



Bayesian semi-individual based model with approximate Bayesian computation for parameters calibration: Modelling Crown-of-Thorns populations on the Great Barrier Reef



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ABSTRACT

Outbreaks of Crown-of-Thorns Starfish (CoTS), *Acanthaster planci*, are a major cause of coral decline on the Great Barrier Reef, second only to cyclones. Although various models have been developed in the past to assist management decision making, most of these models were cohort-based deterministic descriptions with little inclusion of parameter and individual uncertainties, or they were structured around a generic ecological modelling framework, or they were not calibrated with observational data.

A major challenge of statistical modelling occurs when estimation of the likelihood is computationally expensive or even intractable. However, approximate Bayesian computation (ABC) can be a convenient solution to this problem. In this study, we developed a semi-individual agent-based model for CoTS. Unlike previous models, this model amalgamated a species-specific individual-based process model with statistical methods of parameter estimation, namely replenishment ABC (RABC) and ABC-rejection. This Bayesian modelling framework facilitates quantification of the uncertainty in parameter estimation while the individual-based aspect of the model enables it to take into account individual variation in life histories.

In this relatively complex setting and in the absence of an informative prior, ABC-rejection was unable to efficiently estimate the posterior distribution of model parameters within a reasonable time frame. In contrast, RABC demonstrated promising results in estimating model parameters. The results of posterior predictive checks showed that most observations were within the 95% predicted intervals. Therefore, the semi-individual agent-based model developed in this study showed promising ability to accurately predict the general population trends at the three locations studied. The results of modelling identified a strong link between observed sharp declines in CoTS populations and depletion of their food (i.e. coral cover).

As outbreaks of CoTS have caused substantial decline in the coral cover of the Great Barrier Reef, this model should eventually be combined with operation models to predict the outcome of different interventions, and the design of optimal control strategies.

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1. Introduction

The world's coral reefs are in a state of decline. On the Great Barrier Reef (GBR), predation by Crown-of-Thorns Starfish (CoTS), *Acanthaster planci*, at outbreak densities is the major cause of coral decline, second only to cyclones (Deáth et al., 2012). On the GBR, CoTS often occur at low background densities (Moran and Deáth, 1992), but episodically (historically every 15 to 17 years Pratchett et al., 2014) can increase in numbers, presumably triggered by

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an alignment of environmental and biotic factors (Pratchett et al., 2014; Wooldridge and Brodie, 2015; Fabricius et al., 2010). CoTS outbreaks can last several years before a sudden dramatic reduction in the population occurs (Moran, 1986). Since the start of scientific surveys in the late 60s, the GBR has experienced multiple boom-and-bust CoTS cycles, with the size of booms, duration and frequency of cycles varying greatly both spatially and temporally (Moran, 1986; Pratchett et al., 2014). Although there is no general consensus regarding the causes of these population cycles on the GBR, it is generally accepted that there are primary and secondary outbreaks. Pratchett et al. (2014) suggested that primary outbreaks are the result of progressive accumulation of individuals over time in a so-called “initiation box” between Cairns and Cooktown, a relatively small area of reefs with high internal connectivity and episodically high connectivity to the central and southern GBR (Hock et al., 2014; Wooldridge and Brodie, 2015). In contrast, secondary outbreaks result from the accumulation of sexually mature and highly fecund adults in the initiation zone, high larval survival in the water column, and export of large numbers of CoTS larvae to downstream reefs.

Various CoTS meta-population models have been developed in the past to investigate different aspects of CoTS population dynamics (McCallum, 1990; Morello et al., 2014; Fabricius et al., 2010; Scandol, 1993). Fabricius et al. (2010) developed a simulation model to investigate the role of water-column chlorophyll in driving the initiation of CoTS outbreaks. This age-based population model was built on the earlier CoTS simulation model, CotSim (Scandol, 1993), with an additional element enabling the simulation of CoTS abundance with different levels of chlorophyll. The other major difference between these two models is the complexity of the hydrodynamic model of water currents used. Both models used simulated ocean current data to inform larval dispersal. Specifically, CotSim adopted the larval dispersal model developed by Dight (1992) while Fabricius et al. (2010) used the current simulation by James et al. (2002). The latter hydrodynamic model involves a larger number of input variables. All of these simulation models were designed to predict changes in CoTS abundance under a specific scenario, e.g. varying chlorophyll level, while keeping other parameters at predefined levels. These levels, however, were not calibrated against observational data.

Morello et al. (2014) developed an intermediate complexity model for ecosystems (MICE), which is based on the trophic interaction between large predatory fishes, CoTS and fast- and slow-growing corals, to test the effectiveness of different control strategies. This model used quasi-Newton automatic differentiation to infer model parameters from observational data collected around Lizard Island. This is the only model to date that has utilised observational data. Although it is the most recognised CoTS modelling tool for decision making (Babcock et al., 2014), it has various limitations. For example, the model structure was framed around the assumption of a trophic cascade, therefore, the model assumed some level of predation on adult CoTS. Aside from the giant triton, *Charonia tritonis*, which was heavily harvested in the 60s and has yet to recover from over-exploitation, predations on healthy and uninjured adult CoTS by other species has rarely been observed (Cowan et al., 2017; Sweatman, 1997). Furthermore, even though MICE was composed of multiple submodels, only four parameters were inferred directly from the data (i.e. stock-recruitment residual in 1996, immigration residual in 1994, natural mortality and effect of fast growing coral on CoTS mortality) while other major parameters were chosen *a priori* and kept constant. Consequently, in order to fit the data, the model required an *ad hoc* assumption of a low level of immigration and self-recruitment in most years, except for 1994 to 1996 when a sudden pulse of immigration and self-recruitment to reefs around Lizard Island was needed to reconstruct two peaks observed in outbreak years. There is, however, little

empirical evidence to support these assumptions. Furthermore, the CoTS population size-structure from October 1996 to January 1999 does not support the assumption of additional recruitment to Lizard Island (Pratchett, 2005), and most nearby reefs had only a single abundance peak during this outbreak period.

To date, CoTS models have been mostly deterministic and have adopted the age-based approach. While informative, deterministic approaches have two major limitations: they have limited ability to quantify the uncertainty in parameter estimates, and they fail to take into account individual variation in life histories. In a deterministic modelling framework, simulations are carried out using parameters of a fixed value, and to account for parameter uncertainties, additional uncertainty and sensitivity analyses are used to determine parameters which are most or least influential on modelling results and contribute most prediction uncertainty, thus requiring additional research in order to reduce model/output uncertainty (Hamby, 1994).

To address the limitations outlined above, we present a Bayesian probabilistic approach to the problem that places priors on the input parameters and uses empirical data to infer posterior distributions of key parameters. Using posterior distributions to represent uncertainty in parameter values makes it possible to avoid selecting a single set of parameter values, and offers additional uncertainty and sensitivity analyses.

In recent decades, ecological modelling has shifted from the traditional population and bio-geo-chemical dynamic models to individual agent-based models (IBM) (DeAngelis and Mooij, 2005; Grimm and Railsback, 2005, 2012), due to their ability to address two fundamental characteristics of natural populations: (1) that individuals are different, and (2) that interactions between individuals and their environment occur at a local scale (Huston et al., 1988). In IBMs, the simulated population is composed of individual agents representing individuals (or groups) of the species of interest. These may have different traits (DeAngelis and Mooij, 2005), including their foraging behaviour and life histories, and differing degrees of plasticity of those traits determined by their phylogeny. Because each agent is modelled separately, there is in principle no limit to the temporal and spatial resolution that can be taken into account. Modelling at such fine resolutions can also enhance forward prediction to assess the impact of changing local and global environmental conditions. Consequently, IBMs can provide more realistic predictions over longer time frames compared to population-based modelling tools (Judson, 1994).

While useful in this context, IBMs are computationally expensive. As the number of agents increases, the time required to process all individuals increases substantially. Most invertebrates produce an enormously large number of eggs, but this is accompanied by high mortality. Therefore, for computational feasibility, we propose a semi-individual based approach in which individuals born at the same time step are aggregated into a single cohort and later become individual agents.

Parameter estimation for complex process models has long been studied in statistical modelling. In the past, a major challenge occurs when estimation of the likelihood is computationally expensive or even intractable. However, approximate Bayesian computation (ABC, Pritchard et al., 1999) can be a convenient solution to this problem. ABC has been successfully applied in genetic modelling (Beaumont et al., 2002; Toni et al., 2009), macroparasite evolution (Drovandi and Pettitt, 2011), in an ecological predator-prey model (Toni et al., 2009) and to calculate earthworm energy budgets (van der Vaart et al., 2015). There are several variations of ABC (Beaumont, 2010; Marin et al., 2012; Del Moral et al., 2012; Lenormand et al., 2013) that differ by computational method and construction and that have different characteristics with respect to the proposal mechanism, which impacts the efficiency in approximating the posterior. Notwithstanding these differences,

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