comment 1:** *Pg 1, In 1: Unclear opening sentence to abstract. Do you mean laterally perpendicular to shore, alongshore or both (in which case, perhaps "spatially" is a better term)? The lateral change and progradation/accretion/retrogression is responsible for the change in core depth: i.e. they are the same thing are they not?*

**Response:** Following reviewer's comment, we have modified the first sentence and used the term spatially as suggested by the reviewer.

**Comment 2:** *Pg 1, In 5: poorly constrained on centennial to geological timescales, no?*

**Response:** We have changed millennial to geological timescales.

**Comment 3:** *Pg 1, In 6: it doesn't do the inverse though?*

**Response:** Following reviewer's comment, we have remove the term inverse in the sentence as it was misleading.

**Comment 4:** *Pg 2, In 33: Add Hill et al 2012 as a heuristic tool Hill, Jon, Rachel Wood, Andrew Curtis, and Daniel M. Tetzlaff. 2012. "Preservation of Forcing Signals in Shallow Water Carbonate Sediments." Sedimentary*

*Geology 275-276 (1): 79–92.*

**Response:** We have added the reference to Hill et al., 2012.

**Comment 5:** *Pg 3, ln 14: typo You forgot the*

**Response:** We have corrected the typo.

**Comment 6:** *Pg 5, ln 6. Does this need a new paragraph?*

**Response:** We have merged the 2 paragraphs together.

**Comment 7:** *Pg 6, ln 10. So how can you encapsulate this in an algorithm if there's no data? Perhaps some of this needs moving into the discussion? See above general comment.*

**Response:** This point has been addressed now, as explained in our response to the general comment.

**Comment 8:** *Pg 6, ln 10. Remove sentence: "This objective...". I don't think it adds anything.*

**Response:** Following reviewer's suggestion, we have removed the sentence.

**Comment 9:** *Pg 7, ln 9-10: As general comment on moving to discussion.*

**Response:** This point has been addressed now, as explained in our response to the general comment.

**Comment 10:** *Pg 11, sec 4.7. 50% is rather arbitrary! Can you give any insight on how the resultant core varies if this is altered to say 25% or 75%? How did you arrive at 50%!?*

**Response:** First we would like to state that this parameter is user-defined in pyReef-Core and can be changed in the XML file by adjusting the **facOpt** parameter ([http link](#)). Following reviewer's comment, we have modified the section 4.7 and added a new sentence at the end to reflect the fact that this parameter can be set by the user. The change in 'turn-on' criteria value will result in different evolution and therefore can change significantly the resulting core. This is especially true for simulations in which assemblage population number fall to 0 due for example to reef drowning or aerial exposure. Difference between a value of 25% compare to 75% will enable assemblages to start growing even though their optimal environmental conditions are not reached. A high value like 75% could result in simulations in which particular coral assemblages will never be able to grow due to more restrictive environmental conditions.

**Comment 11:** *Pg 22, ln 30+: I'm not sure this is relevant here. You don't tackle the inverse problem in this paper and whilst I don't disagree with this at all (as you know!), the linkage to inverse in the abstract and this is tenuous. Perhaps leave removing the inverse and removing the reference to pyReef-Bayes is sufficient here; i.e. you still get to stake out the fact that the inverse problem is what we are trying to solve (as a community), but it's the implication you are doing that in this paper which I don't think sits well.*

**Response:** Following reviewer's suggestions, we have removed *inverse* in the abstract as well as the reference to pyReef-Bayes from this section, the inverse problem and the MCMC approach is indeed not relevant to the work described in this paper and will be published later.

# Exploring coral reef responses to millennial scale climatic forcings: insights from a 1-D numerical tool ~~pyReef-Core~~pyReef-Core v1.0

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## Abstract.

Assemblages of corals characterise specific reef biozones and the environmental conditions that change ~~laterally~~spatially across a reef and with depth. Drill cores through fossil reefs record the time- and depth-distribution of assemblages, which captures a partial history of the vertical growth response of reefs to changing palaeoenvironmental conditions. The effects of environmental factors on reef growth are well understood on ecological time-scales but are poorly constrained at centennial to ~~millennial~~geological timescales. *pyReef-Core* is a stratigraphic forward model designed to solve the ~~inverse~~ problem of unobservable environmental processes controlling vertical reef development by simulating the physical, biological and sedimentological processes that determine vertical assemblage changes in drill cores. It models the stratigraphic development of coral reefs at centennial to millennial timescales under environmental forcing conditions including accommodation (relative sea level upward growth), oceanic variability (flow speed, nutrients, pH and temperature), sediment input and tectonics. It also simulates competitive coral assemblage interactions using the generalised Lotka-Volterra system of equations (GLVEs) and can be used to infer the influence of environmental conditions on the zonation and vertical accretion and stratigraphic succession of coral assemblages over decadal timescales and greater. The tool can quantitatively test carbonate platform development under the influence of ecological and environmental processes, and efficiently interpret vertical growth and karstification patterns observed in drill cores. We provide two realistic case studies illustrating the basic capabilities of the model and use it to ~~estimate~~reconstruct (1) the Holocene history (from 8,500 years to present) of coral community responses to environmental changes, and (2) the evolution of an idealised coral-reef core since the Last Interglacial (from 140,000 years to present) under the influence of sea-level change, subsidence and karstification. We find that the model reproduces the details of the formation of existing coral-reef stratigraphic sequences both in terms of assemblages succession, accretion rates and ~~deposited~~depositional thicknesses. It can be applied to estimate the impact of changing environmental conditions on growth rates and patterns under many different settings and initial conditions.

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## 1 Introduction

Ecologists and geologists tend to have different spatial and temporal perspectives of coral reefs. This is because the methods and observations which inform both fields differ. While ecologists can make direct oceanographic and biological observations of coral reef ecosystems on daily to decadal timescales, reef geologists must interpret assemblage patterns from fossil outcrops and drill cores to infer persistent biological or sedimentological processes on centennial to millennial timescales. This results in both fields addressing differently the question of how coral reefs respond to environmental conditions (Stocker et al., 2013). Furthermore, as Hughes (2000) argues, the most relevant spatial and temporal scales fall in the gap between both fields; modelling predictions of climate change are most relevant to society on regional to global scales over hundreds of years. Stratigraphic forward modelling (SFM) of carbonate systems offer a solution by simulating sedimentary processes and carbonate production through time (Burgess and Wright, 2003). In this paper, we present a deterministic, one-dimensional (1-D) numerical model, **pyReef-Core**, that simulates the vertical coral growth patterns observed in a drill core, as well as the physical and environmental processes that affect coral growth. The model is capable of integrating ecological processes like coral community interactions over centennial-to-millennial scales using predator-prey or *Generalised Lotka-Volterra Equations* (GLVEs). *pyReef-Core* is the first of its kind to incorporate coral community dynamics into reef growth modelling at reef-scale resolution. We first describe the main model constitutive laws and forcing parameters. Then we present two realistic case studies to illustrate the model's capability. First, we simulate a Holocene shallowing-up fossil reef sequence representing a 'catch-up' growth strategy observed in the Great Barrier Reef (Hopley et al., 2007; Dechnik et al., 2017) and [estimates-estimate](#) assemblage compositions and changes. The second [one-case study](#) simulates the long-term evolution (> 120,000 years) of an idealised reef sequence under the influence of sea-level change and subsidence, commonly observed on passive margins world wide (Montaggioni, 2005; Woodroffe and Webster, 2014; Gischler, 2015).

## 2 SFM of carbonate systems

SFM has become a powerful tool used to predict stratigraphic architecture of sedimentary systems (Warrlich et al., 2008). SFM involves simulating processes acting over geological timescales, and iteratively refining parameters to improve the match between observed and predicted morphologies and stratigraphies. Through this trial-and-error procedure, parameters such as sedimentation and carbonate production rates can be evaluated and quantified, where they ordinarily cannot be directly observed from the fossil record (Dalmasso et al., 2001; Warrlich et al., 2008; Salles et al., 2011; Seard et al., 2013; Huang et al., 2015). In that sense, SFM addresses the short-comings of qualitative investigation techniques applied to carbonate systems (e.g., Cabioch et al., 1999; Abbey et al., 2011; Dechnik et al., 2015). Several numerical models have been developed since the 1960s to investigate the evolution of carbonate systems, yet only recently have the complexity of biological interactions – specific to reefs – started to be addressed (Barrett and Webster, 2017; Clavera-Gispert et al., 2017).

Traditionally stratigraphic modelling of carbonate-siliciclastic systems has been applied to locate oil and gas reservoirs ([Kendall et al., 1991](#)). However, SFM has become a popular heuristic tool to better understand and quantify parameters regulating peritidal carbonates (Burgess and Prince, 2015), the development of coral reef environments (Bosscher and Southam, 1992; Clavera-Gispert

et al., 2017) as well as microbial (Parcell, 2003) and coral reef growth (Paulay and McEdward, 1990; Bosscher and Southam, 1992; Dalmasso et al., 2001). Early forward models were 1-D (Schwarzacher, 1966) or 2-D in formulation (Bosence and Waltham, 1990; Kendall et al., 1991), but improvements in computing led to the development of more complex, 3-D models (e.g., DIONISOS (Granjeon and Joseph, 1999; Searid et al., 2013) and FUZZIM (Nordlund, 1999)).

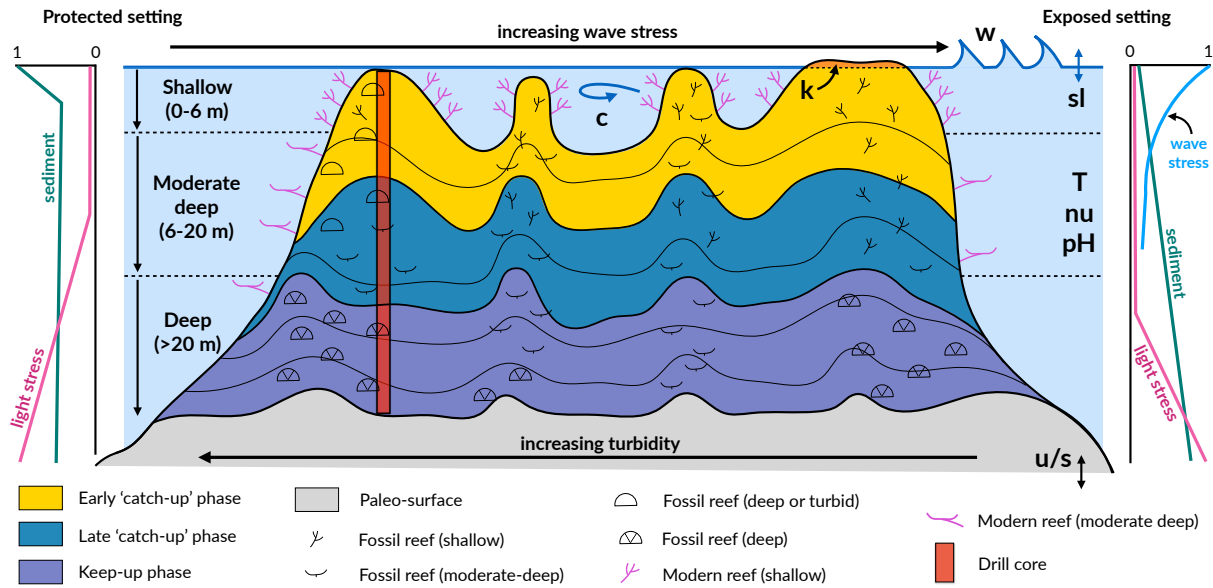
Most recently, three software packages have been developed that represent important antecedents to the modelling effort described in this paper: CARBONATE-3D (C3D) (Warrlich et al., 2008), ReefSAM (Barrett and Webster, 2017), and SIMSAFADIM-CLASTIC (Clavera-Gispert et al., 2017). These models are 3-D and able to simulate hydrodynamic processes, sediment transport and biological production, but with varying degrees of realism. ReefSAM and C3D are both reef-scale models, yet ReefSAM constitutes an improvement from C3D in prediction of more realistic reef growth morphologies (i.e. ~~lagoonal patch reefs~~ mostly sand fill lagoonal patch reefs and mostly sand infilled lagoons) that depends on environmental factors (Barrett and Webster, 2017). However, despite the added complexity, ReefSAM, like C3D, was found to have overly simplistic hydrodynamic and sediment transport models that were unable to simulate important, small-scale morphological features and feedbacks (Barrett and Webster, 2017).

The shortcomings of both ~~textseR~~ ReefSAM and C3D are notable in their inability to model bio-sedimentary facies in any complexity. Limited to basic sedimentary facies only, they also fail to simulate how changing environmental conditions influence the ecological requirements of different coral reef communities (Clavera-Gispert et al., 2017). SIMSAFADIM-CLASTIC offers the possibility to investigate carbonate production as a biological function of species interactions (based on the Lotka-Volterra equations) as well as environmental parameters (i.e., light, hydrodynamic energy and slope) (Clavera-Gispert et al., 2017). However, it has only been applied to model interactions between marine organisms and not between reef building corals. Furthermore, while the approach is promising, SIMSAFADIM-CLASTIC is not applicable at reef-scales due to its coarse > 100 m spatial resolution and with a minimum time interval exceeding the life-span of corals (500 years).

3-D SFM becomes necessary when accounting for the 3-D nature of sediment-driven and hydrodynamic processes like lateral reef accretion and fluid flow, establishing sediment budgets or investigating problems such as the influence of inherited topography (Warrlich et al., 2008). However, the development of complex 3-D models has not necessarily improved the quality of carbonate system modelling. In some cases lower-dimensional and reduced-complexity models are easier to test and constrain (Paola, 2000). Because 1-D forward modelling prioritises accommodation space as the fundamental control over vertical sequences, it is a starting point to understand and constrain other essential influences on reef growth before adding greater complexity. Rationalised this way, *pyReef-Core* serves as a basis for constraining the biological interactive aspect of carbonate production, and the effect of environmental influences. Once an understanding of the complex influence of environmental conditions on vertical coral accretion can be established, extending the model to 2-D and 3-D becomes a less challenging task.

### 3 Environmental controls on reef development

Coral framework production is ~~strongly linked~~ linked, through complicated processes, to biological activity, such that the evolution of reef systems are limited by the growth potential of carbonate producing organisms and their environmental requirements



**Figure 1.** Schematic figure of a hypothetical reef with transitions from deep to shallow reef assemblages occurring up-core, illustrating a catch-up reef growth response to environmental forcing including light, sea-level changes (sl), hydrodynamic energy (w wave conditions and c currents), tectonic (u uplift and s subsidence), oceanic conditions (T temperature, nu nutrients, pH acidityacidification), karstification (k) and sediment flux.

(Flügel, 2004). Environmental factors affecting growth have been classified by Veron (2011) as latitude-correlated factors, and those that are regional or local in character. Latitude-correlated factors include sea surface temperatures (SSTs), solar radiation and water chemistry (Kleypas et al., 1999). Regional and local environmental factors include wave climate, salinity, water clarity, nutrient influx, sedimentation regime and depth/composition of the initial substrate. These factors affect coral species to different extents, controlling the distribution of coral communities across a reef (Hallock, 2001). Over longer time scales, they also shape the rate of calcium-carbonate production, framework building by corals, and the accumulation of sedimentary deposits (Done, 2011).

Despite the significant, short-term impacts cyclonic storms and terrigenous sediment input can have on reef systems (Cubasch et al., 2013), episodic disturbances are smoothed out on geologic scales (10,000's years) where reef systems are characterised by remarkable persistence and resilience (Precht and Aronson, 2016). The persistent factors (e.g., sedimentation, wave climate and accommodation) are those that exert a stronger effect on the distribution of coral communities across a reef (Fig. 1). In the current study, we focus on these three main controls, however the model can simulate the impact of other ocean forcings (temperature, nutrients and aciditypH) on coral reef development.



### 3.1 Accommodation

~~Accommodation is the vertical and lateral space in the water column above the substrate within which corals can grow. The effect of accommodation on coral growth is the most well-understood constraint on the waxing and waning of reef development, and is governed by the relationship between the rate of vertical reef accretion, sea-level rise, subsidence and uplift (Woodroffe and Webster, 2014).~~

Accommodation affects coral growth in two ways (~~Braithwaite, 2016~~)([Davies et al., 1985](#); [Braithwaite, 2016](#)). Firstly, light attenuates with depth in the ocean, and as corals are photosynthetic organisms, carbonate production decreases exponentially with increasing water depth (~~Schlager, 2005~~)([Neumann and Macintyre, 1985](#); [Schlager, 2005](#)). Secondly, wave energy and water flow also decreases with depth, such that corals growing with reduced accommodation (i.e., in shallow depth) experience increased hydrodynamic energy (Montaggioni, 2005). The effect of light is assumed to dominate over the effect of water movement in limiting carbonate production (Dullo, 2005) (Fig. 1), however both effects play a role in determining coral composition and, in turn, rates of vertical accretion (Cabioch et al., 1999; Kayanne et al., 2002).

~~Generally, assemblages within 20 m depth have the highest accretion rates (10-20 m/ky) than those deeper (< 10 m/ky) (Montaggioni, 2005). For example in the Great Barrier Reef (GBR), Holocene reef growth largely occurred due to initially rapid sea-level rise (~10-6 ky), which created new accommodation and favourable conditions for reef 'turn-on' and the potential for vertical aggradation (Hopley et al., 2007; Leonard, 2017). Some reefs were able to keep pace with sea-level rise ('keep-up' reefs), while others caught up after sea-level stabilised ('catch-up' reefs), and others drowned ('give-up' reefs) (Davies et al., 1985; Neumann and Macintyre, 1985).~~

### 3.2 Hydrodynamic energy

~~At the organism level, currents,~~ [Currents](#), water flow and oscillatory motion induced by waves are critical in modulating physiological processes in coral and thus influencing coral growth rates (Falter et al., 2004; Lowe and Falter, 2015). High water flow increases rates of photosynthesis by symbiotic algae (Bruno and Edmunds, 1998), nutrient uptake by corals (Weitzman et al., 2013), particle capture (Houlbrèque and Ferrier-Pagès, 2009) and facilitates sediment removal from coral surfaces (Rogers, 1990), all of which contribute to enhanced primary production. At the extremes, too little flow can be lethal in corals by inducing anaerobiosis, whereas extreme wave events cause mechanical destruction (Done, 2011) and can lead to long-term changes in community diversity and structure (Madin and Connolly, 2006).

~~Waves exert a strong spatial control on hydrodynamics of reef systems (Lowe and Falter, 2015).~~ Wave energy is largely dissipated on shallow reefs from bottom friction and wave breaking, with the former effect dominating the latter on reefs with high surface rugosity of coral communities (~~Rogers et al., 2016~~)([Grossman and Fletcher, 2004](#); [Lowe and Falter, 2015](#); [Rogers et al., 2016](#)). Furthermore the geomorphology and high-rugosity of reefs cause wave refraction, such that wave energy is highest on the ocean-facing margin (Fig. 1 *exposed setting*) and lower in back reef (Fig. 1 *protected setting*) lagoonal and marginal environments that are protected from the prevailing winds and wave energy (Harris et al., 2015, 2018). As a result, wave-induced bottom stress strongly influences coral cover and community composition.

While overall, corals tend to grow more rapidly in higher flow environments (Kuffner, 2001), high wave energy can also have a negatively effect on reef growth in shallow (<6 m) environments (Grossman and Fletcher, 2004; Rogers et al., 2016).  
5 Field studies demonstrate that coral communities form in particular hydrodynamic conditions and adopt specific morphologies suitable to those conditions (Done, 1982). Hence, wave-induced bottom stress affects community organisation spatially, with a clear zonation pattern from the reef crest to the reef slopes (Done, 1982)(Done, 1982; Kuffner, 2001).

While some studies have examined net water flow as it varies across whole reefs (Davies and Hopley, 1983) very few studies have examined the effect of water movement on corals themselves in a variety of environments (Sebens et al., 2003; Baldoek et al., 2014) and  
10 even so, quantitative data on water energy thresholds for assemblages are non-existent. A high flow velocity threshold exists for some corals, beyond which they break (Baldoek et al., 2014), however the reduction in coral growth in response to water flow is poorly studied. The objective and benefit of *pyReef-Core* is its ability to model coral growth under changing flow conditions, thereby contributing to the understanding of the coral reef response to hydrodynamic energy.

### 3.3 Sediment input

15 High fluxes of both terrigenous and autochthonous sediments are widely identified to have both direct and indirect inhibitory effects on coral reef growth (Larcombe et al., 2001; Erftemeijer et al., 2012). Firstly, elevated turbidity attenuates ambient photosynthetically active radiation (PAR), which inhibits the ability of corals to meet energy requirements through photosynthesis (Rogers, 1990). Secondly, smothering and abrasion by sediment blankets can impair feeding and cause physical damage and direct mortality (Sanders and Baron-Szabo, 2005). While the lethality of sediment exposure is determined by the intensity  
20 and duration to exposure, generally the long-lasting impact of turbidity regimes is known to depress coral growth and survival (Larcombe et al., 2001). (Larcombe et al., 2001; Erftemeijer et al., 2012; Sanders and Baron-Szabo, 2005; Salles et al., 2018a). For instance, elevated turbidity on mid-outer platform reefs caused by the suspension of sediment on the Pleistocene reef substrate during initial flooding  $\sim 9$  ky-ka is hypothesised to be responsible for a delayed initiation of coral growth in the southern GBR (Dechnik et al., 2015).  
25 (Dechnik et al., 2015; Salles et al., 2018b). Autochthonous carbonate gravels and sediments (i.e. aragonite, calcite and high-magnesium calcite), produced by the growth and mechanical destruction of reef organisms through physical, biochemical and bio-erosive processes, are important determinants of the spatial and temporal distribution of coral communities on long timescales (Camoin et al., 2012; Kench, 2011). Prevailing wave and current conditions of even moderate energy resuspend fine-grained carbonate sediments and are key in generating stable turbidity regimes on reef systems, particularly in lagoons, on  
30 leeward rims and on reef slopes at moderate depths due to the decreasing water energy gradient both laterally and with depth (Hopley et al., 2007). Similarly, prevailing turbid conditions are less common at shallow sites, especially on the windward rim due to wave-driven sediment removal (Fig. 1). The spatial variation of suspended sediment loads is a critical environmental factor influencing coral community distribution across the reef and with depth (Perry and Larcombe, 2003) (Fig. 1). Turbid conditions are inimical to certain communities such as shallow-water corals, yet some species and communities are tolerant of elevated turbidity conditions on leeward rims (Dechnik et al., 2015) or species that thrive on reef slopes at depth (Perry et al., 2008). Hence, the spatial variation in turbidity is reflected in coral community distribution both across the reef and with depth.

Decades of experimentation carried out on the sensitivity of particular species to sediment have informed generic understanding of the threshold levels of corals to the effect of natural sedimentation (Hubbard, 1986; Rogers, 1983; Stafford-Smith, 1993), however these thresholds have only been partially quantified in the literature, and tolerance at the assemblage level is difficult to constrain due to site and within-species variations (Ertfemeijer et al., 2012). It has been shown that even under uniform sediment input regimes, inter and intra-site variations in sedimentation-resuspension regimes occur depending on water depth and exposure to wave energy (Wolanski et al., 2005). Early measurements supported that sedimentation rates exceeding 50 mg·cm<sup>2</sup>/day produced lethal effects (Rogers, 1990). Yet each coral species has its own tolerance threshold to sediment stress, beyond which sedimentation produces sublethal to lethal effects (Ertfemeijer et al., 2012). ~~Hence, while there is a clear theoretical relationship between duration and rates of sedimentation and coral mortality and live coral cover, determining these thresholds quantitatively have remained difficult to estimate.~~

#### 4 *pyReef-Core* model

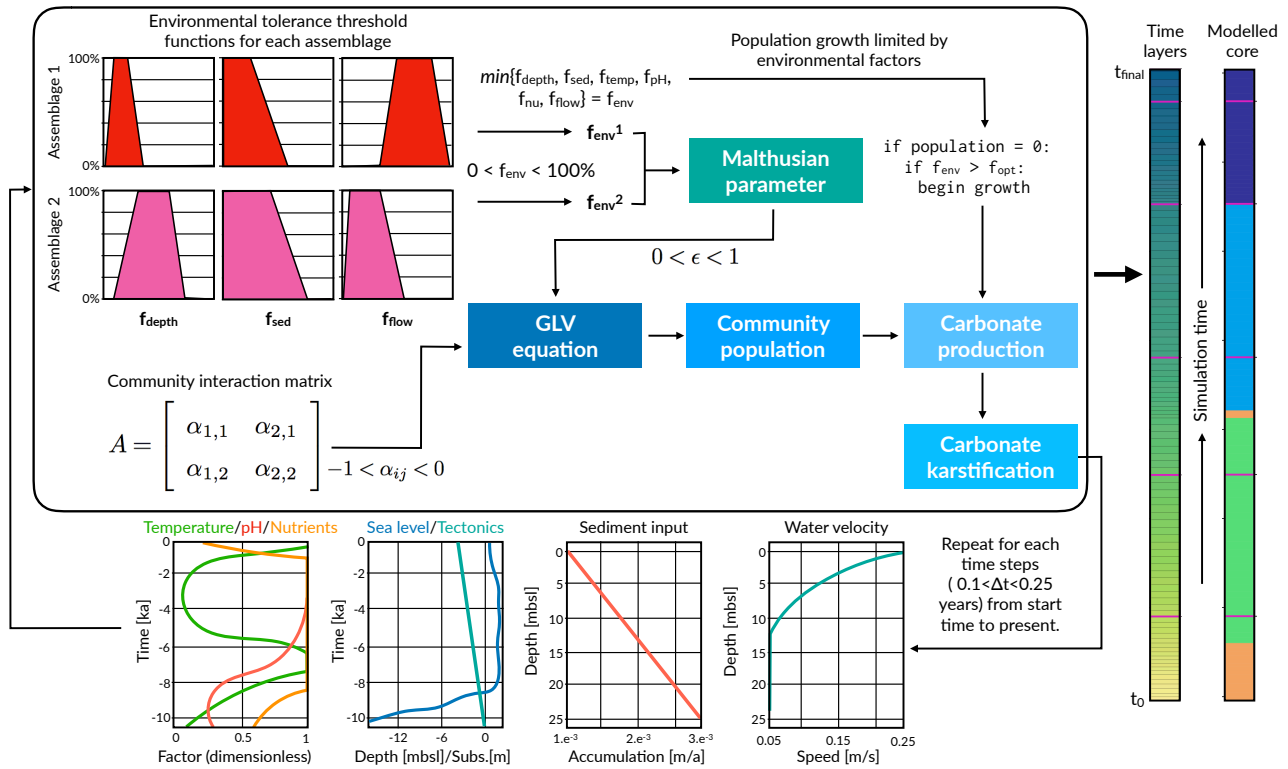
We present a 1-D deterministic, carbonate stratigraphic forward model called *pyReef-Core* that simulates vertical reef sequences comparable to those found in actual fossil reef drill cores. *pyReef-Core* is a tool to represent how dynamic biological and physical processes interact to create predictable, stratigraphic patterns. As shown in figure 2, the main steps in our workflow are: (i) using real geological, geophysical and ecological data to establish environmental boundary conditions, vertical accretion rates of coral assemblages and defining assemblage tolerance thresholds to environmental factors; (ii) defining model input parameters including Malthusian and assemblage interaction matrix parameters, simulation time and those that define model resolution; before (iii) running the model to create a vertical core sequence that records assemblage changes and growth history.

##### 4.1 Vertical reef accretion module

Carbonate production in a 1-D context, as represented by *pyReef-Core*, refers to the thickness of calcium carbonate produced in a core due to vertical framework accretion that is a result of vertical coral growth and sediment supply (Spencer, 2011). Hence, in this context carbonate production corresponds to reef vertical accretion. The model does not consider the destructional processes that occur on the reef due to physical, chemical and biological erosion but does account for erosional process during phases of subaerial exposure (referred as karstification in the model).

In our model, carbonate production is calculated for each time step at a user-defined resolution based on: (i) the maximum vertical accretion rate for each assemblage; (ii) GLVEs determining assemblage populations; and (iii) the environmental conditions that define optimal growth for each assemblage. During periods of subaerial exposure, karstification occurs at an uniform rate independent of the type of assemblages and consists in eroding reef stratigraphic top layers to the extent of the undergoing erosion.

In palaeoenvironmental analysis of real drill cores, assemblages are defined based on the relative abundance of coral species observable at certain intervals (Dechnik et al., 2015). To reflect this in our code, each depth interval in the modelled core records the assemblage that generated the greatest proportion of calcium carbonate at each time step; else if carbonate sedimentation



**Figure 2.** Illustration outlining *pyReef-Core* workflow (left) and of the resulting simulated core (right). First boundary conditions for sea-level, sediment input and flow velocity are set, which describes their relationship to either depth or time. The boundary conditions are used to establish the environment factor  $f_{env}$  which describes the proportion of the maximum growth rate that an assemblage can achieve, depending on whether the environmental conditions exceed the optimal conditions for growth. The environment factor is scaled by the Malthusian parameter, which is in turn used as input in the GLVE equations GLVEs to determine assemblage populations. Larger assemblage populations contribute to a faster rate of vertical accretion (here referred to as carbonate production). At the end of the time step, boundary conditions are updated and the process is repeated.

(defined as a depth-dependent sediment input function – Fig. 2) dominates coral production, sediment characterises the depth interval.

## 4.2 Generalised Lotka-Volterra equations (GLVEs)

The predator-prey ecological model by Lotka (1920) and Volterra (1926) is a well-known and simple model of species population dynamics. Its generalised formulation (GLVEs) allows for an unlimited number of species and their pairwise interactions and is included here to simulate coral assemblage interaction dynamics. GLVEs applied to finding the evolution of species populations typically focus on ecologically-relevant periods (<5 years). The application of GLVEs for this problem is to simulate changes in coral assemblages observed in drill cores, where population dynamics are not the focus but only a means to estimate

production rates over geologically significant periods. This is based on the understanding that internal ecosystem dynamics are partially responsible for the long-term biozonation patterns preserved in fossil reef records (Montaggioni, 2005).

Populations for each coral assemblage are determined by a logistic growth and decay function and a matrix of pair-wise assemblage interactions (Fig. 2), formalised in the equation:

$$10 \quad \frac{dN_i}{dt} = \epsilon_i N_i + \sum_{j=1}^c \alpha_{ij} N_i N_j \quad (1)$$

where  $N_i$  is the population of coral assemblage  $i$  for  $c$  number of assemblages,  $\epsilon_i$  is the intrinsic rate of increase/decrease of assemblage  $i$  (also known as the Malthusian parameter) and  $\alpha_{ij}$  represents the interaction coefficient among assemblages  $i$  and  $j$ . Assemblage populations at time step  $t_{i+1}$  are proportional to both populations at  $t_i$  ( $N_i$  and  $N_j$ ) and to interaction coefficients ( $\alpha_{ij}$ ) (Clavera-Gispert et al., 2017). The equation requires an initial population for each assemblage  $N_i^0$ , which  
 15 is ~~assumed usually set to zero~~ for all populations as the basement substrate is unpopulated at the beginning of reef initiation simulations. Initialisation of any assemblage populations depends on environmental conditions and is related to the 'turn-on' criterion presented in section 4.7. Once these conditions are met for a particular assemblage, its population number is set to 1 and will evolve following the GLVEs defined above (Eq. 1).

### 4.3 Malthusian parameter ( $\epsilon$ )

20 Assemblage populations are proportionate to a Malthusian parameter  $\epsilon$  which takes values between 0 and 1 and reflects the intrinsic reproduction of species through birth and mortality of corals in ecology (Fig. 2 – Clavera-Gispert et al. (2017)). However, in the geologic context of *pyReef-Core*,  $\epsilon$  represents the tendency of corals to spatially dominate under favourable environmental conditions.

Clavera-Gispert et al. (2017) previously incorporated GLVEs to model the geological evolution of large scale carbonate plat-  
 25 forms and assumed that  $\epsilon$  is not meaningful when timescales are beyond the lifespan of an organism and supposed that  $\epsilon = 1$ . Clavera-Gispert et al. (2017) examine carbonate production in 500-year intervals whereas *pyReef-Core* explores much smaller intervals (<10 years), and as coral colonies may live for several decades to centuries (Camoin et al., 1997; Grigg, 2002),  $\epsilon$  is not assumed to be 1. Even when assuming  $\epsilon = 1$ , *pyReef-Core* simulations produced volatile population dynamics where assemblage populations grew exponentially and were unable to replicate long-term ecosystem stability, nor the thousands-of-years of assemblage persistence observed on some reefs (Camoin et al., 1997). Hence, while values of  $\epsilon$  are not yet known at the  
 5 decadal scale,  $\epsilon$  is an important parameter regarding spatial changes in assemblage distributions that occur within centuries. Finally,  $\epsilon$  is scaled according to the environmental factors to take into account the limiting effect of inimical environmental forces on assemblage population growth (section 4.6).

### 4.4 Assemblage interaction matrix

The pair-wise coefficients of interaction between assemblages can be represented as elements  $\alpha_{ij}$  in a square C-by-C matrix,  
 10 where any  $\alpha_{ij}$  is a special case of the effect of a change in assemblage population  $N_i$  on itself. Values of the coefficients

**Table 1.** Interaction possibilities among coral assemblages and the associated range of matrix coefficients, adapted from Clavera-Gispert et al. (2017).

Interactions	Effect on $i$	$\alpha_{ij}$ range	Effect on $j$	$\alpha_{ij}$ range
<b>Competition</b>	Detrimental	$-1 \leq \alpha_{ij} \leq 0$	Detrimental	$-1 \leq \alpha_{ij} \leq 0$
<b>Neutralism</b>	Neutral	$\alpha_{ij} = 0$	Neutral	$\alpha_{ij} = 0$

describe the beneficial, neutral or detrimental effects of one species on another (Table 1). As with  $\epsilon$ , values of  $\alpha_{ij}$  cannot be inferred from previous ecological modelling studies (e.g., Clavera-Gispert et al., 2017) as the temporal scales of study are irreconcilable. It is assumed, however, that competitive-to-neutral effects control the spatial distribution and abundance of coral assemblages at decadal timescales.

- 15 Competitive interactions between corals have received considerable attention in ecology (Lang and Chornesky, 1990), especially regarding their spatial distribution outcomes. As assemblages occupy ecological niches, each will spatially dominate at a location under specific environmental conditions, outcompeting other assemblages for food, space and light (Connell et al., 2004). Hence, competition is an important determinant of reef biozonation which persists over centennial timescales given that coral growth is slow and colony lifespans can be centuries long. Hence in *pyReef-Core*, the interaction matrix is formed by
- 20 competitive-to-neutral interaction coefficients between -1 and 0 (Table 1).

#### 4.5 Computing carbonate production based on assemblage populations

Solved GLVEs determine population growth/decline for each assemblage, and are used to compute carbonate production [cm/y] for each time step. The amount of carbonate produced by each coral assemblage during each time step is defined as:

$$\frac{dp_i}{dt} = \frac{\sum_{i=1}^c A_i \times N_i}{S} \quad (2)$$

- 25 where the carbonate production at every time step of each assemblage  $p_i$  for  $c$  number of assemblages is a product of the population distribution  $N_i$  and the maximum rate of vertical accretion  $A_i$  in proportion to a scalar  $S$ . The scalar is introduced to the vertical growth equation in order to minimise distortionary effects of exponential growth trends for each population occurring in the absence of inter-assemblage competition (i.e., to prevent unreasonably large population growth when only one assemblage can exist under certain conditions). Total vertical reef growth  $G$  recorded in a core is the sum of carbonate sediment deposited  $p_{sed}$  and all calcium carbonate produced by each assemblage:

$$\frac{dG}{dt} = \sum_{i=1}^c p_i + p_{sed} \quad (3)$$

#### 4.6 Environmental factors

Sediment input, water flow and accommodation are the basic environmental factors influencing coral growth in *pyReef-Core*.

- 5 However, the model architecture is such that in the future it is possible to simulate the effect of other important environmental

parameters such as ocean temperature, ~~acidity and nutrient~~ [pH and nutrient flux](#). Tolerance functions are defined for each environmental factor as a set of four points that indicates both the range in which an assemblage would reasonably exist based on published empirical data (Done, 1982; Hopley et al., 2007; Dechnik, 2016) and the rate at which vertical accretion reduces as the environmental conditions exceed upper or lower threshold limits for each assemblage (Fig. 2). As such, they define an ‘optimal growth window’ for each assemblage. The threshold functions for each assemblage to ambient environmental conditions are combined into a single environmental parameter  $f_{env}$  subject to the minimum value rule:

$$f_{env} = \min [f_{depth}^i, f_{sed}^i, f_{temp}^i, f_{pH}^i, f_{nu}^i, f_{flow}^i] \quad (4)$$

where  $f_{depth}$ ,  $f_{sed}$ , ... and  $f_{flow}$  represent the threshold functions for each assemblage  $i$ . Hence,  $f_{env}$  is seen as the combined effect of ambient environmental conditions on optimal growth conditions (Fig. 2). Finally, the Malthusian parameter  $\epsilon$  is scaled by the environmental factor such that:

$$E^i = \epsilon \times f_{env}^i \quad (5)$$

which reflects the limiting effect on environmental factors on the growth potential of each assemblage.

#### 4.7 ‘Turn on’ criterion

At the initialisation of the *pyReef-Core* simulations, assemblage populations are usually set to zero. Population growth only occurs when the initial criterion  $f_{env} > f_{opt}$  is met (Fig. 2). It reflects the notion that reef ‘turn on’ events occur because of a confluence of optimal conditions including a shallow substrate, favourable energy, light and water temperature, pH and nutrients conditions and relatively low sediment supply (Buddemeier and Hopley, 1988; Fabricius, 2005; Dechnik et al., 2015). In other words, *pyReef-Core* only initiates growth when a degree of optimality in growth conditions are met. By default, the value of  $f_{opt}$  is set to 0.5 which stands that the ‘turn-on’ criterion is met when environmental conditions enable at least 50% of the maximum vertical accretion. [The parameter however can be adjusted within the XML input file to reflect different assemblage populations sensitivities to environmental conditions.](#)

## 5 Examples of model application

Two case studies are presented here to assess the ability of *pyReef-Core* to reproduce realistic sequences found in drill core. We simulate the interactions between three assemblages which are estimated based on water depth intervals (shallow, intermediate and deep). We also consider that coral production in these experiments is primarily controlled by accommodation and exposure to sedimentation (Chappell, 1980; Tudhope, 1989) and water flow (Fulton et al., 2005; Comeau et al., 2014).

## 5.1 Experimental settings for model simulations

### 5.1.1 Assemblage maximum vertical accretion rates

Maximum vertical accretion rates in the simulation are user-defined. For shallow assemblages on exposed margins, maximum vertical accretion rates (11 m/kyr) are chosen to reflect known average rates for robust branching coral facies in high-energy environments established for the Indo-Pacific (Montaggioni, 2005). Moderate-deep assemblages represent slightly higher maximum accretion rates (15 m/kyr) with the lowest accretion rates (9 m/kyr) for deep assemblages. These were chosen to reflect the average accretion rates for Indo-Pacific tabular-branching and massive coral facies found in high-energy conditions respectively (Montaggioni, 2005).

### 5.1.2 Ecological dynamics

*pyReef-Core* requires knowledge of the intrinsic rate of assemblage population growth/decline ( $\epsilon_i$ ) and the matrix coefficients ( $\alpha_{ij}$ ) of interactions between distinct assemblages. However, inferring ecological dynamics from ecological studies is challenging. Empirical studies of coral competition and growth are often focused at the species, rather than assemblage, level and explain competitive relationships qualitatively rather than quantitatively (e.g., Connell et al., 2004). Moreover, GLV equations have not been used to model coral population dynamics at the temporal resolution (centennial to millennial) we are interested in. Based on an initial sensitivity analysis, we define a set of values for the Malthusian parameter ( $\epsilon_i$ ) and interaction coefficients among assemblages ( $\alpha_{ij}$ ) which are summarised in Table 2. Chosen coefficients define small competitive interactions between assemblages.

The coral assemblages defined in this study largely do not share the same environmental setting and optimal growth conditions. Therefore, competitive interactions are restricted to only those assemblages that may reasonably co-exist due to overlapping depth, sediment flux or flow velocity thresholds. This translates to an interaction matrix with values only along the main diagonal, super- and sub-diagonals. Everywhere else, interactions are set to 0. Associated to these interactions, we define a series of critical threshold response functions for each assemblages (Fig. 3).

### 5.1.3 Depth threshold functions

Based on a statistical analysis of the depth and environmental distribution of modern coral communities at One Tree Reef (Great Barrier Reef, GBR), Dechnik et al. (2017) calibrated the palaeo-water depositional environments of six fossil coral assemblages (three in protected and three in exposed environments). This calibration was also based on quantitative measurements of crustose coralline algae thickness and vermetid gastropod abundance which are reliable palaeo-depth indicators, allowing for the depth intervals to be more accurately constrained. These assemblages are broadly consistent with shallow- and deep-water coral facies of the Indo-Pacific (Cabioch et al., 1999; Camoin et al., 2012).



Here, three assemblages typically occurring on exposed slopes are modelled according to the estimated depth intervals defined by Dechnik (2016) (Table 2) and represent shallow-water (< 6 m), moderate-to-deep-water (6 – 20 m) and deep-water (20 – 30 m) assemblages respectively.

#### 5.1.4 Water flow

5 The water flow function is constructed according to the theoretical relationship defined by Chappell (1980) whereby wave stress decreases exponentially with depth (Fig. 4). Here, we rely on the velocity-depth relationships on wave-exposed reef slopes from the field study by Sebens et al. (2003). A maximum velocity of 25 cm/s in region  $\leq 1$  m and an exponential decrease up to 25 m below which flow velocity is set to 0. This is consistent with direct observations from exposed algal flat (Davies and Hopley, 1983), and maximum velocities (> 50 cm/s) beyond which branching corals are susceptible to breakage (Baldock et al., 2014).

With lacking specific data on the optimal flow environment for specific corals, assumptions about thresholds for distinct coral assemblages are inferred from boundary conditions. That is, the water flow exposure threshold range for each assemblage  
5 reflects the attenuation of water flow with depth (Fig. 3).

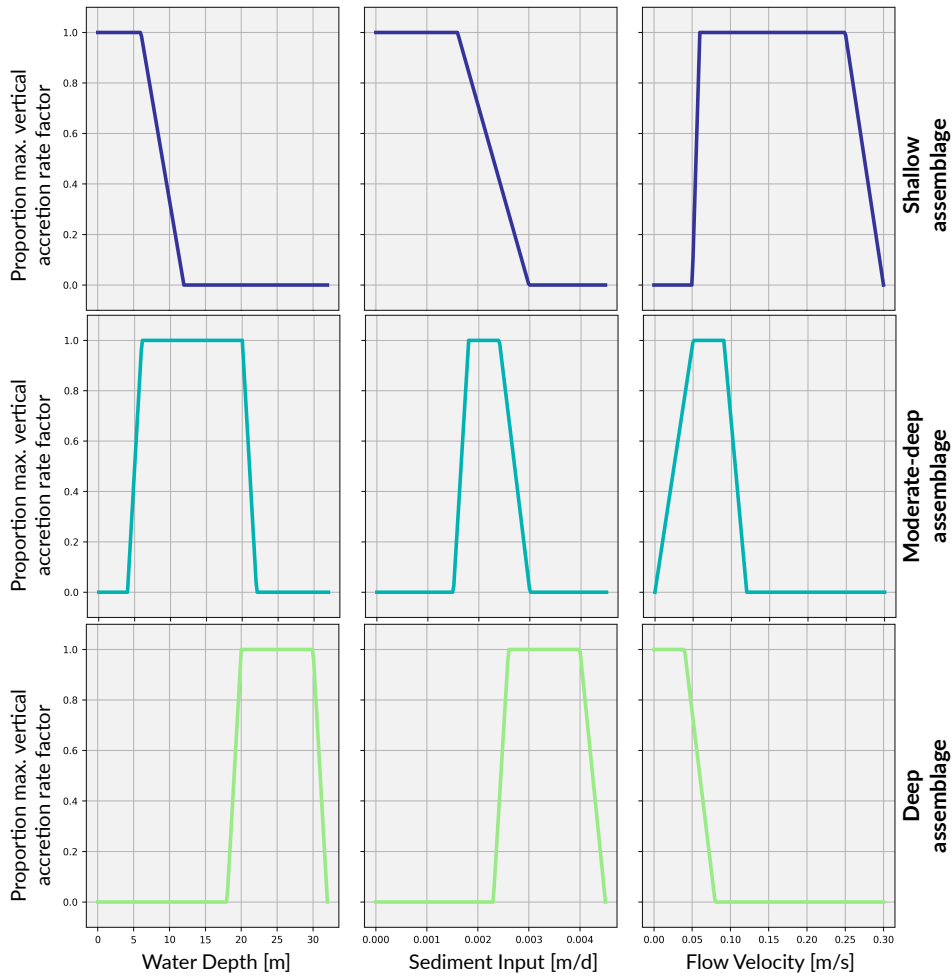
#### 5.1.5 Sediment exposure

*pyReef-Core* can model the vertical sedimentation rate (m/day) as a function of either time or depth. When sediment flux is dependent on depth, it implies that sediments are autochthonous (loose carbonate materials), in contrast to terrigenous sediments transported from outside the reef system (siliclastic materials), which may be represented by sediment flux varying  
10 with time. In our case studies, we use a depth-dependent sedimentation rate input curve to approximate the temporal variations in sediment accumulation along the core (Fig. 4).

Sediment tolerance thresholds for each coral assemblage (Fig. 3) are informed by (Dechnik et al., 2017) before receiving maximum and minimum sedimentation rates corresponding to the sediment input boundary condition (Fig. 4). The boundary condition provides a broad indicator of the sediment load expected at certain depths, and thus what would be tolerated for each depth-specific assemblage. With alternate sediment input boundary conditions, the upper and lower tolerance thresholds can be adjusted to represent how coral communities respond differently to site-specific suspended sediment levels.

#### 5 5.2 Case 1: GBR idealised windward shallowing-upward Holocene reef sequence

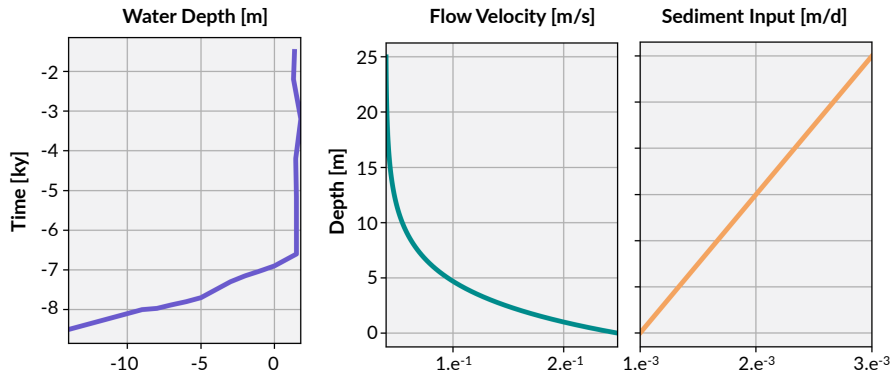
Based on afore described experimental settings, we first simulate a typical shallowing-up sequence of coral assemblages on the exposed rims of several reef in the GBR, expressing a catch-up strategy of reef growth during Holocene sea-level rise (~9.4  
ky-ka to present).



**Figure 3.** Environmental threshold functions for shallow, moderate-deep and deep assemblages characteristic of a synthetic exposed margin. The x-axis indicates the limitation on maximum vertical accretion for conditions outside the optimal maximum vertical accretion rate.

### 5.2.1 Initial parameters

- 10 Considering the simulated temporal scale, neither subsidence nor uplift are considered to be important (Hopley et al., 2007) in this experiment. Instead, accommodation is simulated as a function of Holocene sea-level changes and vertical coral reef growth only. The Holocene relative sea-level (RSL) curve from Sloss et al. (2007) is used to represent sea-level change (Fig. 4). The data ~~implies~~ ~~suggest~~ a RSL history that is characterised by a mid-Holocene highstand of 1.8 m at  $\sim 4$  ~~ky~~ ~~ka~~ before returning slowly to present sea-level, matching other estimates of RSL (Chappell, 1983; Lewis et al., 2013).
- 15 Simulation begins at 8.5 ~~ky~~ ~~ka~~, which is within the take-off envelope for Holocene growth of outer-platform GBR reefs (Hopley et al., 2007). At 8.5 ~~ky~~ ~~ka~~, RSL is 15 m below sea-level (Sloss et al., 2007) and substrate is at 20 m depth in order to simulate

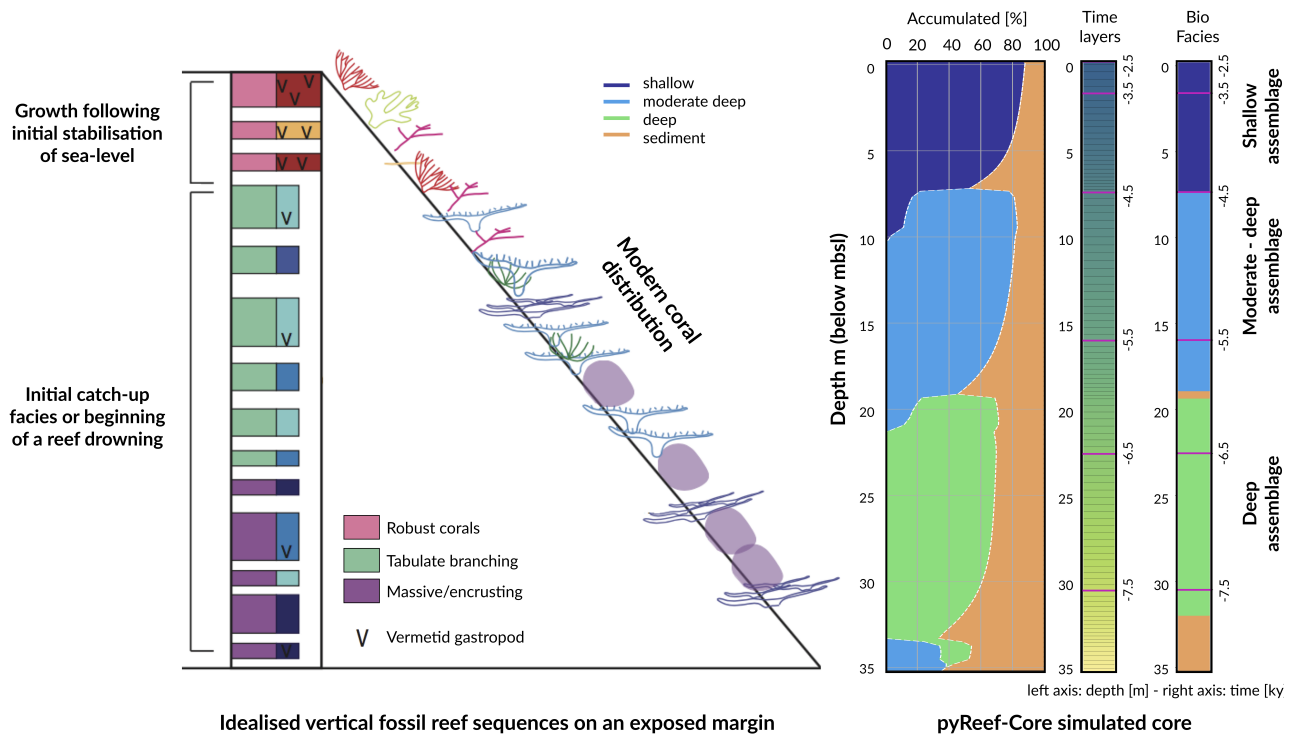


**Figure 4.** Left curve shows the Holocene sea-level curve estimated from Sloss et al. (2007). Right graphs illustrate the boundary conditions established for flow velocity and sediment input used in the experimental simulations.

**Table 2.** Parameter values used in our two experiments. Estimates of maximum production rates for assemblages were determined based on literature surveys of maximum growth rates for coral facies of GBR (Davies and Hopley, 1983) and Indo-Pacific reefs (Montaggioni, 2005).

Parameters	values
<b>Malthusian parameter</b>	$\epsilon_i = 0.004$
<b>Assemblage interaction matrix</b>	
Main diagonal	Detrimental - $\alpha_{ii} = -0.0005$
Sub- and super-diagonal	Detrimental - $\alpha_{ij} = -0.0001$
<b>Assemblage maximum growth rate (m/yr)</b>	
<i>Shallow-water assemblage (0-6 m)</i>	0.011
<i>Moderate-deep-water assemblage (6-20 m)</i>	0.012
<i>Deep-water assemblage (20-30 m)</i>	0.009
<b>Assemblage threshold tolerance variables</b>	
<i>Shallow-water assemblage (0-6 m)</i>	
Absolute water flow threshold range	$0.05 \leq f_{flow} \leq 0.3$
Absolute sediment input threshold range	$0 \leq f_{sed} \leq 0.003$
<i>Moderate-deep-water assemblage (6-20 m)</i>	
Absolute water flow threshold range	$0 \leq f_{flow} \leq 0.12$
Absolute sediment input threshold range	$0.0015 \leq f_{sed} \leq 0.003$
<i>Deep-water assemblage (20-30 m)</i>	
Absolute water flow threshold range	$0 \leq f_{flow} \leq 0.08$
Absolute sediment input threshold range	$0.0023 \leq f_{sed} \leq 0.0045$

a catch-up growth strategy from a deep substrate. We compute the GLVEs at time intervals of 2.5 years and combine each accumulated assemblage as a stratigraphic unit within the core for every 50 years.



**Figure 5.** (Left) Ideal shallowing-up fossil reef sequence representing a ‘catch-up’ growth strategy with associated assemblage compositions and changes, adapted from Dechnik (2016); (Right) Model output of produced *pyReef-Core* sequence representing a similar shallowing-upward, ‘catch-up’ phase.

## 5.2.2 Communities evolution and synthetic core representation

- 20 Figure 5 presents the GBR-representative assemblages summarised by Dechnik (2016) as well as the simulated core by *pyReef-Core*. The modelled core is 35 m long and is composed of three assemblages characteristic of an exposed margin and carbonate sediments. The simulation portrays two distinct assemblage transitions from massive assemblages representing deep (20-30), low-flow conditions to a faster-growing, tabular-and-branching assemblage characteristic of the 6-20 m depth interval, which is succeeded in shallow water (< 6 m) by a robust-branching assemblage representing higher-energy conditions (Figs. 6, 5).
- 25 As sea-level rises from 8.5 to 6.5 [kyka](#), the deeper assemblages have sufficient accommodation space (>20 m) and low-flow to thrive. However, greater sediment input at depth is inhibitive in the early part of the simulation at the base of the core (32-35 m) (Fig. 5. As sea-level begins to stabilise (top right panel Fig. 6), accommodation space decreases and moderate-deep assemblages start to dominate the sequence up to 4.7 [kyka](#) (bottom left panel Fig. 6). Following stabilisation from 4.7 to 3.2 [kyka](#), shallow assemblages develop as a result of the decreased accommodation space (~ 6 m at 4.7 [kyka](#)), high-velocity hydrodynamic
- 30 conditions and reduced sediment input. Assemblage growth rates (bottom right panel Fig. 6) show a pattern similar to the population number curves with values lower than assemblage maximum production rates (Table 2) indicative of the effects of

environmental factors (sediment input and flow velocity) on the growth of each assemblage. The deeper assemblage is 15 m thick and is composed of 30-60 % loose sediment and is succeeded by  $\sim 12$  m of moderate-deep assemblages with a lesser proportion of sediment (Fig.5). The last 6-7 m of core are predominantly formed by shallow assemblages with on average less than 20% of carbonate sediments (Fig. 5). The simulated shallowing-up sequence accurately reflects expected shift from deep to moderately-deep assemblages at  $\sim 15$ -20 m depth, and from moderately-deep to shallow assemblages at  $\sim 6$  m depth proposed by Cabioch et al. (1999) and Dechnik (2016). The simulated sequence relates well with the description proposed by Dechnik (2016) and reproduces the distinct assemblages defined in the idealised reef sequences found on exposed margin along the GBR (Fig. 5).

The modelled core reaches sea-level at around 2.5 ky-ka (Fig. 6 which also correlates well with values reported for several reefs in the GBR (Davies and Hopley, 1983; Dechnik et al., 2015; Salas-Saavedra et al., 2018). Average vertical accretion rate implied by the model is around 4.1 m/ky-kyr (Fig. 6), again in the range of actual drill cores average rates which varies around 3 to 5 m/ky-kyr on exposed reef margins (Davies and Hopley, 1983; Camoin et al., 2012; Dechnik et al., 2015). It is also worth noting that coral growth becomes predominant within the sequence at  $\sim 7.8$  ky-ka in the modelled core which coheres with the observed delay in reef initiation of approximately 1 ky-kyr (Dechnik et al., 2015) after initial flooding of the substrate during the Holocene transgression. We also notice that the transitions between assemblages also correspond to periods where the proportion of carbonate sediment deposited increases (Fig. 5). It mimics a lag between optimal conditions from one assemblage to the other and relates to the choice of environmental threshold functions that were imposed in our simulation (Fig. 3). Overall, the model reproduces the details of the formation of shallowing-upward sequences both in terms of assemblages succession, accretion rates, deposited thicknesses and timing of initiation. It can be applied to estimate the impact of changing environmental conditions on growth rates and patterns under many different settings and initial conditions.

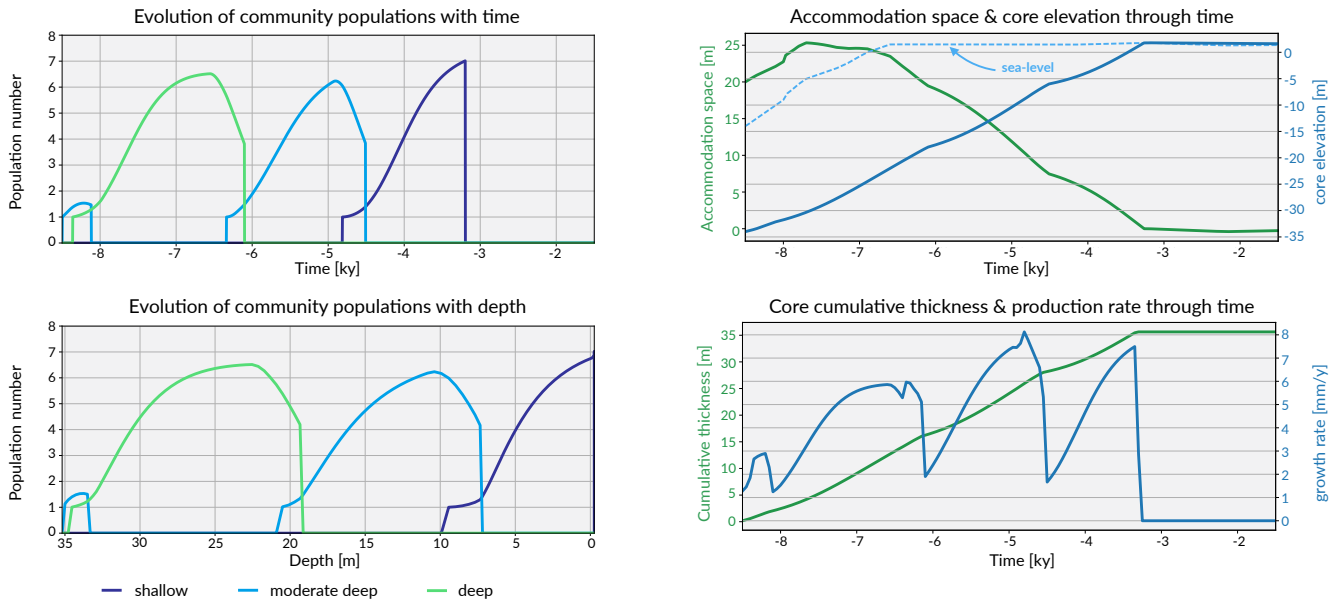
### 5.3 Case 2: GBR idealised reef core reconstruction over the last 140 kykyr

For the second study case, the experimental settings for threshold functions, ecological dynamics, water flow and sediment exposure (presented in section 5.1) remain unchanged. The goal is not to match a specific drill core but to illustrate the influence of forcing conditions on the development of a coral reef sequence with our model.

#### 5.3.1 Initial parameters

We reconstruct using *pyReef-Core* the evolution of an ideal coral reef sequence since the last interglacial (LIG). LIG is represented by marine isotope stage (MIS) 5e, which is a proxy record of low global ice volume and high sea-level (Grant et al., 2012). It is arbitrarily set to begin at approximately 130 ky-ka before present and our simulation runs over 140 kykyr. The GLVEs which control the coral productions dynamic, are updated every 25 years and stratigraphic layers are recorded at time interval of 100 years.

Here we use the sea-level curve proposed by Grant et al. (2012) who estimate sea-level records based on the timing of past ice-volume changes, relative to polar climate change. The relative sea-level change over the simulated period has rates of rise



**Figure 6.** Graphical output from *pyReef-Core* showing on the left the evolution of each community in the form of population number with time and depth. As mentioned previously population number here is a proxy for carbonate production with larger assemblage population corresponding to faster rate of vertical accretion. Right top panel shows the evolution of the accommodation space and core elevation through time in relation to imposed sea-level curve. Right bottom panel presents the temporal evolution of the cumulative thickness as well as the total coral production rate for the considered experiment.

reaching 12 cm/y during all major phases of ice-volume reduction, with values below 7 mm/y when sea-level exceeded present mean sea level (Grant et al., 2012). The applied sea-level curve is shown in top right panel of Fig. 7.

Karstification of Pleistocene reef limestone has been identified as a controlling factor on variations of antecedent topography, which in turn is thought to influence the morphology of modern reefs (Purdy and Winterer, 2001). Rates of karstification are a function of exposure time, rainfall, porosity and original topography of exposed carbonate reefs. Summary of karstification rates from both the Indo-Pacific and Caribbean shows values ranging from 0.01 m/ky-kyr (Barbados, Hopley et al. (2007)) to 0.14 m/ky-kyr (mid-outer platform reefs, Southern GBR, Marshall and Davies (1982)). Here we impose a karstification rate of 0.07 m/ky-kyr consistent with estimates from Ribbon Reef 5 and outer Central GBR shelf (Webster, 1999).

Over such period of time, sea-level fluctuations are not the only factor controlling the accommodation change and uplift/subsidence evolution has to be considered (Spencer, 2011). Based on a comprehensive study of GBR reefs, Dechnik (*unpublished*) estimates that a subsidence rate of  $\sim 0.065$  to  $0.15$   $0.083$  to  $0.13$  m/ky-kyr is required to explain the observed elevation of the upper surface of the LIG reef that provides the antecedent topography of the modern mid-outer platform reefs in the GBR. The proposed range is consistent with values found for other reefs along the GBR (Marshall and Davies, 1982; Webster, 1999). In our model, we use a constant rate of subsidence set to 0.1 m/ky-kyr that corresponds to 14 m of subsidence over the duration

15 of the simulation. In addition, the initial elevation is set 20 m above sea-level position at the start of the simulation (140 kyka), corresponding to a depth of  $\sim 70$  m below current sea-level position.

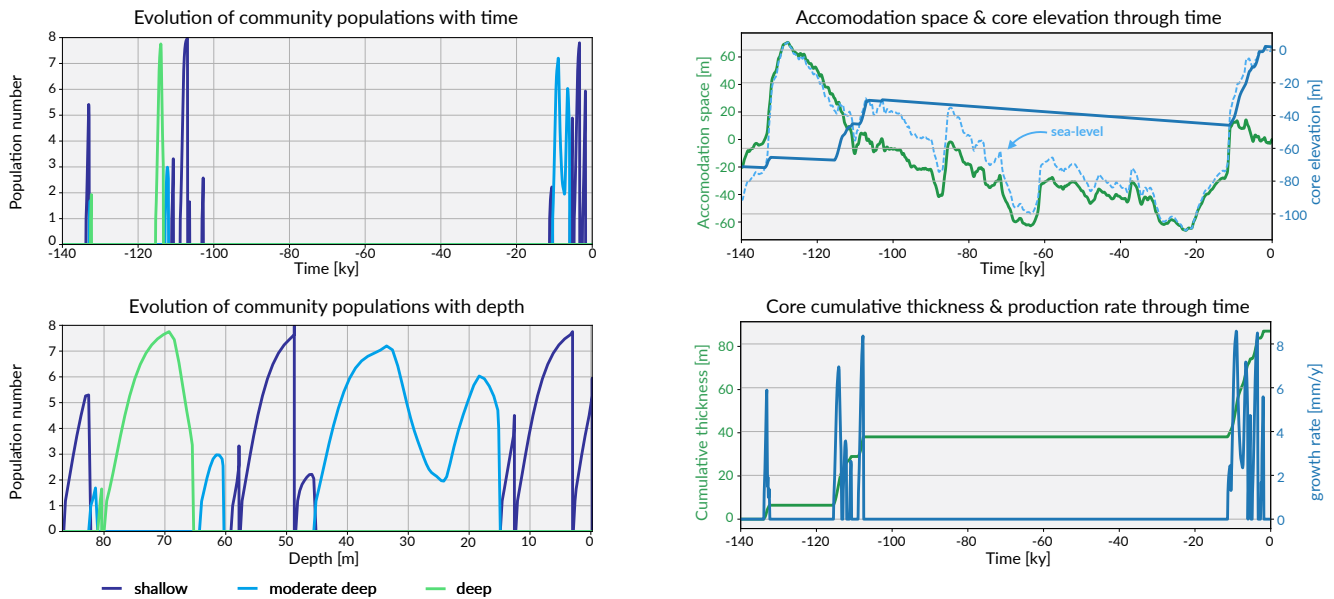
### 5.3.2 Communities evolution and synthetic core representation

Prior to 135 kyka, the model shows a first stage of reef growth characterised by shallow water, high energy coral communities colonisation (left panels Fig. 7 and Fig. 8), following flooding of antecedent platform. The cumulative thickness for this phase is  $< 10$  m (bottom right panel Fig. 7) and is compatible with values estimated for Ribbon Reef 5 and Heron Island (Dechnik et al., 2017).

Following this initial phase, a deepening upwards sequence occurs up to 132 kyka (Fig. 8). Again this sequence has also been identified in similar time interval at One Tree Reef (southern GBR) and Stanley Reef (central GBR) (Dechnik et al., 2017). A lack of significant reef framework ( $< 30\%$ ) characterises the stratigraphic sequence during this interval.

25 The rapid sea-level rise (Grant et al., 2012) during the end of the penultimate deglaciation explains the drowning event observed in the core from 128 to 118 kyka (bottom left panel in Fig. 7). During this period, the accommodation increase is mainly driven by sea-level fluctuations and to a small extent ( $\sim 1$  m) by the imposed subsidence rate.

From 118 to 107 kyka, during the first stage of the regression phase, a shallowing upward sequence ( $\sim 30$  m thick) is identified with three distinct community populations modelled over time (bottom left panel Fig. 7). During this time interval, the



**Figure 7.** Similar to the previous case, these graphs shows on the left the evolution of each community in the form of population number with time and depth. Right top panel shows the evolution of the accommodation space and core elevation through time in relation to imposed sea-level curve. Right bottom panel presents the temporal evolution of the cumulative thickness as well as the total coral production rate.

30 maximum population number for the moderate-deep assemblages is relative lower (<3) than for the 2 other assemblages (>7). Consequently, the percentage of accumulated thickness for this assemblage is below 7%. These assemblage transitions are primarily controlled by high frequency sea-level variations observed in Grant et al. (2012) curve (top right panel Fig. 7). Minor events of karstification (<2 cm of erosion) are triggered by short episodes of sub aerial exposure around 110 kyka. From 107.5 to 104 kyka, high energy coral communities (shallow assemblages) dominate the sequence with a maximum growth rate above 8 mm/yr (bottom right panel Fig. 7).

The following stage from 107 to 12 kyka is characterised by a period of sub aerial exposure due to sea-level fall (bottom right panel Fig. 7). Both subsidence and karstification occur and account for nearly 11 m of elevation offset with about 1 m attributed to karstification processes (Fig. 8). Applied to a real case, *pyReef-Core* can be used to test several scenarios with different rates of subsidence and karstification in order to explain for example the discrepancy in age/elevation data of LIG deposits observed in the GBR (Marshall and Davies, 1982; Dechnik et al., 2017). It can also be used to estimate the contribution of karst dissolution and subsidence (Hopley et al., 2007; Purdy and Winterer, 2001) with a more quantitative approach.

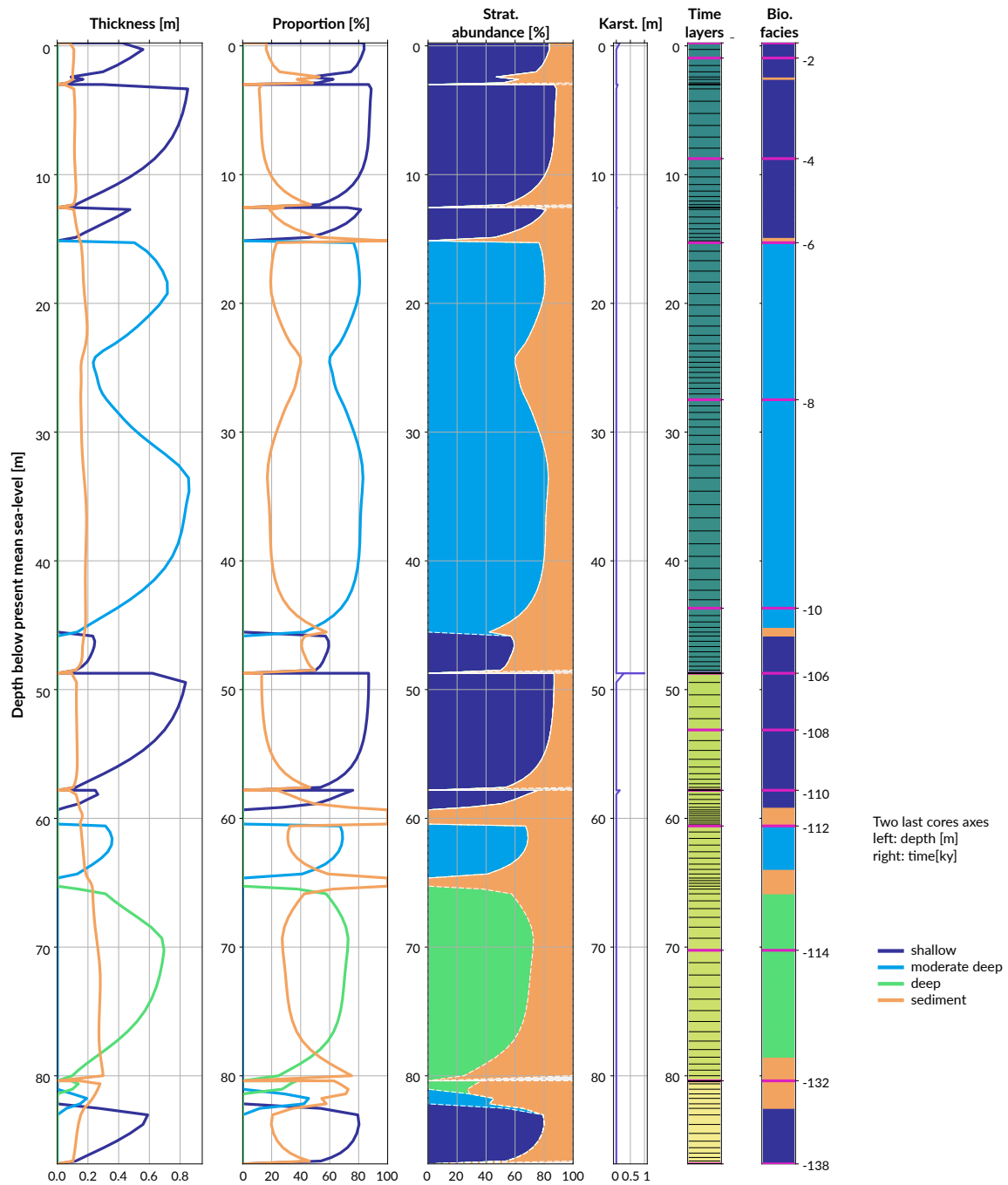
By 13 kyka, sea-level re-floods the LIG reef and Holocene reef growth initiates ~10.5 kyka after in the experiment (Fig. 7). The lag (2.5 kykyr) between flooding and reef growth initiation matches well with observations for the GBR (Fabricius, 2005; Hopley et al., 2007; Camoin et al., 2012). However the timing for the initial flooding occurs 3 kykyr earlier than what is expected for the GBR. This temporal difference is related to both sea-level variations (Grant et al., 2012) and chosen initial starting elevation of the model. The Holocene reef sequence is around 46 m thick (Fig. 8) which is above most of the GBR reef maximum vertical accretion thicknesses (usually < 30 m) but correlates with thicknesses found in reefs from Tahiti and Huon Peninsula (Woodroffe and Webster, 2014). This Holocene sequence is first composed of more than 30 m of moderate-deep assemblage which corresponds to the catch-up phase discussed in the first study case and is associated to the rapid sea-level rise. The reef accretion rate during this time interval is maximum and reaches values above 8.2 mm/y (bottom right panel Fig. 7). The remaining ~15 m of the upper most sequence is built of shallow assemblages that become predominant after 6 kyka when sea-level rise decreases. It is also worth noting the presence of short periods of subaerial exposure which coincide with two small karstification events (karst dissolution < 1 cm, Fig. 8).

The total simulated core has an overall thickness > 86 m. A complete sequence such as the one modelled here is unlikely to be found in natural reef complex mainly due to the 3D nature of such system (Woodroffe and Webster, 2014). Nevertheless the predicted sequence represents in 1D, the idealised succession of coral assemblages produced for a given set of initial and forcing conditions. Therefore it can be compared to series of drill cores at different positions along a given region and used as a quantitative approach to analyse stratigraphic responses of coral reefs to a combination of physical, biological and sedimentological processes.

## 6 Discussion

~~A great amount is still unknown~~ Relatively little is known about how coral reefs grow and respond to environmental conditions at temporal scales exceeding what is measurable (Hughes et al., 2017). ~~In the introduction, the dilemma was posed that~~ (i.e.





**Figure 8.** Simulated reef core reconstruction, showing the different stages of last interglacial reef growth in relation to sea-level, karstification and subsidence.

30 observational record over the last 100 years) (Hughes et al., 2017). It has been a major challenge for both geological and ecological studies ~~have thus been unable~~ to adequately capture coral reef ecological and environmental dynamics on centennial to millennial temporal scales and at reef ~~scale~~ (Stocker et al., 2013). ~~Here we propose a new method to explore these intermediate scales.~~ scales (Stocker et al., 2013). Our new method, *pyReef-Core*, operates on these scales, and offers a coherent, fast and effective way ~~of predicting to predict~~ 1-D reef core ~~stratigraphy~~ stratigraphies and assemblages changes. It can be used to improve our understanding of coral reefs response to climatic and environmental changes (Done, 2011; Harris et al., 2015). The code is most useful in application to reef researchers examining the ~~spatial-vertical~~ distribution of coral assemblages and coral growth dynamics (Montaggioni, 2005; Camoin et al., 2012; Dechnik, 2016) ~~. It can be applied to extrapolate by comparing outputs between modelling cores. This would enable the extrapolation of~~ knowledge gained from examining drill cores to areas of the reef where data ~~is are~~ scarce. It can also be used to understand environmental histories of cores where dating or classification of assemblages is difficult due to poor core recovery. Despite its 1-D limitation, the model can be applied to gain a 3-D picture of the environmental, ecological and geomorphological history of a specific reef. This can be achieved by defining multiple biological and environmental initial conditions representing, for example, the differences in assemblage types and hydrodynamic conditions between the windward and leeward margins of the reef (Cabioch et al., 1999; Dechnik et al., 2015; Salas-Saavedra et al., 2018).

5

10 Necessarily, *pyReef-Core* is also a simplified representation of a coral reef system and required a number of free parameters such as sediments, flow, Malthusian parameter, and community matrix parameters which needs to be defined for modelling. The task of finding these set of parameters that best describes a specific reef site and core data is challenging for several reasons. Firstly, empirical estimates of environmental tolerance thresholds of given assemblages are scarce in the scientific literature making their estimation difficult (Camoin et al., 2012; Baldock et al., 2014; Dechnik et al., 2017). Therefore results interpreted from the modelled environmental threshold represent hypotheses that must be tested and validated against additional real, physical measurements on reefs. Secondly, reefs experience a variety of natural sedimentation regimes due to the variable morphologies (Hopley et al., 2007) and flow regimes due to the position of reefs in respect to the dominant swell (Dechnik, 2016) and proximity to the coast (Larcombe et al., 2001). Consequently, it is difficult to construct a model that ~~represents a full~~ fully represents complex reef system dynamics simultaneously. Thirdly, estimation of the interaction matrix coefficients and Malthusian parameters remains difficult (Clavera-Gispert et al., 2017), specifically when considering coral assemblages ~~dynamic at temporal scale~~ dynamics at the temporal scale (decadal to centennial) relevant to *pyReef-Core*. Yet, interpretations of these parameters from ecological modelling studies provide ~~useful information~~ a useful guide in regards to reef biozonation and assemblages competition (Lang and Chornesky, 1990; Grigg, 2002; Connell et al., 2004). Finally, modelled ~~coral reef vertical~~ vertical accretion or growth patterns in *pyReef-Core* ~~is are~~ non-linear reflecting the natural complexity of coral reef systems and the biological and physical interactions ~~happening occurring~~ at reef scales. It poses the ~~problem of~~ problems for calibrations and the underlying uncertainties inherent to our simplified approach (Burgess and Wright, 2003; Warrlich et al., 2008; Clavera-Gispert et al., 2017). Nevertheless, our model represents a shift from the standard accommodation-forced geometrical models ~~(Gale et al., 2002)~~ (Dalmasso et al., 2001; Gale et al., 2002; Burgess et al., 2006) where coral reef stratigraphy is con-

25

trolled mainly by changes in sea-level. Even if our approach is a simplification of natural processes, the simulated stratigraphic patterns are a sum of simultaneous, interacting tectonic, biological, physical and sedimentological processes.

*pyReef-Core* can be described as a multi-dimensional (i.e. many parameters) and multi-modal (i.e. non-unique solutions) forward model where numerous combinations of interacting parameters could potentially produce identical sequences (Burgess et al., 2006; Burgess and Prince, 2015). Given a specific reef core dataset and *pyReef-Core*, the task of finding the model parameters space that best describes the reef core data can be defined as the inverse modelling problem (Jessell, 2002). Mosegaard and Sambridge (2002) highlighted the importance for Monte Carlo methods in analysis of nonlinear inverse problems where no analytical expression for the forward relation between data and model parameters is available. Markov Chain Monte Carlo (MCMC) methods can straight-forwardly quantify uncertainty in model assumptions and parameters (Andrieu et al., 2003).

- 5 This is particularly useful for SFM approaches (Warrlich et al., 2008) that requires optimisation techniques that lack uncertainty quantification. However, Bayesian inference methods have rarely been applied to reef modelling, despite evidence of their usefulness when handling models with complex, interrelating parameters (Gallagher et al., 2009). ~~One future development avenue for *pyReef-Core* will consist in integrating a Bayesian inference scheme (MCMC) to provide a methodology for estimation of near-optimal values and uncertainty quantification of free parameters in the model.~~ A useful application of such approach would
- 10 involve optimisation of environmental threshold and ecological modelling parameters, and then parametrising of the sediment input and fluid flow boundary conditions based on empirical measurements. ~~Observing cores produced by this method may help in creating 2-D or 3-D conceptualisations of reef stratigraphy.~~

## 7 Conclusions

- Bridging the gap between ecologists and geologists views of coral reef system dynamics is challenging. In this paper, we present
- 15 *pyReef-Core*, a 1-D deterministic, carbonate SFM that simulates vertical reef sequences comparable to those found in actual drill cores. The model serves as a basis for investigating the relationship between the key biological processes (i.e. function of coral assemblages interactions based on the GLV equations) involved in coral reef growth, and the influence of changing environmental factors (e.g. sea-level, tectonics, ocean temperature, [acidity-pH](#) and nutrient). The significance of the approach lies in its ability to incorporate coral community dynamics into reef growth modelling and understand the responses of coral
- 20 reefs to environmental disturbances on centennial to millennial timescales at the reef-scale. Exploration of these intermediate scales is crucial to better understand the enduring growth response of corals in the face of climatic and environmental changes that are expected to have lasting impacts on reefs into the future. As shown in the case studies, generated model predictions cohere well with data and provide a means for explaining observed assemblage patterns. It can help to better constrain the tolerance of shallow-water corals to long-term environmental disturbance, and to quantify the relative dominance of sea-level,
- 25 tectonics, as well as hydrodynamic energy and sediment input on reef growth.

*Code and data availability.* The source code (written in Python 2.7.6) with examples (Jupyter Notebooks) is archived as a repository on [Github](#) and Zenodo ([doi:10.5281/zenodo.1080115](https://doi.org/10.5281/zenodo.1080115)). The code is licensed under the GNU General Public License v3.0. The easiest way to use *pyReef-Core* is via our [Docker](#) container (searching for **pyreef-docker** on Kitematic) which is shipped with the complete list of dependencies and the case studies presented in this paper.

30 *Competing interests.* The authors declare that they have no conflict of interest.

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