Open Communications in Nonlinear Mathematical Physics]ocnmp[Vol.4 (2024) pp 188–211 ARTICLE

The Volterra Integrable case. Novel analytical and numerical results.

M. Scalia[a], *O. Ragnisco*[b], *B. Tirozzi*[c], *F. Zullo*[d]

[a]*Dipartimento di Matematica, Università degli Studi "La Sapienza", P.le A. Moro 2, I-00185 Roma*

[b]*Dipartimento di Matematica e Fisica, Università degli Studi "Roma Tre" (retired), Via della Vasca Navale 84,00146 Roma*

[c] *Dipartimento di Fisica, Università degli Studi "La Sapienza", P.le A. Moro 2, I-00185 Roma*

[d] *DICATAM, Università degli Studi di Brescia, via Branze, 38 - 25123 Brescia, Italy & INFN, Milano Bicocca, Piazza della Scienza 3, Milano, 20126, Italy*

Received July 17, 2024; Accepted October 3, 2024

Abstract

In the present paper we reconsider the integrable case of the Hamiltonian N-species Volterra system, as it has been introduced by Vito Volterra in 1937 and significantly enrich the results already published in the ArXiv in 2019 by two of the present authors (M. Scalia and O. Ragnisco). In fact, we present a new approach to the construction of conserved quantities and comment about the solutions of the equations of motion; we display mostly new analytical and numerical results, starting from the classical predator-prey model and arriving at the general N-species model.

0 Preface

This paper is dedicated to the memory of one of the authors, namely our dearest colleague and friend Massimo Scalia, who sadly died on December 10, 2023, after a dramatic car accident occurred at a crossroad not far from the centre of Rome. In the previous summer, Massimo had been deeply affected by a major personal tragedy, the death of his beloved companion (Adele Vannini) who passed away after a long illness. He was able to react to this tremendous shock, fully devoting himself to the two fields of interest that marked his whole life, politics and science. We could even say that they were not two different interests, inasmuch as, all along his career, he tirelessly struggled to establish a bridge between them. The idea of resuming the brilliant approach to Mathematical Biology introduced by Vito Volterra [1], recently revived by Giorgio Israel in his beautiful monographs [2], has in fact characterized several of his recent papers, among which we just quote the most recent ones [3, 4, 5]. From [1], Massimo took the key idea that conflicting variables, one economical and the other ecological, could be thought as forming a pair of conjugated variables (in the Hamiltonian language) in the spirit of the predator-prey model [6], following the ideas introduced by Goodwin already fifty years ago [7], in his class struggle model.

The analogy could indeed be pushed forward to involve a larger number of competing species, so deriving an N-species generalization of the simplest two-species model. Once recast in a Hamiltonian form, it was then natural to ask whether also such an enlarged model could enjoy the property of complete integrability. In fact we discovered that Volterra himself had already addressed and solved this question, that amounted to require a specific (but simple) structure for the interaction matrix. The present article focusses on the study of the N-species Volterra model in the integrable case, and as such is a reformulation and a significant extension of the preprints appeared in the ArXiv [8], whose contents are here largely incorporated.

1 Introduction.

As well known, the original idea by Vito Volterra [6] was that of determining the evolution of a two species biological system, the so-called predator-prey model, answering a question raised by his son in law, the biologist Umberto d'Ancona [9], who was wondering why the total catch of selachians (mostly sharks) was considerably raising during World War 1, with respect to other more desirable kind of fishes, in correspondence with the decrease of fishing activity [10]. To answer that question, Vito Volterra constructed a dynamical system that enabled him to identify the essential features of what was going on, elucidating the properties entailing the existence of a stable equilibrium configuration and of periodic orbits, and unveiling the asymptotic behavior of the system under general initial conditions. He quickly realized that the predator-prey model was just the simplest example in a large class of biological, or rather ecological systems with pairwise interaction. He was soon interested in understanding the mathematical properties of the N species pairwise interacting model, and expend a considerable effort to find suitable Lagrangian and Hamiltonian formulations, with the final aim of achieving a description where the deep analogy with the well established theory of mechanical systems stemming from the Maupertuis minimal action principle be made transparent. We would say that not the whole Biological-Mechanical dictionary that he proposed in his famous paper (dating back to 1937), *Principes de Biologie Mathématique* [1], resisted the future developments of both disciplines, and some of the notions he tried to introduce look nowadays a bit artificial. But we believe that the core of his derivation is still alive, as it has been witnessed by very widespread applications over about a century in many scientific research subjects, such as Demography, Biophysics, Biomedicine, Ecology, Economics but also chemical reactions modeling and the theory of oriented directed graphs. We notice that in [1] his main aim was the formulation of this generalized model in a Hamiltonian language, with the final purpose of elucidating the algebraic conditions leading to a completely integrable model. Actually, the direction he chose, aiming to establish what he called the "Three fundamental laws of biological fluctuations" [1], pp. 20-21, namely that of looking for a conservative model, is certainly not the only possible generalization of the original predator-prey system. The current literature is quite rich of papers dealing with dissipative models, see for instance [11, 12, 13].

Although [1] has been inexplicably neglected by most of the researchers who worked on Lotka-Volterra systems in their various formulations, we consider it a seminal paper and take it as our starting point. Accordingly, first of we recall his approach and his main results, and then propose a novel approach to integrability, in order to extract new features of the model, first focussing on the three-species case and then generalizing it to an arbitrary number of species. To perform such task we stayed with the basic Volterra's assumption that the interaction matrix A, see (1), be skew-symmetric. We are aware that this assumption could sound unrealistic, but on the other hand, to the best of our knowledge, this property, or better its generalization, the so-called skew-symmetrizability, defined for instance in [11] and in [13], looks fundamental for dealing with conservative systems, and a fortiori with completely integrable ones. Our paper is organized as follows. In Section 2 we recall how Volterra constructed his Lagrangian and Hamiltonian formulation for the general N-species model, and we briefly comment on different Hamiltonian structures existing in the literature. Also, we present the Volterra's approach to complete integrability, and, as a by-product, we exhibit his Hamiltonian description of the predator-prey model; different, possibly more familiar, Hamiltonian formulations, are also recalled here and more explicitly in the Appendix. In the end, we discuss equilibrium configuration for N larger than 2, starting with $N = 3$, so introducing the content of the next section. In Section 3 we present an analytical argument and a geometric evidence to infer the compactness of the space of trajectories for $N = 3$, and display a number of periodic examples. Further, a general argument to deal with the N-species problem is given, and a set of independent integrals of motion is displayed. The proof of their involutivity is confined to Appendix A. Section 4 is the concluding one: we make comments on Volterra's results compared to ours and outline some possible future developments.

2 The N-species system.

The equations for the N-species Volterra System read

$$\dot{N}_r = \epsilon_r N_r + \sum_{s\neq r=1}^{N} A_{rs} N_r N_s \quad (r = 1, \cdots, N) \tag{1}$$

In (1) a dot on a function represents the time derivative and we have set all the parameters introduced in [6] $\beta_r = 1$ $\forall r$ (which is not totally harmless from the biological point of view, as Volterra explains in the second paragraph of the first part of his essay); ϵ_r are the natural growth coefficients of each species and A_{rs} are interaction coefficients between species r and species s that account for the effects of encountering between two individuals (more precisely, according to [1], $(1/\beta_r)A_{rs}N_rN_s$ denotes the decreasing in unit time of the individuals of the specie r, while $(1/\beta_s)A_{sr}N_rN_s$ denotes the corresponding increasing of the species s). If the matrix A, whose elements are A_{rs}, is nonsingular, then the system of equations defining equilibrium configurations (other than the trivial one $\{N_r\} = \{0\}$), namely

$$0 = \epsilon_r + \sum_{s=1}^{N} A_{rs} N_s^{(0)} \tag{2}$$

has a unique solution, say $N_r^{(0)}$, $r = 1, \cdots, N$. If, in addition, according to [6], we require A to be skew-symmetric and N to be even, then the eigenvalues of A will be purely imaginary and complex conjugate in pairs. On the contrary, in the case of an odd number of species, a skewsymmetric A will be singular and the system (2) will not have a single equilibrium solution, but possibly infinitely many. What is more important, however, in the biological context, is that the roots of (2) be all positive. As a necessary condition, the natural growth coefficients ϵ_r cannot have all the same sign. We emphasize that we will assume $N_r > 0$ and $\epsilon_r \neq 0$ $\forall r$ throughout the whole paper

2.1 Lagrangian and Hamiltonian formulation

As many other researchers of his time, Volterra was feeling more assured if a phenomenon quantified by Mathematics could find an analogue with Mechanics, that moreover allowed resorting to the powerful formalism and theorems of the latter. To achieve this goal, Volterra introduced the quantity of life for each species r being defined as $q_r = \int_0^t N_r(\tau) d\tau$. The quantities of life were instrumental for the introduction of a biological, or rather ecological, Lagrangian Φ, defined as:

$$\Phi = \sum_r \epsilon_r q_r + \sum_r \dot{q}_r \log \dot{q}_r - \frac{1}{2} \sum_{rs} A_{rs} \dot{q}_r q_s \tag{3}$$

In terms of (3), (1) can be written as Euler-Lagrange equations

$$\frac{d}{dt}\frac{\partial \Phi}{\partial \dot{q}_r} - \frac{\partial \Phi}{\partial q_r} = 0 \tag{4}$$

yielding the ODEs

$$\ddot{q}_r = (\epsilon_r + \sum_s A_{sr} \dot{q}_s) \dot{q}_r \tag{5}$$

which are just (1), up to the substitution $N_r = \dot{q}_r$. The transition from the Lagrangian to the Hamiltonian description is performed by Volterra in the usual way. The linear momenta, canonically conjugated to the quantities of life, are defined as

$$p_r = \frac{\partial \Phi}{\partial \dot{q}_r} = \log \dot{q}_r + 1 - \frac{1}{2} \sum_s A_{rs} q_s \tag{6}$$

whence

$$\dot{q}_r = \exp(p_r - 1 + \frac{1}{2} \sum_s A_{rs} q_s) \tag{7}$$

Through a transformation of Legendre type Volterra defines the Hamiltonian

$$\mathcal{H} = \Phi - \sum_r \dot{q}_r p_r \tag{8}$$

A straightforward calculation allows to rewrite (8) in the form:

$$\mathcal{H} = \sum_r \epsilon_r q_r - \dot{q}_r = \sum_r \epsilon_r q_r - \exp(p_r - 1 + \frac{1}{2}\sum_s A_{rs} q_s) \tag{9}$$

Note that, in terms of the original ecological variables the expression $\sum_r \epsilon_r q_r - \dot{q}_r$ takes the form:

$$\sum_r \epsilon_r q_r - \dot{q}_r = \sum_r \epsilon_r \int_0^t dt' N_r(t') - N_r \tag{10}$$

Volterra [1] showed that (1) can be written in the standard Hamiltonian form

$$\dot{q}_r = -\frac{\partial \mathcal{H}}{\partial p_r} \tag{11}$$

$$\dot{p}_r = \frac{\partial \mathcal{H}}{\partial q_r} \tag{12}$$

It is easily seen (see again [4]) that the Hamiltonian system (9)-(12) has the following N independent non autonomous integrals of motion:

$$\mathcal{H}_r = \frac{p_r - \frac{1}{2}\sum_s A_{rs} q_s}{\epsilon_r} - t \quad r = 1, \cdots, N. \tag{13}$$

whence one can select $N-1$ autonomous integrals by taking for instance $\mathcal{H}_{1,r} \equiv \mathcal{H}_r - \mathcal{H}_1$, and have a complete set by adding the Volterra $N-1$ species Hamiltonian (9).
We notice that the choice of the signs in (11) and (12) is opposite with respect to the standard approach found in literature (see e.g. [15, 16, 17]). Also, it would be preferable to have a minus sign in the definition of the Hamilton function $\mathcal{H}$ (54), so that $\mathcal{H}(t=0) = \sum_r N_r$. We however prefer here to keep the notation used by Volterra himself in [1]. Also, the term $+1$ appearing in (6) is not crucial and could be replaced by any constant factor for example by adding in the Lagrangian (3) a combination of the variables $\dot{q}_r$. A more modern approach to the Hamiltonian structure underlying the generalized Volterra system can be found for instance in [11, 12, 13] where a Poisson morphism is established between the original system, living in $\mathbb{R}^N$ and equipped with a quadratic Poisson structure, and then one recast, after Volterra, in a canonical Hamiltonian form and thus living in $\mathbb{R}^{2N}$, see also [14]. We will come back to such Hamiltonian formulations, possibly more widely used than Volterra's one, in subsection (2.3) and in the Appendix. Let us remark that different Hamiltonian descriptions of the Lotka-Volterra exist (see e.g. [12], where a map between them is also given): if the Hamiltonian (9) is rewritten in terms of the numerosities N_r with respect to the Poisson bracket given in [12], then the standard logarithmic terms of the numerosities of the populations appears. In our opinion, the question whether there exists a special form of the matrix elements A_{rs} entailing involutivity of the complete set of integrals of motion $(\mathcal{H}, \mathcal{H}_{1,r})$ is a relevant one to ask both mathematically and from the point of view of applications: indeed, broadly speaking, if on one hand the integrability structure leads to a very rich and assorted type of dynamical behavior, on the other hand it is expected that these properties may give a useful insight to the understanding of a

wide variety of phenomena in a number of different fields. It turns out that this form has been found by Volterra himself [1] and is the following:

$$A_{rs} = \epsilon_r \epsilon_s (B_r - B_s) \quad r, s = 1, \cdots N \tag{14}$$

where N is the number of competing populations and the B_r are distinct real numbers. Clearly, (14) can be cast in the compact form:

$$A = \{A_{rs}\} = [B, \epsilon \otimes \epsilon] \tag{15}$$

where $B = diag(B_1, \cdots, B_N)$, and ϵ is the vector $(\epsilon_1, \cdots, \epsilon_N)^t$, meaning that A is the commutator of a diagonal matrix with distinct entries and a rank one matrix.

2.2 A note about the equilibrium conditions.

So, if we require integrability, (15) shows that the invertibility of A has to be given up for $N > 2$. Indeed, in the integrable case Ker(A) has dimension $N-2$, and correspondingly its range is two-dimensional. Accordingly, the equilibrium conditions (2) read:

$$\sum_{s=1}^{N} \epsilon_s (B_s - B_r) N_s^0 = 1$$

where we have denoted by $N_s^0 (s = 1, \cdots, N)$ the equilibrium population numerosities, implying that the equilibrium configuration be defined as the intersection of the two hyperplanes

$$\sum_s \epsilon_s N_s^0 = 0 \tag{16}$$

$$\sum_s \epsilon_s B_s N_s^0 = 1 \tag{17}$$

Consequently an admissible equilibrium configuration can exist only if the ϵ_s have not all the same sign as already remarked at the end of section 2. Moreover, a unique equilibrium position exists only for $N = 2$; setting $\mu = B_1 - B_2$, we get:

$$N_1^0 = \frac{1}{\mu \epsilon_1}; \quad N_2^0 = -\frac{1}{\mu \epsilon_2} \tag{18}$$

For instance, in the case $N = 3$, we have a one parameter family of equilibrium solutions, reading $(0 < \rho < 1)$

$$\epsilon_1 N_1^0 = \frac{\rho}{B_1 - B_3}; \quad \epsilon_2 N_2^0 = \frac{1-\rho}{B_2 - B_3}; \quad \epsilon_3 N_3^0 = -(\epsilon_1 N_1^0 + \epsilon_2 N_2^0). \tag{19}$$

In (19), in order the equilibrium species populations be positive, we have to require $(B_1 - B_3)\epsilon_1$, and $(B_2 - B_3)\epsilon_2$ to be positive quantities, while the ratios ϵ_1/ϵ_3 and ϵ_2/ϵ_3 have to be negative. We end the present subsection by remarking that in all cases, whether they are integrable or not, the N-species Volterra system enjoy a sort of box structure, being equipped with a number of invariant submanifolds, obtaining when only a subset of species is alive, this fact being dictated just by the initial conditions. So, for the two species case, the axes $N_1 = 0$ and $N_2 = 0$ are invariant submanifolds, for the three-species case we have the 6 invariant submanifolds given by the axes and by the planes $N_i = 0$, and so forth. In particular the three-species case gives rise to three Lotka-Volterra systems. Once realized that integrability implies the non-uniqueness of the equilibrium configuration ($\forall$ $N > 2$), we would like to stress that, for the special form of the matrix A given by (14), the integrals of motion are still functionally independent. This is readily seen as (13) shows that the linear dependence of those integrals upon the momenta p_r is in no-way affected by the specific form of the matrix A (while the requirement that the B_r be all distinct is mandatory!), so that the rank of the Jacobian matrix constructed with the gradients of the integrals of motion with respect to the canonical coordinates is maximal (namely N) whatever be that form. So, the integrable version of the N-species Volterra system is again a genuine Hamiltonian system with N degrees of freedom. Here we write down explicitly the expression of the Hamiltonian and of the integrals of motion in the integrable case, resuming what we sketched in formulas (13)-(15). Denoting now by $\mathcal{H}_{int}$ the Hamiltonian (9) we have:

$$\mathcal{H}_{int} = \sum_{r=1}^{N} \epsilon_r q_r - \exp[p_r - 1 + (\epsilon_r/2) \sum_{s=1}^{N} \epsilon_s (B_r - B_s) q_s] \tag{20}$$

and

$$\mathcal{H}_r = p_r/\epsilon_r - (1/2) \sum_{s=1}^{N} \epsilon_s (B_r - B_s) q_s - t \quad r = 1, \cdots, N \tag{21}$$

so that

$$\mathcal{H}_{rl} \equiv \mathcal{H}_r - \mathcal{H}_l = p_r/\epsilon_r - p_l/\epsilon_l - \frac{1}{2}(B_r - B_l) \sum_{s=1}^{N} \epsilon_s q_s, \quad s = 1, \cdots, N. \tag{22}$$

The constants of motion (22) are mutually in involution. So we can take for instance $l = 1$ and get $N - 1$ independent integrals of motion in involution. The set can be completed by adding any function of the Hamiltonian, for instance the Hamiltonian itself. The above formulas clearly show that, in the integrable case, both the Volterra Hamiltonian and the involutive family of integrals of motion depend on the quantities of life only through the inner products (ϵ, Q) and (ϵ, BQ), where Q is the vector of components q_j, while by BQ we have denoted the vector of components $B_j q_j$. However, even in the completely integrable case, we did not succeed in reducing our problem to quadratures for N larger than 2, although this possibility is a well known result in Classical Mechanics [15, 16]. It might be convenient to take as integrals of motion the exponentials of the quantities (21)

$$\exp(\epsilon_r \mathcal{H}_r) = \exp[p_r - \epsilon_r/2 \sum_{s=1}^{N} \epsilon_s (B_r - B_s) q_s - \epsilon_r t] \tag{23}$$

hence choosing $\exp(\mathcal{H}_{rl})$ as an alternative legitimate form for an involutive family of integrals of motion. In the simplest nontrivial case, $N = 2$, (20) reads (the subscript V refers to Volterra):

$$\mathcal{H}_V = \epsilon_1 q_1 + \epsilon_2 q_2 - \exp[p_1 + (1/2)\epsilon_1\epsilon_2(B_1 - B_2)q_2] - \exp[p_2 - (1/2)\epsilon_1\epsilon_2(B_1 - B_2)q_1] \tag{24}$$

The above formula can be slightly simplified through the canonical transformation (in fact, just a rescaling):

$$p_j \to \tilde{p}_j = p_j/\epsilon_j; \quad q_j \to \tilde{q}_j = \epsilon_j q_j \tag{25}$$

that maps (22) into:

$$\mathcal{H}_{rl} = \tilde{p}_r - \tilde{p}_l + (1/2)(B_r - B_l)\sum_j \tilde{q}_j \tag{26}$$

and (24) into:

$$\mathcal{H}_V = \tilde{q}_1 + \tilde{q}_2 - \exp[\epsilon_1(\tilde{p}_1 + 1/2)(B_1 - B_2)\tilde{q}_2)] - \exp[\epsilon_2(\tilde{p}_2 - (1/2)(B_1 - B_2)\tilde{q}_1] \tag{27}$$

2.3 Integration of the $N = 2$ case via the canonical formalism and other Hamiltonian formulations.

Let us slightly simplify the notations in (27), by setting $\mu := B_1 - B_2$, and introducing the new canonical variables:

$$P_1 = \frac{1}{\sqrt{\mu}}(\tilde{p}_1 + \frac{1}{2}\mu\tilde{q}_2); \quad Q_1 = \frac{1}{\sqrt{\mu}}(-\tilde{p}_2 + \mu\frac{1}{2}\tilde{q}_1) \tag{28}$$

$$P_2 = \frac{1}{\sqrt{\mu}}(\tilde{p}_1 - \mu\frac{1}{2}\tilde{q}_2); \quad Q_2 = \frac{1}{\sqrt{\mu}}(\tilde{p}_2 + \frac{1}{2}\mu\tilde{q}_1) \tag{29}$$

In terms of these new variables, the first integral:

$$\mathcal{H}_{12} = \tilde{p}_1 - \tilde{p}_2 - (\mu/2)(\tilde{q}_1 + \tilde{q}_2) \tag{30}$$

takes the form

$$\mathcal{H}_{12} = \frac{1}{\sqrt{\mu}}(P_2 - Q_2) \tag{31}$$

while the two-particle Hamiltonian reads:

$$\mathcal{H}_V = \frac{1}{\sqrt{\mu}}[Q_1 + Q_2 + P_1 - P_2] - \exp\sqrt{\mu}(\epsilon_1 P_1) - \exp[-\sqrt{\mu}(\epsilon_2 Q_1)] \tag{32}$$

Inserting the first integral (31), on the level surface $\mathcal{H}_{12} = C$, up to an irrelevant additive constant we can finally write:

$$\mathcal{H}_V = \frac{1}{\sqrt{\mu}}(Q_1 + P_1) - \exp[\sqrt{\mu}(\epsilon_1 P_1)] - \exp[-\sqrt{\mu}(\epsilon_2 Q_1)] \tag{33}$$

It follows that, in terms of these new coordinates, the above Hamiltonian is a one-body Hamiltonian (integrable by definition), which is nothing but the traditional Lotka-Volterra Hamiltonian. One may pervene to more elegant formulas by defining:

$$x \equiv \exp\sqrt{\mu}(\epsilon_1 P_1); \quad y \equiv \exp[-\sqrt{\mu}(\epsilon_2 Q_1)]$$

leading to:

$$\dot{x} = \epsilon_1 x(1 - \mu\epsilon_2 y) \tag{34}$$

$$\dot{y} = \epsilon_2 y(1 + \mu\epsilon_1 x) \tag{35}$$

The (nontrivial and stable) equilibrium position is the pair $(x^{(0)} = -\frac{1}{\mu\epsilon_1}, y^{(0)} = \frac{1}{\mu\epsilon_2})$ whence it follows that it can belong to the first quadrant only if the coefficients of spontaneous growth have opposite sign, as it is natural if we require that the predator species can survive eating the prey one. As well known [1, 10], the equations for the orbits of (37) and (38) can be written in closed form:

$$(x\exp(\mu\epsilon_1 x))^{\epsilon_2} \;=\; K(y\exp(-\mu\epsilon_2 y))^{\epsilon_1} \tag{36}$$

where K is a positive constant. For the sake of completeness, we recall here the standard form of the predator-prey equations (keeping skew-symmetry) and of their hamiltonian formulation, that might be useful to compare with that described at the beginning of this subsection. Denoting by x and y the two species, we have.

$$\dot{x} = \epsilon_1 x - axy \tag{37}$$

$$\dot{y} = \epsilon_2 y + axy \tag{38}$$

which coincide with (37) and (38) if we set $a = \mu\epsilon_1\epsilon_2$ There are two equiilbrium positions: the trivial one $(0, 0)$, and the center $(\epsilon_1/a, -\epsilon_2/a)$. Assuming $a > 0$ (and thus $\mu < 0$), it belongs to the first quadrant provided $\epsilon_1 > 0,\ \epsilon_2 < 0$. The invariant curve, that defines the family of orbits and plays also the role of Hamiltonian, reads:

$$h(x, y) = \epsilon_2 \ln x - \epsilon_1 \ln y + a(x + y) \tag{39}$$

The equations (37),(38) can be cast in the following Hamiltonian form:

$$\dot{x} = -xy\frac{\partial h}{\partial y} \tag{40}$$

$$\dot{y} = xy\frac{\partial h}{\partial x} \tag{41}$$

which involves the Poisson matrix

$$P = \begin{pmatrix} 0 & -xy \\ xy & 0 \end{pmatrix} \tag{42}$$

The simple change of variables: $x = \exp(\tilde{x}),\ y = \exp(\tilde{y})$ transforms (37,38) into:

$$\dot{\tilde{x}} = \epsilon_1 - a\exp(\tilde{y}) \tag{43}$$

$$\dot{\tilde{y}} = \epsilon_2 + a\exp(\tilde{x}) \tag{44}$$

the Hamiltonian (39) into:

$$\tilde{h}(\tilde{x}, \tilde{y}) = \epsilon_2\tilde{x} - \epsilon_1\tilde{y} + a(\exp(\tilde{x}) + \exp(\tilde{y})) \tag{45}$$

and the Poisson matrix (42) into the canonical one

$$J = \begin{pmatrix} 0 & -1 \\ 1 & 0 \end{pmatrix} \tag{46}$$

2.4 The N-species system: integration through the Volterra's approach.

Here we briefly recall the procedure followed by Volterra to integrate the N-species system in terms of the natural coordinates, i.e.the population numerosities. In the following, we do not preclude the possibility to have an odd number of species, so N can be even or odd. Volterra defines the quantities $\mathcal{N} := \sum_s \epsilon_s N_s$ and $\mathcal{M} := 1 - \sum_s \epsilon_s B_s N_s$, then rewriting the original dynamical system (1) as:

$$\dot{N}_r = \epsilon_r N_r (1 + \sum_s (B_r - B_s) \epsilon_s N_s)$$

or, in other terms:

$$\dot{N}_r = \epsilon_r N_r (B_r \mathcal{N} + \mathcal{M})$$

namely:

$$(1/\epsilon_r) d/dt \log N_r = (B_r \mathcal{N} + \mathcal{M})$$

Note that the previous equation implies $\sum_r (\dot{N}_r - \epsilon_r N_r) = 0$, which is just the conservation of the Hamiltonian (9). It is evident that the involutivity constraints on the coefficients A_{rs} entail a typical Mean Field dynamics. Each species interacts with the others through the collective variables $\mathcal{N}$ and $\mathcal{M}$. By taking two different values of the index r and subtracting, the variable $\mathcal{M}$ can be eliminated, resorting to:

$$\frac{(1/\epsilon_r) d/dt \log N_r - (1/\epsilon_s) d/dt \log N_s}{B_r - B_s} = \mathcal{N},$$

that yields $N - 2$ integrals of motion. Indeed, in term of the variables

$$Y_k \equiv (1/\epsilon_k) \log N_k, \tag{47}$$

we get the linear formula

$$\frac{1}{B_r - B_j}(Y_r - Y_j) - \frac{1}{B_s - B_j}(Y_s - Y_j) = C_{rs}.$$

The simplest non-trivial case is the three-species case, where an elementary calculation shows that the three equations above are indeed the same, yielding:

$$(B_2 - B_3) Y_1 + (B_3 - B_1) Y_2 + (B_1 - B_2) Y_3 = const. \tag{48}$$

We remind the form of the equations of motion for the integrable three species case:

$$\dot{N}_1 = \epsilon_1 N_1 + \epsilon_1 \epsilon_2 \ (B_1 - B_2) N_1 N_2 + \epsilon_1 \epsilon_3 (B_1 - B_3) N_1 N_3 \tag{49}$$
$$\dot{N}_2 = \epsilon_2 N_2 + \epsilon_2 \epsilon_1 (B_2 - B_1) N_2 N_1 + \epsilon_2 \epsilon_3 (B_2 - B_3) N_2 N_3 \tag{50}$$
$$\dot{N}_3 = \epsilon_3 N_3 + \epsilon_3 \epsilon_1 (B_3 - B_1) N_3 N_1 + \epsilon_3 \epsilon_2 (B_3 - B_2) N_3 N_2 \tag{51}$$

and add the expression of the integrals of motion for the system (49)-(51) in terms of the numerosities and of the quantities of life. Taking into account (47), formula (48) takes the form

$$N_1^{(B_2 - B_3)/\epsilon_1} N_2^{(B_3 - B_1)/\epsilon_2} N_3^{(B_1 - B_2)/\epsilon_3} = I_{123} \tag{52}$$

Of course, (52) has a meaning only for nonzero initial data, where it can be written as well as:

$$(N_1/N_1(0))^{(B_2-B_3)/\epsilon_1}(N_2/N_2(0))^{(B_3-B_1)/\epsilon_2}(N_3/N_3(0))^{(B_1-B_2)/\epsilon_3}=1 \tag{53}$$

The Hamiltonian $\mathcal{H}$ is written as:

$$\mathcal{H}=\sum_{r=1}^{N}\epsilon_r\int_0^t N_r(t')dt'-N_r \tag{54}$$

implying that its value equals minus the total population at $t=0$. The involutive integrals $\exp(\mathcal{H}_r)$ read:

$$\exp(\mathcal{H}_r)=N_r\exp[-\sum_s(B_r-B_s)\epsilon_r\epsilon_s\int_0^t N_s(t')dt'] \tag{55}$$

so each of them equals the corresponding initial population. In the next section, in which we will give both analytical and numerical results, we will focus attention on the three species integrable case, which escapes the general analysis presented by Volterra in [1], focussed on the study of an even number of species, mostly assuming invertibility of the interaction matrix A. To our knowledge, Volterra copes with the three species problem only in the case of null spontaneous growth coefficients, where he proves the existence of periodic orbits. By the way, a full treatment of the integrable three species case can be found in [13], denoted as "A three species food chain".

3 Novel numerical and analytical results: from 3 to N.

In this section we propose a way to construct the integrals of motion for the model under scrutiny which is alternative to the one followed by Volterra, recalled in the previous section and in [8]. In the first subsection we present the case $N=3$, by giving also a numerical integration of the equations of motion (49)-(51) for different choices of the relevant parameters. In the second subsection we extend the construction to the generic N-species case.

3.1 The three species case.

We consider the case $N=3$ here. To simplify a little bit the notations, let us set:

$$B_1-B_2=\alpha;\quad B_2-B_3=\beta \tag{56}$$

whence $B_1-B_3=\alpha+\beta$. Recalling (19), we notice that, if ϵ_1,ϵ_2 are positive quantities, we have to require:

$$\beta>0,\ \alpha+\beta>0 \tag{57}$$

implying that, if α is negative, its absolute value has to be less than β. We start from the equations of motion

$$\dot{N}_1=\epsilon_1N_1+\epsilon_1\epsilon_2\alpha N_1N_2+\epsilon_1\epsilon_3(\alpha+\beta)N_1N_3 \tag{58}$$

$$\dot{N}_2=\epsilon_2N_2-\epsilon_2\epsilon_1\alpha N_2N_1+\epsilon_2\epsilon_3\beta N_2N_3 \tag{59}$$

$$\dot{N}_3=\epsilon_3N_3-\epsilon_3\epsilon_1(\alpha+\beta)N_3N_1-\epsilon_3\epsilon_2\beta N_3N_2 \tag{60}$$

and look for an integral of motion written as

$$e^{A(N_1(t)+N_2(t)+N_3(t))}N_1(t)^m N_2(t)^n N_3(t)^k, \tag{61}$$

for suitable constants A, m, n, k. By deriving (61) with respect to time, dividing by (61) itself and making use of (49)-(51) we find

$$\begin{aligned} &\epsilon_1 N_1 \left(A - n\alpha\epsilon_2 - k(\alpha+\beta)\epsilon_3\right) + \epsilon_2 N_2 \left(A + m\alpha\epsilon_1 - k\beta\epsilon_3\right) + \\ &+ \epsilon_3 N_3 \left(A + n\beta\epsilon_2 + m(\alpha+\beta)\epsilon_1\right) + \epsilon_1 m + \epsilon_2 n + \epsilon_3 k = 0. \end{aligned} \tag{62}$$

The coefficients of the $N_i's$, $i = 1, 2, 3$, are all compatible each other if $\epsilon_1 m + \epsilon_2 n + \epsilon_3 k = 0$, giving e.g. $A = k\beta\epsilon_3 - m\alpha\epsilon_1$. So, the following quantity

$$e^{(k\beta\epsilon_3 - m\alpha\epsilon_1)(N_1(t)+N_2(t)+N_3(t))}N_1(t)^m N_2(t)^n N_3(t)^k = I_{m,n,k} \tag{63}$$

is a conserved quantity if the parameters (m, n, k) satisfies $\epsilon_1 m + \epsilon_2 n + \epsilon_3 k = 0$. Notice that (52) can be rewritten as:

$$\frac{N_1^{\beta/\epsilon_1} N_3^{\alpha/\epsilon_3}}{N_2^{(\alpha+\beta)/\epsilon_2}} = I_{123}, \tag{64}$$

This conserved quantity, that corresponds to the choice $(m, n, k) = (\beta/\epsilon_1, -(\alpha+\beta)/\epsilon_2, \alpha/\epsilon_3)$ coincides with that of formula (53). Of the three parameters (m, n, k), only two are independent because of the relation $\epsilon_1 m + \epsilon_2 n + \epsilon_3 k = 0$. It is possible to write two different surfaces by choosing properly the values of the constants m, n, k: if these surfaces intersect by defining a closed curve, the corresponding motion defined by (49-51) will be periodic. Let us make an example. If we take

$$\alpha = 1,\ \beta = 2\ \epsilon_1 = \epsilon_2 = 1,\ \epsilon_3 = -1.$$

Then, two conserved quantities are given by

$$\frac{N_1^2}{N_2^3 N_3} = I_1, \qquad e^{-2(N_1+N_2+N_3)}N_2 N_3 = I_2. \tag{65}$$

We give the plot of the closed orbit $(N_1(t), N_2(t), N_3(t))$ numerically obtained by taking the initial conditions $N_1(0) = N_2(0) = N_3(0) = 1$, the plot of I_1, of I_2 and of the closed orbit all together: as it can be seen from the last figure the two surfaces I_1 and I_2 intersect in a closed curve and the motion is constrained on this curve.

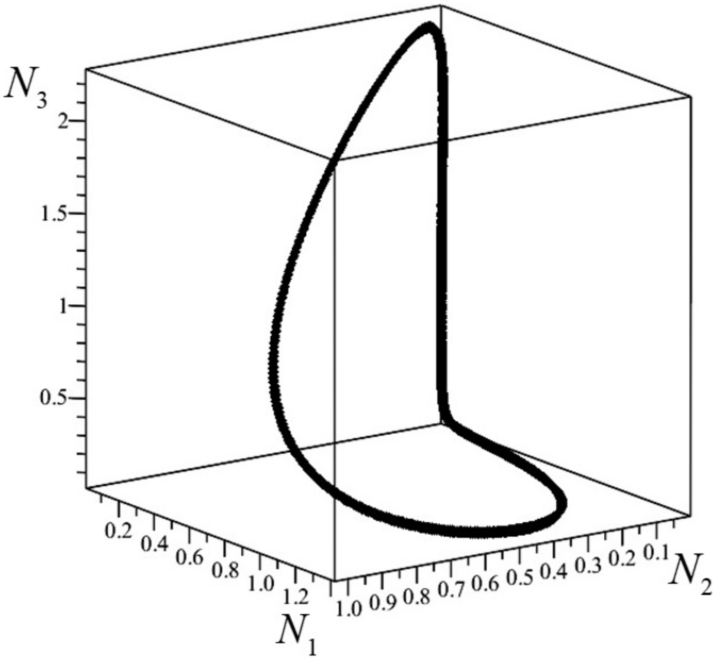

Figure 1. Plot of the closed orbit $(N_1(t), N_2(t), N_3(t))$ corresponding to the initial conditions $N_1(0) = N_2(0) = N_3(0) = 1$

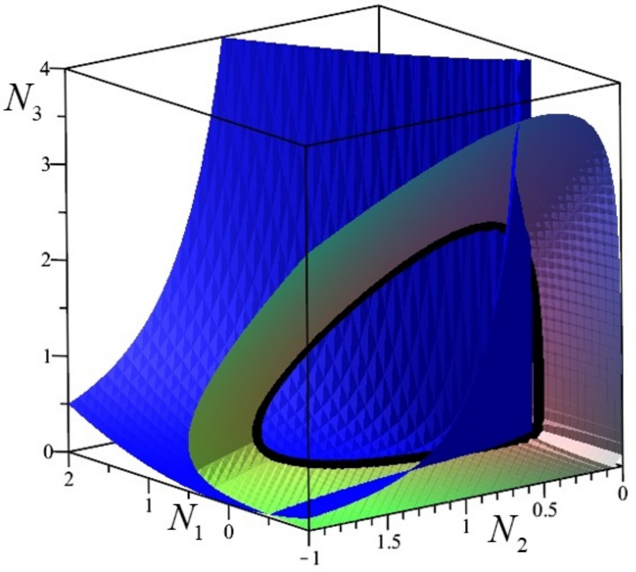

Figure 2. Plot of $N_3 = \frac{N_1^2}{N_2^3}$ and $e^{-2(N_1+N_2+N_3)}N_2N_3 = e^{-6}$ with the numerically obtained closed orbit (in black)

Together with the geometrical picture given by the orbits, we have the dynamical picture associated with the time-behavior of the system. We will consider two different cases of periodic behavior, one with $\alpha > 0$, and the other with $\alpha < 0$, with different initial conditions. Case 1: $\epsilon_1 = \epsilon_2 = 1; \epsilon_3 = -1; \alpha = 0.5; \beta = 2.5$.

$$N_1(0) = 1, N_2(0) = 1, N_3(0) = 1, t \in [0, 30]$$

$$\dot{N}_1 = N_1 + 0.5N_1N_2 - 3N_1N_3, \tag{66}$$
$$\dot{N}_2 = N_2 - 0.5N_1N_2 - 2.5N_2N_3 \tag{67}$$
$$\dot{N}_3 = -N_3 + 3N_1N_3 + 2.5N_3N_2 \tag{68}$$
$$\tag{69}$$

The corresponding plots of N_i, $i = 1, ..., 3$ are given in figure (3). Case 2: $\epsilon_1 = \epsilon_2 = 1; \epsilon_3 = -1, \alpha = -1/2, \beta = 1$.

$$N_1(0) = 1, N_2(0) = 1/2, N_3(0) = 1/2, t \in [0, 30]$$

$$\dot{N}_1 = N_1 - 0.5N_1N_2 - N_1N_3$$

$$\dot{N}_2 = N_2 + 0.5N_1N_2 - 0.5N_2N_3$$

$$\dot{N}_3 = -N_3 + N_1N_3 + 0.5N_3N_2$$

The corresponding plots of N_i, $i = 1, ..., 3$ are given in figure (4).

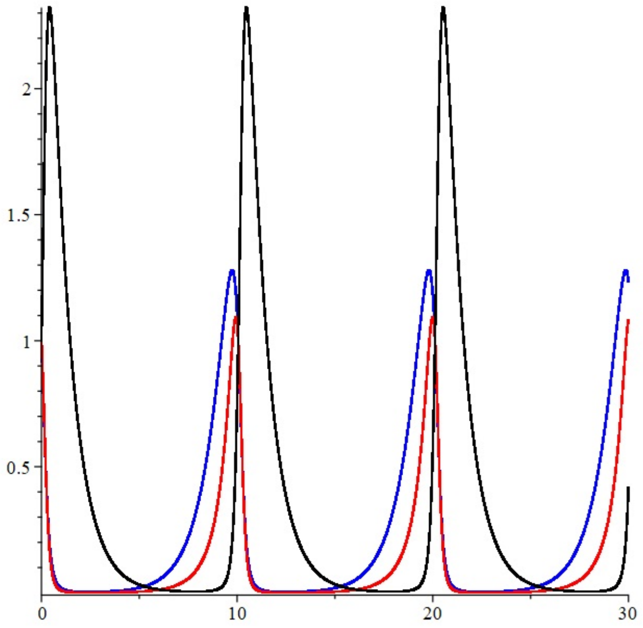

Figure 3. Oscillations of N_1 (in red), N_2 (in blue) and N_3 (in black) corresponding to the initial conditions $N_1(0) = 1, N_2(0) = 1, N_3(0) = 1$ $\alpha = 1/2$, $\beta = 5/2$.

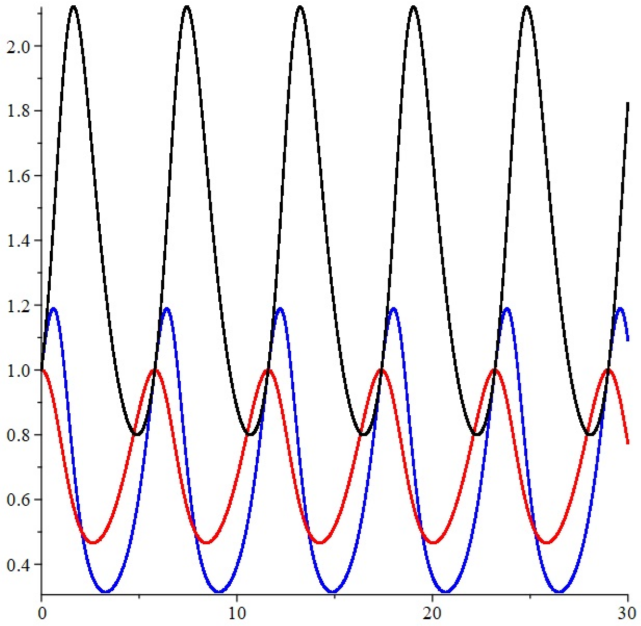

Figure 4. Oscillations of N_1 (in red), N_2 (in blue) and N_3 (in black) corresponding to the initial conditions $N_1(0) = 1, N_2(0) = 1, N_3(0) = 1$ $\alpha = -1/2$, $\beta = 1$.

To conclude this subsection it sounds appropriate comparing the fully nonlinear picture described above with the one corresponding to the linearized evolution in the neighbourhood of (one suitable point) of the equilibrium configuration. To this aim, let us set

$$N_i(t) = N_i^0 + x_i(t), \quad i = 1, 2, 3 \tag{70}$$

where x_i are small quantities. At first order in the x_i, the set of equations (1) becomes

$$\begin{aligned}
\dot{x}_1 &= \frac{B_1 - B_2}{B_1 - B_3}\rho\epsilon_2 x_2 + \rho\epsilon_3 x_3,\\
\dot{x}_2 &= \frac{B_2 - B_1}{B_2 - B_3}(1-\rho)\epsilon_1 x_1 + (1-\rho)\epsilon_3 x_3,\\
\dot{x}_3 &= \left(\frac{B_1 - B_3}{B_2 - B_3} + \rho\frac{B_2 - B_1}{B_2 - B_3}\right)\epsilon_1 x_1 + \left(1 - \rho\frac{B_1 - B_2}{B_1 - B_3}\right)\epsilon_2 x_2.
\end{aligned} \tag{71}$$

We need the eigenvalues of the matrix of the coefficients, given by

$$M = \begin{pmatrix} 0 & \frac{B_1-B_2}{B_1-B_3}\rho\epsilon_2 & \rho\epsilon_3 \\ \frac{B_2-B_1}{B_2-B_3}(1-\rho)\epsilon_1 & 0 & (1-\rho)\epsilon_3 \\ \left(\frac{B_1-B_3}{B_2-B_3} + \rho\frac{B_2-B_1}{B_2-B_3}\right)\epsilon_1 & \left(1-\rho\frac{B_1-B_2}{B_1-B_3}\right)\epsilon_2 & 0 \end{pmatrix} \tag{72}$$

The characteristic polynomial is given by:

$$\lambda^3 - \lambda^2 \mathrm{Tr}(M) + \frac{\lambda}{2}\left(\mathrm{Tr}(M)^2 - Tr(M^2)\right) - \mathrm{Det}(M) = 0, \tag{73}$$

and, since Tr(M) and Det(M) are both equal to zero, it reduces to

$$\lambda(\lambda^2 - \frac{1}{2}\mathrm{Tr}(M^2)) = 0. \tag{74}$$

We see that an eigenvalue is always zero, the sum of the other two is zero. So the three eigenvalues are $(0, \lambda_1, -\lambda_1)$. If λ_1 is real, then the fixed point is unstable. If λ_1 is imaginary (it happens if $\mathrm{Tr}(M^2) < 0$) then the matrix M must have three independent eigenvectors in order the point to be stable [10]. The eigenvector corresponding to the eigenvalue 0 is $(\frac{B_2-B_3}{\epsilon_1}, \frac{B_3-B_1}{\epsilon_2}, \frac{B_1-B_2}{\epsilon_3})$ whereas the other two must be independent. The point is not asymptotically stable obviously. So, if $\mathrm{Tr}(M^2) < 0$ one has periodic orbits, the period being $\mathrm{T} = \frac{2\sqrt{2}\pi}{\sqrt{|\mathrm{Tr}(M^2)|}}$. By setting $B_1 = B_2 + \alpha$ and $B_2 = B_3 + \beta$, we get:

$$\mathrm{Tr}(M^2) = 2\epsilon_3\left(\epsilon_2 + \rho(\epsilon_1 - \epsilon_2)\right) - 2\alpha\rho(1-\rho)\frac{\epsilon_1(\epsilon_2 - \epsilon_3)\alpha + \epsilon_3(\epsilon_2 - \epsilon_1)\beta}{\beta(\alpha + \beta)}$$

Recalling that, in all cases we have considered, we always choose $\epsilon_1 = 1$ $\epsilon_2 = 1$, $\epsilon_3 = -1$, the above expression becomes:

$$-2 - 4\frac{\alpha^2\rho(1-\rho)}{\beta(\beta+\alpha)}$$

which is surely negative, $\forall 0 < \rho < 1$, provided $\frac{\alpha}{\beta} \in (-1, +\infty)$. Once fulfilled, the condition will hold for any point on the equilibrium line. Finally, let us compare the behaviour of the nonlinear model and its linearization, given in subsection (2.2) (see equations (71) and the discussion after these equations). We make two numerical examples by taking the following values of the parameters:

$$\epsilon_1 = \epsilon_2 = 1, \;\; \epsilon_3 = -1, \;\; \alpha = 1, \;\; \beta = 2. \tag{75}$$

The equilibrium positions are given by

$$N_1^0 = \frac{\rho}{3}, \;\; N_2^0 = \frac{1-\rho}{2}, \;\; N_3^0 = \frac{1}{2} - \frac{\rho}{6}. \tag{76}$$

We start with an initial condition close to the equilibrium point $(N_1^0, N_2^0, N_3^0) = (\frac{1}{6}, \frac{1}{4}, \frac{5}{12})$ corresponding to $\rho = \frac{1}{2}$: we choose $(N_1(0), N_2(0), N_3(0)) = (\frac{1}{6} + 0.1, \frac{1}{4}, \frac{5}{12})$. The trajectory determined by the numerical solution of the non-linear system (1) and the one determined by the analytical solution of the set of equation (71) are compared in figure (5). Also, the evolution of the population $N_1(t)$ and the evolution of $N_1^0 + x_1(t)$ is given in figure (6)

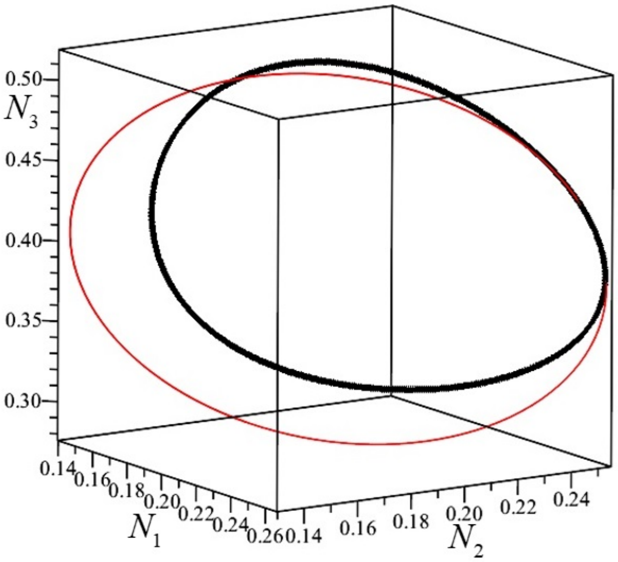

Figure 5. Plot of the closed orbit $(N_1(t), N_2(t), N_3(t))$ for the system (1) corresponding to the initial conditions $N_1(0) = \frac{1}{6} + 0.1$, $N_2(0) = \frac{1}{4}$,$N_3(0) = \frac{5}{12}$ with $\epsilon_1 = \epsilon_2 = 1$, $\epsilon_3 = -1$, $\alpha = 1$, $\beta = 2$ (in black) and of $(\frac{1}{6} + x_1(t), \frac{1}{4} + x_2(t), \frac{5}{12} + x_3(t))$, where $(x_1(t), x_2(t), x_3(t))$ are solution of the system (71) with initial conditions $x_1(0) = 0.1$, $x_2(0) = 0$, $x_3(0) = 0$ (in red).

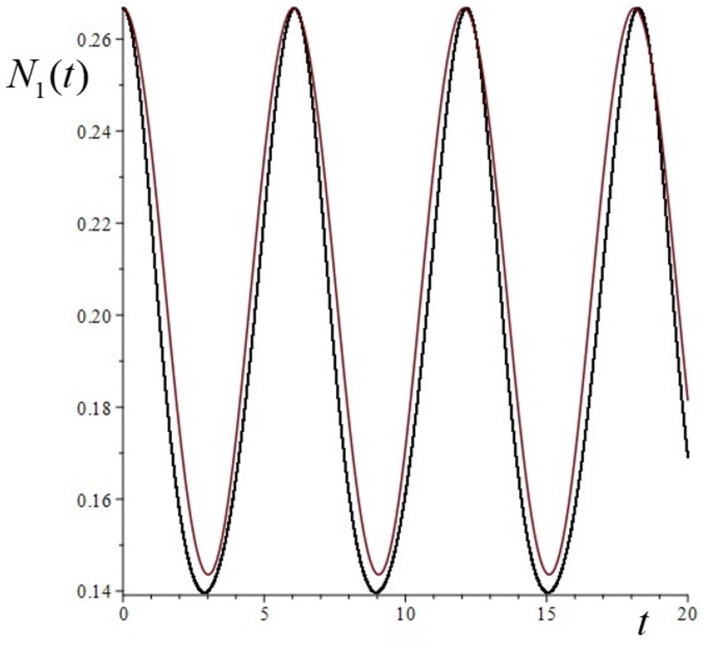

Figure 6. Plot of the evolution of $N_1(t)$ for the system (1) corresponding to the initial conditions $N_1(0) = \frac{1}{6} + 0.1$, $N_2(0) = \frac{1}{4}$,$N_3(0) = \frac{5}{12}$ with $\epsilon_1 = \epsilon_2 = 1$, $\epsilon_3 = -1$, $\alpha = 1$, $\beta = 2$ (in black) and of $\frac{1}{6} + x_1(t)$, where $x_1(t)$ is the solution of the system (71) with initial conditions $x_1(0) = 0.1$, $x_2(0) = 0$, $x_3(0) = 0$ (in red).

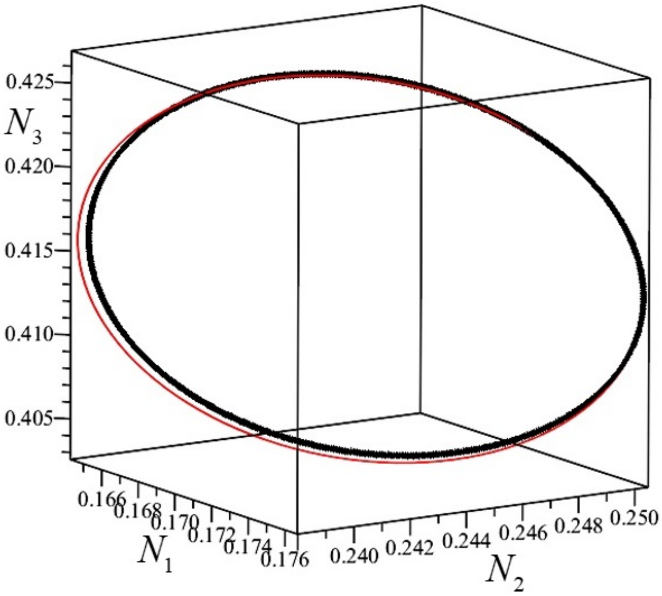

Figure 7. Plot of the closed orbit $(N_1(t), N_2(t), N_3(t))$ for the system (1) corresponding to the initial conditions $N_1(0) = \frac{1}{6} + 0.01$, $N_2(0) = \frac{1}{4}$,$N_3(0) = \frac{5}{12}$ with $\epsilon_1 = \epsilon_2 = 1$, $\epsilon_3 = -1$, $\alpha = 1$, $\beta = 2$ (in black) and of $(\frac{1}{6} + x_1(t), \frac{1}{4} + x_2(t), \frac{5}{12} + x_3(t))$, where $(x_1(t), x_2(t), x_3(t))$ are solution of the system (71) with initial conditions $x_1(0) = 0.01$, $x_2(0) = 0$, $x_3(0) = 0$ (in red).

Now we take an initial condition closer to the equilibrium point $(N_1^0, N_2^0, N_3^0) = (\frac{1}{6}, \frac{1}{4}, \frac{5}{12})$ with respect to the previous one. We choose $(N_1(0), N_2(0), N_3(0)) = (\frac{1}{6} + 0.01, \frac{1}{4}, \frac{5}{12})$. Again, the trajectory determined by the numerical solution of the non-linear system (1) and the one determined by the analytical solution of the set of equation (71) are compared in figure (7). Also, the evolution of the population $N_1(t)$ and the evolution of $N_1^0 + x_1(t)$ is given in figure (8). As it can be seen by the figures the trajectories are really close. Also, the period of the linear system $\mathrm{T} = \frac{2\sqrt{2}\pi}{\sqrt{|\mathrm{Tr}(M^2)|}}$ is a very good approximation for the period of the system in these cases. The agreement between the exact (numeric) nonlinear picture and the linearized (analytic) one looks extremely, and somehow astonishingly, good. The global or local character of this agreement will be discussed in a separate work.

3.2 Extension to N species.

We recall that the integrable case of the Volterra equations with N species reads

$$\frac{dN_r}{dt} = \epsilon_r N_r + \sum_{s \neq r = 1}^{N} A_{rs} N_r N_s \tag{77}$$

where the matrix of the interactions s taken as

$$A_{rs} = \epsilon_r \epsilon_s (B_r - B_s) \quad r, s = 1, \cdots N \tag{78}$$

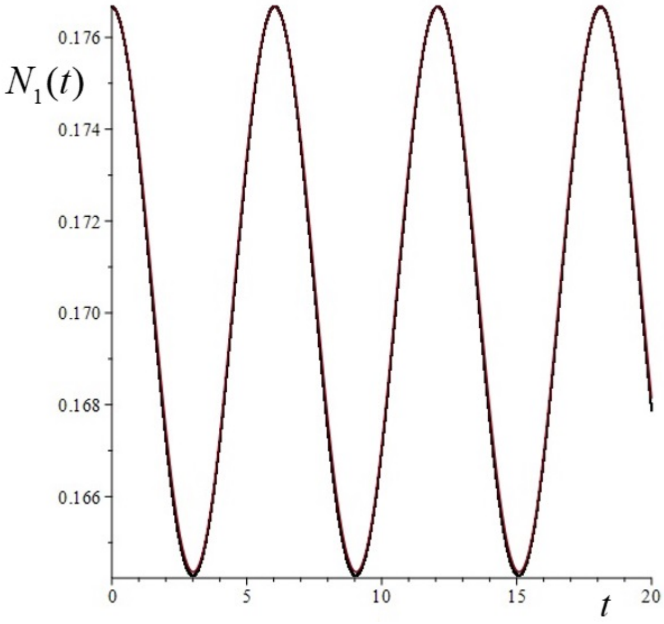

Figure 8. Plot of the evolution of $N_1(t)$ for the system (1) corresponding to the initial conditions $N_1(0) = \frac{1}{6} + 0.01$, $N_2(0) = \frac{1}{4}$,$N_3(0) = \frac{5}{12}$ with $\epsilon_1 = \epsilon_2 = 1$, $\epsilon_3 = -1$, $\alpha = 1$, $\beta = 2$ (in black) and of $\frac{1}{6} + x_1(t)$, where $x_1(t)$ is the solution of the system (71) with initial conditions $x_1(0) = 0.01$, $x_2(0) = 0$, $x_3(0) = 0$ (in red).

Let us look for an integral of motion of the type:

$$e^{A\sum_i N_i(t)} \prod_{i=1}^{N} N_i(t)^{w_i}, \tag{79}$$

where A and w_i are $N+1$ suitable constants. By requiring that the derivative of (79) with respect to time is zero and by using equations (77), we get, after some manipulations:

$$\sum_{k=1}^{N} \epsilon_k w_k = 0, \qquad A = -\sum_{k=1}^{N} B_k \epsilon_k w_k, \tag{80}$$

so that the quantities

$$e^{-\sum_{k=1}^{N} B_k \epsilon_k w_k \left(\sum_i N_i(t)\right)} \prod_{i=1}^{N} N_i(t)^{w_i} = I_{1,..,N}, \tag{81}$$

are a parametric family of conserved quantities, depending on $N-1$ parameters since the constraint $\sum_{k=1}^{N} \epsilon_k w_k = 0$ must be satisfied. Notice that equation (81) can be written as the following product of functions of a single variable:

$$\prod_{i=1}^{N} \frac{N_i^{w_i}}{e^{AN_i}} = I_{1,..,N} \tag{82}$$

where A is defined in (80). The function $f(x) = x^w/e^{ax}$ plays a crucial role in a quite simple proof that the orbits of the original two-populations Volterra model is periodic (see e.g. [10]). Indeed, for x positive, it has a maximum in $x = w/a$ and decreases to zero by going to $x = 0$ and $x = \infty$, similar to a gaussian bell shaped curve. Let us look at equation (82) supposing to vary just the value of the parameter $I_{1,..,N}$ (the other parameters being fixed):

$$f_1(N_1) \cdot f_2(N_2) \cdot \ldots \cdot f_N(N_N) = I_{1,\ldots,N}, \quad f_i(N_i) \doteq \frac{N_i^{w_i}}{e^{AN_i}} \tag{83}$$

Each of the functions $f_i(N_i)$ has a maximum in $N_i = w_i/A$ equal to $M_i = \left(\frac{w_i}{Ae}\right)^{w_i}$: it follows that if

$$I_{1,\ldots,N} > \prod_{i=1}^{N} M_i \tag{84}$$

then the equation (83) has no real solution. Also, if

$$I_{1,\ldots,N} = \prod_{i=1}^{N} M_i \tag{85}$$

then equation (83) has just one real solution, given by $N_i = w_i/A$, $i = 1, \ldots, N$. Let us suppose now that

$$I_{1,\ldots,N} < \prod_{i=1}^{N} M_i. \tag{86}$$

We set

$$I_{1,\ldots,N} = \lambda \prod_{i=2}^{N} M_i, \quad \lambda < M_1 \tag{87}$$

and look at the equation

$$f_1(N_1) \cdot f_2(N_2) \cdot \ldots \cdot f_N(N_N) = \lambda \prod_{i=2}^{N} M_i, \quad \lambda < M_1 \tag{88}$$

The equation $f_1(N_1) = \lambda$ has just two real solutions, let us call them N_1^- and N_1^+, since $f_1(N_1)$ increases from zero to M_1 and then decreases to zero at infinity. Clearly one has $N_1^- < w_1/A$ and $N_1^+ > w_1/A$. It follows that if $N_1 = N_1^-$ or $N_1 = N_1^+$ equation (90) has just one real solution (the other N_i being given by $N_i = w_i/A$, $i = 2, \ldots, n$). When $N_1 < N_1^-$ or $N_1 > N_1^+$ equation (90) has no solution, since one has

$$f_2(N_2) \cdot \ldots \cdot f_N(N_N) = \frac{\lambda}{f_1(N_1)} \prod_{i=2}^{N} M_i > \prod_{i=2}^{N} M_i. \tag{89}$$

Finally it remains the case $N_1 \in (N_1^-, N_1^+)$. In this case, having fixed the value of N_1, we can repeat the above reasoning on N_2, since now we have

$$f_2(N_2) \cdot \ldots \cdot f_N(N_N) = \frac{\lambda}{f_1(N_1)} M_2 \prod_{i=3}^{N} M_i = \hat{\lambda} \prod_{i=3}^{N} M_i, \quad \hat{\lambda} < M_2 \tag{90}$$

and there will be two real solutions to the equation $f_2(N_2) = \hat{\lambda}$, $N_2^- < w_2/A$ and $N_2^+ > w_2/A$. By repeating the same until the last N, we see that equation (90), for $N_i > 0, i = 1, ..., N$, represents a compact closed surface, isomorphic to the N-sphere. We just give two examples. Firstly, we choose again $N = 3$ so that we can also plot the complete surface. We take

$$\frac{N_1^2}{e^{2N_1}} \frac{N_2^3}{e^{2N_2}} \frac{N_3^4}{e^{2N_3}} = 0.001. \tag{91}$$

The maximum of the function $\frac{N_1^2}{e^{2N_1}} \frac{N_2^3}{e^{2N_2}} \frac{N_3^4}{e^{2N_3}}$ equals to $54e^{-9} \sim 0.0067$ so equation (91) possesses solutions. The corresponding surface is plotted in figure (9). The next example is about $N = 4$. We take:

$$\frac{N_1^2}{e^{2N_1}} \frac{N_2^3}{e^{2N_2}} \frac{N_3^4}{e^{2N_3}} \frac{N_4^3}{e^{2N_4}} = 0.0005. \tag{92}$$

Now, the maximum of the function $\frac{N_1^2}{e^{2N_1}} \frac{N_2^3}{e^{2N_2}} \frac{N_3^4}{e^{2N_3}} \frac{N_4^3}{e^{2N_4}}$ equals to $729/4e^{-12} \sim 0.00112$. In order to get a plot in three dimension, we fix the value of N_4 to be equal to 2 (since the value of N_4^3/e^{2N_4} must be greater than $0.0005e^9/54 \sim 0.075$). The corresponding closed surface, projected in the three dimensional space, is given in figure (9). Thanks to our approach we have been able to construct a new (we did not find anything analogous in the literature) $N - 1$ parameter family of integrals of motion, written in terms of the original dynamical variables, and moreover we give a proof of the fact that one can extract from it $N - 1$ first integrals in involution.

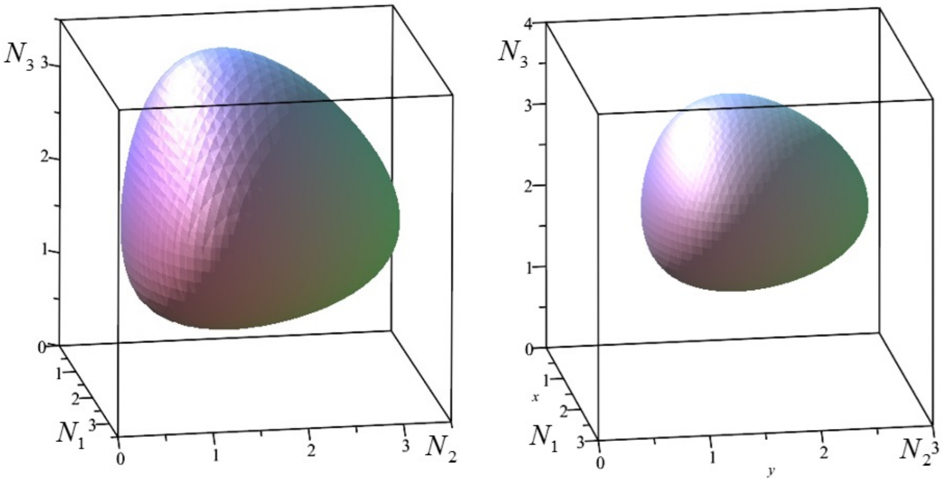

Figure 9. Plot of $\frac{N_1^2}{e^{2N_1}} \frac{N_2^3}{e^{2N_2}} \frac{N_3^4}{e^{2N_3}} = 0.001$ (left) and of the projection of $\frac{N_1^2}{e^{2N_1}} \frac{N_2^3}{e^{2N_2}} \frac{N_3^4}{e^{2N_3}} = 0.0005$ in the space (N_1, N_2, N_3) (right). The value of N_4 has been fixed to be equal to 2.

4 Concluding remarks.

A general comment is needed here, on the comparison between our results and those displayed on pages 245-250 of [1], where the three basic properties of fluctuations in conservative associations are stated and explained. There, first of all Volterra distinguishes between even and odd number of species. In the odd case in fact the coefficient matrix A, being skew symmetric, has to be singular: Volterra concludes that for nonzero growth coefficients equilibrium states will be impossible, and the number of individuals in some species will grow indefinitely or go to zero, and on the long run, only an even number of species will survive. Curiously enough, Volterra did not take into account the fact that complete integrability could change, even drastically, the above scenario. In fact, in section 3 we have shown that even for an odd number of species with nonzero growth coefficients, in spite of the singular nature of the matrix A, there are bounded trajectories and periodic orbits, and we conjecture that such behavior is actually valid for any N, even or odd, just because of integrability. In Appendix A we will come back to the approaches followed in [11, 12, 13] showing that complete integrability holds true for a different Poisson structure, and relies just to the assumed specific form of the matrix A.

Appendix A.

In this Appendix we investigate the following issues:

1. For completeness, we identify the analytic expression of the Hamitonian of the N-species Volterra system associated to the degenerate Poisson bracket (see also [12]):

$$\{f, g\} = \sum_{jk} N_j N_k A_{j,k} \frac{\partial f}{\partial N_j} \frac{\partial g}{\partial N_k} \tag{93}$$

2. We will show that out of the family of first integrals

$$e^{-\sum_{k=1}^{n} B_k \epsilon_k w_k (\sum_i N_i(t))} \prod_{i=1}^{n} N_i(t)^{w_i} = I_{1,..,n}. \tag{94}$$

one can extract $N-1$ independent integrals of motion, in involution with respect to the Poisson bracket (93).

1. For easiness of reading, we remind the explicit form of the N-species Volterra equations:

$$\dot{N}_r = \epsilon_r N_r + \sum_{s=1}^{N} A_{rs} N_r N_s \quad (r = 1, \cdots, N) \tag{95}$$

and look for a Hamiltonian function $\mathcal{K}$ such that (95) can be cast in the form:

$$\dot{N}_r = \{N_r, \mathcal{K}\}$$

where the Poisson bracket is given by (93). Notice that we cannot expect this Hamiltonian to be uniquely defined, as Ker(A) is non-empty, and thus is defined up to Casimir functions. The family of Hamiltonians $\mathcal{K}$ for the system (95) is given by:

$$\mathcal{K} = \sum_{k=1} N_k - N_k^0 \log(N_k) \tag{96}$$

where the constant coefficients N_k^0 belong to the equilibrium configuration and thus satisfy $\epsilon_k + \sum_{s=1}^{N} A_{ks} N_s^0 = 0$. In the three-species case, a possible parametrization is given by equations (19). The proof is by direct computation.

2. Since we are interested in the involutivity, we can take a function of the integrals (94). Let us take the logarithm, by defining:

$$J(w_1 \cdots, w_N) = \sum_{k=1}^{N} \epsilon_k w_k D_k \tag{97}$$

where the coefficients D_k read:

$$D_k = (1/\epsilon_k)\log(N_k) - B_k \sum_j N_j.$$

We are obviously assuming that the matrix A is not just skew-symmetric, but of the form $A_{r,s} = \epsilon_r \epsilon_s (B_r - B_s)$. A troublesome though straightforward calculation yields

$$\{D_k, D_j\} = (B_k - B_j)\left(1 - \sum_i \epsilon_i B_i N_i\right)$$

implying once again that the Poisson brackets $\{D_j - D_r, D_k - D_r\}$ (r fixed, j, k running from 1 to N) vanish, then providing $N-1$ integrals of motion in involution.

So, we have been able to write the Hamiltonian and the integrals of motion in terms of the biological variables. We notice that Volterra was the only one who derived the special, and singular form of the matrix A that ensures complete integrability.

Acknowledgements

F.Z. wishes to acknowledge the support of Università degli Studi di Brescia; INFN, Gr. IV - Mathematical Methods in NonLinear Physics and ISNMP - International Society of Nonlinear Mathematical Physics. O.R. and F.Z. wish to acknowledge the support of GNFM-INdAM.

References

[1] V.Volterra, *Principes de Biologie Mathematiques*, Acta biotheoretica (Leiden, 3, 6-39)(1937)

[2] G.Israel, *Vito Volterra, Book on Mathematical Biology (1931)*, Landmark Writings in Western Mathematics, 1640-1940, edited by I. Grattan-Guinness, Amsterdam, Elsevier, 2005, pp. 936-944.

[3] M. Scalia, A. Angelini, F. Farioli, G.F. Mattioli, O.Ragnisco, M.Saviano, *An Ecology and Economy coupling model.* A global stationary state model for a sustainable economy in the Hamiltonian formalism in Ecological Economics, **172**, 106497(2020)

[4] A.Angelini, F.Farioli, G.Mattioli and M.Scalia, *Le due crisi: crisi del capitalismo e crisi ambientale. Una soluzione sostenibile?* (Parte II),Culture della sostenibilità , **17**, 83-97 (2016)

[5] M.Scalia, A.Angelini, F.Farioli, G.Mattioli and M.L.Saviano, *The chariots of Pharaon at the Red sea: the crises of capitalism and environment. A modest proposal towards sustainability*, I Quaderni di Culture della Sostenibilità, Num. Spec. I Sem. anno IX, 4-64 (2016).

[6] V.Volterra, *Lecons sur la Theorie Mathematique de la lutte pour la vie*, Gauthier-Villars, Paris (1927).

[7] R.M.Goodwin, *A growth Cycle*, in C.H. Feinstein (Editor), Socialism, Capitalism and Economic Growth, Cambridge University Press (1967).

[8] M.Scalia, O.Ragnisco *The Volterra integrable case*, ArXiv 1903 03595 [nlin.si], 2019.

[9] G.Israel, A.M. Gasca, *Letters between Umberto D'Ancona and Vito Volterra* in *The Biology of Numbers* , Birkhauser Basel, 130-200 (2002).

[10] M.Braun, *Differential Equations and Their Applications*, *Predator-Prey problems*,(pp. 441-449), Springer Berlin (1992).

[11] T.J.L. Peixe: Lotka-Volterra Systems and Polymatrix Replicators, Ph.D. Thesis, Universidade de Lisboa, 2015.

[12] R. L. Fernandes and W. M. Oliva, *Hamiltonian dynamics of the Lotka-Volterra equations*, In International Conference on Differential Equations (Lisboa, 1995) (pp. 327-334). World Sci. Publ., River Edge, NJ. (1998).

[13] S.Baigent, Lotka-Volterra Dynamics - An introduction, UCL, March 2 2010.

[14] M.Plank, *Hamiltonian structures for the n-dimensional Lotka-Volterra equations*, J.Math.Phys. **36**,3520 (1995)

[15] V.I. Arnold, *Mathematical Methods of Classical Mechanics (2nd Edition)*, Springer Berlin (1980).

[16] R. Abraham and J. Marsden *Foundation of Mechanics*, Taylor and Francis Ltd (2020).

[17] H. Goldstein, C.P. Poole, J.L. Safko, *Classical Mechanics (3rd Edition)*, Addison-Wesley, New York (2001).