Population dynamics:
interaction between two species.

1 Foreword

The Italian mathematician Vito Volterra is considered to be the principal founder of the modern mathematical theory for the population dynamics. He developed a mathematical foundations for describing biological populations by means of differential and integro-differential equations (Vito Volterra. Lecons sur la Theorie Mathematique de la Lutte pour la Vie. Paris. 1931).

The systems considered by Volterra in his book are usually those of two species. In some particular cases he considers the limitation of the resources (food). The assumptions and hypotheses, which underlie the Volterra's equations describing the interaction between two species, are the following:

1. Food resource is unlimited or its supply over time is strongly regulated.
2. Individuals in a population die out regularly so that per time unit a constant fraction of the population becomes extinct.
3. Predator species consume prey species. Number of consumed preys per time unit is proportional to the probability of "meeting" of the two, which is a product of the two populations sizes.
4. If the food resource is limited and there are several species being able to consume it, then the fraction of it falling per time unit to each of the species is proportional to the size of the species populations (usually, also weighted with species-dependent coefficient).
5. If the food resource is unlimited, the growth of a population consuming it is proportional to the population size.
6. If the food resource is limited, the growth of a population consuming it is proportional to the amount of actually consumed matter.

According to Volterra the interaction between two species, whose population sizes are N_1 and N_2, can be represented through the following system of equations:

$$\frac{dN_1}{dt} = a_1 N_1 + b_{12} N_1 N_2 - c_1 N_1^2$$
$$\frac{dN_2}{dt} = a_2 N_2 + b_{21} N_1 N_2 - c_2 N_2^2 \qquad (1)$$

Here, a_i are the constants of own growth, c_i—self-limitation terms (intra-species competition), b_{ij}—interaction constants. Signs of the latter determine the type of interaction.

2 Types of interaction

There was a suggestion to classify the interaction mechanisms as positive, negative or neutral as a result of increasing, decreasing or non-changing population size of one species in presence of another. Then the basic types of interaction can be:

Interaction type	Effect on 1st	Effect on 2nd	b_{12}, b_{21} coefficients
Symbiosis	+	+	?
Commensalism	+	0	?
Predator-prey	+	-	?
Amensalism	0	-	?
Competition	-	-	?
Neutralism	0	0	?

Table 1: Types of interaction between two species according to Volterra hypotheses.

<u>**Task #1**</u>

Try to identify the signs of b_{12} and b_{21} coefficients by filling in the Table above. One can read more about the types of biological interaction at `http://en.wikipedia.org/wiki/Biological_interaction`.

<u>**Task #2**</u>

Choose one of the interaction types from the Table and perform the dynamical analysis of the system. Namely, a) determine all steady states of the system; b) classify the found steady states according to their stability and roots of the characteristic equation; c) try to find, if any, possible bifurcations of the steady state solutions; d) sketch the phase portrait of the system (if bifurcations are found, sketch the phase portraits "before" and "after" bifurcations).

3 Predator-prey model

Consider the following equations:

$$\begin{aligned}
\frac{dp}{dt} &= p\left[(k-p) - \frac{h}{1+p}\right] \\
\frac{dh}{dt} &= dh\left[\frac{p}{1+p} - ah\right]
\end{aligned} \tag{2}$$

This model describes general relationships between herbivore (h) and plankton (p) species.

Task # 3

Provide for the investigation of the dynamical behavior of the system above. Use the following as the guidelines, but remember to approach the problem creatively.

- Sketch the nullclines and note any qualitative changes as the parameter k varies.
- Demonstrate that a positive steady state (p_0, h_0) exists for all $a > 0$, $k > 0$.
- Determine the signs of the partial derivatives of the RHS of the system (2) evaluated at (p_0, h_0) for this steady state to be stable.
- Show that for $k < 1$ the positive steady state is stable.
- Show that for $k > 1$, and small enough a, the positive steady state may be stable or unstable.
- Show that the necessary condition for oscillations to exist is that a, k lie in the domain bounded by $a = 0$ and $a = 4(k-1)/(k+1)^3$.