

Qualitative behavior of stage-structured populations: application to structural validation

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Abstract. The transient behavior of a class of nonlinear differential systems representing stage-structured populations is studied. The qualitative dynamics are described in terms of succession of extrema for the state variables, or for the integrated difference between two trajectories. The rules giving the possibilities of extrema are derived, they characterize the classical stage-structured models. These rules can be compared with experiments to validate the structure of the model. An explanation for the disagreement of this transition scheme with some experiments could be an unexpected interaction with another variable. A new model taking the interaction into account thus engenders new transition rules, which are to be compared with experiments. These results are illustrated with experiments on copepods, showing how the qualitative experimental features can help the construction and the validation of the models.

Key words: Stage-structured models – Transient behavior – Qualitative study – Validation – Copepods

1 Introduction

For many animal species (crustacean, insects, amphibians, ...), the individuals take on different morphological shapes before reaching their final adult state. This multiplicity of developmental stages gives rise to individuals with a complex life cycle. Copepods are small crustacea whose molting processes determine the succession of the different stages. These different stages are characterized by different shapes, sizes and behaviors, but above all they play very different roles

in marine ecosystems. When considering the dynamics of such a population in the food-web it is therefore very important to determine precisely the evolution of the population composition stage by stage. There is thus a strong need to construct models which represent such complex life cycles.

Because of the multiplicity of the represented stages, the corresponding models often reach high dimensions. Unfortunately, the different functions on which the models are constructed are mainly hypothetical, and have rarely been validated experimentally. Moreover, due to variability and weak sampling rate of data, parameter values, which are not always identifiable (Walter, 1982), are generally not estimated with precision. Under such conditions, the entire characterization of the dynamical behavior of a stage-structured model so that it can be compared with experimental data appears very difficult. For some systems, there exists methods of simplification: logical terms can be considered as an approximation of non-linear functions (Thomas, 1979; Glass and Pasternack, 1978; Snoussi and Thomas, 1993), singular perturbation methods like the quasi steady state assumption (Segel, 1984, 1988) can be used. The qualitative description of the evolution of equilibrium, when one parameter is modified, can also be a means of comparison between model structure and data (Arditi and Ginzburg, 1989; Ginzburg and Akçakaya, 1992). More recently, a dynamical qualitative methodology has been developed to characterize by means of graphs the dynamical behavior of a class of biological systems (Bernard and Gouzé, 1995a, b). With this analysis, the experimentalist can compare the most immediate information from the data (extrema, comparison with reference points) with the possible scenarii of such qualitative events derived from the sign of the jacobian matrix.

Stage-structured models enter in the framework of these models for which qualitative behavior can be entirely determined by the sign of the jacobian matrix: the dynamics of stage i is the balance between an input term in the stage depending on the stage $i - 1$ (recruitment) and an output term (mortality, transfer to the next stage, dilution) depending on the stage i . Hence, the dynamics of each variable only depend on the variable itself and on the precedent one so that the system has a so-called loop structure (Hastings *et al.*, 1977; Mallet-Paret and Smith, 1990; Bernard and Gouzé, 1995a). Nevertheless, the high dimension n of general stage-structured models makes a global qualitative description difficult (it would involve 2^n qualitative states).

In this paper, we focus on the transient behavior of a subsystem involving only a few successive variables, considering the other variables as peculiar inputs applied to the subsystem. We derive from the

structure of the partial system the possibilities of succession of extrema for these variables. We show that this analysis can also be applied to a comparison between two experiments, by integrating the state variables, so that experimental noise is smoothed. We point out that the usual succession rules may be transgressed if an unexpected interaction occurs between a state variable and another variable (predation, competition). This theoretical analysis is illustrated by experimental observations on different experiments with copepods.

2 Structure effects on the succession of extrema

2.1 Presentation and hypothesis

For stage-structured populations, the most common interaction diagram between the variables representing the different stages is presented in Fig. 1a. It is generally assumed that the dynamics of a stage only depend on this stage (mortality growth, dilution) and on the previous one (recruitment, egg laying). If $x_i \in \mathbb{R}^+$ represents biomass or number in stage i , a common way for writing down the associated dynamical system (Σ) is the following differential equations for the n considered stages:

$$(\Sigma) \begin{cases} \dot{x}_1 = f_1(x_n) - g_1(x_1) \\ \dots \\ \dot{x}_n = f_n(x_{n-1}) - g_n(x_n) \end{cases} \quad (1)$$

The system (Σ) has a loop structure, as defined by Bernard and Gouzé (1995a). For sake of simplicity, we will denote indices modulo n , and therefore denote $x_0 = x_n$.

Often the variable x_1 describes eggs, and x_n the adults. Note that some variables x_i may have no biological meaning; they can represent age classes in a stage, or be an aggregation of different stages which have comparable dynamics.

The functions g_p ($\mathbb{R}^+ \rightarrow \mathbb{R}$) represent the output process of the stage p , due to the sum of the transfer to the next stage and the balance between mortality and growth. The functions f_p ($\mathbb{R}^+ \rightarrow \mathbb{R}^+$) are the transfer from the precedent stage. These functions are usually considered as increasing i.e. for all the indexes p : $\forall x_{p-1} \in \mathbb{R}^+ df_p/dx_{p-1} > 0$. We assume that the function f_p and g_p are C^2 .

Some stages may have more complex dynamics. For example in the classical models of age-structured populations of fishes, several

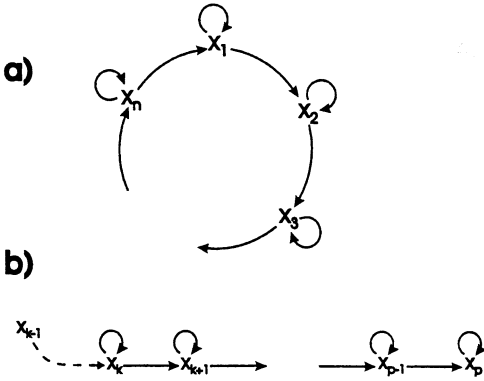


Fig. 1. **a** Graph of interactions for loop models (Σ) (see eq. (1)). The dynamics of each variable depend on the variable itself and on the previous one. **b** Graph of interactions for the chain-structured submodel ($\Sigma_{k,p}$) (see eq. (2)). Variable x_{k-1} acts as an input variable

stages of fish can spawn (Kishi et al., 1991). Such models, which are continuous Leslie models do not have a loop structure: the dynamics of the eggs depend on all the mature stages. Sometimes external interactions (predation, food, ...) can also make what is *a priori* a loop structure disappear. In this case we will focus on a part of the system only, but which still has the following dynamics (assuming $k \leq p$):

$$(\Sigma_{k,p}) \begin{cases} \dot{x}_k = f_k(x_{k-1}) - g_k(x_k) \\ \dots \\ \dot{x}_p = f_p(x_{p-1}) - g_p(x_p) \end{cases} \quad (2)$$

The subsystem ($\Sigma_{k,p}$), is thus a non autonomous system with the input x_{k-1} . The advantage in considering this subsystem is that we do not need to give an analytical formulation for the whole system, which may not be loop-structured.

Definition 1. *The system (2) verifying: $\forall i \in \{k, \dots, p\} \quad \forall x_{i-1} \in \mathbb{R}^+ \quad df_i/dx_{i-1} > 0$, will be called chain-structured with increasing interactions (CSI_2).*

The interaction diagram for a CSI_2 subsystem ($\Sigma_{k,p}$) is presented in Fig. 1b.

2.2 Theorem for succession of extrema

Theorem 1 (CS₂T theorem). *Assuming that the variable x_p obeys the following differential equation:*

$$(\Sigma_p) \{ \dot{x}_p = f_p(x_{p-1}) - g_p(x_p) \} \tag{3}$$

where $\forall x_{p-1} \in \mathbb{R}^+ \text{ df}_p/dx_{p-1} > 0$, then the maxima [resp. minima] of x_p appear during a phase of decline [resp. growth] of x_{p-1} . This transition scheme for the pair (x_{p-1}, x_p) will be called the classical stage-structured transition (CS₂T) scheme.

Proof. Denote $z_p = \dot{x}_p$. By differentiation along time of equation (3) we obtain:

$$\dot{z}_p = \frac{df_p}{dx_{p-1}} z_{p-1} - \frac{dg_p}{dx_p} z_p$$

Suppose that at time t_0 , x_p admits an extremum: $z_p(t_0) = 0$, thus we have

$$\dot{z}_p(t_0) = \frac{df_p}{dx_{p-1}}(t_0) z_{p-1}(t_0).$$

Because $df_p/dx_{p-1} > 0$, the sign of $\dot{z}_p(t_0)$ is the same as that of $z_{p-1}(t_0)$.

If, for example, x_{p-1} is increasing then $\dot{z}_p(t_0) > 0$, and thus z_p is increasing for t_0 . Necessarily, z_p is negative for some $t < t_0$, and z_p is positive for some $t > t_0$. It implies that x_p is decreasing before t_0 and increasing after it: x_p admits a minimum.

We have the symmetric result for x_{p-1} decreasing.

In this approach, we do not consider the set of trajectories, of zero measure, such that x_p and x_{p-1} admits for the same time t_0 an extremum (see Bernard and Gouzé (1995a)). □

Now we propose a series of lemma to characterize the qualitative behavior of these CSI₂ subsystems, in terms of succession of extrema. For given (qualitative) initial conditions and for a given trend of the input x_{p-1} , these lemma predict the extrema that may appear.

We first consider the particular case where x_{p-1} is constant on a time interval.

Lemma 1. *Assume that x_{p-1} is constant for $t \in]t_1, t_2[$. If x_p obeys the CSI₂ subsystem (Σ_p) then x_p is monotonous for this period. If x_k to x_{p-1} also obey a CSI₂ subsystem $(\Sigma_{k,p-1})$ then these variables are constant for this period. If x_1 to x_n obey a loop-structured system (Σ) then the system is at equilibrium.*

Proof. See Appendix 1. □

The following lemma deals now with the other case where the input is strictly monotonous.

Lemma 2. *Consider the CSI_2 system $(\Sigma_{k,p})$. If at time t_i variables x_k to x_p are decreasing [resp. increasing], the only possible extrema at time t_i for these $(p - k + 1)$ variables is a minimum [resp. maximum] of variable x_k which arises if the input x_{k-1} is increasing [resp. decreasing].*

Proof. Suppose that variable i ($k < i \leq p$) admits a minimum. This minimum corresponds to a phase of decline of the variable x_{i-1} , and therefore it is not allowed by the CS_2T theorem.

Lemma 3. *Consider the CSI_2 subsystem $(\Sigma_{k,p})$. If x_k is monotonous for $t \in]t_0, t_1[$, then x_j ($k < j \leq p$) can have at the most $(j - k)$ extrema for $t \in]t_0, t_1[$.*

Proof. While x_k is monotonous, x_{k+1} can have at the most one extremum. Suppose, for example, that it is a maximum: x_{k+1} is thus increasing and then decreasing. During each of these two phases, the variable x_{k+2} can have an extremum. This shows that the variable x_j has, at the most, $(j - k)$ extrema. □

For the loop systems, Lemma 3 can be extended and a stronger result can be given:

Lemma 4. *Assume that the system is loop-structured (eq. (1)) with increasing interactions. If at time t_1 the n state variables of the system are increasing [resp. decreasing] they will remain increasing [resp. decreasing] for all $t \geq t_1$.*

Note. This lemma, consequence of Lemma 2, is a general property of cooperative systems (Smith, 1988).

2.3 Theorem of comparison between two trajectories

We propose here an important extension of the CS_2T theorem, which leads to new ways to determine if the experimental data can be represented by a model with the assumed structure.

Assume that $x_p^1(t)$ and $x_p^2(t)$ are two different trajectories of the same CSI_2 subsystem (Σ_p) associated with two different initial conditions and two different inputs $x_{p-1}^1(t)$ and $x_{p-1}^2(t)$.

Denote by $\delta_p(t)$ the integrated difference between the two trajectories $x_p^1(t)$ and $x_p^2(t)$:

$$\delta_p(t) = \int_0^t (x_p^2(\tau) - x_p^1(\tau)) d\tau \tag{4}$$

Theorem 2. *If the two variables x_p^1 and x_p^2 obey the same CSI_2 subsystem (Σ_p) then the pair (δ_{p-1}, δ_p) satisfies the CS_2T scheme: the maxima [resp. minima] of δ_p appear during a phase of decline [resp. growth] of δ_{p-1} .*

Proof. Let us consider the following function:

$$\phi(\alpha) = f_p(\alpha x_{p-1}^2 + (1 - \alpha)x_{p-1}^1) - g_p(\alpha x_p^2 + (1 - \alpha)x_p^1)$$

If we integrate between 0 and 1 the derivative of ϕ we get:

$$\begin{aligned} \dot{x}_p^2 - \dot{x}_p^1 &= (x_{p-1}^2 - x_{p-1}^1) \int_0^1 f'_p(\alpha x_{p-1}^2 + (1 - \alpha)x_{p-1}^1) d\alpha - (x_p^2 - x_p^1) \\ &\quad \times \int_0^1 g'_p(\alpha x_p^2 + (1 - \alpha)x_p^1) d\alpha \end{aligned}$$

Since the integrated function f'_p is strictly positive, we obtain the following relationship:

$$\ddot{\delta}_p = \dot{\delta}_{p-1} F_p(x_{p-1}^1, x_{p-1}^2) - \dot{\delta}_p G_p(x_p^1, x_p^2)$$

with F_p a strictly positive function.

By applying the same reasoning as in the proof of the CS_2T theorem, we have the result.

Important particular case. It is also possible to compare a trajectory $x_p(t)$ of a CSI_2 (Σ_p) subsystem with the same trajectory translated in time, $x_p(t - T)$. We choose then $x_p^2(t) = x_p(t)$ and, for a positive real T , $x_p^1(t) = x_p(t - T)$. Let us define now the moving average of x_p on the time interval $]t - T, t[$:

$$\bar{x}_p(t) = \frac{1}{T} \int_{t-T}^t (x_p(\tau) - x_p(\tau - T)) d\tau \tag{5}$$

We propose now a straightforward extension of Theorem 2 that characterizes the behavior of the variables which have been filtered by moving average:

Lemma 5. *Assuming that the variable x_p is driven by a CSI_2 subsystem (Σ_p). then the pair $(\bar{x}_{p-1}, \bar{x}_p)$, as defined by eq. (5), satisfies the CS_2T scheme.*

Consequences. If the measurements of the state variables are noisy, which is generally the case in biology, this method provides us a very simple filter to smooth the data, and remains nevertheless in the framework of a qualitative analysis. The example presented in Sect. 2.4 demonstrates the practical efficiency of this methodology.

As for Sect. 2.2, we can derive properties of the dynamical behavior for the integrated difference between two experiments:

Lemma 6. *Consider x_i^1 and x_i^2 the components of two different trajectories of a CSI_2 subsystem ($\Sigma_{k,p}$). If there exists a time t_0 , such that: $\forall i \in \{k, \dots, p\} x_i^1(t_0) < x_i^2(t_0)$ [resp. $x_i^1(t_0) > x_i^2(t_0)$], then the crossing of two components (i.e. $\exists j \in \{k, \dots, p\}, \exists t_c$ s.t. $x_j^1(t_c) = x_j^2(t_c)$) is possible only for components x_k^i , if the inputs verify $x_{k-1}^1 > x_{k-1}^2$ [resp. $x_{k-1}^1 < x_{k-1}^2$].*

Proof. This is the same demonstration as for Lemma 2, by considering the variable δ_i . □

Lemma 7. *Consider x_i^1 and x_i^2 the components of two different trajectories of a CSI_2 subsystem ($\Sigma_{k,p}$). If for all $t \in]t_0, t_1[$: $x_k^1(t) < x_k^2(t)$, then two components x_j^1 and x_j^2 ($k < j \leq p$) can intersect at the most $(j - k)$ times for $t \in]t_0, t_1[$.*

Proof. This is an application of Lemma 3. □

Lemma 8. *Consider x_i^1 and x_i^2 ($i \in \{1, \dots, n\}$) the components of two different trajectories of a loop-structured system with increasing interactions. If at time t_1 , we have for all the components $x_i^1(t_1) < x_i^2(t_1)$ then $\forall t \geq t_1 x_i^1(t) < x_i^2(t)$.*

Proof. This is an application of Lemma 4. Note that it is a general property of cooperative systems (Smith, 1988). □

2.4 Application

The most common application of the CS_2T scheme is the well-known observation of the dynamics of a cohort, obtained by examining the evolution of individuals initially at the same stage. The successions of picks, which is well known from people studying development of stage-structured populations, fit straightforwardly the CS_2T scheme.

Using experimental data, we propose here to show that this CS_2T scheme is also respected for the more complex case where all the stages are present at the initial time. To clarify our analysis, we first use the

result of Lemma 5 to process the data with the moving average filter (see an example of data processing on Fig. 2). Figure 3 presents the processed data for the copepod *Euterpina acutifrons*. The experimental qualitative behavior seems to be in agreement with the CS_2T scheme through the 120 days of the experiment when considering the pair (large naupliar stage, small copepodite stage) for the numerous observed extrema. It can be seen that the level of noise is very low, because it has been smoothed by the filter. Thanks to the filtering effect of the integration, a qualitative analysis can be performed, even for very noisy data, for which the direct observation of extrema would be too uncertain.

Figure 4 presents a comparison between two different experiments with the copepod *Temora stylifera*. For these two experiments the large naupliar stage and the small copepodite stage have been integrated along time (cf eq. (4)). It can be seen that the behavior of this pair follows the CS_2T scheme given by Theorem 2.

This methodology may involve the selection of “reference experiments” to which a given experiment could be compared. If the model is validated for such a reference experiment, the criteria based on the qualitative comparison are a way for the experimentalist to verify whether a given experiment can also be explained by the structure of

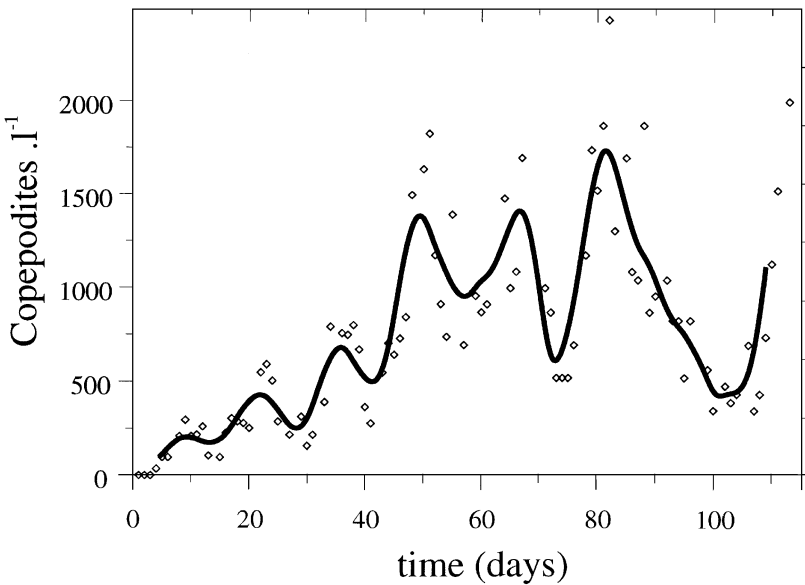


Fig. 2. Example of data processing by moving average for the small copepodite stage of *Euterpina acutifrons*. The symbols represent the original data, the continuous line is the moving average ($T = 6$ days) interpolated by splines function (MATLAB)

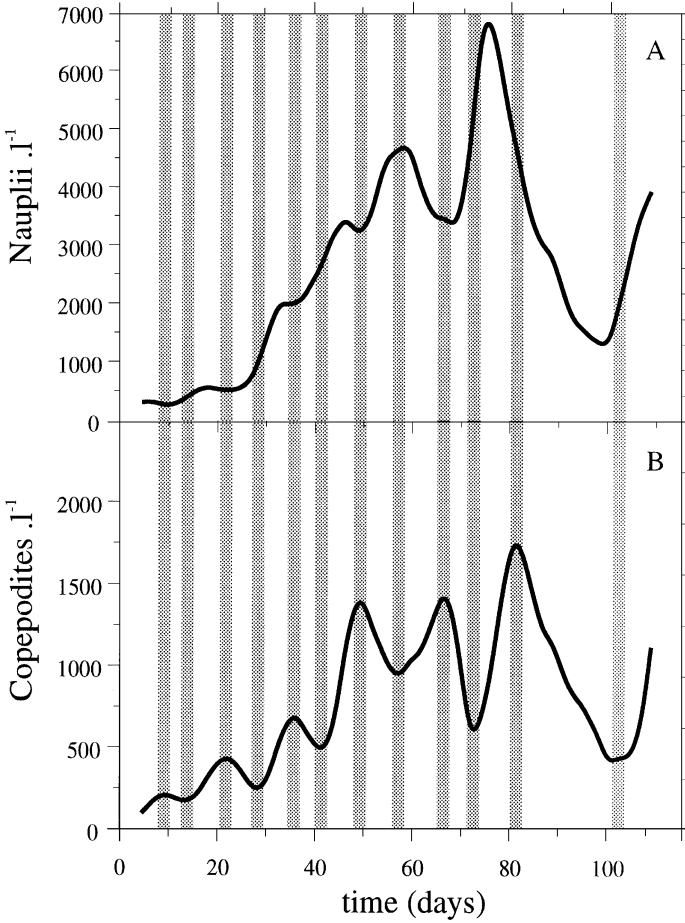


Fig. 3. Development of *Euterpina acutifrons* over several generations (Yassen 1984). Data processed by moving average ($T = 6$ days) for (A) stage $p - 1$ (large naupliar stage) and (B) stage p (small copepodite stage). The extrema for the copepodite are identified by gray strips

the model. The advantage is then to have more tests to compare an experiment and the structure of the model.

3 An unexpected interaction: a reason to transgress the transition rules

3.1 Introduction

Suppose now that an experiment is performed, and that the analysis of its qualitative features does not follow the CS_2T scheme. Clearly it shows

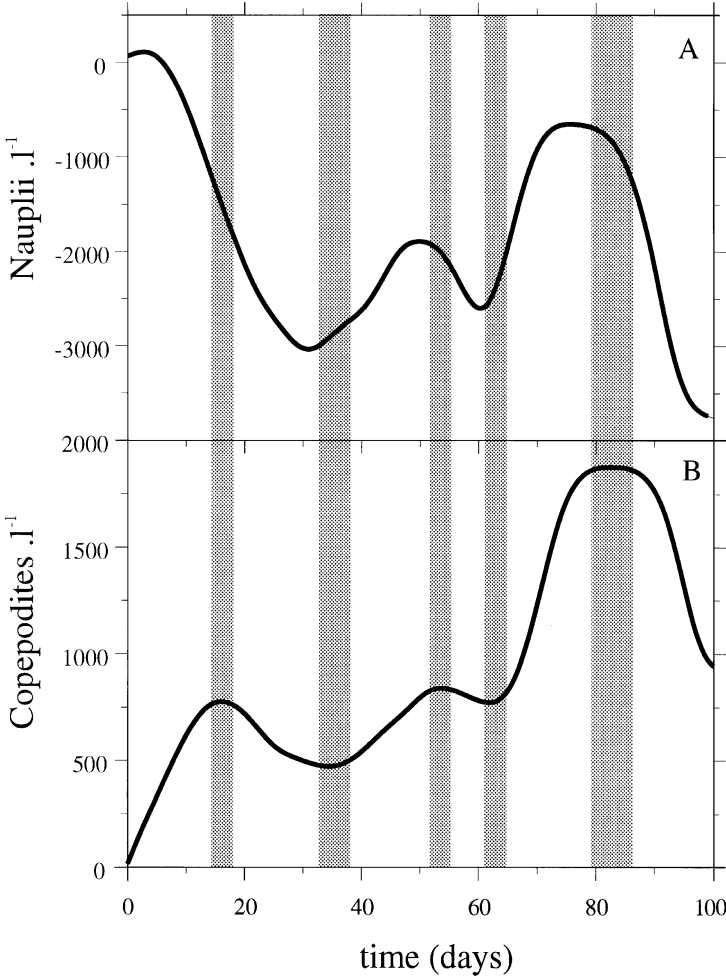


Fig. 4. Comparison of two experiments with *Temora stylifera*. (A) Large naupliar stage: $\delta_3(t) = \int_0^t (x_3^2(\tau) - x_3^1(\tau)) d\tau$. (B) Small copepodite stage: $\delta_4(t) = \int_0^t (x_4^2(\tau) - x_4^1(\tau)) d\tau$. The extrema of δ_4 are represented by gray strips

that the structure of the model is not adapted to the representation of this experiment. More precisely, if stage x_i has an extremum which is not allowed by the CS₂T scheme for the observed trend of x_{i-1} this would mean that the dynamics of stage i can not be described by the equation (Σ_i) . Note that this conclusion is independent of the dynamics of the other stages.

We assume here that the structure of the model is consistent with other experiments, where, for example, ideal growth conditions occur. In other words, we suppose that the stages definition has been

validated, and therefore that the noticed experimental incompatibilities with the CS₂T scheme are not due to aggregation of heterogeneous stages.

In this section, we will go further and try to help the experimentalist to understand why his model did not fit his experiment, in order that he can build a correct model. For this we will show that an unexpected interaction can change the classical transition rules. This interaction may have several sources such as food limitation, predation, competition, ... We will take as an example the case of predation, which often corresponds to the phenomenological question that the biologist wants to answer: does species *a* eat species *b*? Which stages are mostly eaten? We will show that observation of extrema not matching the CS₂T transition scheme can highlight such an interaction between two variables.

3.2 Consequence of an unexpected interaction

Assuming, for example, that some predator of concentration *u* eats the stage *p*. The subsystem driving this stage depends now on two inputs x_{p-1} and *u*:

$$(\Sigma_p^u) \{ \dot{x}_p = f_p(x_{p-1}) - g_p(x_p) - h_p(u, x_p) \} \tag{6}$$

The logical assumption that the loss due to predation increases when *u* increases implies that the function $h_p : (\mathbb{R}^+)^2 \rightarrow \mathbb{R}^+$ verifies:

$$\forall (u, x_p) \in (\mathbb{R}^+)^2, \quad \frac{\partial h_p}{\partial u} > 0 .$$

Theorem 3. *Let x_p be driven by the subsystem (Σ_p^u) where $\forall (u, x_p) \in (\mathbb{R}^+)^2, \partial h_p / \partial u > 0$ and $df_p / dx_{p-1} > 0$. If x_{p-1} increases and *u* decreases [resp. x_{p-1} decreases and *u* increases] x_p can have at the most one extremum, and this extremum is a minimum [resp. a maximum].*

Proof. If we consider the time t_0 when x_p admits an extremum, we have:

$$\dot{z}_p(t_0) = \frac{df_p}{dx_{p-1}} z_{p-1}(t_0) - \frac{\partial h_p}{\partial u} \dot{u}(t_0)$$

Since $z_{p-1}(t_0)$ and $\dot{u}(t_0)$ have opposite signs, using the same principle as for the CS₂T theorem, we can derive the sign of $\dot{z}_p(t_0)$. □

Table 1. Transition rules for the subsystem (Σ_i^u) : The new criteria of appearance of extrema for the variable x_i in relation to the trend of variables x_{i-1} and u

	New possible situations	Situations not permitted
x_{i-1} increasing		
x_{i-1} decreasing		

Note that if x_{p-1} and u have the same trend, both extrema are *a priori* possible for x_p . Especially one can find extrema not compatible with the CS₂T theorem (see Table 1).

Application. If an experimental extremum for variable x_p appears which disagrees with the CS₂T theorem, an interaction between variables x_p and u can be hypothesized. By examining the trend of the three variables x_{p-1} , x_p and u it can be verified if the rules given by Theorem 3 agree with the experiment. This can therefore constitute an indirect method to highlight an interaction between predators and individuals in a stage.

When there are interactions, it is still possible to compare two different experiments. Furthermore we shall see that if the input is the same for both experiments, the CS₂T rules remain valid.

Theorem 4. Consider x_p^1 and x_p^2 two different trajectories from subsystem (Σ_p^u) associated with two sets of input (x_{p-1}^1, u^1) and (x_{p-1}^2, u^2) , respectively. Assume that $\forall x_{p-1} \in \mathbb{R}^+, df_p/dx_{p-1} > 0$ and $\forall (u, x_p) \in (\mathbb{R}^+)^2, \partial h_p/\partial u > 0$, then the same rules as for Theorem 3 are satisfied for $(\delta_{p-1}, U_p, \delta_p)$, with $\delta_p(t) = \int_0^t (x_p^2(\tau) - x_p^1(\tau))d\tau$ and $U_p(t) = \int_0^t (u_p^2(\tau) - u_p^1(\tau))d\tau$.

Proof. Consider the function $\chi(x_{p-1}, x_p, u) = f_p(x_{p-1}) - g_p(x_p) - h_p(u, x_p)$, verifying $\partial\chi/\partial x_{p-1} > 0$ and $\partial\chi/\partial u < 0$. As for the proof of Theorem 2, we define:

$$\varphi_2(\alpha) = \chi(\alpha x_{p-1}^2 + (1 - \alpha)x_{p-1}^1, \alpha x_p^2 + (1 - \alpha)x_p^1, \alpha u^2 + (1 - \alpha)u^1)$$

Then, the principle used for Theorem 2 leads us to the following relationship:

$$\ddot{\delta}_p = \dot{\delta}_{p-1}\Gamma + \dot{\delta}_p\Gamma - \dot{U}\Theta$$

with Γ , A and Θ strictly positive functions of the variables (x_{p-1}^j, x_p^j, u^j) , $j = 1, 2$.

By considering the time when δ_p reaches an extremum, we can conclude in the same way as for Theorem 3. \square

If the predator dynamics are the same for both experiments (i.e. u is the same), a stronger result can be derived:

Theorem 5. Consider x_p^1 and x_p^2 two different trajectories from subsystem (Σ_p^u) associated with the sets of inputs (x_{p-1}^1, u) and (x_{p-1}^2, u) , respectively. Assume that $\forall x_p \in \mathbb{R}^+$, $df_p/dx_{p-1} > 0$, then the pair (δ_{p-1}, δ_p) follows the CS_2T scheme. \square

Proof. The proof is the same as for Theorem 4, with $\dot{U} = 0$.

3.3 Application

In the experiment of Fig. 5, the copepod *Euterpina acutifrons* grows with another copepod *Temora stylifera*. It is hypothesized (Yassen, 1984) that adult stages of *T. Stylifera* eat small stages of *E. acutifrons*. Hence, contrary to a lot of experiments where *E. acutifrons* is reared alone, it can be seen (Fig. 5) that the CS_2T scheme is not respected for the small naupliar stage: a maximum of naupliar stage can be observed during a phase where the eggs, the previous stage, are still increasing. As the number of adults of *T. Stylifera* is increasing, this confirms the suspected interaction with *T. stylifera*. The first naupliar stages are generally non-feeding stages therefore we suggest that the interaction is not a competition for food but a predation of the naupliar stages of *E. acutifrons*.

In another experiment (Fig. 6), eggs and the small naupliar stage are observed for the copepod *Acartia clausi*. In this experiment, a minimum of the nauplii can be seen during a declining phase of the eggs, and a maximum of nauplii follows during an increasing phase of the eggs. These two extrema are not compatible with the CS_2T scheme. For these species, a phenomenon of cannibalism can be hypothesized: adults may eat their own nauplii. As the minimum of the nauplii appears during a phase where adults are decreasing, and the maximum during an increasing phase of the latter, they are now allowed by the result of Theorem 3.

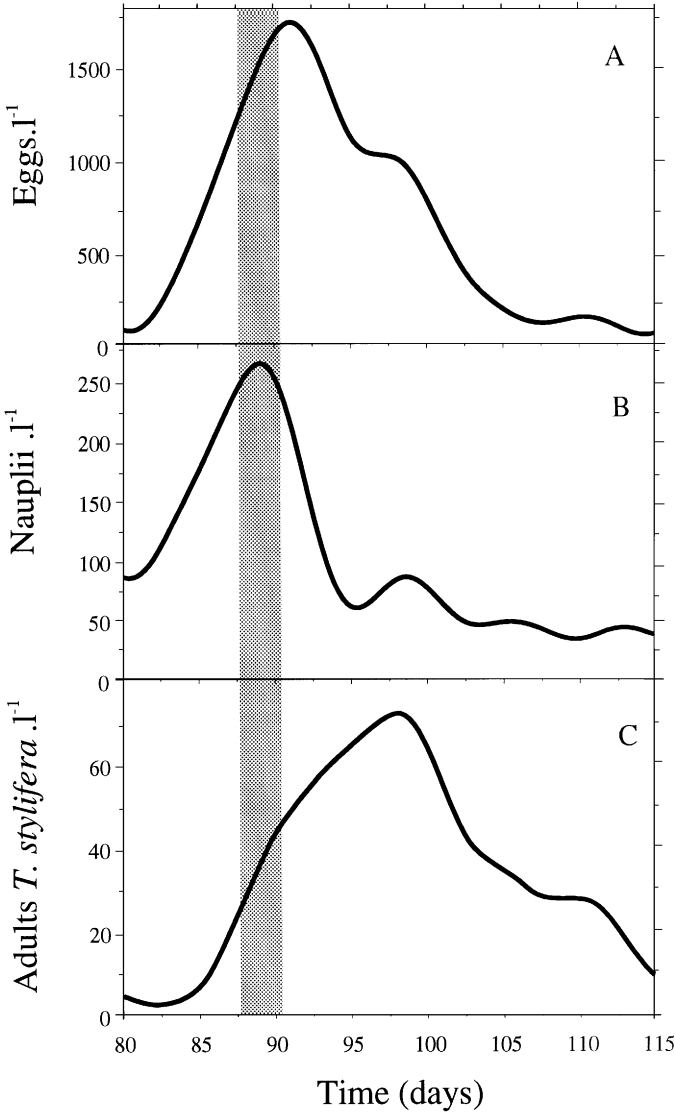


Fig. 5. Bispecific culture *Euterpina acutifrons*–*Temora stylifera*: data processed by moving average ($T = 4$ days) for (A) eggs, (B) small naupliar stage of *E. acutifrons* and (C) adults of *T. stylifera*. The discussed extremum of the small naupliar stage of *E. acutifrons* is represented by a gray strip

4 Conclusions

Models describing stage-structured populations may be very complex, but they are generally loop-structured and have monotonous interactions. Rules governing the succession of qualitative events can therefore

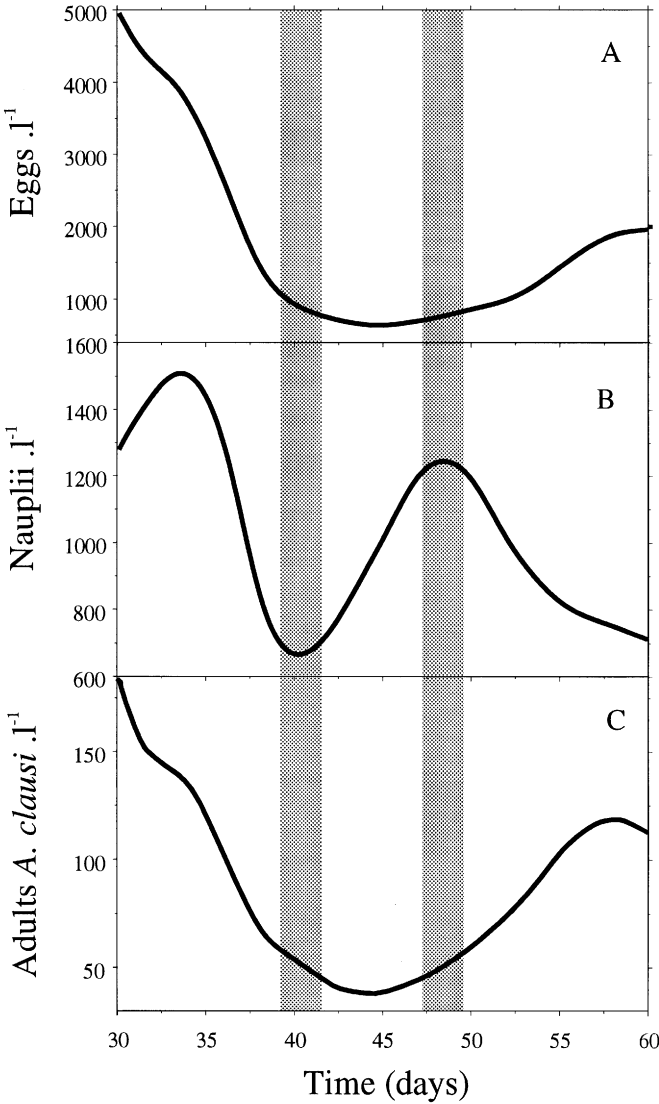


Fig. 6. Bispecific culture *Euterpina acutifrons*–*Acartia clausi*: data processed by moving average ($T = 6$ days) for (A) eggs, (B) small naupliar stage and (C) adults of *A. clausi*. The discussed extrema of the small naupliar stage of *A. clausi* are represented by gray strips

be derived both for the scenarii of extrema for the state variables and for the integrated value of two different trajectories. Some typical results for these systems are shown: during a period where stage i is decreasing, the stage $(i + k)$ can have at the most k extrema. This set of rules gives the experimentalist qualitative criteria with which to test his

model. He can then verify experimentally these rules, in other words compare the structure of his model with his experiments. If the latter are always respected, the structure of the model will be validated.

Sometimes some stages have more complex kinetics, but other stages still have classical stage-structured dynamics. In the work presented here the system is not considered as a whole, and the experimentalist can test separately the structure of the sub-model describing the stages with the classical stage-structure. More precisely, some parts of the model are not required to be explicitly described. It means that the methodology remains valid for complex interactions linking some stages with external variables.

We have shown that the behavior of the stage may qualitatively change if an unexpected interaction between a stage and another variable occurs. In this case the method described may be of substantial help in discovering or proving non-directly observable interactions. In using this methodology we suspect there exists a predation relationship between the two copepods *E. acutifrons* and *T. stylifera*. We have also hypothesized an unexpected cannibalism relationship in the adults of *A. clausi* on his own nauplii.

With such an analysis, the experimentalist can use an information which is easy to obtain because of its qualitative aspect, even if the data are noisy. Since neither the parametric values nor the precise mathematical formulation of the functions is required, this information is very robust and strong enough to invalidate by comparison with experiments an *a priori* supposed structure.

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Appendix 1: Proof of Lemma 1

For x_p obeying the CSI_2 subsystem (Σ_p), let us assume that there exists $t_0 \in]t_1, t_2[$ such that $z_p(t_0) = 0$. Because $z_{p-1}(t_0) = 0$, we have:

$$\dot{z}_p(t_0) = \frac{df_p}{dx_{p-1}} z_{p-1}(t_0) - \frac{dg_p}{dx_p} z_p(t_0) = 0$$

and also:

$$\begin{aligned} \ddot{z}_p(t_0) &= \frac{d^2f_p}{dx_{p-1}^2} z_{p-1}^2(t_0) + \frac{df_p}{dx_{p-1}} \dot{z}_{p-1}(t_0) - \frac{d^2g_p}{dx_p^2} z_p^2(t_0) \\ &\quad - \frac{dg_p}{dx_p} \dot{z}_p(t_0) = 0 \end{aligned}$$

on the same way, the m th derivatives $z_p^{(m)}(t_0) = 0$ for all m , so that the variable x_p does not have a strict extremum.

If x_k to x_{p-1} obey a CSI_2 subsystem $(\Sigma_{k,p-1})$, we have for $t \in]t_1, t_2[$:

$$\dot{z}_{p-1}(t) = \frac{df_{p-1}}{dx_{p-2}} z_{p-2}(t) - \frac{dg_{p-1}}{dx_{p-1}} z_{p-1}(t) = 0 = \frac{df_{p-1}}{dx_{p-2}} z_{p-2}(t)$$

therefore $z_{p-2} = 0$. The calculation of \dot{z}_{p-2} shows that $z_{p-3} = 0$, and so on until $z_k = 0$.

If the system is loop-structured, this reasoning proves that $\forall i, z_i(t) = 0$: the system is at equilibrium.

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