

## **Are crown-of-thorns starfish populations chaotic?**

**Hamish McCallum**

Department of Zoology, University of Queensland,  
St. Lucia QLD 4072

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### **Abstract**

*A model of the interaction between coral and starfish is presented. The model is based on time-delayed differential equations, and addresses the question of whether crown-of-thorns starfish populations display chaotic dynamics. The preliminary conclusion is that they do not appear to do so: for most reasonable parameter combinations the model approaches a stable equilibrium, and even sustained cycles occur only for a narrow range of parameter values. It therefore appears that the apparent unpredictability in starfish population dynamics is generated mostly by stochastic variation, rather than by intrinsic properties of the interaction. This conclusion must, however, be qualified until further work is completed.*

### **Introduction**

The suggestion that the population dynamics of the crown-of-thorns starfish may be chaotic has been made a number of times (eg. Bradbury *et al.* 1985, McCallum 1992a). The life history of the starfish has features that contain the "seeds of chaos": a very high reproductive potential per generation, coupled with over-exploitation of a slowly recovering resource (coral).

Apart from the theoretical interest in demonstrating that the population dynamics of the starfish are chaotic, there are issues of practical importance. If the underlying dynamics of the coral-starfish interaction are chaotic, then very small changes in the

amount of interchange of larvae between reefs may result in very large differences in population behaviour (McCallum 1992a, b). Conversely, if the underlying dynamics of the interaction are not chaotic, and the observed variation in starfish numbers is caused purely by stochastic factors, then small changes in the rate of larval interchange will make only small changes in the resulting behaviour of the system. If a system is governed by deterministic chaos, long term prediction of its behaviour is impossible because of the sensitivity to initial conditions which is one of the hallmarks of chaos. However, since the underlying processes are deterministic, short term predictions of the behaviour of the system may be possible (Sugihara and May 1990).

Detection of deterministic chaos in any natural population is difficult. There are two possible approaches. First, an extended time series of population data may be interpreted, and either an attractor reconstructed (Takens 1981, Schaffer 1985) or a form of non-linear forecasting used (Sugihara and May 1990). Analysis of time series is unlikely to be successful with *Acanthaster*, because of the short run of available data (covering less than 30 years and two outbreaks for the Great Barrier Reef; Reichelt 1990). A second approach is to develop a model appropriate to the system, and demonstrate that, with appropriate parameter values, the model behaviour is chaotic. This was the approach used by Hassell, Lawton and May (1975) in their (largely unsuccessful) search for chaos in single-species insect systems, and is the approach taken in this paper.

## A Simple Model

### *Rationale*

The model which follows attempts to represent the following features of the starfish-coral interaction:

(a) Starfish have four distinct life history stages: pelagic eggs and larvae (approximately 30 days from spawning to settlement); algal feeding juveniles (approximately 6 months duration post settlement), coral feeding pre-reproductive juveniles (from 6 months to approximately 2 years post settlement); and reproductive adults, with an indefinite life span, but a life expectancy of approximately 2 years post maturity (provided coral is available). Larvae and algal feeding juveniles are assumed to have density-independent death rates, and hence are not explicitly included in the model, although the time delay caused by transition through these stages is included. For simplicity, and so that a stage-structured approach (Gurney, Nisbett and Lawton 1983) can be used, all pre-reproductive coral feeders are considered to be identical, as are all starfish of reproductive age. Two basic variables thus describe the starfish population:  $A(t)$  the number of coral feeding juveniles at time  $t$ ; and  $N(t)$ , the number of reproductive adults.

(b) Coral communities on the Barrier Reef have very high species diversity, and one of the main concerns about the crown-of-thorns is that it may have irreversible and fundamental effects on this diversity (Done 1990, Endean *et al.* 1989). Nevertheless, corals of the genus *Acropora* are the preferred prey of *Acanthaster*, the dominant taxon in terms of cover and amongst the most rapidly-recovering corals following crown-of-thorns attack. Coral is therefore included in this model as a single variable,  $C(t)$ , representing the coral cover per hectare, with parameters appropriate to *Acropora*.

Coral dynamics are represented by a simple logistic equation with carrying capacity  $K$  and intrinsic growth rate  $r$ . This simple representation assumes that coral recovery occurs through vegetative growth from colony remnants, rather than requiring settlement from off the reef.

(c) Starfish eat coral at a constant *per capita* rate, unless coral cover is very low, in which case the consumption rate will be restricted by the ability of starfish to locate coral. Although there is little evidence on the functional response of starfish to corals, a type II response seems reasonable, given the above argument. As obligate corallivores, there is little possibility that starfish will be able to switch to alternative prey at low coral densities, and thus generate a type III functional response. As reproductive age-starfish  $N(t)$  are much larger than immature starfish  $A(t)$ , I assume that only mature starfish have a noticeable effect on coral cover. Coral cover, however, has an effect on the death rate of both age classes of starfish, and also on the development rate of immature starfish.

There is no doubt that recruitment is highly stochastic in the crown-of-thorns, and that starfish populations on the scale of single reefs (of a size from 0.5 to 20 km) are open, and subject to substantial larval inflow and outflow. The objective of this paper, however, is to examine the possibility that the observed extreme temporal variability in crown of thorns populations may be at least in part a function of intrinsic population processes, rather than purely a result of environmental variation. Initially, stochastic effects are therefore not included.

## Model Structure

The model is constructed as a variant of the basic stage-structured approach of Gurney, Nisbett and Lawton (1983), in which the length of one or more stages is allowed to be a dynamic variable (Nisbett and Gurney 1983).

The following equations describe the system:

### Stages

#### Coral feeding juveniles $A(t)$

Duration of period  $\tau_A$  depends on coral cover, as does mortality  $\delta_A(t)$ . As juveniles are much smaller than adults, their impact on coral cover is negligible. Algal feeding juveniles must pass through an algal feeding stage of fixed duration  $\tau_j$ , during which they have a constant mortality rate of  $\delta_j$ .

**Adults  $N(t)$**

Indefinite lifespan, though mortality  $\delta_N(t)$  is dependent on coral cover, as is fecundity  $\lambda(t)$ . Starfish eat coral according to a type II functional response.

**Coral  $C(t)$**

Grows according to a simple logistic, with intrinsic growth rate  $r$  and carrying capacity  $K$ . It is significantly consumed only by adults, following a type II functional response, represented as

$$\text{consumption} = \frac{C(t)\eta}{C(t)+q} \quad (1)$$

where  $\eta$  is the coral consumption rate at high coral densities, and  $q$  describes the coral cover at which searching limitations become important.

**Auxiliary variables:  $P(t)$  and  $\tau_A(t)$**

The stage-structured formulation with variable time lags requires two variables in addition to the life history stages themselves for each stage with an explicit delay: one for the time lag, and a second for the proportion of individuals that survive through the stage.  $P(t)$  is the proportion of individuals surviving through  $A(t)$  at time  $t$  and  $\tau_A(t)$  is the time these individuals have spent as subadults. Thus, the basic equations are:

$$\frac{dA}{dt} = R_A(t) - \frac{g(t)}{g(t-\tau_A(t))} R_A(t-\tau_A(t)) P(t) - \delta_A(t) A(t) \quad (2)$$

$$\frac{dN(t)}{dt} = -\frac{g(t)}{g(t-\tau_A(t))} R_A(t-\tau_A(t)) P(t) - \delta_N(t) N(t) \quad (3)$$

$$\frac{dC(t)}{dt} = rC(t) \left(1 - \frac{C(t)}{K}\right) - \frac{N(t)C(t)\eta}{C(t)+q} \quad (4)$$

$$\frac{dP(t)}{dt} = P(t) \left[ \frac{g(t)\delta_A(t-\tau_A(t))}{g(t-\tau_A(t))} - \delta_A(t) \right] \quad (5)$$

$$\frac{d\tau_A(t)}{dt} = 1 - \frac{g(t)}{g(t-\tau_A(t))} \quad (6)$$

$$g(t) = \frac{bC(t)}{q+C(t)} \quad (7)$$

Here,  $g(t)$  is the growth rate of subadults at time  $t$ . The scaling parameter  $b$  is arbitrary. The death rate of subadults, as a function of coral cover, is given by:

$$\delta_A(t) = \frac{\mu_{A1}q + \mu_{A2}C(t)}{q+C(t)} \quad (8)$$

and the death rate of adult starfish is:

$$\delta_N(t) = \frac{\mu_{N1}q + \mu_{N2}C(t)}{q+C(t)} \quad (9)$$

The reproductive rate of starfish is similarly a function of their coral consumption rate. At high coral cover, it is assumed to reach a maximum of  $\Lambda$ , but is assumed to decrease with coral cover following the type II functional response. Hence, the per capita rate of larval production  $\lambda(t)$  is given by:

$$\lambda(t) = \frac{C(t)\Lambda}{q+C(t)} \quad (10)$$

As starfish are thought to spawn annually, a pulsed recruitment function  $R_A(t)$  is used, in which starfish reproduce only in the first two months of the year.

If  $T(t-\tau_j) < 60$ ,

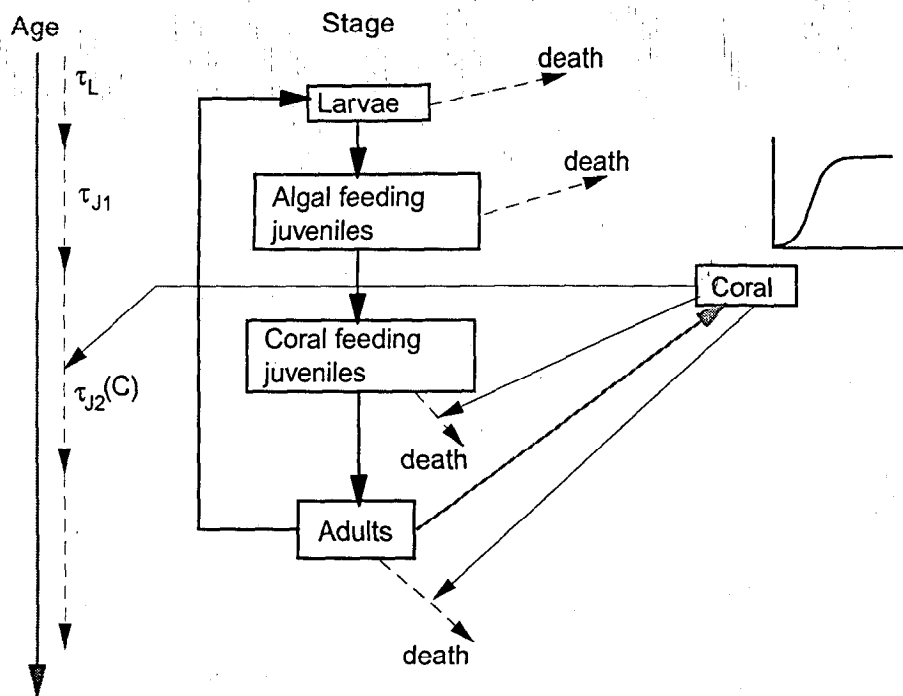
$$R_A(t) = \lambda(t-\tau_j) N(t-\tau_j) \exp(-\tau_j \delta_j) \quad (11)$$

otherwise,  $R_A(t) = 0$ .

Here,

$$T(t) = t - \text{Int}\left(\frac{t}{365}\right) \times 365 \quad (12)$$

The model structure is shown schematically in *Figure 1*.



**Figure 1: Structure of the model:** Compartments within the model are represented as boxes. Heavy black arrows represent transitions between life history stages of the starfish, and the heavy grey arrow represents removal of coral biomass by starfish. Time delays are represented on the time line to the left of the figure, and light arrows represent effects of coral cover on various parameters.

## Model Parameters

Parameter values used in these initial simulations are given in Table 1. These were derived from a variety of sources, principally Moran (1986), and will require extensive sensitivity testing. Time units for all parameters are days. Population density or other spatial units are in square metres.

| Parameter   | meaning   | value   |
|-------------|---|---------|
| $\tau_j$    | time in algal feeding stage                           | 180     |
| $\delta_j$  | death rate of algal feeders                           | 0.02    |
| $\mu_{A1}$  | death rate of juvenile coral feeders without food     | 0.05    |
| $\mu_{A2}$  | death rate of juvenile coral feeders with excess food | 0.002   |
| $\mu_{N1}$  | death rate of adults without food                     | 0.02    |
| $\mu_{N2}$  | death rate of adults with excess food                 | 0.002   |
| $b$         | arbitrary scaling parameter for growth                | 1       |
| $K$         | maximum coral cover                                   | 5,000   |
| $\eta$      | maximum rate of coral consumption by adults           | 0.164   |
| $r$         | rate of coral recovery                                | 0.00082 |
| $\Lambda$   | maximum annual starfish fecundity (recruits/adult)    | 100,000 |
| $\tau_A(0)$ | Time delay in subadult stage with excess coral        | 547     |

## Model Results

A complex model such as this requires extensive sensitivity analysis and exploration with a full range of parameter combinations. In this preliminary investigation, however, I have focussed attention on one particularly important parameter,  $q$ , which describes the way the coral consumption rate of the adult starfish (and hence their mortality) depends on coral cover. Biologically, this parameter will be a function both of the behaviour of the starfish and the physical patchiness of the coral resource. Figure 2 shows the functional response of the starfish (equation 1) for various values of  $q$ . The main point to be gained from this figure is that  $q=400$ ,  $q=350$  and  $q=330$  would be essentially indistinguishable in practice, and in each, the predation rate of starfish is not markedly reduced until coral cover drops to about 20%. In contrast, when  $q=800$ , the predation rate does not asymptote until coral cover is close to the carrying capacity of 5000 m<sup>2</sup>. Runs of the model for each of the values of  $q$  in Figure 2 are shown in Figures 3-6. When  $q=800$  (Figure 3), the system settles quite rapidly to an equilibrium with coral cover slightly depressed and a "chronic" starfish population of less than 10 ha<sup>-1</sup>. (Note that the short-period oscillations in both starfish and coral are a function of the pulsed annual recruitment, and are not related to predator-prey cycling.)

### Consumption rate

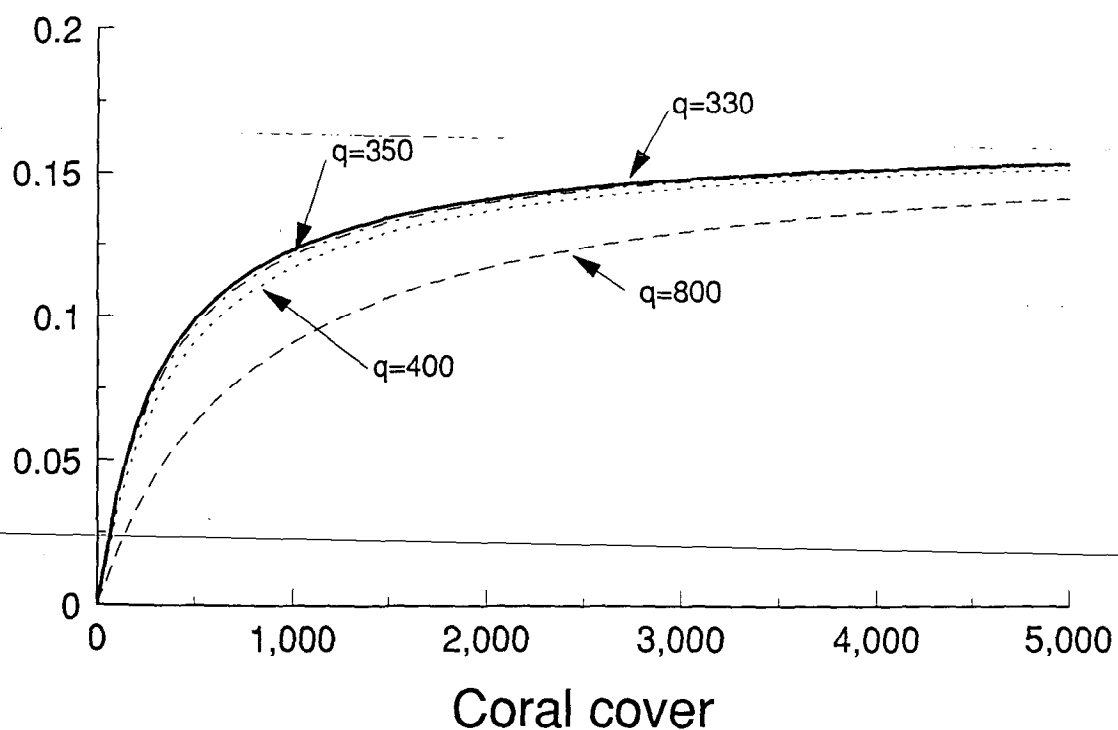


Figure 2: Representative starfish functional responses.

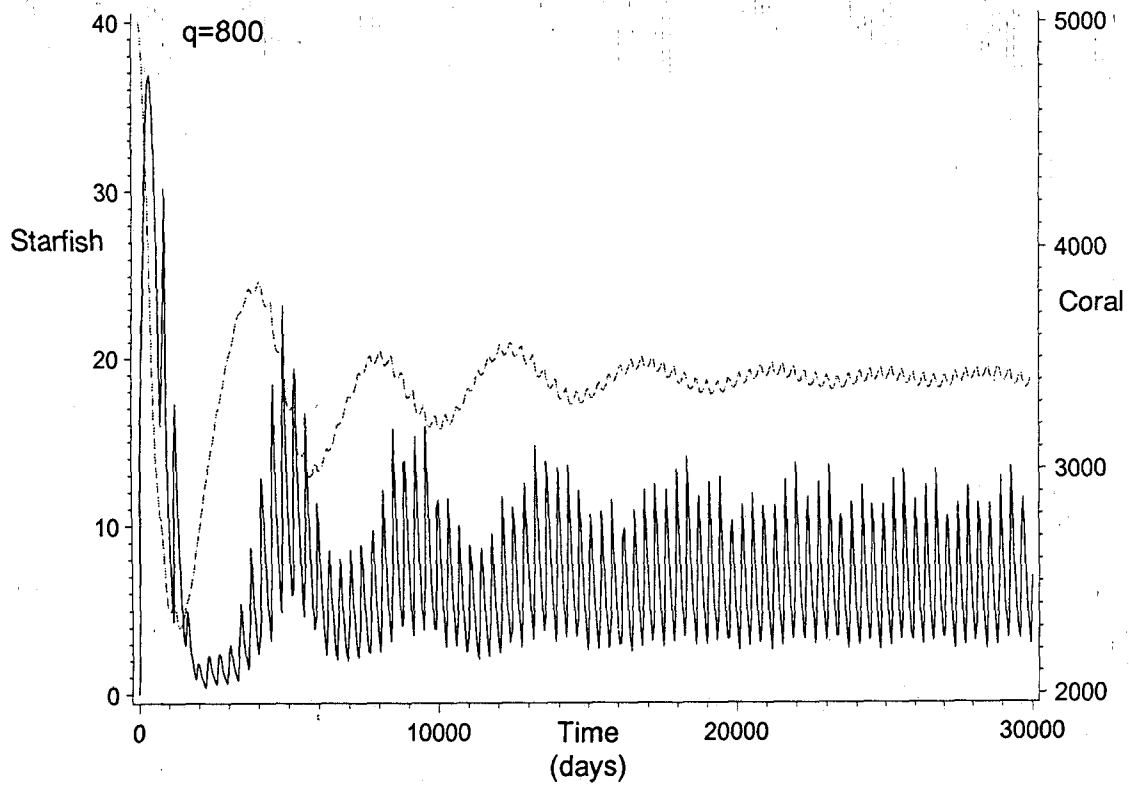


Figure 3: Adult starfish numbers and coral cover with  $q=800$ . Adult starfish numbers ( $\text{ha}^{-1}$ ) are shown as a solid line, scaled on the axis to the left of the figure. Coral cover ( $\text{m}^2\text{ha}^{-1}$ ) is shown as a dashed line, scaled on the axis to the right.

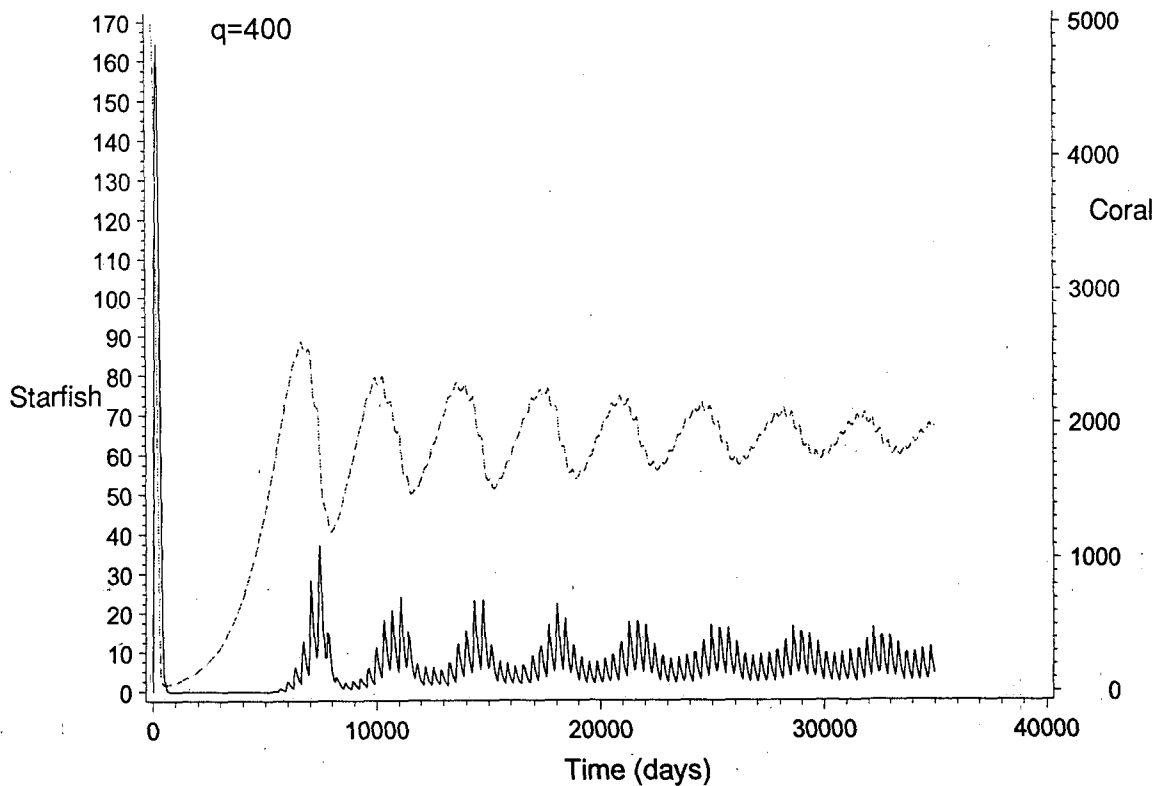
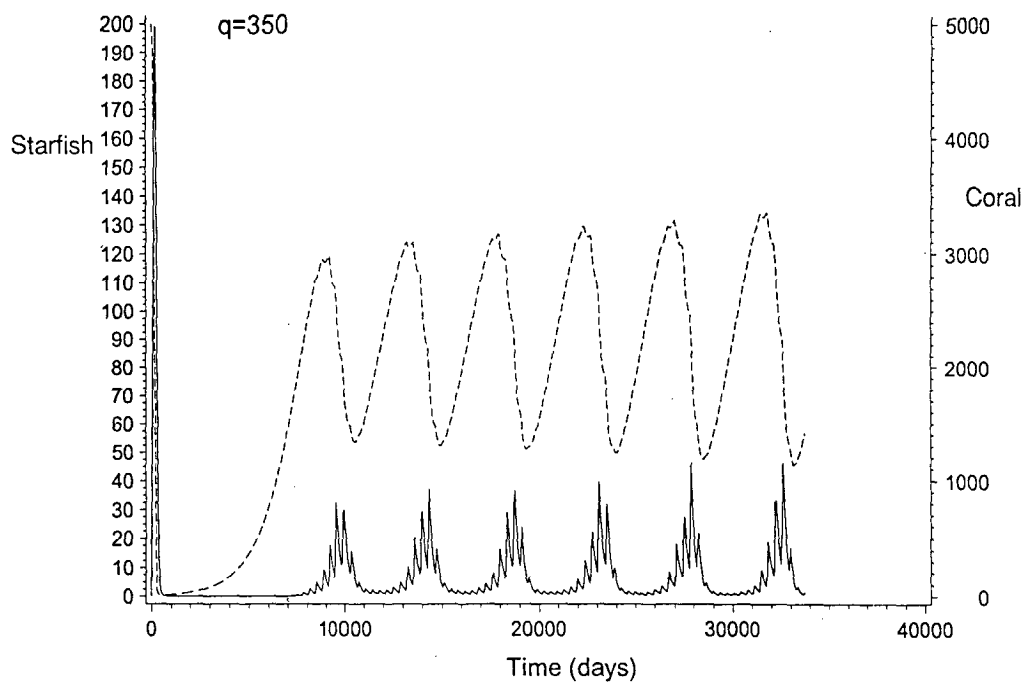
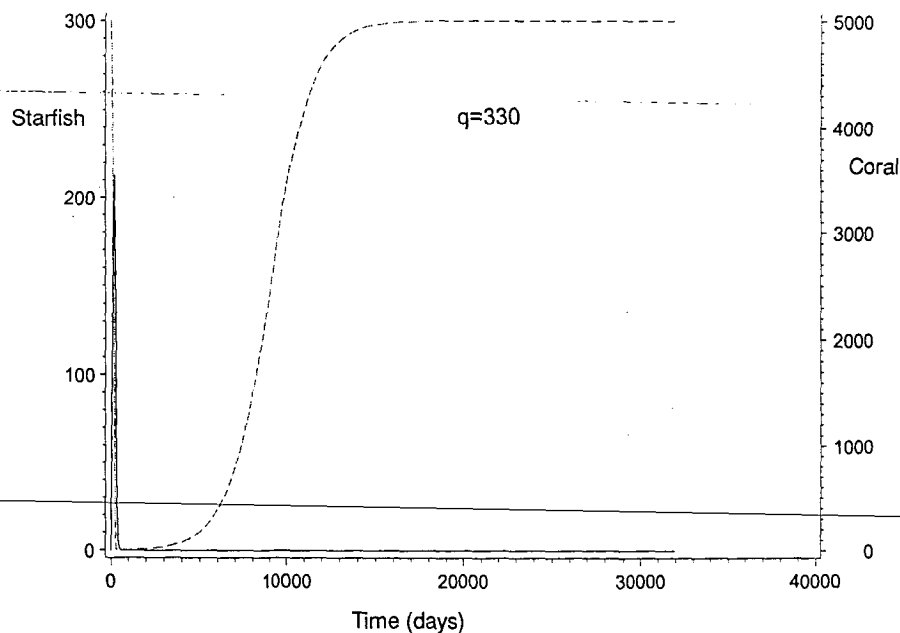


Figure 4: Adult starfish numbers and coral cover with  $q=400$ . Details as in Figure 3.



**Figure 5:** Adult starfish numbers and coral cover with  $q=350$ . Details as in Figure 3.



**Figure 6:** Adult starfish numbers and coral cover with  $q=330$ . Details as in Figure 3.

At  $q=400$  (Figure 4), starfish feeding efficiency is maintained at lower coral cover, and as might be expected, this results in both lower coral cover, and a less stable coral-starfish interaction. Nevertheless, the system appears to be settling toward an equilibrium. A slight decrease in  $q$  to 350 produces a very different result: the cycles do not damp out at all: a stable limit cycle with coral cover varying between approximately 1000 and 3500  $\text{m}^2$  occurs (Figure 5). Decreasing  $q$  to 330 (Figure 6) appears to result in a single starfish outbreak which depresses coral cover to such a level that there is no successful starfish recruitment in the next generation at all.



## Discussion

The results reported here are very preliminary investigations of a model which is likely to have extremely complex behaviour. A full analysis with far more runs together with stability analysis is now in progress. These preliminary results are nevertheless interesting. They suggest that *Acanthaster* population dynamics are not of the type that can be expected readily to generate deterministic chaos. This means that the apparent unpredictability in *Acanthaster* dynamics probably is not a result of deterministic processes: it is rather a function of environmental stochasticity. A further somewhat surprising result is that persistent cycles are apparent for a narrow range of parameter values only. For most values of  $q$ , the cycles damp to a constant "chronic" starfish population fairly rapidly. Thus "qualitatively stable cycles" (Bradbury *et al.* 1985) are unlikely to be generated purely by a deterministic coral-starfish interaction. As the approach to equilibrium is oscillatory, however, random variations may maintain cyclical behaviour indefinitely. The conclusion that *Acanthaster* populations do not exhibit chaotic behaviour must, at this stage, be qualified extensively. Although a wider range of parameter combinations has been explored informally than is reported on here, a systematic survey of the entire plausible parameter space has not yet been completed. It may be that an extensive region of chaos exists which has yet to be found. One problem of particular concern is the behaviour for small values of  $q$ . As reported above, the starfish go extinct if  $q$  is too small. This can be prevented by setting a "floor" on coral cover (corresponding to some sort of refuge from predation) but the level at which this floor should be set is hard to determine. As the size of such a floor can determine whether chaos occurs in much simpler models (McCallum 1992a), addition of a floor to this model may considerably complicate the results. A second possibility is that there may be a "chaotic repeller" existing somewhere in the system. Very few mathematical models have been published which combine, as this model does, the inherent cyclicity of exploiter-victim interactions together with extrinsic seasonal cyclical forcing. One of the few such models was developed by Rand and Wilson (1991), and is based on seasonally-forced measles and chickenpox epidemics. The model was found to have an equilibrium annual cycle, but the approach to this cycle was such that it took a very long time to reach it, and the transitory behaviour was chaotic in nature, around a "chaotic repeller". This meant that relatively small amounts of stochastic variation were sufficient to maintain very unpredictable behaviour in the long term. In other words, the deterministic structure of the model was acting as an "amplifier" of the random variation. This crown-of-thorns model may well behave in a similar manner. It has similarities in structure to Rand and Wilson's model, and it appears that whether the cycles and stable points shown in Figures 3-6 are reached depends quite sensitively on the starting conditions. The difficulty with confirming this possibility is that it is hard to distinguish numerical difficulties with the integration procedure from complex behaviour caused by the underlying model. Work is continuing on this problem. If the existence of chaotic repellers is confirmed, the practical implication will be that the amount of unpredictability or variation in adult crown-of-thorns numbers is very much greater than that expected on the basis of variable larval survival alone. In these initial investigations, I have focussed attention on the parameter  $q$ . This single parameter encompasses several features of the coral-starfish interaction. Whilst it represents the searching efficiency of the starfish, describing the way in which the feeding rate varies as a function of coral density, it is in fact a function of the spatial configuration of the coral as much as it is a feature of the feeding behaviour of the starfish. On a reef where

coral is present in a large, contiguous area, the rate of coral consumption by starfish will not decline markedly until the coral is greatly depleted: starfish move across the coral in a "feeding front" (McCallum *et al.* 1989) and can maintain maximal feeding rates until there is no longer live coral in front of the advancing starfish. Conversely, on reefs or reef systems where coral cover is very patchy, relatively small amounts of coral depletion will result in particular patches being depleted, causing the starfish to traverse areas with no coral in order to continue feeding, thus depressing the feeding rate. This raises an obvious and important question: on what scale and where is this model intended to be applicable? As the model implicitly assumes a stock-recruitment relationship, the starfish population must be defined at a level and in a region in which most recruitment is internal. Spatial structure within this population is then expressed through the parameter  $q$ . At present, it is unclear what physical scale this requirement corresponds to. The model is most useful in seeking to explain the origin of "primary outbreaks" in the area around 16°S (Johnson 1992) rather than the "secondary outbreaks" which appear to move southward down the reef in response to primary outbreaks. Whilst hydrodynamic models (James, Dight and Bode 1990) convincingly demonstrate that larvae may be dispersed over substantial distances, even in the northern part of the GBR, they cannot predict the proportion of larvae that are transported between reefs. It may be that most larvae are captured in the boundary layer and never leave their home reef.

## Acknowledgements

This work was funded by the Great Barrier Reef Marine Park Authority (GBRMPA) through the COTSREC research program, and partially undertaken whilst on Study Leave at the Centre for Population Biology, Imperial College, London.

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