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PLANKTONS DISCRETE-TIME DYNAMICAL SYSTEMS

U. A. ROZIKOV, S. K. SHOYIMARDONOV, R. VARRO

ABSTRACT. In this paper, we initiate the study of a discrete-time dynamical system modelling a trophic network connecting the three types of plankton (phytoplankton, zooplankton, mixoplankton) and bacteria. The nonlinear operator V associated with this dynamical system is of type 4-Volterra quadratic stochastic operator (QSO) with twelve parameters. We give conditions on the parameters under which this operator maps the five-dimensional standard simplex to itself and we find its fixed points. Moreover, we study the limit points of trajectories for this operator. For each situations we give some biological interpretations.

1. INTRODUCTION

The conventional view of species divides organisms into two distinct classes:

- *Autotroph* species like plants, are able to synthesize all the organic matter that composes them from mineral elements taken from the environment.
- *Heterotroph* organisms like animals, must absorb preformed organic matter present in their environment to constitute the organic matter that composes them.

Beside these two modes of trophism there is a third:

- *The mixotrophy*, that combines the other two modes. Mixotroph organisms are able to constitute their organic matter by autotrophy as well as by heterotrophy. Mixotrophy is very rare among terrestrial organisms, but since the 1980s many studies have shown that mixotrophy is very abundant in ocean plankton [15].

Plankton plays important role in marine ecosystems, it provides the base for the aquatic food chain [2, 6, 14].

Generally¹ small or microscopic, the plankton organisms are capable of limited movement, but unable to move against the current and drift with the currents.

There are two types of plankton: plant-like plankton also called *phytoplankton* and animal-like plankton called *zooplankton*.

Phytoplankton mainly consist of unicellular photosynthetic organisms, therefore autotroph organisms absorbing mineral elements such as nitrogen, phosphorus, calcium, iron and transform these elements into organic matter using energy from sunlight. It is estimated that phytoplankton contributes

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¹see <https://en.wikipedia.org/wiki/Phytoplankton> and references therein.

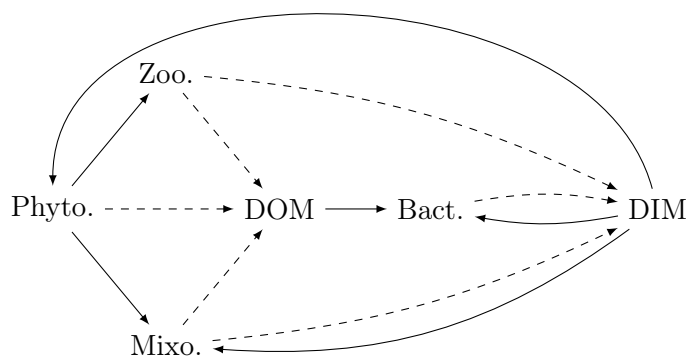
about half of the photosynthesis on the planet and absorbs one-third of the carbon dioxide.

Zooplankton includes holoplankton or permanent zooplankton composed of organisms that are born, reproduce and die as zooplankton and meroplankton or temporary zooplankton consisting of eggs and larvae of many species (fish, crustaceans, shells ...) that leave the plankton stage when they metamorphose. Zooplankton feed on organic matter, phytoplankton or zooplankton.

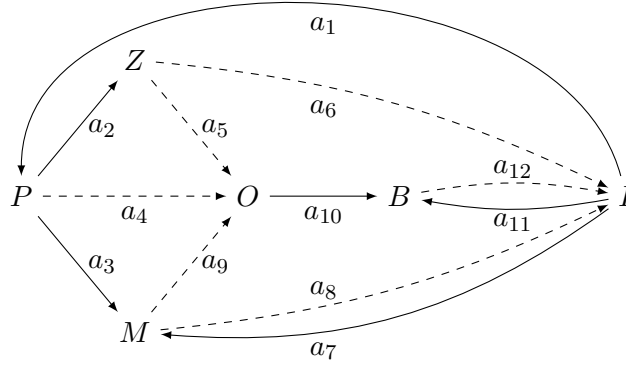
Research over the last decade showed that zooplankton is subdivided into protozooplankton (incapable of phototrophy) and mixoplankton (capable of phototrophy and phagotrophy). Long regarded as a curiosity, it appears today that mixotrophy is common [3] and that many organisms considered as phytoplankton are mixotroph and that 50% of zooplankton is mixoplankton. Mixoplankton is subdivided into three functional groups: constitutive mixoplankton whose physiology allows photosynthesis, general non-constitutive mixoplankton which extracts the organelles necessary for photosynthesis in their preys and specialist non-constitutive mixoplankton which attack specific prey to extract certain parts allowing photosynthesis.

When they die, phytoplankton, zooplankton and mixoplankton elements are decomposed into dissolved organic matter (DOM) that are consumed and transformed by bacteria into dissolved inorganic matter (DIM) that are in turn consumed by phytoplankton, mixoplankton and bacteria.

This cycle [8] is summarized in the following diagram.



If the quantities, measured by concentrations or weights, of phytoplankton, zooplankton, mixoplankton, bacteria, dissolved organic matter and dissolved inorganic matter are respectively denoted P, Z, M, B, O and I . And if we denote a_1, \dots, a_{12} the transfer rates between the different compartments according to the graph below.



Then the corresponding model is

$$(1.1) \quad \begin{cases} \frac{dP}{dt} &= a_1PI - a_2PZ - a_3PM - a_4P \\ \frac{dZ}{dt} &= a_2PZ - a_5Z - a_6Z \\ \frac{dM}{dt} &= a_3PM + a_7MI - a_8M - a_9M \\ \frac{dO}{dt} &= a_4P + a_5Z + a_9M - a_{10}BO \\ \frac{dB}{dt} &= a_{10}BO + a_{11}BI - a_{12}B \\ \frac{dI}{dt} &= a_6Z + a_8M + a_{12}B - a_1PI - a_7MI - a_{11}BI \end{cases}$$

Remark 1. We note that the study of the role of mixoplankton is very recent and the system (1.1) is not analytically studied yet. To the best of our knowledge this paper is a first exploration of the field. It remains to be studied what happens when consumption rates are higher than death rates.

For simplicity we have assumed that the dissolved inorganic matter produced by bacteria is immediately assimilated and available for food.

We notice that $\frac{d}{dt}(P + Z + M + O + B + I) = 0$, from this we deduce that the total weight of this closed system remains constant over time, by convention we put $P + Z + M + O + B + I = 1$. Coefficients a_4, a_5, a_9 are decomposition rates in dissolved organic matter and a_6, a_8, a_{12} decomposition rates in dissolved inorganic matter, we can assume that these coefficients are strictly positive and interpret $a_4, a_5 + a_6, a_8 + a_9, a_{12}$ as death rates. Similarly, the coefficients $a_1, a_2, a_3, a_7, a_{10}$ and a_{11} being consumption rates, we can also assume that these coefficients are also strictly positive.

2. ℓ -VOLTERRA QUADRATIC STOCHASTIC OPERATORS

The quadratic stochastic operator (QSO) [5], [7] is a mapping of the standard simplex.

$$(2.1) \quad S^{m-1} = \{x = (x_1, \dots, x_m) \in \mathbb{R}^m : x_i \geq 0, \sum_{i=1}^m x_i = 1\}$$

into itself, of the form

$$(2.2) \quad V : x'_k = \sum_{i=1}^m \sum_{j=1}^m P_{ij,k} x_i x_j, \quad k = 1, \dots, m,$$

where the coefficients $P_{ij,k}$ satisfy the following conditions

$$(2.3) \quad P_{ij,k} \geq 0, \quad P_{ij,k} = P_{ji,k}, \quad \sum_{k=1}^m P_{ij,k} = 1, \quad (i, j, k = 1, \dots, m).$$

Thus, each quadratic stochastic operator V can be uniquely defined by a cubic matrix $\mathbb{P} = (P_{ij,k})_{i,j,k=1}^m$ with conditions (2.3).

Note that each element $x \in S^{m-1}$ is a probability distribution on $\llbracket 1, m \rrbracket = \{1, \dots, m\}$. Each such distribution can be interpreted as a state of the corresponding biological system.

For a given $\lambda^{(0)} \in S^{m-1}$ the *trajectory* (orbit) $\{\lambda^{(n)}; n \geq 0\}$ of $\lambda^{(0)}$ under the action of QSO (2.2) is defined by

$$\lambda^{(n+1)} = V(\lambda^{(n)}), \quad n = 0, 1, 2, \dots$$

The main problem in mathematical biology consists in the study of the asymptotical behaviour of the trajectories. The difficulty of the problem depends on given matrix \mathbb{P} . One of simple cases is Volterra QSO, i.e., the matrix \mathbb{P} satisfies

$$(2.4) \quad P_{ij,k} = 0 \text{ if } k \notin \{i, j\} \text{ for any } i, j \in \llbracket 1, m \rrbracket.$$

In [4] the theory for Volterra QSO was developed by using the theories of the Lyapunov function and of tournaments. But non-Volterra QSO (i.e., not satisfying condition (2.4)) were not exhaustively studied, because there is no general theory that can be applied to the study of non-Volterra operators (see [5] for a review). In this paper we reduce our operator to a non-Volterra operator which is known as a ℓ -Volterra QSO (see [10], [11], [12]):

ℓ -Volterra QSO. Fix $\ell \in \llbracket 1, m \rrbracket$ and assume that elements $P_{ij,k}$ of the matrix \mathbb{P} satisfy

$$(2.5) \quad \begin{aligned} &P_{ij,k} = 0 \text{ if } k \notin \{i, j\} \text{ for any } k \in \{1, \dots, \ell\}, i, j \in \llbracket 1, m \rrbracket; \\ &P_{ij,k} > 0 \text{ for at least one pair } (i, j), i \neq k, j \neq k \\ &\text{for any } k \in \{\ell + 1, \dots, m\}. \end{aligned}$$

Definition 2. [10] For any fixed $\ell \in \llbracket 1, m \rrbracket$, the QSO defined by (2.2), (2.3) and (2.5) is called ℓ -Volterra QSO.

Definition 3. A QSO V is called regular if for any initial point $\lambda^{(0)} \in S^{m-1}$, the limit

$$\lim_{n \rightarrow \infty} V^n(\lambda^{(0)})$$

exists, where V^n denotes n -fold composition of V with itself (i.e. n time iterations of V).

3. REDUCTION TO 2-VOLTERRA QSO

In this paper we study the discrete time dynamical systems associated to the system (1.1).

For simplicity of notations we denote

$$x_1 = P, \quad x_2 = Z, \quad x_3 = M, \quad x_4 = B, \quad x_5 = O, \quad x_6 = I.$$

Define the evolution operator V by $V : S^5 \rightarrow \mathbb{R}^6$, $(x_1, \dots, x_6) \mapsto (x'_1, \dots, x'_6)$

$$(3.1) \quad V : \begin{cases} x'_1 = x_1 (1 - a_4 + a_1x_6 - a_2x_2 - a_3x_3) \\ x'_2 = x_2 (1 - a_5 - a_6 + a_2x_1) \\ x'_3 = x_3 (1 - a_8 - a_9 + a_3x_1 + a_7x_6) \\ x'_4 = x_4 (1 - a_{12} + a_{10}x_5 + a_{11}x_6) \\ x'_5 = x_5 + a_4x_1 + a_5x_2 + a_9x_3 - a_{10}x_4x_5 \\ x'_6 = x_6 (1 - a_1x_1 - a_7x_3 - a_{11}x_4) + a_6x_2 + a_8x_3 + a_{12}x_4 \end{cases}$$

Note that the operator V has a form of 4-Volterra QSO, but the parameters of this operator are not related to $P_{ij,k}$. Here to make some relations with $P_{ij,k}$ we find conditions on parameters of (3.1) rewriting it in the form (2.2) (as in [9]). Using $x_1 + \dots + x_6 = 1$ we change the form of the operator (3.1) as following:

$$V : \begin{cases} x'_1 = x_1 ((1 - a_4)(x_1 + \dots + x_6) + a_1x_6 - a_2x_2 - a_3x_3) \\ x'_2 = x_2 ((1 - a_5 - a_6)(x_1 + \dots + x_6) + a_2x_1) \\ x'_3 = x_3 ((1 - a_8 - a_9)(x_1 + \dots + x_6) + a_3x_1 + a_7x_6) \\ x'_4 = x_4 ((1 - a_{12})(x_1 + \dots + x_6) + a_{10}x_5 + a_{11}x_6) \\ x'_5 = (x_5 + a_4x_1 + a_5x_2 + a_9x_3)(x_1 + \dots + x_6) - a_{10}x_4x_5 \\ x'_6 = x_6 (x_1 + \dots + x_6 - a_1x_1 - a_7x_3 - a_{11}x_4) + \\ \quad (a_6x_2 + a_8x_3 + a_{12}x_4)(x_1 + \dots + x_6) \end{cases}$$

From this system and QSO (2.2) for the case $m = 6$ we obtain the following relations between $P_{ij,k}$:

$$\begin{aligned}
 (3.2) \quad & P_{11,1} = 1-a_4, & 2P_{12,1} &= 1-a_2-a_4, & 2P_{13,1} &= 1-a_3-a_4, \\
 & 2P_{14,1} = 1-a_4, & 2P_{15,1} &= 1-a_4, & 2P_{16,1} &= 1+a_1-a_4, \\
 & 2P_{12,2} = 1+a_2-a_5-a_6, & P_{22,2} &= 1-a_5-a_6, & 2P_{23,2} &= 1-a_5-a_6, \\
 & 2P_{24,2} = 1-a_5-a_6, & 2P_{25,2} &= 1-a_5-a_6, & 2P_{26,2} &= 1-a_5-a_6, \\
 & 2P_{13,3} = 1+a_3-a_8-a_9, & 2P_{23,3} &= 1-a_8-a_9, & P_{33,3} &= 1-a_8-a_9, \\
 & 2P_{34,3} = 1-a_8-a_9, & 2P_{35,3} &= 1-a_8-a_9, & 2P_{36,3} &= 1+a_7-a_8-a_9, \\
 & 2P_{14,4} = 1-a_{12}, & 2P_{24,4} &= 1-a_{12}, & 2P_{34,4} &= 1-a_{12}, \\
 & P_{44,4} = 1-a_{12}, & 2P_{45,4} &= 1+a_{10}-a_{12}, & 2P_{46,4} &= 1+a_{11}-a_{12}, \\
 & P_{11,5} = a_4, & 2P_{12,5} &= a_4+a_5, & 2P_{13,5} &= a_4+a_9, \\
 & 2P_{14,5} = a_4, & 2P_{15,5} &= 1+a_4, & 2P_{16,5} &= a_4, \\
 & P_{22,5} = a_5, & 2P_{23,5} &= a_5+a_9, & 2P_{24,5} &= a_5, \\
 & 2P_{25,5} = 1+a_5, & 2P_{26,5} &= a_5, & P_{33,5} &= a_9, \\
 & 2P_{34,5} = a_9, & 2P_{35,5} &= 1+a_9, & 2P_{36,5} &= a_9, \\
 & 2P_{45,5} = 1-a_{10}, & P_{55,5} &= 1, & 2P_{56,5} &= 1, \\
 & 2P_{12,6} = a_6, & 2P_{13,6} &= a_8, & 2P_{14,6} &= a_{12}, \\
 & 2P_{16,6} = 1-a_1, & P_{22,6} &= a_6, & 2P_{23,6} &= a_6+a_8, \\
 & 2P_{24,6} = a_6+a_{12}, & 2P_{25,6} &= a_6, & 2P_{26,6} &= 1+a_6, \\
 & P_{33,6} = a_8, & 2P_{34,6} &= a_8+a_{12}, & 2P_{35,6} &= a_8, \\
 & 2P_{36,6} = 1-a_7+a_8, & P_{44,6} &= a_{12}, & 2P_{45,6} &= a_{12}, \\
 & 2P_{46,6} = 1-a_{11}+a_{12}, & 2P_{56,6} &= 1, & P_{66,6} &= 1,
 \end{aligned}$$

other $P_{ij,k}=0$.

Proposition 4. *We have $V(S^5) \subset S^5$ if the strictly positive parameters a_1, \dots, a_{12} verify the following conditions*

$$\begin{aligned}
 (3.3) \quad & a_1 \leq 1, & a_6 \leq 1, & a_{10} \leq 1, & a_{12} \leq 1, \\
 & a_2 + a_4 \leq 1, & a_3 + a_4 \leq 1, & a_5 + a_6 \leq 1, & a_8 + a_9 \leq 1, \\
 & & |a_7 - a_8| \leq 1, & |a_{11} - a_{12}| \leq 1.
 \end{aligned}$$

Moreover, under conditions (3.3) the operator V is a 4-Volterra QSO.

Proof. The proof can be obtained by using equalities (3.2) and solving inequalities $0 \leq P_{ij,k} \leq 1$ for each $P_{ij,k}$. \square

Remark 5. In the sequel of the paper we consider operator (3.1) with parameters a_1, \dots, a_{12} which satisfy conditions (3.3). This operator maps S^5 to itself and we are interested to study the behaviour of the trajectory of any initial point $x \in S^5$ under iterations of the operator V .

Remark 6. The conditions of Proposition 4 are sufficient for the quadratic operator to map simplex to itself. A criterion for a quadratic operator with real coefficients $\gamma_{ij,k}$ (not necessary positive) to map the $(n-1)$ -dimensional simplex to itself is known ([13]):

- i) $\sum_{k=1}^n \gamma_{ij,k} = 1$, for all $i, j = 1, \dots, n$;
- ii) $0 \leq \gamma_{ii,k} \leq 1$, for all $i, k = 1, \dots, n$;
- iii) $-\sqrt{\gamma_{ii,k}\gamma_{jj,k}} \leq \gamma_{ij,k} \leq 1 + \sqrt{(1-\gamma_{ii,k})(1-\gamma_{jj,k})}$.

4. FIXED POINTS OF THE OPERATOR (3.1)

Definition 7. [1]. A fixed point p for $F : \mathbb{R}^m \rightarrow \mathbb{R}^m$ is called *hyperbolic* if the Jacobian matrix $\mathbf{J} = \mathbf{J}_F$ of the map F at the point p has no eigenvalues on the unit circle.

There are three types of hyperbolic fixed points:

- (1) p is an attracting fixed point if all of the eigenvalues of $\mathbf{J}(p)$ are less than one in absolute value.
- (2) p is a repelling fixed point if all of the eigenvalues of $\mathbf{J}(p)$ are greater than one in absolute value.
- (3) p is a saddle point otherwise.

To find fixed points of operator V given by (3.1) we have to solve $V(x) = x$.

By the following proposition we give all possible fixed points of the operator V .

Proposition 8. *The operator (3.1) has the following fixed points with conditions (3.3) for parameters:*

- 1) $\lambda_1 = (0, 0, 0, 0, \lambda, 1 - \lambda)$ with $\lambda \in [0, 1]$.
- 2) $\lambda_2 = \left(0, 0, 0, 1 - \frac{a_{12}}{a_{11}}, 0, \frac{a_{12}}{a_{11}}\right)$ if $a_{12} \leq a_{11}$.
- 3) $\lambda_3 = \left(0, 0, \frac{a_7 a_{12} - a_9 a_{11} - a_8 a_{11}}{a_7 a_9} \lambda, \lambda, \frac{a_7 a_{12} - a_9 a_{11} - a_8 a_{11}}{a_7 a_{10}}, \frac{a_9 + a_8}{a_7}\right)$ if

$$a_{12} a_7 - a_{11} (a_8 + a_9) \geq 0 \text{ and } a_7 (a_{10} - a_{12}) - (a_8 + a_9) (a_{10} - a_{11}) \geq 0$$

where

$$\lambda = \frac{a_9 (a_7 a_{10} - a_9 a_{10} - a_8 a_{10} - a_7 a_{12} + a_9 a_{11} + a_8 a_{11})}{a_{10} (a_7 a_9 + a_7 a_{12} - a_8 a_{11} - a_9 a_{11})}.$$

- 4) $\lambda_4 = \left(\frac{a_1 a_{12} - a_4 a_{11}}{a_1 a_4} \lambda, 0, 0, \lambda, \frac{a_1 a_{12} - a_4 a_{11}}{a_1 a_{10}}, \frac{a_4}{a_1}\right)$ if

$$a_{12} a_1 - a_{11} a_4 \geq 0 \text{ and } a_{10} a_1 - a_{10} a_4 - a_{12} a_1 + a_{11} a_4 \geq 0,$$

where

$$\lambda = \frac{a_4 (a_{10} a_1 - a_{10} a_4 - a_{12} a_1 + a_{11} a_4)}{a_{10} (a_{12} a_1 - a_{11} a_4 + a_4 a_1)}.$$

- 5) $\lambda_5 = \left(\frac{a_8 + a_9 - a_7 a_6}{a_3}, 0, \frac{a_1 \lambda - a_4}{a_3}, \frac{a_4 a_8 + (a_1 a_9 - a_4 a_7) \lambda}{a_3 (a_{12} - a_{11} \lambda)}, \frac{a_{12} - a_{11} \lambda}{a_{10}}, \lambda\right)$ where λ is a root of

$$(4.1) \quad ax^2 + bx + c = 0$$

where

$$a = a_3 a_{11}^2 + a_{10} a_{11} (a_7 - a_1 - a_3),$$

$$b = a_{10} a_{11} (a_3 + a_4 - a_8 - a_9) + a_{10} a_{12} (a_3 + a_1 - a_7) +$$

$$a_{10} (a_1 a_9 - a_4 a_7) - 2a_3 a_{11} a_{12},$$

$$c = a_{10} a_{12} (a_8 + a_9 - a_3 - a_4) + a_3 a_{12}^2 + a_4 a_8 a_{10},$$

if $a_4 < a_1$ and λ verify

$$\frac{a_4}{a_1} < \lambda < \min\left\{\frac{a_{12}}{a_{11}}, \frac{a_8 + a_9}{a_7}\right\} \quad \text{if } a_1 a_9 \geq a_4 a_7,$$

$$\frac{a_4}{a_1} < \lambda < \min\left\{\frac{a_{12}}{a_{11}}, \frac{a_8 + a_9}{a_7}, \frac{a_4 a_8}{a_4 a_7 - a_1 a_9}\right\} \quad \text{if } a_1 a_9 < a_4 a_7.$$

- 6) $\lambda_6 = \left(\frac{a_5+a_6}{a_2}, \frac{a_1\lambda-a_4}{a_2}, 0, \frac{a_4a_6+a_1a_5\lambda}{a_2(a_{12}-a_{11}\lambda)}, \frac{a_{12}-a_{11}\lambda}{a_{10}}, \lambda \right)$ if $a_4 < a_1$ and $\frac{a_4}{a_1} < \lambda < \frac{a_{12}}{a_{11}}$, where λ is a root of

$$(4.2) \quad \alpha x^2 + \beta x + \gamma = 0$$

where

$$\alpha = a_2 a_{11}^2 - a_{10} a_{11} (a_1 + a_2),$$

$$\beta = a_{10} a_{11} (a_2 + a_4 - a_5 - a_6) + a_{10} a_{12} (a_1 + a_2) + a_1 a_5 a_{10} - 2a_2 a_{11} a_{12},$$

$$\gamma = a_{10} a_{12} (a_5 + a_6 - a_2 - a_4) + a_2 a_{12}^2 + a_4 a_6 a_{10}.$$

- 7) $\lambda_7 = \left(\frac{a_5+a_6}{a_2}, x_2, \lambda, x_4, x_5, \frac{a_2(a_8+a_9)-a_3(a_5+a_6)}{a_2 a_7} \right)$ where

$$x_2 = \frac{a_1(a_2 a_8 + a_2 a_9 - a_3 a_5 - a_3 a_6) - a_2 a_4 a_7 - a_2 a_3 a_7 \lambda}{a_2^2 a_7},$$

$$x_4 = \frac{a_7(a_4 a_5 + a_4 a_6 + a_2 a_5 x_2 + a_2 a_9 \lambda)}{a_2 a_7 a_{12} - a_{11}(a_2 a_8 + a_2 a_9 - a_3 a_5 - a_3 a_6)},$$

$$x_5 = \frac{a_2 a_7 a_{12} - a_{11}(a_2 a_8 + a_2 a_9 - a_3 a_5 - a_3 a_6)}{a_2 a_7 a_{10}},$$

$$\lambda = 1 - \frac{a_5+a_6}{a_2} - x_2 - x_4 - x_5 - \frac{a_2(a_8+a_9)-a_3(a_5+a_6)}{a_2 a_7},$$

if

$$\frac{a_2 a_4 a_7}{a_1} < a_2 a_8 + a_2 a_9 - a_3 a_5 - a_3 a_6 < \frac{a_2 a_7 a_{12}}{a_{11}}$$

and

$$\lambda < \frac{a_1(a_2 a_8 + a_2 a_9 - a_3 a_5 - a_3 a_6) - a_2 a_4 a_7}{a_2 a_3 a_7}.$$

Proof. Recall that a fixed point of the operator V is a solution to $V(x) = x$.

If $x_6 = 0$, from $x_6^{(1)} = x_6$ in (3.1) and $a_6, a_8, a_9 > 0$ we deduce $x_2 = x_3 = x_4 = 0$, therefore with $x_1' = x_1$ and $a_4 > 0$ we get $x_1 = 0$ and from $x_1 + \dots + x_6 = 0$ we deduce $x_5 = 1$ and the fixed point $(0, 0, 0, 0, 1, 0)$.

We assume now that $x_6 \neq 0$.

1) If $x_4 = 0$, from $x_5^{(1)} = x_5$ in (3.1) we get $x_1 = x_2 = x_3 = 0$ and from $x_5 + x_6 = 1$ we find fixed points λ_1 .

2) If $x_4 \neq 0$ and $x_5 = 0$, from $x_5^{(1)} = x_5$ in (3.1) we get $x_1 = x_2 = x_3 = 0$, with this and $x_6^{(1)} = x_6$ we have $x_6 = \frac{a_{12}}{a_{11}}$ from where $x_4 = 1 - x_6$, we find the fixed point λ_2 .

We assume now $x_4 \neq 0$ and $x_5 \neq 0$.

3) If $x_1 = 0$, from $x_2^{(1)} = x_2$ we get $x_2 = 0$, then from $x_5^{(1)} = x_5$ we get $x_3 \neq 0$, it follows from $x_3^{(1)} = x_3$ that $x_6 = \frac{a_8+a_9}{a_7}$, next with $x_4^{(1)} = x_4$ we get $x_5 = \frac{a_{12}-a_{11}x_6}{a_{10}} = \frac{(a_{12}a_7-a_{11}a_9-a_{11}a_8)}{a_7 a_{10}}$ and with $x_5^{(1)} = x_5$ we get $x_3 = \frac{(a_{12}-a_{11}x_6)}{a_9} x_4 = \frac{a_{12}a_7-a_{11}a_9-a_{11}a_8}{a_7 a_9} x_4$, and by $x_1 + \dots + x_6 = 1$ we obtain $x_4 = \frac{a_9(a_7 a_{10} - a_9 a_{10} - a_8 a_{10} - a_{12} a_7 + a_{11} a_9 + a_{11} a_8)}{a_{10}(a_{12} a_7 - a_{11} a_9 - a_{11} a_8 + a_9 a_7)}$, thus we have the fixed point λ_3 .

Here provided that all parameters are positive and since the sum of them equal to one, we can say that they are less than one.

4) If $x_1 \neq 0$. In the case $x_2 = 0$ and $x_3 = 0$, let $x_4 = \lambda \neq 0$, then from $x_1^{(1)} = x_1$ we get $x_6 = \frac{a_4}{a_1}$, from $x_4^{(1)} = x_4$ we get $x_5 = \frac{a_{12}a_1-a_{11}a_4}{a_{10}a_1}$ and from $x_6^{(1)} = x_6$ we deduce $x_1 = \frac{(a_{12}a_1-a_{11}a_4)}{a_4 a_1} \lambda$. In all cases $x_1 + \dots + x_6 = 1$ implies $\frac{(a_{12}a_1-a_{11}a_4)}{a_1 a_4} \lambda + \lambda + \frac{(a_{12}a_1-a_{11}a_4)}{a_{10}a_1} + \frac{a_4}{a_1} = 1$, from this we find

$\lambda = \frac{a_4(a_{10}a_1 - a_{10}a_4 - a_{12}a_1 + a_{11}a_4)}{a_{10}(a_{12}a_1 - a_{11}a_4 + a_4a_1)}$ and thus we have λ_4 . By conditions to the parameters, all coordinates are positive. Moreover, sum of them equal to one. It means that the fixed point belongs to the simplex S^5 . We note that by conditions $a_{12}a_1 - a_{11}a_4 \geq 0$ and $a_{10}a_1 - a_{10}a_4 - a_{12}a_1 + a_{11}a_4 \geq 0$ we have $a_4 \leq a_1$.

5) If $x_1 \neq 0$. In the case $x_2 = 0$ and $x_3 \neq 0$, let $x_6 = \lambda \neq 0$. From $x_3^{(1)} = x_3$ we get $x_1 = \frac{a_8 + a_9 - a_7\lambda}{a_3}$, from $x_1^{(1)} = x_1$ we deduce $x_3 = \frac{a_1\lambda - a_4}{a_3}$, from $x_4^{(1)} = x_4$ we get $x_5 = \frac{a_{12} - a_{11}\lambda}{a_{10}}$ and from $x_5^{(1)} = x_5$ we obtain $x_4 = \frac{a_4x_1 + a_9x_3}{a_{10}x_5} = \frac{a_4a_8 + \lambda(a_1a_9 - a_4a_7)}{a_3(a_{12} - a_{11}\lambda)}$. By replacing these values in $x_1 + \dots + x_6 = 1$ we obtain a quadratic equation (4.1) and by solving it we find λ and for the positiveness of each coordinate get boundary conditions for λ and thus, we obtain λ_5 .

6) Let $x_1 \neq 0, x_2 \neq 0$. If $x_3 = 0$, with $x_6 = \lambda \neq 0$, from $x_2^{(1)} = x_2$ we deduce $x_1 = \frac{a_5 + a_6}{a_2}$, from $x_1^{(1)} = x_1$ we get $x_2 = \frac{a_1\lambda - a_4}{a_2}$, from $x_4^{(1)} = x_4$ it comes $x_5 = \frac{a_{12} - a_{11}\lambda}{a_{10}}$ and from $x_5^{(1)} = x_5$ it follows $x_4 = \frac{a_4x_1 + a_5x_2}{a_{10}x_5} = \frac{a_4a_6 + a_1a_5\lambda}{a_2(a_{12} - a_{11}\lambda)}$. Here also by $x_1 + \dots + x_6 = 1$ we deduce that λ is root of a quadratic equation (4.2), by solving it we find λ and for the positiveness of each coordinate we get boundary conditions for λ and finally, we get λ_6 .

7) Here more difficult case is when all coordinates of fixed point are non-zero. Let $x_1 \neq 0, x_2 \neq 0, x_3 = \lambda \neq 0, x_4 \neq 0, x_5 \neq 0, x_6 \neq 0$. Then from $x_2^{(1)} = x_2$ we get $x_1 = \frac{a_5 + a_6}{a_2}$, from $x_3^{(1)} = x_3$ it follows $x_6 = \frac{a_2(a_8 + a_9) - a_3(a_5 + a_6)}{a_2a_7}$, from $x_1^{(1)} = x_1$ we deduce $x_2 = \frac{a_1x_6 - a_4 - a_3\lambda}{a_2}$, and from $x_4^{(1)} = x_4$ and $x_5^{(1)} = x_5$ we deduce respectively $x_5 = \frac{a_{12} - a_{11}x_6}{a_{10}}$ and $x_4 = \frac{a_4x_1 + a_5x_2 + a_9\lambda}{a_{12} - a_{11}x_6}$. By $x_1 + \dots + x_6 = 1$ we have linear equation with respect to λ and for positiveness of coordinates we get conditions to the parameters. We note that if we request positiveness, then by $x_1 + \dots + x_6 = 1$ we do not need to show coordinates less than 1. Thus, we found all possible fixed points of the operator (3.1). \square

Remark 9. We note that all coordinates of each fixed point must belong to $[0, 1]$ and from the vertices of the simplex only $(0, 0, 0, 0, 1, 0)$ and $(0, 0, 0, 0, 0, 1)$ can be fixed points (see λ_1).

Next we study the type of fixed points. First, we find the Jacobian of the operator (3.1):

$$\begin{bmatrix}
 \frac{\partial x_1^{(1)}}{\partial x_1} & -a_2x_1 & -a_3x_1 & 0 & 0 & a_1x_1 \\
 a_2x_2 & \frac{\partial x_2^{(1)}}{\partial x_2} & 0 & 0 & 0 & 0 \\
 a_3x_3 & 0 & \frac{\partial x_3^{(1)}}{\partial x_3} & 0 & 0 & a_7x_3 \\
 0 & 0 & 0 & \frac{\partial x_4^{(1)}}{\partial x_4} & a_{10}x_4 & a_{11}x_4 \\
 a_4 & a_5 & a_9 & -a_{10}x_5 & 1 - a_{10}x_4 & 0 \\
 -a_1x_6 & a_6 & -a_7x_6 + a_8 & -a_{11}x_6 + a_{12} & 0 & \frac{\partial x_6^{(1)}}{\partial x_6}
 \end{bmatrix}$$

where

$$\begin{aligned}\frac{\partial x_1^{(1)}}{\partial x_1} &= 1 - a_4 + a_1x_6 - a_2x_2 - a_3x_3, & \frac{\partial x_2^{(1)}}{\partial x_2} &= 1 - a_5 - a_6 + a_2x_1, \\ \frac{\partial x_3^{(1)}}{\partial x_3} &= 1 - a_8 - a_9 + a_3x_1 + a_7x_6, & \frac{\partial x_4^{(1)}}{\partial x_4} &= 1 - a_{12} + a_{10}x_5 + a_{11}x_6, \\ \frac{\partial x_6^{(1)}}{\partial x_6} &= 1 - a_1x_1 - a_7x_3 - a_{11}x_4.\end{aligned}$$

By solving simple determinant of 6th order, we can define that at the fixed point λ_1 the Jacobian has two eigenvalues equal to 1, so this fixed point is non-hyperbolic.

At the fixed point λ_2 the Jacobian is:

$$\begin{aligned}\det(J(\lambda_2) - \mu I) &= (1 - \mu) \left(1 - a_4 + \frac{a_1a_{12}}{a_{11}} - \mu\right) \left(1 - a_8 - a_9 + \frac{a_7a_{12}}{a_{11}} - \mu\right) \times \\ &\quad (1 - a_5 - a_6 - \mu) \left(1 - a_{10} + \frac{a_{10}a_{12}}{a_{11}} - \mu\right) (1 - a_{11} + a_{12} - \mu),\end{aligned}$$

from this, one eigenvalue $\mu_4 = 1$, so the fixed point λ_2 also non-hyperbolic. In the general case, finding the eigenvalues of Jacobian for the other fixed points is more difficult.

Let $e_i = (\delta_{1i}, \dots, \delta_{mi}) \in S^{m-1}$, $i = 1, \dots, m$ be the vertices of the simplex S^{m-1} , where δ_{ij} the Kronecker's symbol, and by \mathcal{V}_l we denote the set of all l -Volterra QSOs.

Proposition 10. ([10])

(1) The vertex e_i is a fixed point for an l -Volterra QSO if and only if $P_{ii,i} = 1$, ($i = 1, \dots, m$).

(2) For any collection $I_s = \{e_{i_1}, \dots, e_{i_s}\} \subset \{e_{l+1}, \dots, e_m\}$, ($s \leq m - 1$) there exists a family $\mathcal{V}_l(I_s) \subset \mathcal{V}_l$ such that $\{e_{i_1}, \dots, e_{i_s}\}$ is an s -cycle for each $V \in \mathcal{V}_l(I_s)$.

Using this proposition and the conditions to the parameters (3.3) we formulate the following proposition.

Proposition 11.

(1) The following vertices e_1, e_2, e_3 and e_4 can not be fixed points for the QSO (3.1)

(2) Vertices $\{e_5, e_6\}$, and any collection $\{e_{i_1}, \dots, e_{i_s}\} \subset \{e_1, \dots, e_4\}$, ($1 < s \leq 4$) can not be a periodic orbit for the QSO (3.1).

Proof. (1) By Proposition 10 the vertices e_1, e_2, e_3 and e_4 are fixed points if and only if $P_{11,1} = 1, P_{22,2} = 1, P_{33,3} = 1$ and $P_{44,4} = 1$ respectively. But for the operator (3.1) all parameters are positive and $P_{ii,i} \neq 1$ for any $i = 1, 2, 3, 4$, so e_i can not be fixed point for any $i = 1, 2, 3, 4$.

(2) By Proposition 10 only the collection $\{e_5, e_6\}$ can be 2-cycle for the 4-Volterra QSO. But for the 4-Volterra operator (3.1), $V(e_5) = e_5 \neq e_6$ and $V(e_6) = e_6 \neq e_5$. The remaining part of this assertion follows from Remark 3.4 in [10]. The proposition is proved. \square

5. THE LIMIT POINTS OF TRAJECTORIES

In this section we step by step study the limit behavior of trajectories of initial points $\lambda^{(0)} \in S^5$ under operator (3.1), i.e the sequence $V^n(\lambda^{(0)})$,

$n \geq 1$. Note that since V is a continuous operator, its trajectories have as a limit some fixed points obtained in Proposition 8.

5.1. Case no dissolved inorganic matter. We study here the case where in the model there is no dissolved inorganic matter.

Proposition 12. *For an initial point $\lambda^{(0)} = (x_1^{(0)}, x_2^{(0)}, x_3^{(0)}, x_4^{(0)}, x_5^{(0)}, x_6^{(0)}) \in S^5$ (except fixed points), with $x_6^{(0)} = x_6^{(1)} = 0$, the trajectory (under action of operator (3.1)) has the following limit*

$$\lim_{n \rightarrow \infty} V^{(n)}(\lambda^{(0)}) = (0, 0, 0, 0, 1, 0).$$

Proof. If $x_6^{(0)} = x_6^{(1)} = 0$, from the sixth equation of (3.1) we deduce $x_2^{(0)} = x_3^{(0)} = x_4^{(0)} = 0$ which implies according to the second, third and fourth equations of (3.1) $x_2^{(n)} = x_3^{(n)} = x_4^{(n)} = 0$ for every $n \geq 0$. With these results the sixth equation of (3.1) becomes $x_6^{(n+1)} = x_6^{(n)} (1 - a_1 x_1^{(n)})$ from $x_6^{(1)} = 0$ we deduce recursively that $x_6^{(n)} = 0$ for every $n \geq 0$. Then the first equation of (3.1) becomes $x_1^{(n+1)} = (1 - a_4) x_1^{(n)}$ which implies $x_1^{(n)} = (1 - a_4)^n x_1^{(0)}$ with $1 - a_4 < 1$ thus $\lim_{n \rightarrow \infty} x_1^{(n)} = 0$ and therefore $\lim_{n \rightarrow \infty} x_5^{(n)} = 1$. \square

Biological interpretation: Without zooplankton, mixoplankton and bacteria there is no more production of dissolved inorganic matter. Due to absence of food the amount of phytoplankton decreases until it disappears, as the dissolved organic matter is no longer degraded by bacteria, it accumulates in the environment until it is saturated.

5.2. Case no dissolved organic matter.

Proposition 13. *For an initial point $\lambda^{(0)} = (x_1^{(0)}, x_2^{(0)}, x_3^{(0)}, x_4^{(0)}, x_5^{(0)}, x_6^{(0)}) \in S^5$ (except fixed points), with $x_5^{(0)} = x_5^{(1)} = 0$, the trajectory has the following limit*

$$\lim_{n \rightarrow \infty} V^{(n)}(\lambda^{(0)}) = \begin{cases} (0, 0, 0, 0, 0, 1) & \text{if } a_{11} \leq a_{12} \\ (0, 0, 0, 1 - \frac{a_{12}}{a_{11}}, 0, \frac{a_{12}}{a_{11}}) & \text{if } a_{11} > a_{12}. \end{cases}$$

Proof. From $x_5^{(0)} = x_5^{(1)} = 0$ and the fifth equation of (3.1) we get $x_1^{(0)} = x_2^{(0)} = x_3^{(0)} = 0$ which implies recursively according to the first three equations of (3.1) that $x_1^{(n)} = x_2^{(n)} = x_3^{(n)} = 0$ for any $n \geq 0$, consequently from the fifth equation we get $x_5^{(n)} = 0$ for any $n \geq 0$. Using these results the system (3.1) is reduced to

$$\begin{cases} x_4^{(n+1)} = x_4^{(n)} (1 - a_{12} + a_{11} x_6^{(n)}) \\ x_6^{(n+1)} = x_6^{(n)} + x_4^{(n)} (a_{12} - a_{11} x_6^{(n)}) \end{cases}$$

We see that $x_4^{(n+1)} + x_6^{(n+1)} = x_4^{(n)} + x_6^{(n)}$ thus $x_6^{(n)} = 1 - x_4^{(n)}$ for any $n \geq 1$, with this we get $x_4^{(n+1)} = x_4^{(n)} (1 + a_{11} - a_{12} - a_{11} x_4^{(n)})$. Consider the function $f(x) = x(1 + a_{11} - a_{12} - a_{11}x)$, it has two fixed points 0 and $1 - \frac{a_{12}}{a_{11}}$. Since $f'(0) = 1 - a_{12} + a_{11}$ the fixed point 0 is attracting if and

only if $a_{11} < a_{12}$, non-hyperbolic if $a_{11} = a_{12}$ and repelling if $a_{11} > a_{12}$. Similarly, by $f'(1 - \frac{a_{12}}{a_{11}}) = 1 + a_{12} - a_{11}$ we have that $1 - \frac{a_{12}}{a_{11}}$ is attracting if $a_{11} > a_{12}$ and non-hyperbolic if $a_{11} = a_{12}$. Moreover, for $a_{11} \leq a_{12}$ the sequence $x_4^{(n)} = f^n(x_4^{(0)})$ is decreasing. Finally for any $x_4^{(0)} \in [0, 1]$ we have

$$\lim_{n \rightarrow \infty} f^{(n)}(x_4^{(0)}) = \begin{cases} 0, & \text{if } a_{11} \leq a_{12} \\ 1 - \frac{a_{12}}{a_{11}}, & \text{if } a_{11} > a_{12}. \end{cases}$$

□

Biological interpretation: The absence of dissolved organic matter is due to the absence of plankton. When the bacteria disappearance rate is higher than their consumption rate of dissolved inorganic matter, bacteria disappear completely. When the comparison of these rates is reversed, the composition of the environment tends towards a balance between bacteria and dissolved inorganic matter.

5.3. Case no bacteria.

Proposition 14. *For any initial point $\lambda^{(0)} = (x_1^{(0)}, x_2^{(0)}, x_3^{(0)}, 0, x_5^{(0)}, x_6^{(0)}) \in S^5$ (except fixed points), the trajectory has the following limit*

$$\lim_{n \rightarrow \infty} V^{(n)}(\lambda^{(0)}) = (0, 0, 0, 0, \bar{\lambda}, 1 - \bar{\lambda}),$$

where $\bar{\lambda} = \bar{\lambda}(\lambda^{(0)})$.

Proof. When $x_4^{(0)} = 0$, according to the fourth equation of (3.1) we have $x_4^{(n)} = 0$ for all $n \geq 0$. Then $x_5^{(n+1)} = x_5^{(n)} + a_4x_1^{(n)} + a_5x_2^{(n)} + a_9x_3^{(n)} \geq x_5^{(n)}$ so, the sequence $x_5^{(n)}$ has a limit $\bar{\lambda}$ and $\lim_{n \rightarrow \infty} (a_4x_1^{(n)} + a_5x_2^{(n)} + a_9x_3^{(n)}) = 0$, but $a_4x_1^{(n)} + a_5x_2^{(n)} + a_9x_3^{(n)} \geq a_4x_1^{(n)} \geq 0$ which leads to $\lim_{n \rightarrow \infty} x_1^{(n)} = 0$ and in a similar way $\lim_{n \rightarrow \infty} x_2^{(n)} = \lim_{n \rightarrow \infty} x_3^{(n)} = 0$. Then with $x_6^{(n)} = 1 - \sum_{i=1}^5 x_i^{(n)}$ we deduce that $\lim_{n \rightarrow \infty} x_6^{(n)} = 1 - \bar{\lambda}$. □

Biological interpretation: In the absence of bacteria, compartments between dissolved inorganic and organic matters are not connected, the trophic network is open. Dissolved organic matter (DOM) resulting from plankton mortality are no longer transformed into dissolved inorganic matter (DIM), the environment is no longer supplied with DIM. The supply of phytoplankton and mixoplankton decreases the amount of DIM which causes an increase in plankton mortality and contributes to increase the amount of DOM until reaching a point of equilibrium between the amounts of DOM and DIM.

5.4. Case no phytoplankton. The following lemma is useful.

Lemma 15. *For an initial point $\lambda^{(0)} = (x_1^{(0)}, x_2^{(0)}, x_3^{(0)}, x_4^{(0)}, x_5^{(0)}, x_6^{(0)}) \in S^5$ (except fixed points), if $x_4^{(n)}$ converges to zero and two among the sequences $x_1^{(n)}, x_2^{(n)}, x_3^{(n)}$ have zero limit then remaining (third) sequence has zero limit and the limit of the trajectory is the fixed point λ_1 .*

Proof. – If $\lim_{n \rightarrow \infty} x_i^{(n)} = 0$ for $i = 2, 3$.

Suppose that $\lim_{n \rightarrow \infty} x_1^{(n)} = \nu \neq 0$. Then from the first equation of (3.1) we get $\lim_{n \rightarrow \infty} x_6^{(n)} = \frac{a_4}{a_1}$, which by the sixth equation of (3.1) gives that $a_1\nu = 0$, thus we have a contradiction.

– If $\lim_{n \rightarrow \infty} x_i^{(n)} = 0$ for $i = 1, 3$.

Suppose that $\lim_{n \rightarrow \infty} x_2^{(n)} \neq 0$, then from the second equation of (3.1) we deduce $\lim_{n \rightarrow \infty} x_1^{(n)} = \frac{a_5 + a_6}{a_2} \neq 0$, this is a contradiction.

– If $\lim_{n \rightarrow \infty} x_i^{(n)} = 0$ for $i = 1, 2$.

Suppose that $\lim_{n \rightarrow \infty} x_3^{(n)} = \mu \neq 0$, then it follows from the third equation of (3.1) that $\lim_{n \rightarrow \infty} x_6^{(n)} = \frac{a_8 + a_9}{a_7}$. Now by the equality

$$x_5^{(n)} = 1 - \sum_{\substack{i=1 \\ i \neq 5}}^6 x_i^{(n)}$$

we deduce that the sequence $x_5^{(n)}$ has a limit. Consequently, from the fifth equation of (3.1) we get $a_9\mu = 0$, again a contradiction. \square

Biological interpretation: If bacteria and two species of plankton disappear then the third plankton also disappears.

Lemma 16. *For an initial point $\lambda^{(0)} = (x_1^{(0)}, x_2^{(0)}, x_3^{(0)}, x_4^{(0)}, x_5^{(0)}, x_6^{(0)}) \in S^5$ (except fixed points), if $a_{10} + a_{11} \leq a_{12}$ (resp. $a_3 + a_7 \leq a_8 + a_9$) then $x_4^{(n)}$ (resp. $x_3^{(n)}$) converges to zero.*

Proof. From the condition $a_{10} + a_{11} \leq a_{12}$ we have $a_{12} - a_{10}x_5^{(0)} - a_{11}x_6^{(0)} > 0$, because, $x_5 = x_6 = 1$ never occurs, and by Proposition 4 it follows $a_{12} \leq 1$, from this we get $a_{12} - a_{10}x_5^{(0)} - a_{11}x_6^{(0)} \leq 1$, it means that $0 \leq 1 - (a_{12} - a_{10}x_5^{(0)} - a_{11}x_6^{(0)}) < 1$, so we have

$$\lim_{n \rightarrow \infty} x_4^{(n)} = 0.$$

Similarly, if $a_3 + a_7 \leq a_8 + a_9$ then $\lim_{n \rightarrow \infty} x_3^{(n)} = 0$. \square

Proposition 17. *If $a_7 \leq a_8 + a_9$ and $a_{10} + a_{11} \leq a_{12}$ then for any initial point $\lambda^{(0)} = (0, x_2^0, x_3^0, x_4^0, x_5^0, x_6^0) \in S^5$ (except fixed points), the trajectory has the following limit*

$$\lim_{n \rightarrow \infty} V^{(n)}(\lambda^{(0)}) = (0, 0, 0, 0, \bar{\lambda}, 1 - \bar{\lambda}).$$

where $\bar{\lambda} = \bar{\lambda}(\lambda^{(0)})$.

Proof. If $x_1^{(0)} = 0$ according to (3.1) we have $x_1^{(n)} = 0$ for all $n \geq 0$. Then the operator V becomes

$$(5.1) \quad V : \begin{cases} x'_2 = x_2(1 - a_5 - a_6) \\ x'_3 = x_3(1 - a_8 - a_9 + a_7x_6) \\ x'_4 = x_4(1 - a_{12} + a_{10}x_5 + a_{11}x_6) \\ x'_5 = x_5 + a_5x_2 + a_9x_3 - a_{10}x_4x_5 \\ x'_6 = x_6(1 - a_7x_3 - a_{11}x_4) + a_6x_2 + a_8x_3 + a_{12}x_4 \end{cases}$$

We have $x_2^{(n+1)} = x_2^{(0)}(1 - a_5 - a_6)^n$ since $1 - a_5 - a_6 < 1$ the sequence $x_2^{(n)}$ has limit $\lim_{n \rightarrow \infty} x_2^{(n)} = 0$. Moreover, from condition $a_{10} + a_{11} \leq a_{12}$ and according Lemma 16 we have $\lim_{n \rightarrow \infty} x_4^{(n)} = 0$.

If $a_7 \leq a_8 + a_9$ then $x_3^{(1)} \leq x_3^{(0)}(1 - (a_8 + a_9 - a_7x_6)) \leq x_3^{(0)}$. So the sequence $x_3^{(n)}$ has limit and according Lemma 15 it has zero limit.

From the fourth equation of the system (5.1) we deduce

$$\left| x_5^{(n+1)} - x_5^{(n)} \right| \leq a_5x_2^{(n)} + a_9x_3^{(n)} + a_{10}x_4^{(n)}.$$

Then for all $m > n$ we have

$$\left| x_5^{(m)} - x_5^{(n)} \right| \leq \sum_{k=n}^{m-1} \left| x_5^{(k+1)} - x_5^{(k)} \right| \leq a_5 \sum_{k=n}^m x_2^{(k)} + a_9 \sum_{k=n}^m x_3^{(k)} + a_{10} \sum_{k=n}^m x_4^{(k)}$$

using the upper bounds of sequences $x_2^{(n)}$, $x_3^{(n)}$, $x_4^{(n)}$ obtained previously, we get

$$\begin{aligned} \left| x_5^{(m)} - x_5^{(n)} \right| &\leq a_5x_2^{(0)} \sum_{k=n}^{+\infty} (1 - a_5 - a_6)^k + a_9x_3^{(0)} \sum_{k=n}^{+\infty} (1 + a_7 - a_8 - a_9)^k + \\ &\quad a_{10}x_4^{(0)} \sum_{k=n}^{+\infty} (1 + a_{10} + a_{11} - a_{12})^k \end{aligned}$$

from this we deduce that $x_5^{(n)}$ is a Cauchy sequence, thus we can say that this sequence has limit $\bar{\lambda}$, but it always depends the initial point $\lambda^{(0)}$. In this case we know that operator called *regular*, i.e., every initial point has its limit point.

□

Biological interpretation: If no phytoplankton and if death rates of mixoplankton and bacteria are higher than their consumption rates of dissolved inorganic compounds, then after some time the populations of zooplankton, mixoplankton and bacteria gradually disappears and finally it stay only dissolved inorganic and organic matters, of course they depend the initial amount of each other organisms.

5.5. Case neither zooplankton nor mixoplankton.

Proposition 18. *If $a_1 \leq a_4$ and $a_{10} + a_{11} \leq a_{12}$ then for any initial point $\lambda^{(0)} = (x_1^{(0)}, 0, 0, x_4^{(0)}, x_5^{(0)}, x_6^{(0)}) \in S^5$ (except fixed points), the trajectory has the following limit*

$$\lim_{n \rightarrow \infty} V^{(n)}(\lambda^{(0)}) = (0, 0, 0, 0, \bar{\lambda}, 1 - \bar{\lambda}),$$

where $\bar{\lambda} = \bar{\lambda}(\lambda^{(0)})$.

Proof. If $x_2^{(0)} = x_3^{(0)} = 0$ then $x_2^{(n)} = x_3^{(n)} = 0$ for all $n \geq 0$, the system (3.1) becomes

$$(5.2) \quad \begin{cases} x_1' = x_1(1 - a_4 + a_1x_6) \\ x_4' = x_4(1 - a_{12} + a_{10}x_5 + a_{11}x_6) \\ x_5' = x_5 + a_4x_1 - a_{10}x_4x_5 \\ x_6' = x_6(1 - a_1x_1 - a_{11}x_4) + a_{12}x_4 \end{cases}$$

By the condition $a_{10} + a_{11} \leq a_{12}$ using Lemma 16 we have $\lim_{n \rightarrow \infty} x_4^{(n)} = 0$. If $a_1 \leq a_4$ then $x_1^{(1)} \leq (1 - (a_4 - a_1x_6))x_1^{(0)} \leq x_1^{(0)}$ so the sequence $x_1^{(n)}$ has limit. Thus, by Lemma 15 we have $\lim_{n \rightarrow \infty} x_1^{(n)} = 0$. From the fourth equation of (5.2) we get

$$\left| x_6^{(n+1)} - x_6^{(n)} \right| \leq a_{12}x_4^{(n)} \leq a_{12}(1 + a_{10} + a_{11} - a_{12})^n x_4^{(0)},$$

therefore for any $m > n$ we have

$$\left| x_6^{(m)} - x_6^{(n)} \right| \leq a_{12} \sum_{k=n}^{+\infty} a_{12}(1 + a_{10} + a_{11} - a_{12})^k x_4^{(0)},$$

so $x_6^{(n)}$ is a Cauchy sequence thus the sequence $x_6^{(n)}$ has a limit. □

Biological interpretation: Without zooplankton and mixoplankton, if the consumption rates of dissolved inorganic compounds of phytoplankton and bacteria is less than their death rates, then after some time the populations of phytoplankton and bacteria gradually disappears, ultimately it only stays in the environment dissolved inorganic and organic matters whose proportions whose proportions depend of course on the initial conditions.

5.6. Cases with three types of plankton and bacteria at initial stage.

We formulate a proposition for general case where all coordinates of an initial point are non zero.

Proposition 19. *If $a_1 \leq a_4$, $a_2 \leq a_5 + a_6$, $a_3 + a_7 \leq a_8 + a_9$, $a_{10} + a_{11} \leq a_{12}$ then for any initial point $\lambda^{(0)} = (x_1^{(0)}, x_2^{(0)}, x_3^{(0)}, x_4^{(0)}, x_5^{(0)}, x_6^{(0)}) \in S^5$ (except fixed points) the following holds*

$$\lim_{n \rightarrow \infty} V^{(n)}(\lambda^{(0)}) = (0, 0, 0, 0, \bar{\lambda}, 1 - \bar{\lambda}),$$

where $\bar{\lambda} = \bar{\lambda}(\lambda^{(0)})$.

Proof. From conditions $a_3 + a_7 \leq a_8 + a_9$, $a_{10} + a_{11} \leq a_{12}$ according Lemma 16 we obtain $x_3^{(n)}$ and $x_4^{(n)}$ have zero limits. We will study the 4 cases according to whether the inequalities $a_1 \leq a_4$, $a_2 \leq a_5 + a_6$ are equalities or strict inequalities.

If $a_1 \leq a_4$, $a_2 \leq a_5 + a_6$, we deduce from the first two equations of (3.1) the following inequalities

$$(5.3) \quad x_1^{(1)} \leq (1 + a_1 - a_4)x_1, \quad x_2^{(1)} \leq (1 + a_2 - a_5 - a_6)x_2,$$

If $a_1 = a_4$, from (5.3) the sequence $x_1^{(n)}$ is decreasing so it has a limit noted μ_1 . Analogously, if $a_2 = a_5 + a_6$ the sequence $x_2^{(n)}$ has a limit μ_2 .

Case 1: Two strict inequalities.

If $a_1 < a_4$, $a_2 < a_5 + a_6$ from the first two equations of (3.1) we get

$$(5.4) \quad x_1^{(n)} \leq (1 + a_1 - a_4)^n x_1^{(0)}, \quad x_2^{(n)} \leq (1 + a_2 - a_5 - a_6)^n x_2^{(0)}.$$

So the sequences $x_1^{(n)}$, $x_2^{(n)}$ converge to zero, and the limit of the trajectory is the fixed point of type λ_1 (cf. Proposition 8).

Case 2: One equality and one strict inequality.

In each of the two possible cases, one of the sequences $x_1^{(n)}$, $x_2^{(n)}$ has limit zero, therefore according to Lemma 15, the remaining sequence also has limit zero, thus the limit of the trajectory is the fixed point of type λ_1 .

Case 3: Two equalities.

3.1. If $a_1 = a_4$ and $a_2 = a_5 + a_6$.

We suppose $\mu_1 \neq 0$ and $\mu_2 \neq 0$, otherwise according to Lemma 15 we have $\lim_{n \rightarrow \infty} x_i^{(n)} = 0$ for $1 \leq i \leq 4$ and the limit of the operator V is the fixed point of type λ_1 . Then from the second equation of (3.1) we get $\mu_1 = \frac{a_5 + a_6}{a_2} = 1$ and thus $\mu_2 = 0$, this is contradiction. Consequently, the limit of the trajectory is the fixed point of type λ_1 .

□

6. CONJECTURE FOR MORE GENERAL CASES.

Recall that $\lambda_2, \lambda_3, \lambda_4$ are the fixed points defined in Proposition 8.

Based on the numerical analysis, the explicit form of the operator and the fixed points we make the following conjectures:

Conjecture 1. Let the initial point $\lambda^{(0)} = (x_1^{(0)}, x_2^{(0)}, x_3^{(0)}, x_4^{(0)}, x_5^{(0)}, x_6^{(0)})$, with $x_4^{(0)} > 0$ and $a_{11} > a_{12}$, $a_3 \leq a_7 \leq a_8 + a_9$ (or $x_3^{(0)} = 0$). Then

(1) If $x_1^{(0)} > 0$, $a_4 < a_1$, and $a_{12}a_1 - a_{11}a_4 > 0$, $a_{10}a_1 - a_{10}a_4 - a_{12}a_1 + a_{11}a_4 > 0$ then

$$\lim_{n \rightarrow \infty} V^{(n)}(\lambda^{(0)}) = \lambda_4.$$

(2) If $a_{12}a_1 - a_{11}a_4 \leq 0$ then

$$\lim_{n \rightarrow \infty} V^{(n)}(\lambda^{(0)}) = \lambda_2.$$

Conjecture 2. If $a_{11} > a_{12}$, $a_7 > a_8 + a_9$, $a_1 \leq a_4$ (or $x_1^{(0)} = 0$), $a_{12}a_7 - a_{11}(a_8 + a_9) > 0$, $a_{10}(a_7 - (a_8 + a_9)) - (a_{12}a_7 - a_{11}(a_8 + a_9)) > 0$, $x_3^{(0)} > 0$, $x_4^{(0)} > 0$, then

$$\lim_{n \rightarrow \infty} V^{(n)}(\lambda^{(0)}) = \lambda_3.$$

We note that for the other cases an investigation of the limit behavior of the operator (3.1) seems very difficult.

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