Modeling Coral Reef Bleaching Recovery Through KCC-Theory

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Abstract

We use Volterra-Hamilton systems theory and their associated cost functional to study the population dynamics and productive processes of coral reefs in recovery from bleaching and show that the cost of production remains the same after the process. The KCC-theory geometrical invariants are determined for the model proposed to describe the renewed symbiotic interaction between coral and algae.

1 Introduction

There is no doubt that increasing seawater temperature leads to coral bleaching [1]. This process occurs when corals are stressed by changes in environmental conditions such as temperature, light, or nutrients, leading to the expelling of the symbiotic algae which lives in the coral’s tissues, causing it to turn white. So global warming causes coral bleaching as increasing local seawater temperature stresses symbiotic algae (commonly called \textit{zooxanthellae}) in hermatypic coral (\textit{reef-building}) [2] which leads to a breakdown in the symbiotic relationship between the coral animal and its zooxanthellae. This kind of seaweed has been severely affected by global warming around the world [3, 4]. It is important to note that an individual coral is compound by thousand or even million of polyps which are animals of a few millimeters thick. The symbiotic algae living within the polyp makes energy from sunlight; they share that energy with polyp in exchange for a comfortable environment and their interaction produce CaCO3 for the reef building. If there are no symbionts, the polyp run out of energy and dies within a few weeks or months, causing the coral to appear white or "bleached" [5], unless they take more symbionts among those algae that naturally floating in the water around the coral barrier. Some coral reefs have been observed to recover from bleaching in appropriate situations [6, 7]. In order to model this recovering we suppose that before bleaching each polyp contains symbiotic algae living inside in a stable symbiotic relationship, and that there exist different kinds of algae outside the polyp, which benefit from the coral but do not influence it (\textit{commensal}) some of which are possibly better adapted to higher seawater temperatures.

2 Interactive Population Dynamics

Let \( \Sigma \) denote a population at a fixed location. Whenever we refer to \( \Sigma \) it is implicit that there exists at least one individual living at this location. Let
$N(t) \geq 0$ be the population density (or number of individuals per unit volume) in $\Sigma$ at time $t \in [0, T]$, $T > 0$. We assume that $N(t)$ is a continuous function of time $t$ and satisfies Hutchinson’s axioms [9] throughout this paper. We reserve the symbol $\Pi$ for the set of distinct species sharing the same location with no isolated species, i.e., it is a simple community. Let $\Pi$ be a simple $n$ species community. We can describe this interaction by the system of equations:

$$\frac{dN_i}{dt} = \lambda_i N^i \left( 1 - \frac{N^i}{K_i} - \delta_j \frac{N^j}{K_i} \right), \quad i, j = 1, 2, \ldots, n. \quad (1)$$

where $\lambda_i$ and $K_i$ are positive constants denoting intrinsic growth rate and carrying capacity for specie $i$, respectively. The coefficient $\delta_{(j)}$ represents how much the specie $i$ is affected by the specie $j$ in the interaction. The sign of $\delta_j$ tells what kind of interaction it is. Consider the system of two equations taking any $i, j \in \{1, \ldots, n\}, i \neq j$, in $[1]$. There are three possibilities to this system as follow:

- Parasitism: $\delta_i > 0, \delta_j < 0$ or $\delta_{(i)} < 0, \delta_j > 0$;
- Competition: $\delta_i > 0, \delta_j > 0$;
- Symbiosis: $\delta_i < 0, \delta_j < 0$.

According to [8] we see that Competition case in a Gause Witt model. Assuming $\delta_i, \delta_j > 0$, the competition case, set $i = 1, j = 2$ for $n = 2$. Then we have the following theorem (see [10], page 21):

**Theorem 1**

1. If $\delta_1 > \frac{K_1}{K_2}$ and $\delta_2 > \frac{K_2}{K_1}$, then only one of the two species will persist after the competition and the winner will be determined entirely by the starting proportions.

2. If $\delta_1 > \frac{K_1}{K_2}$ and $\delta_2 < \frac{K_2}{K_1}$, then the specie 1 will be eliminated by the competition.

3. If $\delta_1 < \frac{K_1}{K_2}$ and $\delta_2 > \frac{K_2}{K_1}$, then the specie 2 will be eliminated by the competition.

4. If $\delta_1 < \frac{K_1}{K_2}$ and $\delta_2 < \frac{K_2}{K_1}$, then both species persist together at equilibrium.

We are interested in study Gause-Witt equations whose coefficients satisfies hypothesis of items 2 and 3.

**Remark.** Gause-Witt model is just a particular case of a more general system of equation which describes ecological interaction of species in a simple community $\Pi$:

$$\frac{dN_i}{dt} = -\Gamma_{jk}^i N^j N^k + \lambda_{(i)} N^i, \quad i, j, k = 1, \ldots, n \quad (2)$$
where the $n^3$ quantities $\Gamma_{jk}^i$ are all constants (here, use is made of the Einstein summation convention on summing over repeated upper and lower indices with the only exception being $\lambda_{(j)} N^i$ where the parentheses indicates no summation).

Now we introduce a natural measure of production $x^i$ of a population $N^i(t)$, the Volterra’s Production Variable [11], by defining

$$x^i(t) = k_i \int_0^t N^i(\tau) d\tau + x^i(0) \quad (3)$$

where $k_i > 0$ is the per capita production rate.

An $n$-species Volterra-Hamilton (VH) system $(\Pi, \Gamma)$ is pair consisting of $\Pi$, a set of $n$ producer populations whose sizes are denoted by $N^1, \ldots, N^n$, together with a system of equations $\Gamma$ (2), (3):

$$\Gamma : \begin{cases} \frac{dx^i}{dt} = k_i N^i \\ \frac{dN^i}{dt} = -\Gamma_{jk}^i N^j N^k + \lambda_{(i)} N^i \end{cases} \quad (4)$$

### 3 Bleaching Recovery Model

Let $N(t)$, $A^1(t)$ and $A^2(t)$ be continuous functions of time which denote coral, symbiotic alga and commensal alga population density, respectively. We split this modelling in three stages: (I) Commensal + Symbiosis; (II) Symbiosis + Competition; (III) Symbiosis. Here, it is initially assumed $\lambda_{(N)} = \lambda_{(A^1)} = \lambda_{(A^2)} = \lambda$, where these constants have the same meaning as in (1). Following this symbiont assumptions, we can describe these three stages of interactions between coral and algae.

**Remark.** The first stage describes how these three species live in the coral reef barrier before bleaching; Second stage is the dynamic produced by bleaching, but we will focus our attention at the competition between the algae; in the last one, we suppose alga $A^2$ will develop a symbiotic relation with the coral which was invaded by the outside algae, creating the condition to stop bleaching and start the recovering process.

• Commensal + Symbiosis

At this stage we suppose water temperature is adequate for both species of Algae and to the Coral. First, note that algae $A^2$ lives outside the Polyp (commensal relation), then this interaction is beneficial only one to alga $A^2$. By the other hand, alga $A^1$ and coral have a symbiotic interaction. So, we can describe this relation by extended Gause-Witt equations (1) as follow:

$$\begin{cases} \frac{dN}{dt} = \lambda N - \frac{\lambda(N)^2}{K} + \delta \frac{\lambda N A^1}{K} \\ \frac{dA^1}{dt} = \lambda A^1 - \frac{\lambda(A^1)^2}{K_1} + \delta_1 \frac{\lambda A^1 N}{K_1} \\ \frac{dA^2}{dt} = \lambda A^2 - \frac{\lambda(A^2)^2}{K_2} + \delta_2 \frac{\lambda A^2 N}{K_2} \end{cases} \quad (5)$$
where $\delta > 0$ to describe the symbiosis. If $N$ was affected by $A_2$, there would be a 4th term in the 1st equation.

- Symbiosis + Competition

Here we assume that water warming is less lethal to $A_2$ than to $A_1$. The increasing water temperature produce a decreasing population density of algae $A_1$, since this specie is not adjusted to live in these conditions. This situation provides adequate conditions to algae $A_2$ penetrate the Polyp to establish the symbiotic relation that coral needs to live. In this case we have a dynamic where each specie interact to each other described as follow:

\[
\begin{cases}
\frac{dN}{dt} = \lambda N - \frac{\lambda (N)^2}{K} + \delta \frac{\lambda N (A_1 + A_2)}{K} \\
\frac{dA_1}{dt} = \lambda A_1 - \frac{\lambda (A_1)^2}{K_1} + \delta_1 \frac{\lambda A_1 N}{K_1} - \mu_1 \frac{\lambda A_1 A_2}{K_1} \\
\frac{dA_2}{dt} = \lambda A_2 - \frac{\lambda (A_2)^2}{K_2} + \delta_2 \frac{\lambda A_2 N}{K_2} - \mu_2 \frac{\lambda A_1 A_2}{K_2}
\end{cases}
\]

where $\mu_i (i = 1, 2)$ are positive contants and $\mu_i$ is the impact that $A_i$ suffers by interaction with especie $A_j$. We expect that competition between $A_1$ and $A_2$ is so strong that we can assume $\mu_1, \mu_2 \gg \delta, \delta_1, \delta_2$. Therefore (6) becomes a classical Gause-Witt competition system:

\[
\begin{cases}
\frac{dA_1}{dt} = \lambda A_1 - \frac{\lambda (A_1)^2}{K_1} - \mu_1 \frac{\lambda A_1 A_2}{K_1} \\
\frac{dA_2}{dt} = \lambda A_2 - \frac{\lambda (A_2)^2}{K_2} - \mu_2 \frac{\lambda A_1 A_2}{K_2}
\end{cases}
\]

(7)

As we have supposed that warmer water is more lethal to $A_1$ than $A_2$, then $\mu_2 < \mu_1$ because this competition is harder $A_1$. Thus, by item 2 of theorem 1 we can conclude that $A_1$ is eliminated by the competition described in (7).

- Symbiosis

After elimination of $A_1$ by competition with $A_2$, the coral $N$ has a new alga population to establish a symbiotic relation and then stop bleaching. The situation before bleaching and after recovering is quite the same in the sense of system of equations as follow:

\[
\begin{cases}
\frac{dN}{dt} = \lambda N - \frac{\lambda (N)^2}{K} + \delta \frac{\lambda N A_2}{K} \\
\frac{dA_2}{dt} = \lambda A_2 - \frac{\lambda (A_2)^2}{K_2} + \delta_2 \frac{\lambda A_2 N}{K_2}
\end{cases}
\]

(8)

Remark. Equations (8) have the same form of the Gause-Witt system to describe interaction of $N$ and $A_1$ in (5). This occurs because $A_1$ is supplanted by $A_2$. 

4
4 Proposal of the model

Before bleaching disruption, it is known that coral and symbiotic alga develop a by-product as a result of their interaction. The same occurs after bleaching recovery since we are assuming alga $A_2$ becomes the symbiotic alga before the coral dies completely. Volterra-Hamilton is well suited to describe this production. For simplicity, we suppose all three populations have the same percapita rate of production (set $k_i = 1, i = 1, 2, 3$), so (I) describes production before bleaching and (II) after recovery:

\[ I: \begin{align*}
\frac{dx}{dt} &= N, \\
\frac{dy_1}{dt} &= A_1, \\
\frac{dN}{dt} &= \lambda N - \frac{\lambda(N)^2}{K} + \delta \frac{\lambda N A_1}{K}, \\
\frac{dA_1}{dt} &= \lambda A_2 - \frac{\lambda(A_1)^2}{K_1} + \delta_1 \frac{\lambda A_1 N}{K_1}.
\end{align*} \]

\[ II: \begin{align*}
\frac{dx}{dt} &= N, \\
\frac{dy_2}{dt} &= A_2, \\
\frac{dN}{dt} &= \lambda N - \frac{\lambda(N)^2}{K} + \delta \frac{\lambda N A_2}{K}, \\
\frac{dA_2}{dt} &= \lambda A_2^2 - \frac{\lambda(A_2)^2}{K_2} + \delta_2 \frac{\lambda A_2 N}{K_2}.
\end{align*} \]

Using the change of parameter $s = e^t$ we obtain another system equivalent to system (I):

\[ \begin{align*}
\frac{d^2x}{ds^2} + \frac{\lambda}{K} \left( \frac{dx}{ds} \right)^2 + \delta \lambda \frac{dx \, dy_1}{K \, ds \, ds} &= 0, \\
\frac{d^2y_1}{ds^2} + \frac{\lambda}{K_1} \left( \frac{dy_1}{ds} \right)^2 + \delta_1 \lambda \frac{dy_1 \, dx}{K_1 \, ds \, ds} &= 0.
\end{align*} \] (9)

One can prove that

\[ F(x, y^1, N, A^1) = e^{\psi(x, y^1)} \frac{(A^1)^{1+(1/\lambda)}}{(N)^{\frac{1}{\lambda}}} \] (10)

is conserved along the flow (9), i.e., $dF/ds = 0$, even these equations are not Euler-Lagrange for the functional $F$, where $\psi$ is of the form:

\[ \psi(x, y^1) = \left( \frac{\lambda \delta_1}{K} + \frac{-K + \delta_1 K}{K^2} \right) x + \left( \frac{\lambda \delta}{K} + \frac{(1 + \lambda)(-K + \delta K)}{K^2} \right) y^1. \] (11)

By symmetry,

\[ \begin{align*}
\frac{d^2x}{ds^2} + \frac{\lambda}{K} \left( \frac{dx}{ds} \right)^2 + \delta \lambda \frac{dx \, dy_2}{K \, ds \, ds} &= 0, \\
\frac{d^2y_2}{ds^2} + \frac{\lambda}{K_2} \left( \frac{dy_2}{ds} \right)^2 + \delta_2 \lambda \frac{dy_2 \, dx}{K_2 \, ds \, ds} &= 0.
\end{align*} \] (12)
represents system (II) in an intrinsic time scale, longer than t, which is just a adaptation of original system. Replacing $A^1$ for $A^2$, $y^1$ for $y^2$, $K_1$ for $K_2$ and $\delta_1$ for $\delta_2$ in (10) and (11) we conclude that after recovering, the cost of production is the same as before bleaching and $dF/ds = 0$ along (12), provided that we assume that the new alga replace the original one in the same ecological niche, or, in other words, $K_2$ appractically equal $K_1$. This is interpreted as representing an adaptation process, as oppose to an evolutionary one, where the cost of production is supposed to dimish, leading to a more efficient interaction pattern.

5 KCC-Theory and Volterra-Hamilton System

Let $(x^1, \ldots, x^n) = (x)$, $(\frac{dx^1}{dt}, \ldots, \frac{dx^n}{dt}) = (\dot{x})$, and t be $2n + 1$ coordinates in an open connected subset $\Omega$ of the Euclidean $(2n+1)$-dimensional space $\mathbb{R}^n \times \mathbb{R}^n \times \mathbb{R}$. For our purpose, suppose that we have

$$\frac{d^2 x^i}{dt^2} + g^i(x, \dot{x}, t) = 0, \quad i = 1, \ldots, n,$$

where each $g^i$ is $C^\infty$ in some neighborhood of initial conditions $((x)_0, (\dot{(x)}_0, t_0) \in \Omega$. The intrinsic geometry properties of (8) under non-singular transformations of the type:

$$\begin{cases} \tilde{x}^i = f^i(x^1, \ldots, x^n), & i = 1, \ldots, n, \\ \tilde{t} = t \end{cases}$$

are given by the five KCC-differential invariants, named after by D. Kosambi [12], E. Cartan [13] and S. S. Chern [14], given below. Let us first define the KCC-covariant differential of a contravariant vector field $\xi^i(x)$ on $\Omega$ by

$$\mathbb{D} \xi^i = \frac{d\xi^i}{dt} + \frac{1}{2} g^i_{r\sigma} \xi^r$$

where the semi-colon indicates partial differentiation with respect to $\tilde{x}^r$, and use of the Einstein summation convention on repeated indices. Using (14), equation (8) becomes

$$\mathbb{D} \xi^i = \epsilon^i = \frac{1}{2} g^i_{r\sigma} \tilde{x}^r - g^i$$

defining the first KCC-invariant of (8), the contravariant vector field on $\Omega$, $\epsilon^i$, which represents an ‘external force’. Varying trajectories $x^i(t)$ of (8) into nearby ones according to

$$\tilde{x}^i(t) = x^i(t) + \xi^i(t) \eta$$

where $\eta$ denotes a parameter, with $|\eta|$ small and $\xi^i(t)$ the components of some contravariant vector field defined along $x^i = x^i(t)$, we get, substituting (16) into (8) and taking the limit as $\eta \to 0$

$$\frac{d^2 \xi^i}{dt^2} + g^i_{r\sigma} \frac{d\xi^r}{dt} + g^i_{r\sigma} \xi^r = 0$$

where the comma indicates partial differentiation with respect to $x^r$. Using the KCC-covariant differentiation (14) we can express this as

$$\mathbb{D}^2 \xi^i = \mathcal{P}^i_{r\sigma} \xi^r$$
where
\[
P^i_j = -g^i_j - \frac{1}{2}g^r_{i;j} + \frac{1}{2}g^r_{j;i} + \frac{1}{4}g^r_{i;j} + \frac{1}{2} \frac{\partial}{\partial t} g^i_j.
\] (20)

The tensor \( P^i_j \) is the second KCC-invariant of (8). The third, fourth and fifth invariants are:
\[
\begin{align*}
R_{i;j} &= \frac{1}{3} (P_{i;k}^j - P_{k;j}^i) \\
B_{j;kl} &= R_{i;jk}^i \\
D_{j;kl} &= g_{i;jk}^i 
\end{align*}
\] (21)

The main result of KCC-theory is the following:

**Theorem 2** Two systems of the form (8) on \( \Omega \) are equivalent relative to (13) if and only if the five KCC-invariants are equivalent. In particular, there exist coordinates \((\bar{x})\) for which \( g_{i;jk}^i \) all vanish if and only if all KCC-invariants are zero. The tensor \( D \) vanishes if and only if \( g^i_j \) is quadratic in \((\dot{x})\), in the case when the first KCC-invariant vanishes.

The theorem above provides a great tool to obtain equivalence between our system before bleaching and system after recover as is stated in the last section. A complete discussion about KCC-Theory can be found at [15, 16]. Setting \( s = 1/\lambda \exp (\lambda t) \) defines an intrinsic time scale, longer than \( t \), for which (4) with \( k \) \((i) = 1 \) for \( i = 1, \ldots, n \) takes the form defined as in (8):
\[
\frac{d^2 x^i}{ds^2} = -\Gamma^i_{jk} \frac{dx^j}{ds} \frac{dx^k}{ds}.
\] (22)

where \( g^i_j = \Gamma^i_{jk} \frac{dx^j}{ds} \frac{dx^k}{ds} \), \( \dot{x} = \frac{dx}{ds} \).

Now we evaluate the KCC-invariants for a general system of (9) and (10) using techniques of Maple [19] where was made use of [18].
restart;

with(Finsler);

\begin{align*}
& \text{coordinates}(x_1, x_2); \\
& \text{The coordinates are:} \\
& \quad X^1 = x_1 \\
& \quad X^2 = x_2
\end{align*}

\begin{align*}
& \text{coordinates}(y_1, y_2); \\
& \text{The d-coordinates are:} \\
& \quad Y^1 = y_1 \\
& \quad Y^2 = y_2
\end{align*}

\begin{align*}
& G_1 := \left( \frac{\lambda_1}{K_1} \right) y_1^2 + \frac{\lambda_2 \delta_{11} y_1 y_2}{K_1} + \frac{\lambda_2 \delta_{12} y_1 y_2}{K_1} \\
& G_2 := \left( \frac{\lambda_2}{K_2} \right) y_2^2 + \frac{\lambda_2 \delta_{12} y_1 y_2}{K_2} + \frac{\lambda_2 \delta_{22} y_1 y_2}{K_2}
\end{align*}

\begin{align*}
& \text{connection}(G_1, G_2); \\
& G^1 = \frac{\lambda_1 y_1^2}{K_1} + \frac{\lambda_2 \delta_{12} y_1 y_2}{K_1} \\
& G^2 = \frac{\lambda_2 y_2^2}{K_2} + \frac{\lambda_2 \delta_{22} y_1 y_2}{K_2}
\end{align*}

\begin{align*}
& \text{definetsensor}(\epsilon[i, j] = N[i, j] \cdot Y) - 2 \cdot G (i); \\
& e^{i} = N^{i} \cdot Y^{j} - 2G^{j}
\end{align*}

\begin{align*}
& \text{eval}(\epsilon[i, j]); \\
& e^{i} = 0
\end{align*}

\begin{align*}
& \text{show}(B[i, j]); \\
& B^{i} = \frac{\lambda_2 \delta^{i_2} y_2 \left( K_1 y_1 \delta^{x_2} - K_2 y_2 \delta^{x_1} + 2 K_1 y_2 \right)}{K_1^2 K_2} \\
& B^{i} = \frac{-\lambda_2 \delta^{i_2} y_1 \left( K_1 y_1 \delta^{x_2} - K_2 y_2 \delta^{x_1} + 2 K_1 y_2 \right)}{K_1^2 K_2} \\
& B^{i} = \frac{\lambda_2 \delta^{i_2} y_1 y_2 \left( K_1 y_1 \delta^{x_2} - K_2 y_2 \delta^{x_1} - 2 y_1 K_2 \right)}{K_2^2 K_1}
\end{align*}
Making the appropriated adaptations in the coefficients of the computation above \((K_1 = K_2 = K')\) we see that the systems \([9]\) and \([10]\) are equivalent by the main result of KCC-Theory.

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