
Predator-prey theory: hidden twins in ecology and microbiology

Christian Jost, Institut national agronomique Paris-Grignon, Ecologie des populations et communautés, 16, rue Claude Bernard, F-75231 Paris cedex 05, France (christian.jost@inapg.inra.fr).

Consumption of a resource by an organism is a key process in both microbiology and population ecology. Recently, there has been a debate in population ecology about the importance of organism density in functions describing this process. Actually, microbiologists have had this debate over the last 40 years. In reviewing their main results I show that even for the most simple systems there is no unique correct function to describe consumption. Organism density influences consumption to various degrees. I conclude that, for predictions based on model simulation, one should use a pluralistic approach, working with different models to identify robust predictions (that is, common to all studied models) and guide further research to understand model-specific predictions.

Describing the consumption process in predator-prey interactions has been a research topic in population ecology since the early theoretical works of Lotka and Volterra. The quantitative description of this process has faced several questions: does the instantaneous consumption depend only on food (prey) availability, or on consumer (predator) abundance as well? What function should be used in mathematical models? How should parameters for these functions be estimated?

Microbiologists have often faced similar problems in describing the growth of bacteria or protozoa on some substrate or in the study of competition through resource depletion (see Grover (1997) for a recent review). In this note I want to draw attention to their work and its relevance to current debates in population ecology. Substrate uptake (e.g., in batch or chemostat cultures) is analogous to predation in simple systems. Although hidden behind different names and notations, several mathematical forms of consumption used in ecology have an equivalent microbiological growth function (Table 1). Most interestingly, there is also a twin (Contois's model) to a model that has aroused a heated debate in ecology: the ratio-dependent model introduced by Arditi and Ginzburg (1989). I will review

the results in microbiology with respect to this twin model and discuss how they can help find a consensus in the ecological debate.

The functional response (prey eaten per predator per unit of time, Solomon 1949) is traditionally considered to be a function of prey abundance only (termed prey-dependent by Arditi and Ginzburg 1989). However, predator density can also influence individual consumption rate, an effect termed predator dependence in Arditi and Ginzburg (1989). Such predator dependence (usually a functional response that is decreasing with increasing consumer density) has been observed in many vertebrate and invertebrate species (reviews: Hassell 1978, Sutherland 1996). A particularly simple way to include predator dependence has been proposed in the ratio-dependent model where the functional response is modelled as an increasing and bounded function of the ratio prey density to predator density. In contrast to prey-dependent models, this approach predicts the experimentally observed decreasing feeding rates with increasing predator densities. It also predicts the positive correlations between population abundances of producers and consumers observed along gradients of productivity (see Arditi et al. (1991a) and the review in Pimm (1991: 290)). Despite the empirical evidence supporting it, there is an on-going debate about the validity of the ratio-dependent approach (Arditi et al. 1992, Ruxton and Gurney 1992, Abrams 1994, 1997, Akçakaya et al. 1995).

In microbiology, Contois (1959) introduced a particular ratio-dependent growth function much earlier. It has served there as an alternative to the well-known growth function of Monod (1942), a twin to the popular (prey-dependent) Holling type II functional response (Table 1). Microbiologists have worked during the last 40 years with Contois's function, compared it to others or elaborated it further. I have followed citations of Contois's paper during this period of time. The results

that are relevant for the on-going ecological debate will be highlighted. I will indicate in brackets the parallels and similar concepts in ecological predator-prey theory.

A short historical perspective

The introduction of Monod's (1942) function as an empirical description of bacterial growth on some substrate s ,

$$\mu(s) = \mu_{\max} \frac{s}{K_s + s}, \quad (1)$$

(parameters are explained in Table 1) together with its mathematical handiness and strong experimental and theoretical/methodological support, was a major breakthrough in the mathematical description of bacterial growth. Microbiologists have applied Monod's model successfully in the context of chemostat and batch cultures (reviews: Fredrickson 1977, Jannasch and Egli 1993). These chemostats can be described by two rate equations:

$$\frac{ds}{dt} = D(s_0 - s) - Q\mu(s)x$$

$$\frac{dx}{dt} = \mu(s)x - D(x - x_0) \quad (2)$$

with organism concentration x , resource quota Q , dilution rate D , inflowing substrate concentration s_0 , and inflowing organism concentration x_0 (usually equal to 0). The last three parameters can be controlled entirely by the researcher. [These equations correspond mathe-

matically to predator-prey equations with constant prey immigration and a constant emigration or death rate of both populations. In this sense, studying $\mu(s)$ in (2) is related to studying the functional response in predator-prey systems.]

Despite its initial success, there were experimental results that could not be explained with Monod's function (see details below). At first, these were attributed to apparatus effects such as incomplete mixing or growth on chemostat walls (e.g., Herbert et al. 1956). Contois (1959) was the first to suggest and to present experimental results that the half saturation 'constant' K_s is not necessarily a constant (estimates of this 'constant' varied up to three orders of magnitude (Jannasch and Egli 1993)) but that it might be proportional to inflowing substrate concentration, $K_s = ks_0$. Together with the occurrence of mass balance ($ds/dt + Q dx/dt = 0$ in system (2), which suggests the relation $Q(x - x_0) \stackrel{x_0=0}{=} Qx = (s_0 - s)$) model (1) changes to

$$\begin{aligned} \mu(s, x) &= \frac{\mu_{\max}s}{k(Qx + s) + s} = \frac{\mu_{\max}s}{(kQ)x + (k+1)s} = \frac{\mu's/x}{K' + s/x} \\ &= \mu\left(\frac{s}{x}\right) \end{aligned} \quad (3)$$

(with $\mu' = \mu_{\max}/(k+1)$ and $K' = kQ/(k+1)$) which is a particular case of a growth function that depends on the ratio substrate to organism [this corresponds in ecology to a ratio-dependent functional response]. Contois's equation (3) has later also been derived by mechanistic reasoning (Fujimoto 1963, Characklis 1978) based on enzyme kinetics or saturation kinetics applied to mass transfer limited growth.

Contois's function predicts that the growth rate μ decreases with increasing organism concentration, while

Table 1. References to the same model in ecology and microbiology. s is prey density or substrate concentration, x is predator density or density of organism that grows on substrate s , a is predator attack rate, h is handling time, μ_{\max} is the maximum growth rate, K_s the Michaelis-Menten or half saturation constant, α total searching efficiency and c, m, s_m, s_b are empirical positive constants.

functional response or growth rate	reference in ecology	reference in microbiology
$\begin{cases} as & s \leq s_b \\ as_m & s \geq s_b \end{cases}$	Holling (1959) type I with added upper limit	Blackman (1905)
$\frac{as}{1+ahs} = \mu_{\max} \frac{s}{K_s + s}$	Holling (1959) type II	Monod (1942)
$a(1 - e^{-cs})$	Ivlev (1961)	Teissier (1936)
$\frac{as^m}{1+ahs^m}$	Real (1977)	Moser (1958)
$\frac{\alpha s/x}{1 + \alpha hs/x} = \frac{\alpha s}{x + \alpha hs}$	Arditi and Ginzburg (1989), Arditi and Akçakaya (1990)	Contois (1959)
$\mu_{\max} \frac{s}{K_s + s} \frac{1}{x}$	Hassell and Rogers (1972) (special case)	Ashby (1976)
$\mu_{\max} \frac{s}{K_s + s + cx}$	Beddington (1975), DeAngelis et al. (1975)	Roques et al. (1982) (special case)

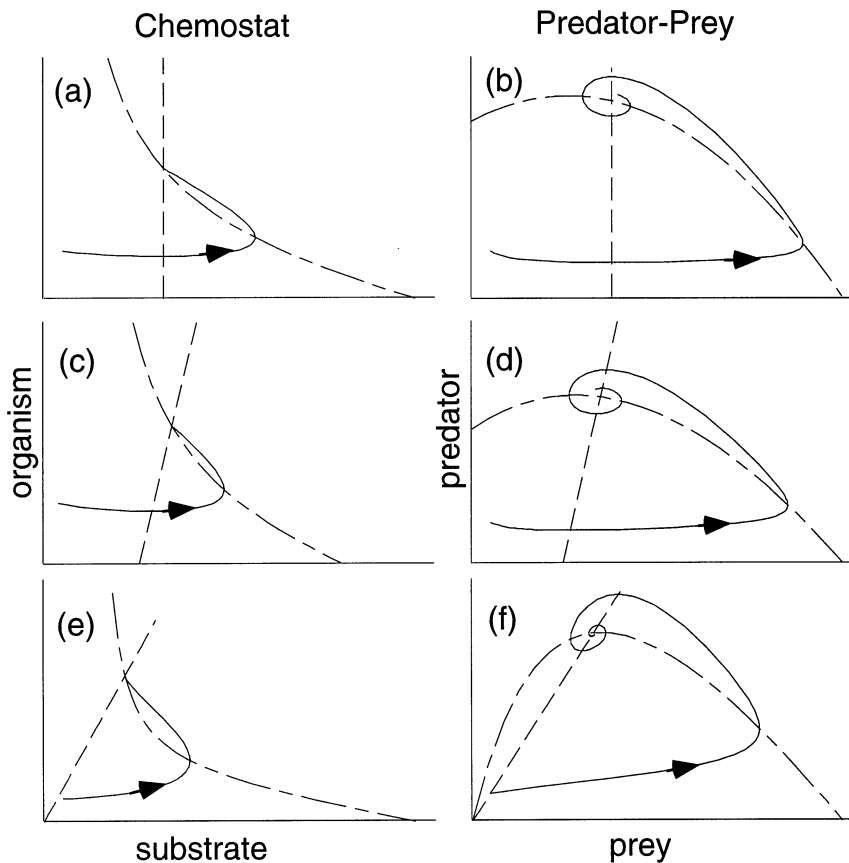


Fig. 1. Typical isoclines in chemostats (left) and predator-prey systems (right) with prey-dependent Monod/Holling type II growth functions (a, b), Roques/DeAngelis-Beddington type growth functions (c, d) and Contois/ratio-dependent growth functions (e, f). Prey isoclines are long-short dashed, predator isoclines are short dashed. Straight lines represent typical trajectories.

Monod's function assumes that the growth rate should be independent of organism concentration. This negative dependence of the growth rate on organism concentration was experimentally shown in a number of studies (Aiba et al. 1968, Curds and Cockburn 1968, Fayyaz et al. 1971, Wilhelm 1993) and was usually explained as the result of accumulation of metabolic byproducts that inhibit growth.

Monod's function (1) also predicts that effluent substrate concentration in chemostats (2) at equilibrium should only depend on dilution rate D , $s^* = \mu^{-1}(D)$, and be independent of inflowing substrate concentration s_0 . [This is equivalent to the vertical predator isocline in Lotka-Volterra or Rosenzweig-MacArthur predator-prey systems, see Fig. 1.] This prediction was tested by varying dilution rates and influent substrate concentration, letting the chemostat reach steady state and measuring the effluent substrate concentration s^* . Monod's prediction was confirmed for pure cultures growing on glucose (Grady et al. 1972), but the results consistently diverged from this prediction when working with mixed cultures (e.g., in wastewater treatment or fermentation processes) (Grady et al. 1972, Grady and Williams 1975, Elmaleh and Ben Aim 1976, Daigger and Grady 1977). In the latter, the outflowing substrate concentration was proportional to inflowing

concentration, as predicted from the chemostat equations (2) with Contois's function (3). [It corresponds in ecology to the prediction that the prey equilibrium in a ratio-dependent predator-prey system is proportional to prey carrying capacity K , in the sense that K replaces s_0 as the growth limiting factor.]

The first approach to reconcile theory and experiment was to introduce flexible models that contain both Monod's and Contois's functions as special cases (Roques et al. 1982, Borja et al. 1995)

$$\mu(s, x) = \frac{\mu s}{K_s + s + cx} \quad (4)$$

[This form was introduced independently in ecology by DeAngelis et al. (1975) and by Beddington (1975).] Another intermediate function (Kargi and Shuler 1979) attempted to unify Monod's, Contois's, Teissier's and Moser's growth functions in the context of chemostats. However, experimentalists rarely use these intermediate functions because of the effort required to estimate the additional parameter, while theoreticians do not like them because of the considerably more complicated analytical expressions. [The DeAngelis-Beddington function encounters the same fate in ecology.]

The second approach was to confront data statistically with different functional forms of the growth rate, by fitting either the dynamic model (2) to time series data of substrate and organism abundances, or by fitting direct measurements of the growth rate as a function of organism and substrate concentration. Model selection was then based on the goodness-of-fit criterion. Table 2 lists these studies together with the tested models (the best fitting model in capitals). Often Contois's function fitted best, but the differences in goodness-of-fit were usually small. In a more qualitative analysis of predator-prey time series data Bazin and Saunders (1978) applied catastrophe theory to "determine the variable that governs the response of an amoebal predator to its prey". They showed that "a comparatively simple mechanism can account for the observed behaviour" if the ratio prey per predator (rather than the prey density) is taken as the critical variable, and thus concluded that Contois's function is a parsimonious way to model this observation.

The mentioned ambiguity in model selection in many direct statistical confrontations of Contois's and Monod's model to experimental data (Table 2) indicates that the intermediate model (4) or other more complex models might sometimes be more appropriate to describe the data. Bohannan and Lenski (1997, 1999) tested such a case by modeling susceptible and resistant bacteria (with a phage as consumer species) either separately with a linearized form of Monod's model (Lotka-Volterra) and a delay between consumption and consumer reproduction or by combining them into one single compartment and modeling the system as a simple food chain with consumption in a linearized form of Contois's model and without any delay. Their complex model conforms qualitatively better to the observed destabilization with enrichment than the simple food chain.

In summary, the reviewed experimental results illustrate that Contois's model was successfully used in the context of mixed cultures on multicomponent substrates such as wastewater treatment, fermentation pro-

cesses or biogas production from manure (e.g., Lequerica et al. 1984, Bala and Satter 1990, Ghaly and Echiegu 1993, Benitez et al. 1997). It has only been contradicted by experimental results for monospecific cultures growing on pure medium or when trying to collapse resistant and susceptible strains into a single trophic species. In most other cases (mixed medium or several species/strains present) it was rather Monod's model that should have been rejected. [Similarly in ecology, the particular predictions of prey-dependent food chains (response of equilibrium abundances to enrichment) could only be found in protozoan laboratory systems with pure strains for prey and predator species (Kaunzinger and Morin 1998) or in *Daphnia*-algae systems with homogeneous population distributions (Arditi et al. 1991b).] Monod's function remained nevertheless the predominant one in the microbiological literature (as stated by Barford and Hall (1978), Janasch and Egli (1993) and Wetzel (1994)).

Lessons for ecology

Microbiological experiments are usually done in well-controlled laboratory situations, following the observed processes with precise measurement techniques. In contrast, field ecology has to cope with various stochastic influences and unprecise census techniques. Therefore, empirical validation of a model from data is more highly valued in microbiology than in ecology where model rejection because of data incompatibility is rare. However, Table 2 also lists results where several growth functions fitted equally well to the same (microbiological) data. This can be either due to inadequacy of all compared (simple) models, as mentioned in the previous section, or due to poor data quality. Therefore, as a first lesson, if model selection based on goodness-of-fit is ambiguous already with microbiological data, then model selection based on ecological field data cannot be expected to be any better. I would speculate that this is one of the reasons why many ecologists consider mechanistic underpinning an essential part for the validity of a model, even though the models, by their very simplicity, cannot be much more than a phenomenological account of the observed biological processes. This is especially true for models describing natural food chains or food webs where many mechanisms are at work. Furthermore, "one scientist's mechanism is another scientist's phenomenon" (Pimm 1991). This quotation best summarizes that the very definition of 'mechanistic' is controversial and 'mechanisms' can be rather a methodological support than a true representation of what is happening in a population. Ratio dependence was first introduced as an empirical (and parsimonious) way to include predator dependence, only recently have mechanistic derivations been developed (Poggiale et al. 1998, Cosner et al. 1999). How-

Table 2. Collection of studies that compared Contois's function quantitatively with other functions (the tested models are noted in the third column with the best fitting model, if there was one, in capitals).

reference	studied system	tested functions
Chiu et al. (1972)	microbial sewage	Moser, Monod, Contois
Morrison et al. (1987)	nutrient limited phytoplankton growth	Monod, CONTOIS, LOGISTIC
Dercová et al. (1989)	growth and glucose consumption of yeast	CONTOIS, Monod
Wilhelm (1993)	protozoan feeding rate on bacteria	Contois, Monod and 9 others*

* best fits were obtained with functions that are sigmoid with respect to substrate concentration, either Contois or Monod type.

ever, these works also show that ratio dependence as well as prey dependence are only special cases in the complex real world. This must be kept in mind when working with these models.

Let us now interpret the ecological meaning of the cited results in microbiology. The most often tested prediction of Monod's approach has been that the effluent substrate concentration in chemostats should be independent of influent substrate concentration. This prediction is equivalent to the one that in predator-prey systems with prey-dependent functional response $g(s)$,

$$\begin{aligned} \frac{ds}{dt} &= r \left(1 - \frac{s}{K} \right) s - g(s)x \\ \frac{dx}{dt} &= eg(s)x - qx, \end{aligned} \quad (5)$$

the equilibrium prey-density $s^* = g^{-1}(q/e)$ is independent of carrying capacity K and that the predator isocline is vertical (as in Lotka-Volterra or Rosenzweig-MacArthur predator-prey systems). See Fig. 1a and b for examples in chemostats or predator-prey systems. This prediction from Monod's function has been confirmed only in the case of growth of a single organism type on a single substrate within the constant environment of chemostat cultures. Deviations from these conditions lead to effluent substrate concentration being proportional to in-flowing concentration. This result can only be explained with a slanted predator isocline (see Fig. 1c to f), and it is also an essential prediction of the ratio-dependent model. The second series of results in batch and continuous cultures shows that the growth function is decreasing with increasing predator density whenever heterogeneities occur either in consumer species composition or in the substrate, again suggesting that the predator isocline should be slanted. In addition to the first series of results, predator dependence of the functional response is now clearly identified as a cause for this slanted isocline. Such a slanted predator isocline seems to be the rule rather than the exception and ratio dependence with its isocline through the origin (Fig. 1e and f) can be considered a parsimonious way to model it, although other ways to obtain a slanted predator isocline exist (e.g., if there is consumer immigration in eq. (2) or (5), but see also DeAngelis et al. (1975) and Gatto (1991)). Note that the functional response in eq. (5) is only proportional to the microbiological growth function μ in eq. (2), but not equal. However, this difference does not affect the conclusions in this review.

The consideration of a vertical predator isocline lies also at the base of two so-called paradoxes: the paradox of enrichment (Rosenzweig 1971) that predicts that richer systems (high K) should be less stable, and the paradox of biological control (termed in Arditi and Berryman 1991) that predicts that biologically con-

trolled pests should have unstable dynamics. When these predictions disagree with observations, the problem is often resolved by creating more complex models with additional state variables (e.g., the Droop (1968) model that puts an internal storage compartment between substrate and organism) or additional parameters (e.g., McCauley et al. 1988, Scheffer and de Boer 1995). While such additions may sometimes be necessary (Bohannan and Lenski 1999), they also rapidly lead to analytically very complex models that (unfortunately) often discourage any further investigation. Instead, we might start (or complement) our investigations in a simple modeling framework that inherently has a slanted predator isocline. After all, "modeling philosophies...should be treated in the same way as models – retained only as long as they assist progress" (Nisbet and Gurney 1982).

Some authors have argued that the "recent focus on ratio dependence is unfortunate" because it deflects attention from more general forms of predator dependence (Murdoch et al. 1998). I think that, on the contrary, ratio-dependent theory has enhanced the status of predator dependence: it provides a simple mathematical framework to test whether strong predator dependence changes predictions that were originally derived from prey-dependent concepts, and it can guide further research when these predictions are not 'robust' against predator dependence such as the two paradoxes mentioned above. For example, what is the influence of predator dependence on fundamental mechanisms in communities such as omnivory, keystone predation or competitive exclusion? Substrate uptake as well as predation are processes of resource consumption, a concept that is at the base of Grover's (1997) recent book on the theoretical and experimental analysis of competition through resource depletion (this book is another example to show that microbiological experiments can still contribute a lot to ecological questions). Predator dependence is briefly discussed in the example of competition for biotic resources (predation) as reducing the consumptive pressure on the resource. Two of the studies mentioned in Table 2 indicate that consumer dependence can already occur at the level of substrate/nutrient uptake. Will there still be competitive exclusion in food webs with predator dependence on all levels? The mathematical tools to model such food webs need careful consideration because of logical constraints (Arditi and Michalski 1995). The simplicity of the ratio-dependent approach can result in analytically tractable food webs to answer such questions.

The ratio-dependent approach cannot and should not replace the prey-dependent one (or the more general predator-dependent one) in every case. While modeling frameworks based on prey-dependent interactions can be linked to top-down mechanisms (Arditi and Ginzburg 1989) and account for cyclic systems (Rosenzweig 1971, Bohannan and Lenski 1999), the ratio-de-

pendent approach includes elements of both top-down and bottom-up regulation (Arditi and Ginzburg 1989, Poggiale et al. 1998) and offers the possibility of deterministic extinction (Jost et al. 1999).

The reviewed results show that, in general, natural and laboratory systems contain predator dependence in the functional response (slanted predator isocline). In this case, the most appropriate model would be one with a flexible slanted predator isocline, but the microbiological example confirms that these complex models are rarely used either due to intractability or by insufficient data to parameterize them. Thus, often compelled to use simpler models, the problems in microbiology to distinguish experimentally between Monod's and Contois's functions (Table 2) show that we have to accept the fact that there is also much model uncertainty in population ecology. In the absence of modeling techniques that take this uncertainty into account we should not limit our investigations to one particular type of model. Using several alternative models and comparing their predictions can serve to guide further research in the case of differing predictions, while converging predictions give confidence of having found 'robust' features of the systems studied.

Acknowledgements – I thank R. Arditi for initially pointing out the relation between Contois's model and ratio dependence and for supporting this study. Additional thanks go to P. Inchausti for helpful discussions and a careful reading of the manuscript. This research was supported by the Swiss National Science Foundation (grant 31-43440.95 to R. Arditi) and by the French 'Programme Environnement, Vie et Société' (CNRS).

References

- Abrams, P. A. 1994. The fallacies of "ratio-dependent" predation. – *Ecology* 75: 1842–1850.
- Abrams, P. A. 1997. Anomalous predictions of ratio-dependent models of predation. – *Oikos* 80: 163–171.
- Aiba, S., Shoda, M. and Nagatani, M. 1968. Kinetics of product inhibition in alcohol fermentation. – *Biotechnol. Bioengineering* 10: 845–864.
- Akçakaya, H. R., Arditi, R. and Ginzburg, L. R. 1995. Ratio-dependent predation: an abstraction that works. – *Ecology* 76: 995–1004.
- Arditi, R. and Ginzburg, L. R. 1989. Coupling in predator-prey dynamics: ratio-dependence. – *J. Theor. Biol.* 139: 311–326.
- Arditi, R. and Akçakaya, H. R. 1990. Underestimation of mutual interference of predators. – *Oecologia* 83: 358–361.
- Arditi, R. and Berryman, A. A. 1991. The biological control paradox. – *Trends Ecol. Evol.* 6: 32.
- Arditi, R. and Michalski, J. 1995. Nonlinear food web models and their responses to increased basal productivity. – In: Polis, G. A. and Winemiller, K. O. (eds), *Food webs: integration of patterns and dynamics*. Chapman & Hall, pp. 122–133.
- Arditi, R., Ginzburg, L. R. and Akçakaya, H. R. 1991a. Variation in plankton densities among lakes: a case for ratio-dependent predation models. – *Am. Nat.* 138: 1287–1296.
- Arditi, R., Perrin, N. and Saïah, H. 1991b. Functional responses and heterogeneities: an experimental test with cladocerans. – *Oikos* 60: 69–75.
- Arditi, R., Ginzburg, L. R. and Perrin, N. 1992. Scale invariance is a reasonable approximation in predation models – reply to Ruxton and Gruney. – *Oikos* 65: 336–337.
- Ashby, R. E. 1976. Long term variations in a protozoan chemostat culture. – *J. Exp. Mar. Biol. Ecol.* 24: 227–235.
- Bala, B. K. and Satter, M. A. 1990. Kinetic and economic considerations of biogas production systems. – *Biol. Wastes* 34: 21–38.
- Barford, J. P. and Hall, R. J. 1978. An evaluation of the approaches to the mathematical modelling of microbial growth. – *Process Biochem.* 11: 22–29.
- Bazin, M. J. and Saunders, P. T. 1978. Determination of critical variables in a microbial predator-prey system by catastrophe theory. – *Nature* 275: 52–54.
- Beddington, J. R. 1975. Mutual interference between parasites or predators and its effect on searching efficiency. – *J. Anim. Ecol.* 44: 331–340.
- Benitez, J., Beltran-Heredia, J., Torregrosa, J. et al. 1997. Aerobic degradation of olive mill wastewaters. – *Appl. Microbiol. Biotechnol.* 47: 185–188.
- Blackman, F. 1905. Optima and limiting factors. – *Ann. Bot.* 19: 281–295.
- Bohannan, B. J. M. and Lenski, R. E. 1997. Effect of resource enrichment on a chemostat community of bacteria and bacteriophage. – *Ecology* 78: 2303–2315.
- Bohannan, B. J. M. and Lenski, R. E. 1999. Effect of prey heterogeneity on the response of a model food chain to resource enrichment. – *Am. Nat.* 153: 73–82.
- Borja, R., Banks, C.J., Martin, A. and Khalifaoui, B. 1995. Anaerobic digestion of palm oil mill effluent and condensation water waste: an overall kinetic model for methane production and substrate utilization. – *Bioprocess Engineer.* 13: 87–95.
- Characklis, W. G. 1978. Microbial reaction rate expressions. – *J. Environ. Engineer. Div.* 104: 531–534.
- Chiu, S. Y., Erickson, L. E., Fan, L. T. and Kao, I. C. 1972. Kinetic model identification in mixed populations using continuous culture data. – *Biotechnol. Bioengineer.* 14: 207–231.
- Contois, D. E. 1959. Kinetics of bacterial growth: relationship between population density and specific growth rate of continuous cultures. – *J. Gen. Microbiol.* 21: 40–50.
- Cosner, C., DeAngelis, D. L., Ault, J. S. and Olson, D. B. 1999. Effects of spatial grouping on the functional response of predators. – *Theor. Popul. Biol.* 56: 65–75.
- Curds, C. R. and Cockburn, A. 1968. Studies on the growth and feeding of *Tetrahymena pyriformis* in axenic and monoxenic culture. – *J. Gen. Microbiol.* 54: 343–358.
- Daigger, G. T. and Grady, C. P. L., Jr. 1977. A model for the bio-oxidation process based on product formation concepts. – *Water Res.* 11: 1049–1057.
- DeAngelis, D. L., Goldstein, R. A. and O'Neill, R. V. 1975. A model for trophic interactions. – *Ecology* 56: 881–892.
- Dercová, K., Derco, J., Hutňan, M. and Králik, M. 1989. Effect of formaldehyde on kinetics of glucose consumption. – *Chemical Papers* 43: 41–50.
- Droop, M. R. 1968. Vitamin B₁₂ and marine ecology. IV. the kinetics of uptake, growth and inhibition in *Monochrysis lutheri*. – *Mar. Biol. Assoc. UK* 48: 689–733.
- Elmaleh, S. and Ben Aim, R. 1976. Influence sur la cinétique biochimique de la concentration en carbone organique à l'entrée d'un réacteur développant une polyculture microbienne en mélange parfait. – *Water Res.* 10: 1005–1009.
- Fayyaz, A. M., Prokop, A. and Fencel, Z. 1971. Growth and physiology of a yeast cultivated in batch and continuous culture systems. – *Folia Microbiol.* 16: 249–259.
- Fredrickson, A. G. 1977. Behavior of mixed cultures of microorganisms. – *Annu. Rev. Microbiol.* 31: 63–87.
- Fujimoto, J. 1963. Kinetics of microbial growth and substrate consumption. – *J. Theor. Biol.* 5: 171–191.
- Gatto, M. 1991. Some remarks on models of plankton densities in lakes. – *Am. Nat.* 137: 264–267.

- Ghaly, A. E. and Echiegu, E. A. 1993. Kinetics of a continuous-flow no-mix anaerobic reactor. – *Energy Sources* 15: 433–449.
- Grady, C. P. L., Jr., Harlow, L. J. and Riesing, R. R. 1972. Effects of growth rate and influent substrate concentration on effluent quality from chemostats containing bacteria in pure and mixed culture. – *Biotechnol. Bioengineer.* 14: 391–410.
- Grady, C. P. L., Jr. and Williams, D. R. 1975. Effects of influent substrate concentration on the kinetics of natural microbial populations in continuous culture. – *Water Res.* 9: 171–180.
- Grover, J. P. 1997. Resource competition. – Chapman & Hall.
- Hassell, M. P. 1978. The dynamics of arthropod predator-prey systems. – Princeton Univ. Press.
- Hassell, M. P. and Rogers, D. J. 1972. Insect parasite responses in the development of population models. – *J. Anim. Ecol.* 41: 661–676.
- Herbert, D., Elsworth, R. and Telling, R. C. 1956. The continuous culture of bacteria: a theoretical and experimental study. – *J. Anim. Ecol.* 14: 601–622.
- Holling, C. S. 1959. Some characteristics of simple types of predation and parasitism. – *Can. Entomol.* 91: 385–398.
- Ivlev, V. S. 1961. Experimental ecology of the feeding of fishes. – Yale Univ. Press.
- Jannasch, H. W. and Egli, T. 1993. Microbial growth kinetics: a historical perspective. – *Antonie Leeuwenhoek J. Microbiol.* 63: 213–224.
- Jost, C., Arino, O. and Arditi, R. 1999. About deterministic extinction in ratio-dependent predator-prey models. – *Bull. Math. Biol.* 61: 19–32.
- Kargi, F. and Shuler, M. L. 1979. Generalized differential specific rate equation for microbial growth. – *Biotechnol. Bioengineer.* 21: 1871–1875.
- Kaunzinger, C. M. K. and Morin, P. J. 1998. Productivity controls food chain properties in microbial communities. – *Nature* 395: 495–497.
- Lequerica, J. L., Vallés, S. and Flors, A. 1984. Kinetics of rice straw fermentation. – *Appl. Microbiol. Biotechnol.* 19: 70–74.
- McCauley, E., Murdoch, W. and Watson, S. 1988. Simple models and variation in plankton densities among lakes. – *Am. Nat.* 132: 383–403.
- Monod, J. 1942. Recherches sur la croissance des cultures bactériennes. – Hermann et Cie, Paris.
- Morrison, K. A., Thérien, N. and Marcos, B. 1987. Comparison of six models for nutrient limitations on phytoplankton growth. – *Can. J. Fish. Aquat. Sci.* 44: 1278–1288.
- Moser, H. 1958. The dynamics of bacterial populations maintained in the chemostat. – Carnegie Institution of Washington Publ.
- Murdoch, W. W., Nisbet, R. M., McCauley, E. et al. 1998. Plankton abundance and dynamics across nutrient levels: tests of hypothesis. – *Ecology* 79: 1339–1356.
- Nisbet, R. M. and Gurney, W. S. C. 1982. Modelling fluctuating populations. – John Wiley & Sons.
- Pimm, S. L. 1991. The balance of Nature. – Univ. of Chicago Press.
- Poggiale, J.-C., Michalski, J. and Arditi, R. 1998. Emergence of donor control in patchy predator-prey systems. – *Bull. Math. Biol.* 60: 1149–1166.
- Real, L. A. 1977. The kinetics of the functional response. – *Am. Nat.* 111: 289–300.
- Roques, H., Yue, S., Saipanich, S. and Capdeville, B. 1982. Faut-il abandonner le formalisme de monod pour la modélisation des processus de dépollution par voie biologique? – *Water Res.* 16: 839–847.
- Rosenzweig, M. L. 1971. Paradox of enrichment: destabilization of exploitation ecosystems in ecological time. – *Science* 171: 385–387.
- Ruxton, G. D. and Gurney, W. S. C. 1992. The interpretation of tests for ratio-dependence. – *Oikos* 65: 334–335.
- Scheffer, M. and de Boer, R. J. 1995. Implications of spatial heterogeneity for the paradox of enrichment. – *Ecology* 76: 2270–2277.
- Solomon, M. E. 1949. The natural control of animal populations. – *J. Anim. Ecol.* 18: 1–35.
- Sutherland, W. J. 1996. From individual behaviour to population ecology. – Oxford Univ. Press.
- Teissier, G. 1936. Quantitative laws of growth. – *Ann. Physiol. Biochim. Biol.* 12: 527–586.
- Wetzel, R. L. 1994. Modeling the microbial loop: an estuarine modeler's perspective. – *Microb. Ecol.* 28: 331–334.
- Wilhelm, R. 1993. Dynamics and persistence of a microbial predator-prey system in laboratory culture. – Technical Report 2835, Forschungszentrum Jülich.