

INTERACTIVE INSTRUCTION ON POPULATION INTERACTIONS

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Abstract – An interactive computer system for teaching and investigating models formulated in terms of differential or (stochastic) difference equations is presented. Population models are used as examples to demonstrate the use of the system.

It is argued that (simulation) models should contain not only the dynamics of the system to be simulated, but also default parameter values and a notion about the qualitative dissimilarity of the parameter values. The latter notion is provided in the present system by graphical representation of the static structure of the state space. Thus the system exploits the strong points in both man and machine in the interaction as it relies for the generation of complex graphical display on the computer and for complex pattern recognition on the human being.

Graphical display Isocline-planes Simulation Ecological models Population models
Eutrophication

INTRODUCTION

In this paper we present an interactive graphic computer system for the investigation of models formulated in terms of differential – or (stochastic) difference equations. The system was originally developed for the investigation of population models and we have used it so far mainly in this context. Obviously it is by no means restricted to this subject matter as it can be used for the investigation of any model of up to ten coupled differential or difference equations. Nevertheless we present the system in the context of population models, not only because this is the subject of our own research, but also because of the state of the art in population modelling which demands preeminently the advantages which the system provides. These advantages include a fast access to a variety of models and an easy grasp of especially the qualitative properties of the models, while the representation is quantitative enough to avoid misleading results which purely qualitative solutions may yield.

In building and debugging one's own internal representation of the facts the best aid seems to be, to be confronted with different representations of the facts, to match them and to amend for wrong expectations. Computers have possibilities of communicating concepts which most people lack, like (three dimensional) pictures, but they are, unlike humans, relatively poor in verbal utterances. Here we present a program system for graphical presentation of models as static and dynamic properties of the state space. The system can be used:

1. for classroom demonstrations of ecosystem models,
 2. to familiarize individual students with the properties of models, in particular relative to the setting of parameter values (after all it is the parameter value, not the structure of the interaction, which makes the difference between viable and non-viable circumstances for populations),
 3. to investigate the properties of new models by research workers.
- The greatest satisfaction is obtained from working with the system when one's expectations of the behaviour of the model are just slightly wrong.

SIMULATION

It is often argued that a severe shortcoming of simulation models is that, in contrast to analytical solutions of the corresponding models, they do not provide "true understanding"

of the phenomenon; this statement is implicitly based on the fact that simulation requires full specification of parameter values. We think that this evaluation stems from an often held, but misleading, image of science, i.e. the image that science consists of sets of true, general statements with as few parameter bindings as possible. A better image is that science consists of a set of fully specified paradigm models, each demonstrating a particular aspect or approach to a class of phenomena. Such example models include prototypes, counter examples, borderline cases, teaching examples etc. [5, 6].

ECOLOGICAL MODELS

Many housewives wipe away spiderwebs to get rid of spiders. Even the simplest ecological models show that this merely results in an increase of mosquitos, while the spider population remains constant. Like in this example, ecological problems have, for many people, counterintuitive solutions.

The theoretical framework of ecology consists of "mini" models of population interactions [2-4, 7-12]. These "mini" models are known to be wrong in all (or almost all) cases, but they do provide an, heuristically useful, conceptual framework for thinking about ecology.

These models are most often given in the form of sets of differential or difference equations. However, they are actually not sufficiently specified that way, because the behaviour of the model is a useful paradigm for (some aspect of) the behaviour of ecological systems for a limited number of sets of parameter values only. For example, a population passing through a state of e.g. 10^{-10} individuals and recovering to a moderate or high population size is not a representation of an observable ecological situation. Thus we need default parameter values in order to give the models their heuristic value for ecology. If we want to study the models in different circumstances, we need, moreover, some sort of (dis)similarity criterion on parameter values, otherwise the search space becomes too large. However, numerical (dis)similarity of the parameter values will in general not suffice for this purpose and we need more sophisticated, model-dependent, ways. Here we will use, for example, the representation of the structure of the state-space by means of the \emptyset -isocline planes of the populations, i.e. the planes in which the change of one of the populations is zero, to provide knowledge about which differences in parameter values give rise to qualitatively (dis)similar situations in the particular model.

A scientific model should contain all the ingredients mentioned i.e. a representation of the interactions of the variables, default parameter values, and a notion about the (dis)similarity of sets of parameter values. If we incorporate all these ingredients in simulation implementations of the models, these implementations can provide a thorough understanding of the models.

A TOOL FOR TEACHING AND STUDYING (POPULATION) MODELS

The tool we present here for teaching and investigating population models is called *TRICLE*, Program for tridimensional representation of trajectories and isoclines.

TRICLE can handle deterministic models in terms of differential and difference equations, and stochastic models in terms of difference equations. It handles up to 10 coupled equations and it incorporates for each model not only the structure of the interactions, but also default parameter values and a representation to show the dissimilarity of the parameters, and it provides the following facilities for displaying the current status of the model:

1. *alphanumerical* representation of the population's interactions and the parameter values;
2. representation of the \emptyset -isocline planes of each of the populations in the first quadrant (only positive population numbers are meaningful) in a three-dimensional sub-state-space of three selected populations (the display space). Qualitatively different parameter values are shown as qualitatively different geometrical configurations of the

isocline planes. This display therefore guides the user in selecting parameter values, in such a way that all possible, qualitatively different, sets can be covered. This display also guides the user in selecting initial population sizes: the outcome of the simulation may depend on the initial state. In order to be sure to observe all qualitatively different behaviours of the system, initial states can be chosen in each of the sections of the state-space divided by the isocline planes.

3. representation of the trajectories in the display space, for selected initial values in this space.
4. representation of changes in time; all populations are displayed in this case.

The \emptyset -isocline planes can be represented by:

1. their intersections with $X=0$, $Y=0$ and $Z=0$ planes
2. shaded planes in the first quadrant
3. their intersections with other isocline planes in the first quadrant.

A *TRICLE* session runs as follows:

1. The user selects one of the available population models.
2. The system displays the structure of the population interactions and the current (default) parameter values.
3. The user changes some parameter values.
4. The system displays the current (default) values of the drawing specification parameters, i.e. which intersections of which isoclines-planes should be drawn, which should be shaded, how the direction of shading is to be, whether the lines should be dashed, on which scale it should be displayed and where the viewpoint of the user is with regard to the projection of the three-dimensional state-space.
5. The user can change any of these.
6. The system draws the requested isoclines.
7. The user inspects these, and checks his own expectations about the effect of the changes in parameter values he made.
8. The system prints *NSTEP X Y Z DT*, requesting the number of simulation steps and the initial state for a simulation and the time increment (if $DT = 0$ variable step integration is used).

If $NSTEP < 0$, the system returns to 2.

If $NSTEP = 0$, the system displays a trajectory it has computed in the previous simulation phase in the current display space.

If $NSTEP > 0$, the trajectory is computed and displayed in the current display space; the last coordinates in display space are printed; the system returns to 8.

9. The system requests whether a time display is wanted by requesting first time and last time. If last time > 1 , a time plot is shown, and the system returns to 9.

If last time = -99 , the system returns to 6, i.e. the isoclines are drawn again as specified before, but "focused" to the current values of the variables not displayed.

If, moreover, first time = -99 , the new isoclines are drawn without paging the screen, i.e. in the current picture.

Program organisation

TRICLE was developed in FORTRAN IV on the CYBER 7328 with a TEKTRONIX 4010 graphics terminal connected through INTERCOM 4, at 300 baud. It is presently being adapted for a PDP 11/45 configuration with the same terminal. The program is organised in such a way that the models for population interaction are incorporated in separate modules, which can be provided by the user, and so that several (up to 10) models can be present in the system simultaneously. Each model is represented in two procedures:

1. *POPdynn* in which the differential (difference) equations governing the dynamics of the model are given.
2. *ISODEFn* in which the \emptyset -isoclines are expressed in terms of each (or some) of the other

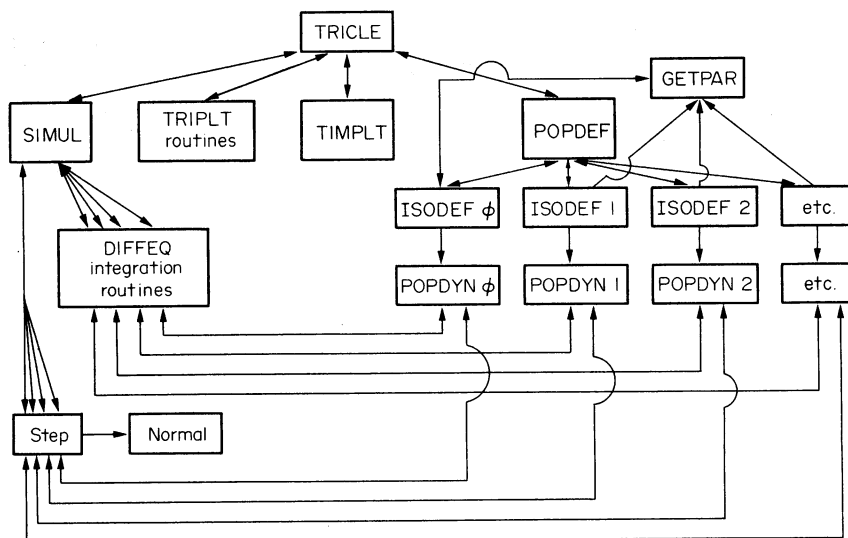


Fig. 1. Chart of program organisation.

populations. These expressions will in general be in the form of a call to the corresponding *POPDYN_n* procedure. (*n* is a digit (0–9) to distinguish ten different simultaneously available models). A chart of the program organisation is given in Fig. 1.

The procedure *GETPAR* is available to the model-specification routines for parameter specification and default setting. *GETPAR* is called by the *ISODEF* modules, which provide it with the dimensions of the parameter arrays, default model parameters, and default preferences for the display parameters (i.e. shading direction and intersections). The latter are used to generate the default parameters in accordance with the requested display space. *GETPAR* accepts user requests for changes in the model parameters. The usage of *GETPAR* may be omitted if the *ISODEF* procedure sets its own parameters.

The main program *TRICLE* organises the main flow through the program and does the displaying of the state-space. For this purpose it displays the current display parameters and accepts changes thereof, and it calls the procedure *POPDEF*, which provides it with the required model definition *ISODEF_n*. The three-dimensional display is obtained through calling the *TRIPLT* routines, which are organised analogous to the two-dimensional *CALCOMP* routines. After drawing the isoclines in the first quadrant of the state-space, *TRICLE* requests the specification of the simulation from the user and initiates the simulation phase by calling *SIMUL*. *SIMUL* passes the control either to the integration routines *DIFFEQ* (for continuous models) or to *STEP*, for discrete time step models or rectangular integration of continuous models with the appropriate model definition (*POPDYN_n*), and draws the trajectories in the display space. Both types of integration use the same model specification, i.e. the *POPDYN_n* procedure. In the discrete time step simulation some (or all) of the model parameters may be stochastic variables. They should be specified as such in *GETPAR* by specifying besides the mean value (which is used for calculating the ϕ -isocline) also the variance. The integration is done according to the rational extrapolation method of Bulirsch and Stoer (1966). This method has been chosen because of its speed and accuracy (see Bulirsch and Stoer 1966). High accuracy is necessary for models such as ours (e.g. inaccuracy in integration of the classical Volterra models may change its qualitative behaviour of neutral stable oscillations to oscillations with rapidly increasing amplitude). The method uses variable timesteps, which are chosen on the basis of computability. The rigorous minimisation of the amount of computation so acquired is useful for obtaining an insight in the (long term) behaviour of the model. However for elegant representation a fixed step for output purposes is to be preferred, because the system's response is limited by the baud rate rather than by computation. Therefore, if a fixed output

interval is used, the speed of drawing of the trajectories corresponds to time dynamics of the system, and therefore contains extra information above the mere form of the trajectories. This information is very useful in applications such as ours; it demonstrates for example the relative stability of instable equilibrium points (the population numbers may, in the neighbourhood of such an unstable equilibrium change barely for many generations). Therefore the system provides for the possibility of fixing the output interval (at the expense of computation time) by coding negative timesteps in stage 8 of the typical session as described above.

Finally the main program asks the user the time stretch to be displayed as a time plot and/or returns to the parameter specification phase (i.e. letting the *ISODEF* procedure call *GETPAR*).

AN EXAMPLE OF INTERACTIVE INSTRUCTION ON POPULATION INTERACTIONS

A problem in theoretical (as well as applied) ecology is eutrophication. The issue is the following:

A surplus of nutrients can have disastrous consequences for the prevailing ecosystems as it can lead to e.g. algal bloom or "dead water" (in the former case an excessive large algal population occurs, while in the latter case all populations die out). These phenomena appear to occur, however, for varying total amounts of available nutrients: certain amounts of nutrients will lead in some cases to such effects, while in other cases a rich ecosystem prevails under apparently similar circumstances. Theoretical ecology has partially succeeded in explaining these phenomena. Models of predator-prey interactions (developed independently from the eutrophication problem), do indeed show destabilisation for a large amount of nutrients for the prey, leading to large fluctuations in the sizes of both populations. These large fluctuations explain the observed phenomena of algal bloom (large amounts of prey) and dead water in nutrient-rich ecosystems.

The destabilisation of the predator-prey interactions is illustrated by *TRICLE* in Fig. 2. Predator-prey interaction is modeled as:

$$\begin{aligned} dA/dt &= p_1A - p_2B\{1 - \exp(-p_3A)\} - p_4A^2 \\ dB/dt &= -p_5B + p_6B\{1 - \exp(-p_7A)\} - p_8B^2, \end{aligned} \quad (1)$$

in which A is the prey, B is the predator and $p_1 \dots p_8$ are positive (or zero) parameters.

Eutrophication, i.e. increase of the amount of food available to the prey, is brought into the model by decreasing the self-limitation of the prey (i.e. decreasing p_4).

Figures 2(a), (c) and (e) show the effect of eutrophication in a deterministic differential equation model. Figures 1(b), (d) and (f) show the same in a stochastic difference equation model, in which p_1 and p_5 are stochastic variables with a variance of 0.1 times the mean.

From the figures it can be seen that the prey isocline changes by the eutrophication with respect to the intersection with the X -axis (i.e. the maximal number of prey in absence of the predator) and the position of the hump, which becomes higher and moves to the right (note the changes in scale!). In the differential equations a qualitative change in the behaviour of the system occurs as the intersection of the isoclines changes from right to left of the hump: in the former case the trajectories approach the equilibrium point, in the latter case they diverge from the equilibrium point and approach a limit cycle. The approach, c.q. divergence from the equilibrium point is the slower the nearer the intersection is to the tip of the hump; moreover, the limit cycles increase in diameter the farther the intersection is to the left of the hump. The behaviour of the stochastic difference-equation model is analogous to the deterministic differential equation system: the effect of eutrophication causes ever larger fluctuation to occur in the predator and the prey populations. The differences with the differential equation system are that fluctuation occurs already for less eutrophication (the intersection being still to the right of the hump), and that extinction of the predator population or both populations can occur, which is never the case in the differential equation

model, however large the cycles are. As was mentioned, this should, however, be considered as an artefact of the differential equation model, and we conclude that the present system gives a satisfactory explanation for the occurrence of "dead water" in environments with an excessive amount of nutrients.

However, it does not explain the discrepancy observed in the effect of a certain amount of nutrients in different cases. A hypothesis to explain this was derived by analysing models for three populations with *TRICLE*. In Fig. 3 a third population is added to the system. This third population predate on the predator of the two-species system.

For the parameters of Fig. 2(e), plus the new population the isocline planes are shown in Fig. 3(a), the trajectory in Fig. 2(c): the system approaches a stable equilibrium point. This could be predicted from the position of the isoclines: the *B* isocline is curved to the right such that the equilibrium point is at the right of the hump of the *A* isocline; the intersection of the *C* isocline (the upper predator) and the intersection of the *A* and *B* isocline planes is also at the right side of the hump of the latter. Further eutrophication leads eventually also to destabilisation of this equilibrium point. In Fig. 3(d) a large limit cycle occurs; and in Fig. 3(e) a double limit cycle occurs. In general the trajectories of three-species systems will converge to a toroidal plane.

From the analysis of the three population systems, of which a more detailed account will be presented elsewhere, the above-mentioned paradox can be solved. If the third population is introduced in the system while the nutrient level is as in Fig. 2(c) (i.e. a stable two-species system) and is allowed to settle before the eutrophication becomes too strong, a smooth "straight" path will be traced up to the new stable point, while when eutrophication is too fast (the upper predator cannot develop fast enough) the large limit cycles as in Fig. 1(e) will occur before the stable point is reached [as is the case in Fig. 3(c)], which may lead to extinction in the stochastic case.

Thus, we hypothesise that the unfavourable effects of eutrophication as frequently observed in polluted areas can be caused not only by the total amount of nutrients, but primarily by the fast rate of change in the amount of nutrients (or by the non-availability of the upper-predator).

In this example, the use of *TRICLE* to illustrate well-known ecological theory as well as its use as research tool were demonstrated.

Note that, contrary to the figures, the display includes the rate of movement along the trajectories. The observation of these movements increases the comprehensibility of the display significantly.

DISCUSSION

Interactive computer systems most often use one of two strategies for interaction with the user:

1. Extensive, sequential question answering and prompting for input specification. The user needs in this case no or very few *a priori* ideas about what he wants to do, and what the system is for.
2. Few guidelines are provided by the system for input specification. The user needs a precise and complete *a priori* idea about what he wants and what he can do with the system.

Contrary to these types of interaction, the here described system *TRICLE* confronts the user with the current status of the model and leaves it up to the user to adapt the system (or his own ideas) on the basis of this information. Thus, the user is supposed to have ideas about likely behaviour of the model, and the system helps him in debugging and expanding these ideas.

The system tries to optimise man-machine co-operation in analysing the model under consideration by using the strong points of each. The computer contributes its display generating power and the human his pattern recognition power. The display puts less

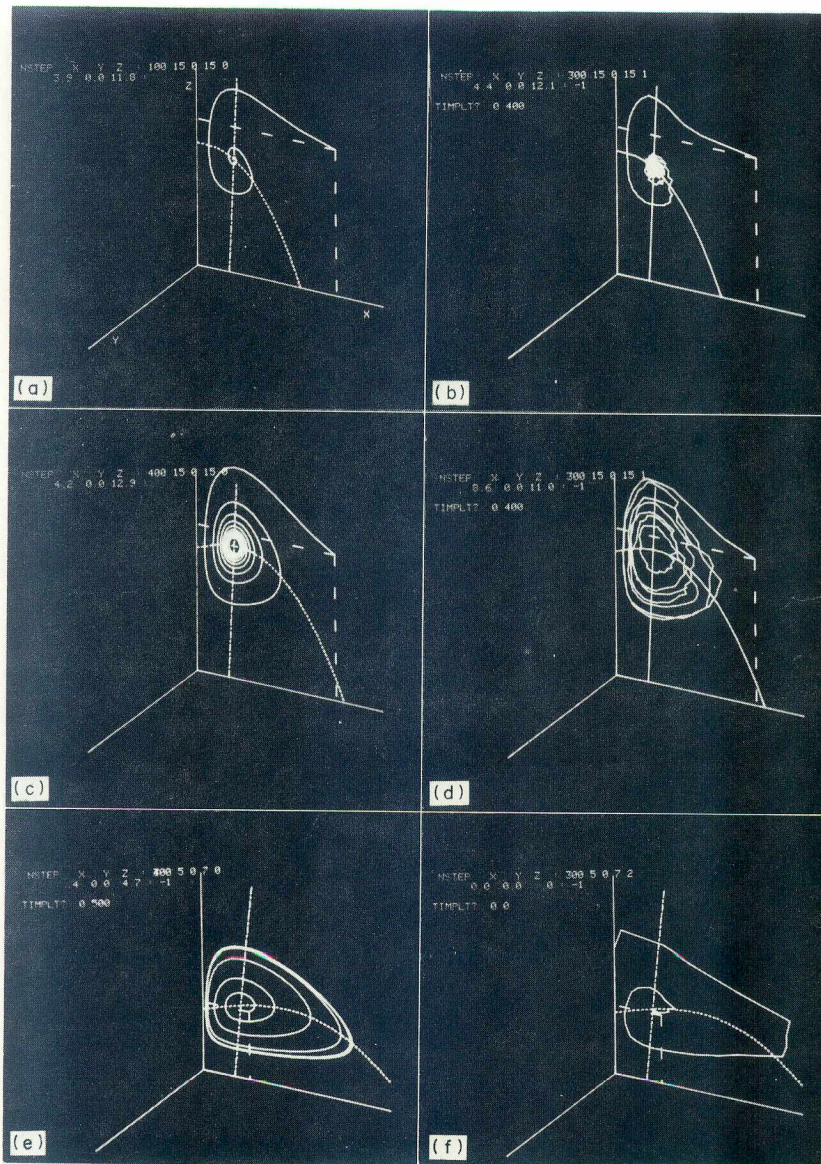


Fig. 2. Eutrophication in a predator-prey system, state space representation as provided by TRICLE.

A , the size of the prey population, is represented on the X -axis.

B , the size of the predator population, is represented on the Z -axis.

X, Y, Z axes as indicated in Fig. 2(a).

- $dA/dt = 0$
- - - - - $dB/dt = 0$
- indicates the starting point of the trajectory
- trajectory.

The dynamics of the interaction between the predator and the prey population are given in equation (1).

- (a) $p_1 = 0.5, p_2 = 1.0, p_3 = 0.02, p_4 = 0.0045, p_5 = -0.08, p_6 = 0.2, p_7 = 0.015, p_8 = 0.0004$. Scale: $x = 0.1, y = 0.5$.

Stable equilibrium of 39 prey and 23.4 predators.

- (b) Idem 2(a), except that variance (p_1) = 0.05 and variance (p_5) = 0.008. Small fluctuations around the equilibrium point.
- (c) Idem 2(a), except for larger eutrophication: $p_4 = 0.00315$. Stable equilibrium point, which is approached very slowly.
- (d) Idem 2(c), but variance of p_1 and p_5 as in 2(b). Oscillations around the equilibrium point.
- (e) Idem 2(c), except for larger eutrophication: $p_4 = 0.00221$. Scale: $x = 0.1, y = 0.25$. Divergence from the equilibrium point to a limit cycle, which passes through a state of a very small prey population.
- (f) Idem 2(e), except for the variances of p_1 and p_5 , which are as in 2(b). Both populations die out.

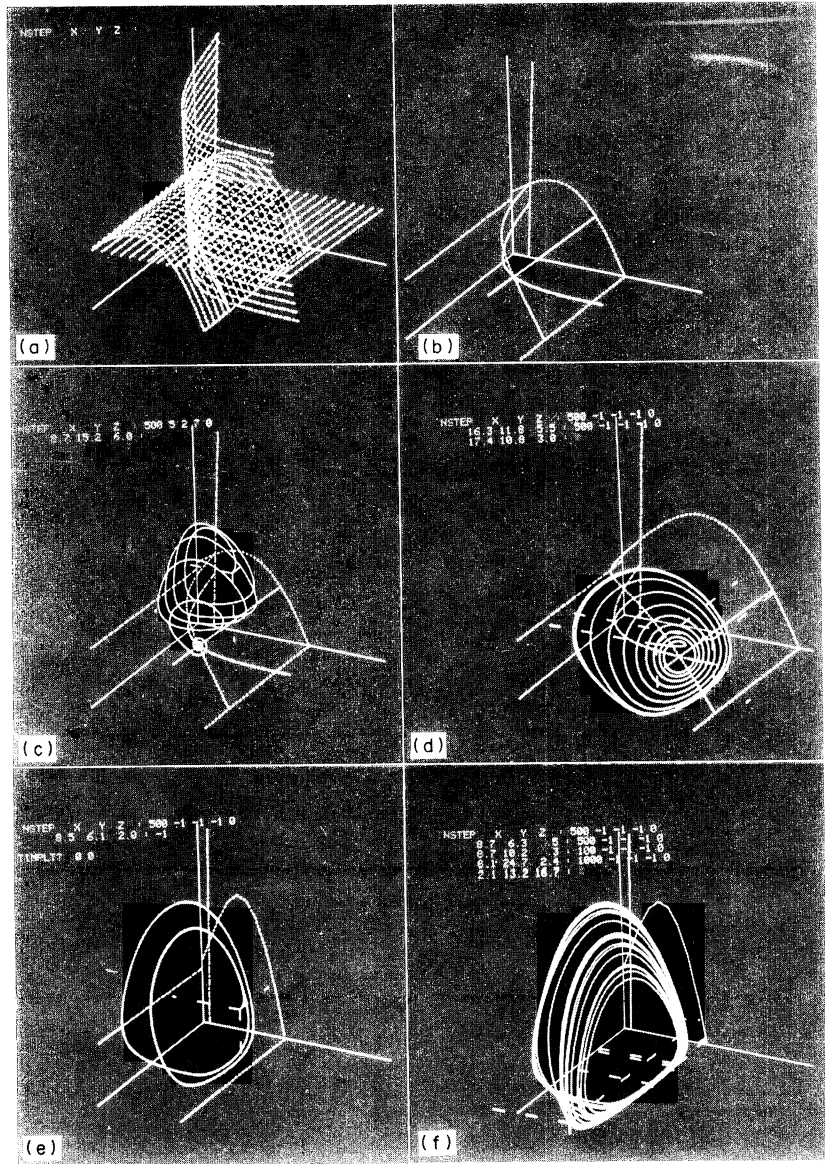


Fig. 3. Eutrophication in a three species system, state-space representation as provided by *TRICLE*. The interaction between *A*, *B* and *C* (*A* is prey for *B* and *B* is prey for *C*) is governed by:

$$\begin{aligned}
 dA/dt &= p_1A - p_2B\{1 - \exp(-p_3A)\} - p_4A^2 \\
 dB/dt &= -p_5B + p_6B\{1 - \exp(-p_7A)\} + \\
 &\quad - p_9C\{1 - \exp(-p_{10}B)\} - p_8B^2 \\
 dC/dt &= -p_{11}C + p_{12}C\{1 - \exp(-p_{13}B)\} - p_{14}C^2
 \end{aligned}$$

A, *B*, *C* are represented on the *X*, *Z*, *Y* axis respectively (see Fig. 2(a)). Dashing of lines as indicated in Fig. 2, and

----- $dC/dt = \emptyset$.

Intersections of \emptyset -isoclines have dashing of first population.

- (a) p_1 - p_8 as in Fig. 2(e); $p_9 = 0.4$, $p_{10} = 0.015$, $p_{11} = 0.04$, $p_{12} = 0.2$, $p_{13} = 0.0!$, $p_{14} = 0.001$. Scale: $X = 0.05$, $Y = 0.25$, $Z = 0.5$. \emptyset -isocline planes of the three populations.
- (b) Idem 3(a). Only intersections of isocline planes are shown.
- (c) Idem 3(b). A trajectory starting near the equilibrium point of the corresponding two-species system reaches the equilibrium point after several large oscillations.
- (d) Idem 3(e), except $p_4 = 0.0126$. Divergence from equilibrium point to large limit cycle.
- (e) Idem 3(d), except for $p_4 = 0.00114$. Scale: $X = 0.02$, $Y = 0.25$, $Z = 0.5$. "double" limit cycle.
- (f) Idem 3(e), but $p_{12} = 0.1$, $p_{13} = 0.04$, $p_{11} = 0.035$. A toroidal path giving rise to aperiodic oscillations.

demands on the latter than the Figs. 2 and 3 of this paper do, because the isocline–planes and intersections are drawn sequentially.

Moreover, the display contains more information than the figures, because not only the position of the trajectories is displayed, but also the speed with which the system moves along the trajectories. The human pattern recognition capabilities are improved by suitable prior knowledge. Therefore, the greater satisfaction is obtained from working with the system the better one's expectations about the behaviour of the system are.

Simulation models play a rapidly increasing role in science. Besides the strongly fact-based simulation models which may be of predictive value, the here discussed conceptual "mini" models can be of considerable heuristic value.

Simulation studies of such mini-models can be even more useful than analytical studies, not only because analytical results may be difficult to obtain, but also because the latter tend to yield either too quantitative (analytical expressions), or too qualitative (e.g. by linear stability theory) results.

Simulation models enforce full specification of the parameters. Search in a large parameter space is only feasible if a model-dependent notion on the dissimilarity of sets of parameters is incorporated in the model. In our system this notion is provided by the representation of the isoclines. If such a notion is available in a suitable form, simulation studies are likely to yield results of the required generality and of the required detail.

Finally we note that the incorporation of all ingredients of (scientific) knowledge in a simulation model almost automatically leads to an improved interaction between the user and the machine.

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The program *TRICLE* is available on request from the authors.

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