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Age and Growth of An Outbreaking *Acanthaster* cf. *solaris* Population within the Great Barrier Reef

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Abstract: Despite having been studied for more than 40 years, much about the basic life history of crown-of-thorns starfish (CoTS; *Acanthaster* spp.) remains poorly understood. Size at age—a key metric of productivity for any animal population—has yet to be clearly defined, primarily due to difficulties in obtaining validated ages and potentially indeterminate growth due to factors such as starvation; within-population variability is entirely unknown. Here we develop age and growth estimates for an outbreaking CoTS population in Australian waters by integrating prior information with data from CoTS collected from multiple outbreaking reefs. Age estimates were made from un-validated band counts of 2038 individual starfish. Results from our three-parameter von Bertalanffy Bayesian hierarchical model show that, under 2013–2014 outbreak conditions, CoTS on the GBR grew to a 349 (326, 380) mm (posterior median (95% uncertainty interval)) total diameter at a 0.54 (0.43, 0.66) intrinsic rate of increase. However, we also found substantial evidence ($\Delta\text{DIC} > 200$) for inter-reef variability in both maximum size (SD 38 (19, 76)) and intrinsic rate of increase (SD 0.32 (0.20, 0.49)) within the CoTS outbreak initiation area. These results suggest that CoTS demography can vary widely with reef-scale environmental conditions, supporting location-based mechanisms for CoTS outbreaks generally. These findings should help improve population and metapopulation models of CoTS dynamics and better predict the potential damage they may cause in the future.

Keywords: age estimation; Bayesian modeling; Great Barrier Reef

1. Introduction

Population outbreaks of crown-of-thorns starfish (CoTS; *Acanthaster* spp.) are a major contributor to coral loss throughout the Indo-Pacific [1–4]. On the Great Barrier Reef (GBR), for example, there have been four distinct episodes of outbreaks since the 1960s [5], and coral loss caused by these outbreaks is equal or greater than that caused by other major disturbances (e.g., severe tropical storms and climate-induced coral bleaching [3]). Moreover, minimizing or preventing outbreaks of *Acanthaster* spp. is considered one of the foremost management strategies to reverse sustained coral loss on the GBR (e.g., [6]). Effective management of CoTS outbreaks is, however, currently constrained by limited knowledge of CoTS demography [5,7], which is fundamental to understanding both the proximal and ultimate causes of outbreaks [8].

Outbreaks of *Acanthaster* spp. are variously attributed to their inherent life history characteristics, such as exceptional fecundity [9,10], versus anthropogenic and environmental changes that disrupt normal regulatory processes [11–13]. However, there is limited data on differences in population demographics within outbreak or non-outbreak populations of CoTS, which would help to resolve the relative importance of intrinsic versus extrinsic processes. Most studies of CoTS (e.g., [14–16]) are initiated after starfish densities have already increased to outbreak levels, and demographic information is largely limited to estimates of abundance and size structure. Some studies have used size structure to estimate age structure, and thereby reconstruct the events that led to the particular outbreak (e.g., [17,18]), and resolving when and where CoTS outbreaks are initiated is fundamental for establishing potential causes or triggers for outbreaks [13]. However, the relationship between size and age for CoTS may be obscured by vagaries in growth due to food availability and environmental conditions [19,20], leaving an important gap in our ability to quantify demographic rates from size alone.

Size-independent proxies of individual age have been explored, including spine length, age pigments, and growth-ring-like pigment bands on spines [21], with the most promising technique for estimating individual ages based on pigment banding [22]. Validation of band counts has been made for some younger age classes (age three to five years) in a mark-recapture context, with 21 of 22 recaptured individuals having added a single growth band after 12 months at liberty on Davies Reef, Australia [23], and evidence of spine growth (mean \pm SE 0.72 ± 0.08 mm in eight months) via tetracycline markers present in 85 recaptured individuals 15.5–46.5 cm with estimated ages of one to nine years [24]. However, much about the relationship between size and age in CoTS remains unknown, including the exact mechanism by which banding occurs. However, seasonality in the reproductive physiology and life history of CoTS on the GBR is a strong candidate [25].

The current outbreak of CoTS on the GBR was first spotted in 2011, near Lizard Island in the northern management sector [26]. Given repeated association with the initiation of outbreaks [13,17,27,28] in the area between Lizard Island (14.7 S) and Cairns (16.9 S), this region has been dubbed the CoTS ‘initiation box’ and is subject to intense surveillance and research (Figure 1). To explore potential inter-reef variability in CoTS demographics within this critical area, we undertook pigment banding of wet CoTS spines to estimate size at age for CoTS collected among reefs within or near the initiation box, using a Bayesian hierarchical approach.

2. Materials and Methods

A total of 3759 CoTS were collected between October 2013 and September 2014 from four to five reefs within each of four different sub-areas of Australia’s Great Barrier Reef (Table 1). All starfish were collected while snorkeling or diving using hooks and poles. Starfish were kept alive in 500 L tanks connected to high flow-through sea-water systems on live-aboard boats or at the research station on Lizard Island for a maximum of 20 h before being processed. During processing, starfish were removed from the water and placed on flat surface for 30–90 s before measuring maximum diameter along two perpendicular axes. Ages were estimated from a total 2038 CoTS based on sampling of replicate spines from a maximum of 200 starfish per reef (Table 1), for individuals from which we could extract band counts. For those individuals selected for inclusion in demographic analyses, the longest spine from the upper portion of each of three to six arms (close to the disc) was removed and stored dry for later processing. Spines were soaked in 5 mL of 10% sodium hypochlorite solution for a minimum of 2 h to remove tissue. The spines were then thoroughly rinsed with fresh water and then soaked in freshwater for a minimum of 3 h before visually inspecting banding patterns (Figure 1), following [22]. Age readers recorded both the number of distinct bands observed on each spine, as well as a subjective quality score (Q_{score}) between 0 (unreliable) and 1 (highly reliable) that reflected their belief in their ability to resolve clear individual bands.

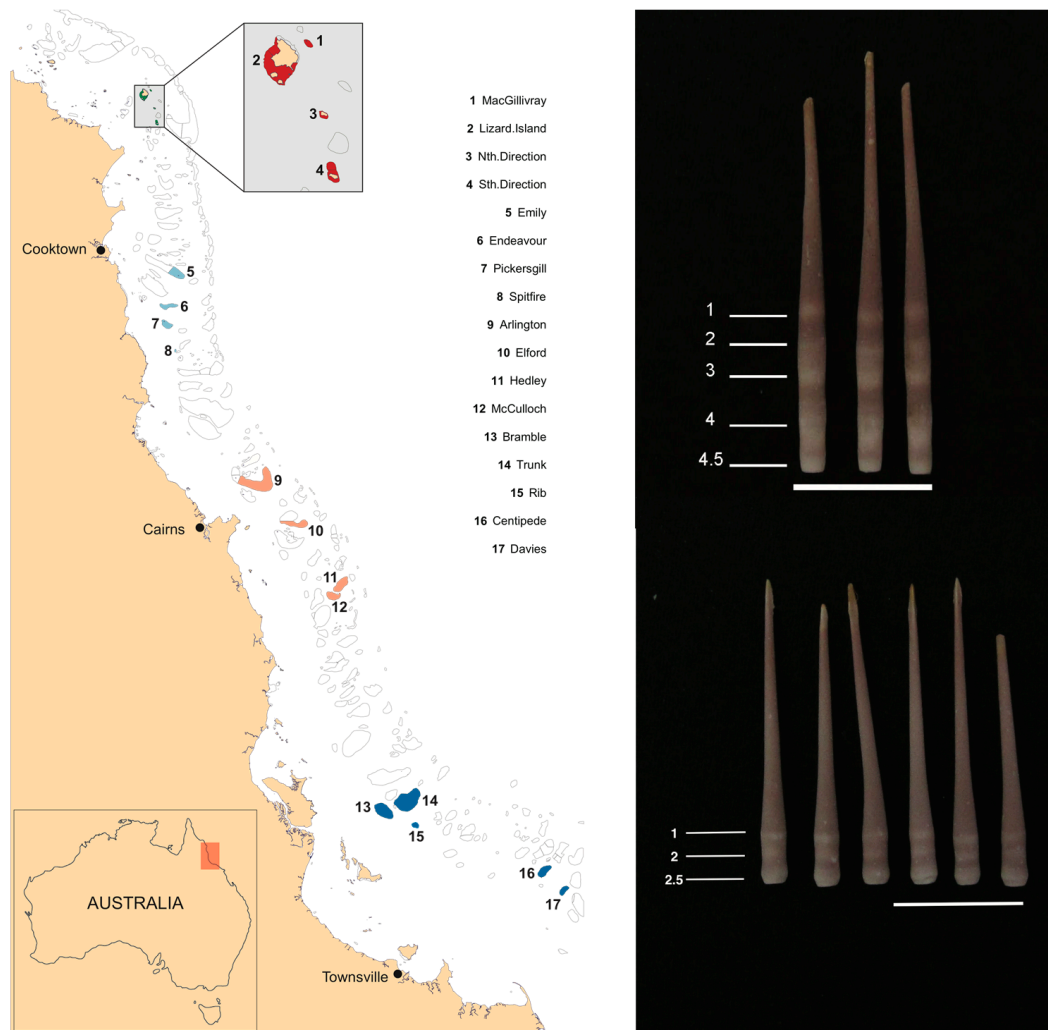


Figure 1. Great Barrier Reef study region reefs sampled for crown-of-thorns starfish (CoTS; *Acanthaster* spp.), October 2013 and September 2014 (left panel). Reefs are colored according to region. Spines selected for band counting from two starfish (right panels), showing distinct banding counts from 1 to 4.5 (top panel) and 1 to 2.5 (bottom panel), scale bar represents 1 cm.

Table 1. Summary table of collections of crown-of-thorns starfish on the GBR between October 2013 and November 2014. Only a subset of starfish (≤ 202 individuals per reef) was used in demographic analyses.

Region	Reef	Reef Size (km ²)	n (Abundance)	n (Demographics)
Northern sector of the initiation box (around Lizard Island)	Lizard Island	13.62	333	202
	MacGillivray Reef	0.92	333	200
	North Direction	0.69	305	198
	South Direction	3.32	259	200
Total			1230	
Central sector of the initiation box (off Cooktown)	Emily Reef	35.31	348	200
	Endeavour Reef	20.40	340	200
	Pickersgill Reef	18.82	322	200
	Spitfire Reef	3.12	300	200
Total			1310	

Table 1. Cont.

Region	Reef	Reef Size (km ²)	<i>n</i> (Abundance)	<i>n</i> (Demographics)
Southern sector of the initiation box (off Cairns)	Arlington Reef	127.75	334	200
	Elford Reef	39.68	89	89
	McCulloch Reef	26.31	308	200
	Hedley Reef	39.84	328	200
	Total		1059	
Southern edge of the outbreak (off Townsville)	Bramble Reef	62.99	75	75
	Centipede Reef	30.01	4	4
	Davies Reef	16.62	3	3
	Rib Reef	10.45	36	36
	Trunk Reef	121.60	42	42
	Total		160	
	Grand Total		3759	

Statistical Methods

We estimated the size-at-age relationship for CoTS from around the initiation box using a three-parameter formulation of the von Bertalanffy growth model, implemented in a Bayesian framework. The basic von Bertalanffy model defines growth relative to length as:

$$L_t = L_\infty - (L_\infty - L_0)e^{-kt}$$

where L_t is length-at-age t (typically in years, in our analysis the band counts), L_∞ is the maximum size, k is a growth coefficient and L_0 is the length-at-age zero. For our analysis, we modified this basic form to reflect specific dependencies in the data, with the various L parameters corresponding to CoTS diameters. Specifically, the model was parameterized as:

$$\begin{aligned} DIA_i &\sim N(\mu_i, \sigma_{obs}) \\ \mu_i &= L_{\infty r} - (L_{\infty r} - L_0)e^{-k_r IC_i} \\ IC_i &\sim N(5, 100) \\ C_{i,o} &\sim N(IC_i, \sigma_c / Q_{score,i,o}) \\ k_r &\sim N(k, \sigma_k) \\ L_{\infty r} &\sim N(L_\infty, \sigma_L) \\ \sigma_{obs}, \sigma_k, \sigma_L, \sigma_c &\sim U(0, 1000) \\ k &\sim N(0.235, 0.303) \\ L_\infty &\sim N(562.7, 37.6) \\ L_0 &\sim N(0.83, 2.11) \end{aligned}$$

where DIA_i was the observed diameter of an individual CoTS from reef r , and COU_i was the wet band count recorded by a single age reader. The IC_i parameter was an estimated latent band count for each individual CoTS, given the observed count from each reader ($C_{i,o}$) and an estimated standard deviation scaled by their subjective quality scores ($Q_{score,i,o}$). The σ parameters represent standard deviations. This approach allowed us to build on previous size at age data (from Figure 5 of [5]; model results presented in Supplemental Table S1); explicitly integrate band counts and quality scores; and hierarchically estimate reef-scale demographics based on sub-populations collected from individual

reefs. Models were coded using the PyMC3 framework [29] in Python, with inferences made using gradient-based Hamiltonian MCMC sampling in the form of a No-U-Turn Sampler (NUTS). The NUTS sampler is particularly appropriate for efficient sampling when parameters are highly correlated, as is common between parameters L_∞ and k .

Given that we lacked a validation approach for the wet band counts used for inference, we undertook an inter-reader comparison between the main age reader and a second age reader, both of whom read a sub-group of spines using a dry band count method. The dry band counts were used initially by both readers before switching to the wet count method that readers felt better resolved individual bands. A solitary reader then wet band counted the full set of 2038 starfish from which spines had been collected. We calculated within-reader variability, relative to the other, taking 95% percentiles overlapping with zero as lack of evidence for individual reader bias. It is important to note that this approach did not validate the ages reported, but demonstrated reliability of band counts.

3. Results

3.1. Age and Growth Estimates

Overall, the estimated maximum size of CoTS within the current outbreak was a 349 (326, 380) mm (posterior median (95% uncertainty interval)) total diameter, with an average 0.54 (0.43, 0.66) intrinsic rate of increase. However, the observed distribution of CoTS collected had a median size of a 285 (150, 400) (95% quantiles) mm diameter, with median band counts at age four, putting 93% of the data below age eight, where sizes begin to asymptote. Despite this, the reef-scale hierarchical model estimates showed a good fit to the observed data (Figure 2), capturing apparent reef-level differences in growth that were well supported compared with an alternative model that did not include the reef-level hierarchical structure ($\Delta\text{DIC} > 200$).

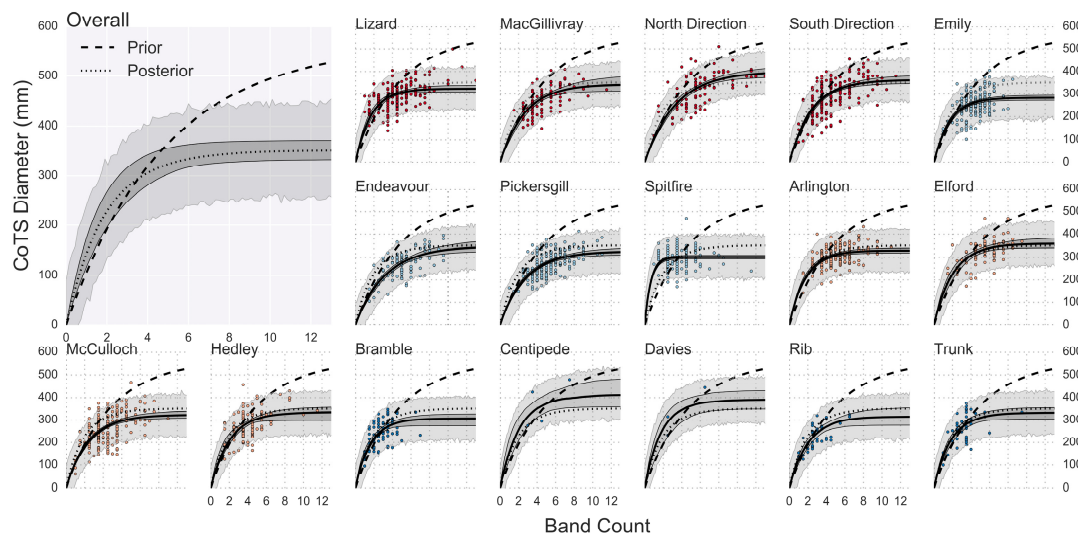


Figure 2. Bayesian hierarchical von Bertalanffy model posterior fit for the relationship between band counts and observed diameter of CoTS collected in the Great Barrier Reef CoTS initiation box, 2013–2014. Overall (grey panel, upper left) hierarchical posterior median von Bertalanffy curve (dotted line), 50% (dark grey area), and 95% (light grey area) uncertainty intervals (given highest posterior density); overall prior curve (dashed line) is from previous age and growth studies reported in [5]. Hierarchical model fits for each study reef (white panels) show inter-reef variation in posterior median curved (black lines) and uncertainty intervals, with points representing samples from the northern initiation box (red), central initiation box (light blue), southern initiation box (tan), and southern outbreak edge (dark blue).

Inter-reef variation in both L_∞ and k was substantial, with non-overlapping 95% uncertainty intervals both within and among sampling regions (Figure 3). As expected, the correlation between L_∞ and k was high, averaging -0.78 among reefs; however, posterior traces from the NUTS algorithm showed no evidence for lack of convergence and the overall (global) L_∞ and k estimates were uncorrelated (-0.01). Individual reef estimates for L_∞ ranged between 283 mm (Emily Reef) and 415 mm (Centipede Reef), with the majority lying around 340 mm; reef estimates of k ranged between 0.30 (North Direction Reef) and 1.5 (Spitfire Reef), averaging 0.54 overall.

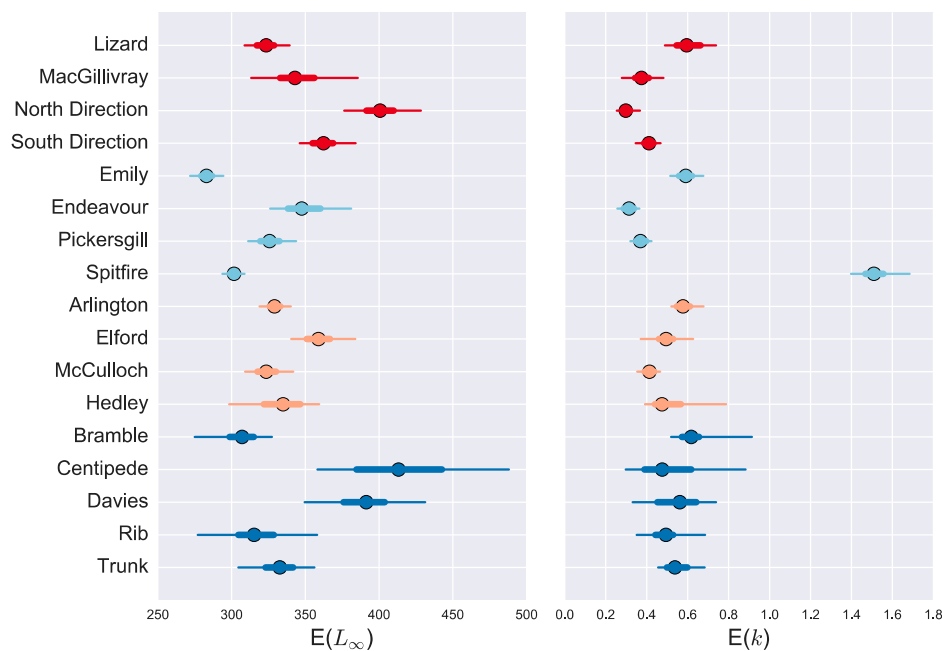


Figure 3. Bayesian hierarchical von Bertalanffy parameter posterior effect sizes for the relationship between band counts and observed diameter of CoTS collected in the Great Barrier Reef CoTS initiation box, 2013–2014. Points are highest posterior density medians, with 50% (thick lines) and 95% (thin lines) uncertainty intervals. Plot includes reefs sampled from the northern initiation box (red), central initiation box (light blue), southern initiation box (tan), and southern outbreak edge (dark blue).

3.2. Age Reliability

Dry band counts between agers A and B were broadly comparable, with equivalent average counts between ages two to seven, and a slight underestimation by ager B, relative to A, above age eight (Supplemental Figure S1); this relative discrepancy was less pronounced in estimates of ager A relative to B. Therefore, we found no suggestion of reader-specific bias in CoTS dry band counts across the range of assessed ages.

4. Discussion

The demography of *Acanthaster* spp. is considered to be extremely plastic, whereby adult growth and longevity are strongly dependent on local environmental conditions, such as food availability, temperature, and wave exposure [19,20,30]. For this reason, the relationship between size and age (and the capacity to reliably assign starfish to a given cohort based on size) has been highly contentious. Our results provide substantial support for this theory, with the demography of age and growth varying substantially among closely related reefs and at varying stages of outbreak. Most notably, the asymptotic size of CoTS sampled across the 17 reefs in the northern GBR ranged from a <300 mm total diameter at Emily Reef to a >400 mm total diameter at North Direction.

Inter-reef variation in the life history of *A. cf. solaris* within the northern GBR, during the latest outbreak, is likely due to extrinsic factors (e.g., local environmental settings) rather than intrinsic population processes. Notably, extensive genotyping of the same CoTS sampled for this study found no genetic structure among reefs [31], suggesting that all starfish sampled are highly related and have a common origin. Variation in growth is unlikely, therefore, to have any genotypic basis. More relevant is the local density of *Acanthaster* spp. and the stage of the outbreak at each reef, whereby high asymptotic sizes (L_{∞}) occur at reefs (Centipede Reef and Davies Reef) with low abundance of CoTS, especially relative to the size of the reefs. Moreover, outbreaks are yet to become established at these locations, such that the larger CoTS sampled have likely grown up with very limited competition for food. At high densities (during outbreaks), *Acanthaster* spp. appear to have highly constrained, finite growth and survivorship, which has been linked to strong intraspecific competition and rapid depletion of prey resources [32]. The smaller L_{∞} estimates from this study come from reefs (e.g., Lizard Island, Emily Reef and Spitfire Reef) where outbreak densities have been well established for several years. The smallest asymptotic sizes recorded during this study also correspond with modal sizes of CoTS recorded (300–350 mm total diameter) during established outbreaks on the GBR in the 1990s [17,33].

Despite inter-reef differences in the demography of CoTS, the general pattern of growth is characterized by rapid initial growth (when starfish are one to three years of age), followed by decelerating growth approximately three to four years post-settlement, and finally, an extended period of very limited growth (Figure 2). This is consistent with determinate growth shown by [20] for individual CoTS that were reared from in vitro fertilization of gametes obtained from CoTS collected on the GBR and then maintained in captivity for eight years. However, [20] readily acknowledged that determinate growth (with asymptotic sizes of 300–400 mm TL) was inconsistent with records of very large (>750 mm) *Acanthaster* spp. from the GBR [23], and may have been an artifact of captivity or limited food availability. Conversely, determinate growth may occur due to the increasing diversion of energy from somatic growth to gametogenesis [34], which is consistent with disproportionate investment in reproduction with the increasing size of CoTS on the GBR [10]. Elsewhere, sustained growth of *Acanthaster* spp. has been documented for up to seven to 13 years [18], resulting in asymptotic sizes >450 mm, as used to generate priors for this study, which may have occurred due to an abundance of prey resources, limited reproductive investment, or in low density populations.

While comparisons of estimated ages across two different readers show remarkable consistency, and demonstrate reliability in band counts, this does not necessarily mean that density banding on the spines of *Acanthaster* spp. is an effective proxy for the age of individual CoTS. Validation of age estimates fundamentally requires absolute determination of growth increment frequency, particularly the age of initial band formation [35], which has only been conducted in a single mark-recapture study that we are aware of [25]. Because our study duration was only a single year, we were unable to validate the ages estimated. Herein, we assumed the first band count represents the start of year two, based on the reported emergence of CoTS around age two [5]. Despite this important issue, the consistent annual reproductive cycle of CoTS along the GBR [5,25] suggests that our ages should be consistent with the seasonal banding previously reported from this area [23].

5. Conclusions

These findings point to fundamental differences in demographics of CoTS between outbreaking and non-outbreaking populations as alluded to by [8], who explained sporadic CoTS outbreaks using a bifurcated invasion model, where outbreaking populations are limited by their coral prey (a Holling Type-II functional response [36]) and non-outbreaking populations are governed by predation (a Type-III functional response). In light of our results, the implications of multi-modal population dynamics are that food-limited outbreaking populations grow more slowly and to a smaller ultimate size than those in non-outbreaking populations. Although such a mechanism remains unproven, our results emphasize that a clear understanding of variable CoTS demography under a

range of outbreak and environmental conditions will be fundamental to understanding the underlying cause(s) of population outbreaks. That we have failed to develop these kinds of flexible population models over the past three decades of CoTS research highlights a major gap in devising effective interventions for their control.

Supplementary Materials: The following are available online at www.mdpi.com/1424-2818/9/1/18/s1, Figure S1: Inter-reader comparability for dry counts of crown-of-thorns starfish (*Acanthaster cf. solaris*) spines; Table S1: Posterior parameter estimates for a Bayesian von Bertalanffy three-parameter model; Table S2: Reef-specific posterior parameter estimates for a Bayesian von Bertalanffy three-parameter model; Data S1: *cots_spines_wet_data.csv*; Wet band count data from CoTS initiation box, 2013–2014.

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Conflicts of Interest: The authors declare no conflict of interest.

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