

Large-amplitude periodic fluctuations in starfish–coral dynamics caused by feeding preferences

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(Received 26 May 1992; accepted 30 June 1992)

ABSTRACT

Antonelli, P. and Křivan, V., 1993. Large-amplitude periodic fluctuations in starfish–coral dynamics caused by feeding preferences. *Ecol. Modelling*, 67: 251–257.

In this paper we construct a model for the starfish, *Acanthaster planci*, feeding on several corals. The model is based on a control system with a strategy map. This allows to model food-preferences for the starfish. We show that food-preferences alone can induce robust large-amplitude periodic fluctuations.

INTRODUCTION

The crown-of-thorns starfish *Acanthaster planci* is a large coral-eating echinoderm and one of the most well-known animals on the Great Barrier Reef (GBR) of Australia. This notoriety derives from its periodic large-scale outbreaks recorded over the last 25 years. There are still many questions about this beast that are not fully answered (Moran, 1986). Perhaps the most important is: are *A. planci* outbreaks man-induced? There have been at least two International Conferences devoted to this and related questions (Antonelli, 1990; Bradbury, 1990). These two proceedings will bring the reader up-to-date.

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¹ Partially supported by NSERC A-7667.

² Partially supported by NSERC A-7667, University of Alberta Research Fund and CAS 18002.

The most basic behaviour of *Acanthaster* is perhaps its tendency to form large adult aggregations and, indeed, the vast majority of the modelling on its outbreaks have employed this mechanism to show how both local large amplitude fluctuations and global (whole GBR) starfish waves can be induced (Antonelli et al., 1992). In these models, every factor which alters aggregation behaviour directly influences the amplitude, period and stability of the cycle or its corresponding starfish-wave. Thus, for example, accumulative overfishing of several fish species together, can cause aggregations to surge to outbreak levels, as may freshwater run-off and other environmental conditions (cyclones etc.).

So from the presently accepted point-of-view secondary behavioural characteristics, like food-preference asymmetry, may not be relevant to understanding starfish outbreaks. In fact, while *A. planci* does exhibit such behaviour, 95% of all its coral prey species are largely devoured by the end of a particular outbreak (Moran, 1986). But, it is possible that food-preference still plays a major role in the early stages (or later) of a developing outbreak by stabilizing its continuance, for example. Whereas, in the most recent published paper (Antonelli et al., 1992) aggregation dynamics without food-preferences over the whole GBR is considered, in the present study we show that food-preferences alone can induce robust large-amplitude periodic fluctuations.

The point-of-view taken is fundamentally different from previous models in that *Acanthaster* is considered to be a strategist and controller of its own behaviour in regard to what it eats.

More specifically, the starfish chooses optimal control in myopic fashion, because it can only make decisions based on immediate circumstances in its local environment. We do *not* suppose that *Acanthaster planci* has knowledge of the past or future. Several factors are believed to determine the coral species consumed by the crown-of-thorns (Moran, 1986). They comprise for example abundance of corals, accessibility of corals, nutritional value of corals, etc.

Using optimal myopic strategies approach for food webs (Colombo and Krivan, 1993) we built a model for the starfish and n different corals that takes into account different feeding strategies of *A. planci*. The techniques of control systems, differential inclusions and discontinuous differential equations are used because the myopic strategies employed lead to such objects (Aubin and Cellina, 1984). We also give some simulations.

MODEL

The model consists of n different corals and the starfish. The densities of corals are denoted by x_1, \dots, x_n and the density of starfish is denoted

by x_{n+1} . In this paper we deal, for simplicity, only with autonomous case. Reformulation to non-autonomous case is straightforward. We assume that the dynamics are described by the following control system

$$x'(t) = f(x(t), u(t)) \tag{1}$$

$$u(t) \in U \tag{2}$$

where $U \subset \mathbf{R}^n$ is a given set of possible controls. We assume that

$$U = \{(u_1, \dots, u_n) \mid u_1 + \dots + u_n = 1, u_i \geq 0, i = 1, \dots, n\}$$

The meaning of the component u_i of the control vector is how much starfish feeds on the i -th coral. We want to stress here that it is starfish who “chooses” this control vector according to some criteria that are given below.

We specify the right hand side of the control system (1). We assume

$$f_i(x, u) = a_i x_i - \sum_{j=1}^n b_{ij} x_j x_i - u_i k_i x_i x_{n+1}, \quad i = 1, \dots, n \tag{3}$$

$$f_{n+1}(x, u) = \sum_{i=1}^n u_i x_i x_{n+1} - m x_{n+1}$$

Here a_i is the intrinsic natality of the i -th coral, b_{ij} is the interaction coefficient between the i -th and j -th corals, k_i is efficiency coefficient and m denotes the mortality rate of the starfish. All parameters are assumed to be non-negative.

Since it is assumed that the starfish shows feeding preferences, we will model these preferences using a strategy map $S(t, x)$ (Colombo and Křivan, 1993). In general we assume the following form of the strategy map

$$S(x) = \left\{ u \in U \mid d(x, u) = \max_{v \in U} d(x, v) \right\}$$

where $d: \mathbf{R}^n \times U \rightarrow \mathbf{R}$ is a given map. Let us note that $S(x)$ is a set-valued map, i.e. a map whose values are sets (Aubin and Frankowska, 1990). Optimal myopic solutions are trajectories of the following system

$$\begin{aligned} x'(t) &= f(s(t), u(t)) \\ u(t) &\in S(x(t)) \end{aligned} \tag{4}$$

Let us note that (4) may be rewritten as a differential inclusion

$$x'(t) \in F(x(t)) \tag{5}$$

where

$$F(x) := \{f(x, u) \mid u \in S(x)\}$$

For more information on differential inclusions we refer to Aubin and Cellina (1984). Any absolutely continuous function that satisfies (5) for almost all t is a solution of (5).

Now we give some possible forms for the function $d(x, v)$, following Moran (1986).

1. *Abundance of corals.* This strategy assumes that the starfish feeds on the most abundant coral. If we set

$$d_1(x, u) = \sum_{i=1}^n x_i u_i$$

we get the corresponding strategy map. Indeed, if for example $x_1(t) > x_i(t)$, $i = 2, \dots, n$, for some fixed t , using this map $d_1(x, u)$ we get the corresponding control vector to be $(1, 0, \dots, 0)$. Consequently, the starfish feeds on the most abundant coral, i.e. $x_1(t)$. Observations indicated this genus is *Acropora* (Moran, 1986).

2. *Maximal growth strategy.* Feeding on different corals gives different growth rates for the starfish, depending on the nutritional value of each coral. Let n_i denote the growth rate of the starfish feeding only on the i -th coral. Then the strategy when starfish maximizes its own growth rate corresponds to the following function

$$d_2(x, u) = \sum_{i=1}^n n_i x_i u_i$$

3. *Accessibility of corals on a reef to *A. planci*.* We may define a function $a_i(x_i)$ that measures "the accessibility" of the i -th coral for the starfish, a reasonable assumption is

$$a_i(x_i) = a_i x_i$$

Then, the strategy when starfish chooses the most accessible coral, corresponds to the following function

$$d_3(x, u) = \sum_{i=1}^n a_i x_i u_i$$

We believe that many other strategies one may think of will lead to the same (or similar) function form, $d(x, u)$.

Since the starfish may show not only one feeding preference, but in fact it may show several feeding preferences, we take the weighted sum of these

preferences that are given by functions $d_i(x, u)$, $i = 1, \dots, k$, namely we define

$$d(x, u) = \sum_{i=1}^k w_i d_i(x, u)$$

where w_i are given weights to each possible preference. It is assumed that $\sum_{i=1}^k w_i = 1$. These weights will depend on given locality, since it is well known that feeding preferences vary geographically (Moran, 1986). If we consider functions $d_i(x, u)$, $i = 1, 2, 3$ specified above, then function $d(x, u)$ may be written as

$$d(x, u) = \sum_{i=1}^n r_i x_i u_i \tag{6}$$

where r_i are nonnegative constants.

Two questions must be answered now. The first question concerns the existence of a solution to (4), the second one uniqueness of this solution. The existence of a solution of (4) with the right hand side given by (3) and the strategy map given by the function $d(x, u)$ in (6) follows from Colombo and Křivan (1993). Moreover, for function $d(x, u)$ defined by (6), uniqueness theorem was obtained in Kastner-Maresh and Křivan (1993). The uniqueness theorem is based on uniqueness theorem for discontinuous differential equations (Filipov, 1988).

A MODEL OF STARFISH FEEDING ON TWO CORAL SPECIES

In this part we give some simulations for a system consisting of the starfish and two different corals. Such system is described by

$$\begin{aligned} x'_1(t) &= a_1 x_1(t) - b_{11} x_1^2(t) - b_{12} x_1(t) x_2(t) - k_1 u_1 x_1(t) x_3(t) \\ x'_2(t) &= a_2 x_2(t) - b_{21} x_2(t) - b_{22} x_2^2(t) - k_2 u_2 x_2(t) x_3(t) \\ x'_3(t) &= u_1 x_1(t) x_3(t) + u_2 x_2(t) x_3(t) - m x_3(t) \end{aligned} \tag{7}$$

Let

$$d(x, u) = r_1 x_1 u_1 + r_2 x_2 u_2$$

and let

$$g(x_1, x_2) = r_1 x_1 - r_2 x_2$$

The corresponding optimal myopic strategy for the starfish will be

$$\begin{aligned} u_1 &= 1 && \text{if } g(x_1, x_2) > 0 \\ u_2 &= 1 && \text{if } g(x_1, x_2) < 0 \\ u_1 + u_2 &= 1 && \text{if } g(x_1, x_2) = 0 \end{aligned}$$

Numerical simulations for different values of parameters are given in Fig. 1. The following parameters were used: $a_1 = 1.0$, $a_2 = 2.0$, $b_{12} = b_{21} = 0.05$, $r_1 = 1$, $r_2 = 2$, $m = 0.5$. The parameter b_{11} was varied. Moreover for simulations we set $b_{11} = b_{22}$. Although our system is in fact Filippov regularization of a differential equation with discontinuous right-hand side, we see similar behaviour as in the case of the Hopf bifurcation for differential

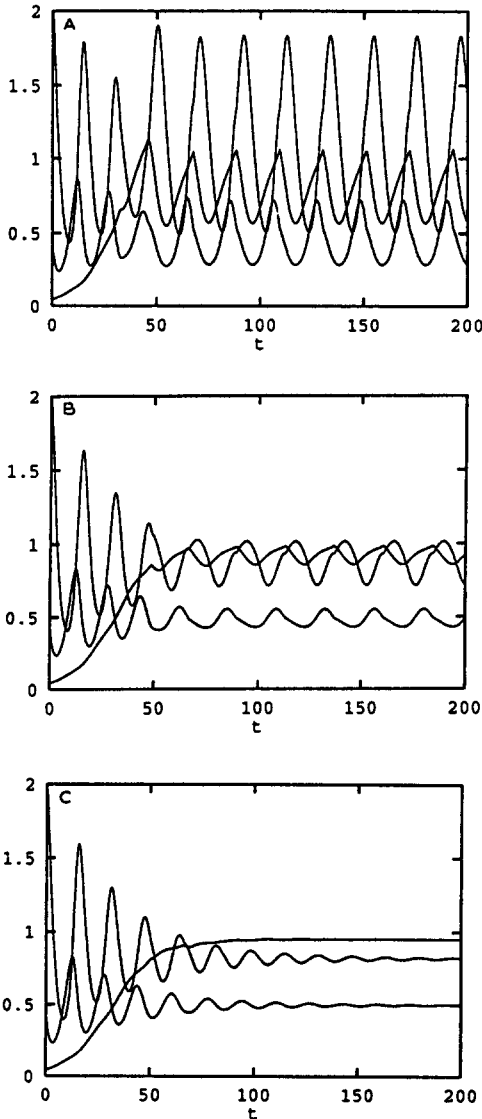


Fig. 1. Simulations of system (7) with the following values of parameter b_{11} : (a) $b_{11} = 0.01$; (b) $b_{11} = 0.09$; (c) $b_{11} = 0.1$.

equations. If the system is controlled mostly by the starfish (Fig. 1a) it exhibits large fluctuations as the result of "switching" between two prey. When the "environmental carrying capacities" $b_{11} = b_{22}$ are growing, i.e. prey are becoming more and more limited by the environment, the fluctuations are decreasing (Fig. 1b). Eventually, the behaviour exhibits stable equilibrium (Fig. 1c).

ACKNOWLEDGEMENT

The authors thank Dr. Alois Kastner-Maresch for numerical simulations.

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