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Mathematical modelling of the growth rate and lag time for *Listeria monocytogenes*

Jean-Christophe Augustin*, Vincent Carlier

Service d'Hygiène et Industrie des Denrées Alimentaires d'Origine Animale, Ecole Nationale Vétérinaire d'Alfort, 7 avenue du Général de Gaulle, F-94704 Maisons-Alfort Cedex, France

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Abstract

Growth data for *Listeria monocytogenes* were collected from the literature and a global model built with existing secondary models describing independently the effects of environmental factors on the growth rate and lag time was based on these data. The growth rates calculated with this model were consistent with the published ones but the fit was poor near the limits of growth of the micro-organism. The model was also less accurate to describe the lag time. It seems then that reliable predictions of the growth rate of *L. monocytogenes* could be obtained in a wide range of growth conditions, but models should take into account interactions between environmental factors. Furthermore, it is necessary to better model the lag phase duration and particularly to model the effect of the history of the inoculum on the subsequent lag time.

Keywords: Growth rate; Lag time; *Listeria monocytogenes*; Predictive microbiology

1. Introduction

Listeria monocytogenes is a well known food-borne pathogen which has been extensively studied since the early 1980s. Numerous studies deal with the growth and survival characteristics of the micro-organism in foods. At the same time, interest in predictive microbiology increased and today several mathematical models are available to describe the effects of environmental factors on growth of micro-organisms. The aim of this work was then to use existing predictive models in order to obtain a global model describing the effect of the environment on the growth parameters of *L. monocytogenes* and to point out the cases where improvements of these predictive models are required.

2. Growth data for *Listeria monocytogenes*

Growth data for *L. monocytogenes* in mi-

*Corresponding author. Tel.: +33-1-4396-7043; fax: +33-1-4396-7121.

E-mail address: augustin@vet-alfort.fr (J.-C. Augustin)

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crobiological media, dairy products, meats, liquid eggs and seafoods were taken from 74 published papers and from unpublished personal data (Table 1).

2.1. Growth parameters

Growth data included growth kinetics, and/or maximum specific growth rates (μ_{max}) or maximum exponential growth rates ($\mu = \mu_{max}/\ln(10)$) or generation times ($Tg = \ln(2)/\mu_{max}$), and/or lag times (*lag*). Only growth parameters obtained from viable counts were taken into account. The growth data obtained with other techniques, i.e. turbidimetry or conductimetry, were used to model the effect of growth conditions on growth parameters but were not included in the database because these techniques can under-estimate the growth parameters (Baranyi et al., 1993a; Dalgaard et al., 1994; Hudson and Mott, 1994; Augustin et al., 1999). The no growth data (growth not observed by authors within the experimental period considered), i.e. nil growth rates, obtained with turbidimetry or conductimetry were included in the database.

Models were fitted to the transformed growth parameters to stabilize the variances of the residuals. The most appropriate transformations seem to be the square root transformation for μ_{max} (Zwietering et al., 1990; Ratkowsky et al., 1991, 1996; Schaffner, 1994), and the log transformation for *Tg* (Alber and Schaffner, 1992; Ratkowsky et al., 1996), *lag* (Zwietering et al., 1990; Ratkowsky et al., 1991; Alber and Schaffner, 1992; Delignette-Muller, 1998) and *lag*/*Tg* (Delignette-Muller, 1998).

The procedure used to obtain growth kinetics from published graphs was validated by comparing growth parameters estimated from growth curves with the corresponding published growth parameters obtained by authors. The square roots of 35 estimated growth rates were not significantly different from the square roots of the published ones ($P = 0.26$) and the logarithm of 34 estimated lag times were not significantly different from the logarithm of the published ones ($P = 0.86$).

Estimated growth parameters from published growth kinetics were obtained by fitting the logistic equation with delay, i.e. with a breakpoint at the transition between the lag and the exponential phase (Kono, 1968; Baranyi et al., 1993b; Rosso et al., 1996):

$$x(t) = \begin{cases} x_0, & t \le lag \\ \dfrac{x_{max}}{1 + \left(\dfrac{x_{max}}{x_0} - 1\right) \cdot \exp(-\mu_{max} \cdot (t - \text{lag}))}, & t > lag \end{cases} \quad (1)$$

where $x(t)$ is bacterial concentration (cfu.ml^{-1}) at the instant t (h), x_0 is the initial bacterial concentration, x_{max} is the maximum bacterial concentration, *lag* is the lag time (h), and μ_{max} is the maximum specific growth rate (h^{-1}). The logarithm of this function was fitted to the logarithm of $x(t)$.

Published growth parameters (μ_{max} and *lag*) were obtained by authors by fitting the Gompertz, the logistic or the Baranyi equation, or by log-linear regression (growth rate estimated from the regression line in the exponential growth phase and lag time estimated from the line as the time corresponding to the initial bacterial count). Differences between the estimated growth parameters were observed according to the growth model used. The use of the Gompertz equation led to a significant ($P = 0$) and large over-estimation of μ_{max} as it has been previously reported (Whiting and Cygnarowicz-Provost, 1992; Labuza and Fu, 1993; Baranyi et al., 1993a; Dalgaard, 1995; Farber et al., 1996; Membré et al., 1999). The lag times are too systematically over-estimated (Whiting and Cygnarowicz-Provost, 1992; Labuza and Fu, 1993; Farber et al., 1996). The same results were observed with the logistic equation.

The growth parameters published were then corrected to eliminate a bias due to the growth model used and the logistic equation with delay (Eq. (1)) was chosen as the reference growth model. Growth parameters estimated by fitting 505 growth curves with the different growth models were compared to the estimates obtained with the reference one. For all models, good linear correlations were observed between transformed growth parameters obtained with Gompertz, logistic, Baranyi or log-linear model and those obtained with the logistic model with delay. Linear regressions were made with transformed growth parameters obtained with the reference model as the dependent variables and trans-

Table 1
Growth database for *L. monocytogenes*

Substrate	No. publi.[a] μ_{max}	No. estim.[b] μ_{max}	No. publi. *lag*	No. estim. *lag*	Refs.
Culture broths	56	–	14	7	El-Shenawy and Marth (1988a)
	48	8	29	9	El-Shenawy and Marth (1988b)
	20	–	–	–	George et al. (1988)
	56	–	8	–	Ahamad and Marth (1989)
	160	–	131	–	Buchanan et al. (1989)
	–	3	–	3	Denis and Ramet (1989)
	14	–	–	–	Katoh (1989)
	2	–	–	–	McClure et al. (1989)
	27	–	–	–	Petran and Zottola (1989)
	38	–	–	–	Sorrells et al. (1989)
	10	–	4	–	Buchanan and Klawitter (1990)
	11	4	11	4	Buchanan and Phillips (1990)
	11	–	–	–	Cole et al. (1990)
	5	–	–	–	Conner et al. (1990)
	20	50	18	39	Pearson and Marth (1990b)
	6	–	–	4	Pearson and Marth (1990c)
	16	10	14	10	Walker et al. (1990)
	14	–	14	–	Buchanan and Klawitter (1991)
	123	–	–	–	McClure et al. (1991)
	12	–	–	–	Tapia de Daza et al. (1991)
	14	–	12	–	Yousef et al. (1991)
	26	–	24	–	George and Lund (1992)
	23	–	10	–	Miller (1992)
	16	–	–	–	Nolan et al. (1992)
	15	–	14	–	Duh and Schaffner (1993)
	54	–	–	46	Oh and Marshall (1993)
	14	–	14	–	Duffy et al. (1994b)
	4	5	11	2	Johansen et al. (1994)
	3	–	–	–	Brocklehurst et al. (1995b)
	23	–	–	–	Bajard et al. (1996)
	9	–	–	–	Bal'a and Marshall (1996b)
	–	–	21	–	Buncic and Avery (1996)
	43	–	40	–	Farber et al. (1996)
	19	6	–	8	George et al. (1996)
	2	–	–	–	Patchett et al. (1996)
	–	–	60	–	Avery and Buncic (1997)
	3	–	–	–	Blom et al. (1997)
	6	–	6	–	Dufrenne et al. (1997)
	11	6	–	7	Fernández et al. (1997)
	44	–	44	–	McKellar et al. (1997)
	–	14	–	4	Membré et al. (1997)
	14	–	10	–	Wang and Johnson (1997)
	37	–	37	–	Robinson et al. (1998)
	4	–	5	–	Membré et al. (1999)
	–	144	–	144	Unpublished personal data
Dairy products	–	35	–	35	Donnelly and Briggs (1986)
	56	–	–	32	Rosenow and Marth (1987a)
	12	4	–	16	Rosenow and Marth (1987b)
	15	4	–	19	Marshall and Schmidt (1988)
	24	–	–	–	Ryser and Marth (1988)
	–	14	–	14	Schaack and Marth (1988a)
	–	18	–	18	Schaack and Marth (1988b)
	–	4	–	4	Denis and Ramet (1989)

Table 1. Continued

Substrate	No. publi.[a] μ_{max}	No. estim.[b] μ_{max}	No. publi. *lag*	No. estim. *lag*	Refs.
	16	–	–	8	Papageorgiou and Marth (1989)
	16	28	–	36	Pearson and Marth (1990a)
	6	–	–	4	Pearson and Marth (1990c)
	10	2	8	2	Walker et al. (1990)
	2	–	2	–	Buchanan and Klawitter (1991)
	30	6	–	36	El-Gazzar et al. (1991)
	4	–	–	–	Lanciotti et al. (1992)
	5	–	5	–	Gay et al. (1996)
	13	–	13	–	Murphy et al. (1996)
	–	10	–	10	Wang and Johnson (1997)
Meats	3	–	–	–	Kaya and Schmidt (1989)
	6	–	6	–	Buchanan and Klawitter (1991)
	–	8	–	2	Hart et al. (1991)
	–	9	–	9	Marshall et al. (1991)
	–	19	–	12	Chen and Shelef (1992)
	8	–	6	1	Grant et al. (1993)
	76	–	73	–	Grau and Vanderlinde (1993)
	4	–	4	–	Hudson and Mott (1993a)
	4	–	4	–	Hudson and Mott (1993c)
	5	–	–	–	Manu-Tawiah et al. (1993)
	53	–	53	–	Duffy et al. (1994a)
	4	–	3	–	Hudson et al. (1994)
	7	–	4	–	Beumer et al. (1996)
	–	6	–	3	Blom et al. (1997)
	–	7	–	5	Wang and Johnson (1997)
Liquid eggs	16	–	–	–	Foegeding and Leasor (1990)
Seafoods	–	4	–	3	Wang and Shelef (1992)
	3	–	–	2	Dorsa et al. (1993)
	4	–	4	–	Hudson and Mott (1993b)
	2	–	–	–	Oh and Marshall (1994)
Total	1437	428	736	558	

[a] Published.
[b] Estimated from published growth kinetics.

formed growth parameters obtained with the models to test as the independent ones. For square roots of growth rates, the constant terms of regression lines were not significantly different to 0.0 so the ratios of reference and model to test growth rates could be considered constant. From the medians of the square roots, ratios between maximum specific growth rates of respectively 0.84, 0.86, 0.97, and 1.00 for the Gompertz, logistic, Baranyi, and log-linear model were obtained. For the log of lag times, the slopes of the regression lines were not significantly different to 1.0 so the ratios of reference and model to test lag times could be considered constant. From the medians of the log of lag times, ratios between lag times of respectively 0.82, 0.97, 0.95, and 1.00 for the Gompertz, logistic, Baranyi, and log-linear models were obtained.

As no correlations were found between the ratios and the growth parameters obtained with the logistic equation with delay, i.e. $\log_{10}(x_0)$, $\log_{10}(x_{max})$, $\mu_{max}^{0.5}$, and ln(*lag*), maximum specific growth rates and lag times published in papers were corrected in accordance with ratios obtained. The database contained then growth parameters assumed estimated with the

same growth model: the logistic equation with delay (Eq. (1)). The distributions of the 1865 μ_{max}-values and the 1294 *lag*-values considered in the study are shown in Fig. 1. The 453 values of μ_{max} equal to 0 and the 29 values of *lag* equal to 0 were not included in these histograms.

2.2. Environmental factors

Temperature was always given in papers, but the pH and water activity were not specified for, respectively, 20 and 65% of the data.

In these cases, the pH of culture broths was set at 7.10. For milk, the pH was set at 6.6 which was the median of 8 published values (6.2 to 6.9) for this product. The pH of butter was set at 7.0 (Murphy et al., 1996). The pH of cream was set at 6.4 (Murphy et al., 1996). The pH of canned meat was set at 6.3 which is a published value for corned beef (Grau and Vanderlinde, 1992). The pH of chicken nuggets was set at 5.85 which was the median of published pH for chicken breast (5.8 to 6.3). The pH of liquid whole egg was set at 6.56 (Erickson and Jenkins, 1992), and the pH of crawfish tail meat was set at 6.0 (George et al., 1996).

For not reported water activities (a_w), knowing the amounts of solutes (sodium chloride, glycerol, sucrose) used in the liquid media, their a_w were calculated by applying the Ross equation (Ross, 1975) or were found in the literature (Petran and Zottola, 1989; Nolan et al., 1992; Brocklehurst et al., 1995a). The a_w of culture broths and milk containing

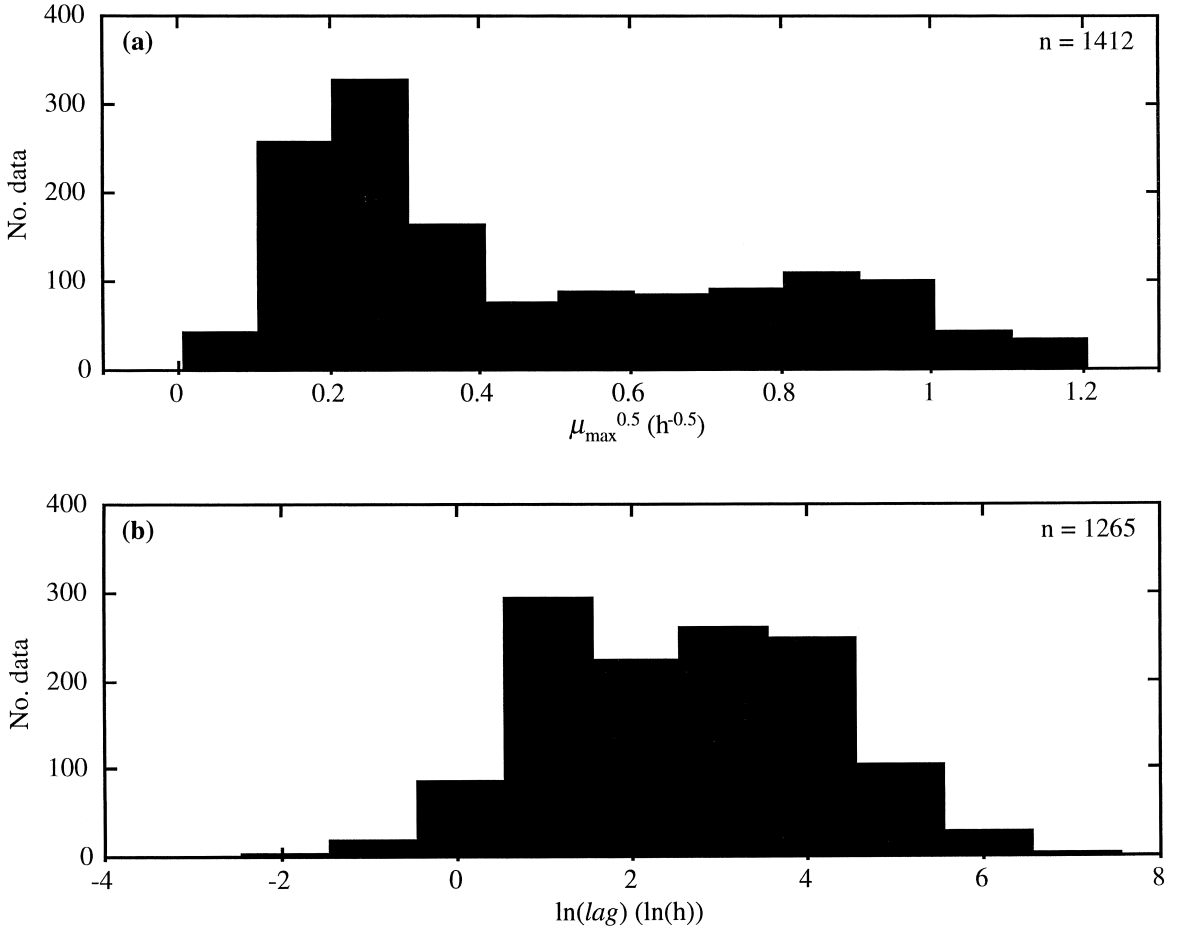

Fig. 1. Distributions of (a) $\mu_{max}^{0.5}$ and (b) ln(*lag*) for *L. monocytogenes* included in the database.

no added solutes were set at 0.997 (Nolan et al., 1992). The sodium chloride concentrations of chocolate milk, cream, Camembert cheese, liquid whole egg, and crawfish tail meat were assumed to be, respectively, 2.5% (Buchanan and Phillips, 1990), 0.5% (McClure et al., 1997), 2.4% (McClure et al., 1997), 0.5% (Erickson and Jenkins, 1992; McClure et al., 1997), and 3% (Hudson and Mott, 1993b). These concentrations correspond to a_w of, respectively, 0.986, 0.997, 0.986, 0.997, and 0.976. The a_w of fresh meat was set at 0.994 (Chen and Shelef, 1992; Duffy et al., 1994a). The a_w of canned meats and ham were set at 0.97 (Grau and Vanderlinde, 1992).

3. Effect of growth conditions on maximum specific growth rate

3.1. Effect of temperature, pH and water activity on μ_{max}

The changes of μ_{max} as a function of temperature, pH, and water activity were described by the cardinal models of Rosso (1998b):

$$\mu_{max} = \mu_{opt(X)} \cdot CM_n(X) \quad (2)$$

$$CM_n(X) = \begin{cases} 0, & X \le X_{min} \\ \dfrac{(X - X_{max}) \cdot (X - X_{min})^n}{(X_{opt} - X_{min})^{n-1} \cdot [(X_{opt} - X_{min}) \cdot (X - X_{opt}) - (X_{opt} - X_{max}) \cdot ((n-1) \cdot X_{opt} + X_{min} - n \cdot T)]}, & X_{min} < X < X_{max} \\ 0, & X \ge X_{max} \end{cases}$$

where X is temperature, pH or water activity, X_{min} is the value below which no growth occurs, X_{opt} is the value at which μ_{max} is equal to its optimal value $\mu_{opt(X)}$ (h^{-1}), X_{max} is the value above which no growth occurs, and n is a shape parameter.

The effect of temperature, T (°C), throughout the entire biokinetic temperature range was then described by the CTMI model (Rosso et al., 1993):

$$\mu_{max} = \mu_{opt(T)} \cdot \tau(T), \text{ where } \tau = CM_2.$$

When growth was only observed at sub-optimal temperatures, the change of μ_{max} as a function of temperature was described by the square root model of Ratkowsky (Ratkowsky et al., 1982; Zwietering et al., 1991):

$$\mu_{max} = \begin{cases} 0 & , T \le T_{min} \\ [b \cdot (T - T_{min})]^2 & , T > T_{min} \end{cases} \quad (3)$$

where b ($°C^{-1}.h^{-0.5}$) is a constant parameter. This model was only used to estimate T_{min}.

The change of μ_{max} as a function of pH was described by the CPM model (Rosso et al., 1995):

$$\mu_{max} = \mu_{opt(pH)} \cdot \rho(pH), \text{ where } \rho = CM_1.$$

When growth was only observed at sub-optimal pH, the CPM model was used with the following relation: $pH_{max} = 2 \cdot pH_{opt} - pH_{min}$.

The change of μ_{max} as a function of water activity, a_w, was described by the CAM model (Rosso, 1998a):

$$\mu_{max} = \mu_{opt(a_w)} \cdot \alpha(a_w), \text{ where } \alpha = CM_2$$

The $a_{w,max}$ value was set at 1.

3.2. Effect of inhibitory substances on μ_{max}

The change of μ_{max} as a function of the concentration of inhibitory substance, c, was assumed to be described by a square root type model (Dalgaard, 1995). The following equation was used:

$$\mu_{max} = \mu_{opt(c)} \cdot \gamma(c) \quad (4)$$

$$\gamma(c) = \begin{cases} \left(1 - \dfrac{c}{MIC}\right)^2, & c < MIC \\ 0, & c \ge MIC \end{cases}$$

where MIC is the minimal inhibitory concentration above which no growth occurs, $\mu_{opt(c)}$ (h^{-1}) is the optimal value of μ_{max} when the concentration of inhibitory substance, c, is 0.

3.3. Effects of qualitative factors on μ_{max}

Qualitative factors (nature of the substrate, agitation . . .) were assumed to have a proportional effect on $\mu_{\max}$ and the following equation was used to described the effect of the different levels of studied factors:

$$\mu_{\max(l)} = k_l \cdot \mu_{\max(0)} \quad (5)$$

where $\mu_{\max(l)}$ is the maximum specific growth rate for the l-th level of the factor, k_l is the coefficient corresponding to the l-th level, $\mu_{\max(0)}$ is the maximum specific growth rate for the level 0 which is the reference one ($k_0 = 1$).

3.4. Global effect of growth conditions on μ_{max}

As proposed by several authors (Zwietering et al., 1992; Wijtzes et al., 1993, 1998; Rosso et al., 1995; Baranyi et al., 1996), the growth conditions were supposed to have independent effects and the following model was used to describe the global effect of growth conditions on $\mu_{\max}$:

$$\mu_{\max} = \mu_{\text{opt}} \cdot \omega(T, pH, a_w, c_{1:n}, k_{1:p}) \quad (6)$$

$$\omega(T, pH, a_w, c_{1:n}, k_{1:p}) = \tau(T) \cdot \rho(pH) \cdot \alpha(a_w) \cdot \prod_{i=1}^{n} \gamma(c_i) \cdot \prod_{j=1}^{p} k_{jl}$$

where μ_{opt} is the maximum specific growth rate (h^{-1}) in the reference medium for optimal conditions (T_{opt}, pH_{opt}, $a_{w,\text{opt}}$, $c_{1:n} = 0$, $k_{1:p} = 1$). The parameters of this model are: μ_{opt}, $T_{\min}$, T_{opt}, $T_{\max}$, $pH_{\min}$, pH_{opt}, $pH_{\max}$, $a_{w,\min}$, $a_{w,\text{opt}}$, $MIC_{1:n}$, $k_{1:p}$.

4. Effect of growth conditions on lag time

By assuming initially that the ratio of lag time and generation time, that is the work that a cell needs to do to adapt to its environment (Robinson et al., 1998), is constant (not significantly influenced by the growth conditions) for cells in the same initial state, we have:

$$\frac{lag}{Tg} = K \quad (7)$$

where K is a constant depending on the physiological state of the inoculum.

5. Model fit

Fits were performed by linear or non-linear regression using the least squares criterion (Box et al., 1978). Estimation of parameters was carried out by minimizing the sum of the squared residuals (SSR) where SSR is defined as follows: $SSR = \Sigma_{i=1}^{n}(value(i)_{observed} - value(i)_{fitted})^2$where n is the number of data points.

The minimum SSR values were computed with the REGRESS and NLINFIT subroutines of MATLAB 5.2 software (The MathWorks Inc., Natick, MA, USA).

6. Estimation of model parameters

Data used to estimate cardinal values and *MIC*-values were taken in papers where the studied environmental factors showed at least three levels and when concomitant variables varied in the same manner for all the levels (complete balanced designs).

Median values of these estimations were chosen to estimate the model parameter values for the whole database since they are less sensitive to outliers than means (Delignette-Muller et al., 1995).

6.1. Estimation of cardinal values

CTMI, square root, CPM, and CAM models were fitted to maximum specific growth rates to determine cardinal temperatures, pH, and water activities for *L. monocytogenes*.

The median $T_{\min}$- and $T_{\max}$-values were, respectively, −2.7 and 45.5°C (Table 2). The T_{opt}-values obtained from the 3 datasets including the entire biokinetic range temperature (Petran and Zottola, 1989; Duh and Schaffner, 1993; Bajard et al., 1996) were greater than 30–37°C which is commonly observed as the optimal temperature for growth of *L. monocytogenes* (Gray and Killinger, 1966; Farber and Peterkin, 1991; Lou and Yousef, 1999). These discrepancies were linked to a poor fit of the CTMI model on these data. On corresponding plots of growth rate against temperature, it could be observed

Table 2
Estimated cardinal values for growth of *L. monocytogenes*

Factor X	No. levels [range]	No. points	X_{min}	X_{opt}	X_{max}	Concomitant variables	Refs.
T (°C)	23 [−2;42]	23	−2.7	38.7	42.3	–	Bajard et al. (1996)
	15 [4;45]	15	−0.7	39.0	45.5	–	Duh and Schaffner (1993)
	9 [4;45]	9	0.5	39.7	47.7	–	Petran and Zottola (1989)
	19 [0;35.0]	32	−2.4	–	–	pH	Grau and Vanderlinde (1993)
	15 [0;30.6]	18	−2.2	–	–	–	Grau and Vanderlinde (1993)
	11 [0;9.3]	18	−3.0	–	–	pH, inoculum	Walker et al. (1990)
	10 [4.0;35.4]	74	−2.7	–	–	Strain	unpublished personal data
	7 [4;35]	14	−2.7	–	–	Atmosphere	Katoh (1989)
	7 [5;30]	33	−1.5	–	–	Inoculum	McKellar et al. (1997)
	5 [4;35]	56	−1.0	–	–	pH, a_w, strain, substrate	Rosenow and Marth (1987a)
	5 [0;9.3]	10	−4.4	–	–	inoculum	Walker et al. (1990)
	5 [5;25]	15	0.8	–	–	a_w	Robinson et al. (1998)
	4 [4;35]	58	2.6	–	–	pH, sodium benzoate	El-Shenawy and Marth (1988a)
	4 [4;35]	56	0.6	–	–	pH, potassium sorbate	El-Shenawy and Marth (1988b)
	4 [7;35]	80	−4.4	–	–	pH, acid, strain	Ahamad and Marth (1989)
	4 [5;28]	8	9.1	–	–	Atmosphere	Buchanan and Klawitter (1990)
	4 [4;30]	12	−6.6	–	–	Strain	Foegeding and Leasor (1990)
	4 [4.4;10.2]	25	−3.3	–	–	Pre-incubation	unpublished personal data
	3 [4;22]	26	−6.1	–	–	Strain, substrate	Donnelly and Briggs (1986)
	3 [5;28]	120	0.1	–	–	pH, a_w, atmosphere, nitrite	Buchanan et al. (1989)
	3 [4;12]	3	−3.9	–	–	–	Kaya and Schmidt (1989)
	3 [3;11]	9	−3.8	–	–	Atmosphere	Marshall et al. (1991)
	3 [0;12]	3	−4.8	–	–	–	Dorsa et al. (1993)
	3 [4;10]	36	−0.7	–	–	pH, CO_2	Farber et al. (1996)
	3 [3;9]	9	−3.1	–	–	pH, a_w, substrate	Murphy et al. (1996)
	[5;35]	–	−2.6	–	–	–	Wijtzes et al. (1993)
pH	15 [4.0;10.0]	24	4.56	7.10	9.40	–	Petran and Zottola (1989)
	39 [5.87;6.89]	53	5.08	–	–	a_w	Duffy et al. (1994a)
	25 [5.46;6.98]	58	4.14	–	–	Temperature	Grau and Vanderlinde (1993)
	7 [4.70;7.30]	7	4.38	–	–	–	Robinson et al. (1998)
	6 [4.45;7.10]	64	4.88	–	–	Temperature, acid, strain	Ahamad and Marth (1989)
	4 [4.7;6.0]	98	4.77	–	–	Acid	Young and Foegeding (1993)
	3 [5.6;6.8]	24	4.89	–	–	a_w, strain, *Penicillium*	Ryser and Marth (1988)
	3 [5.0;7.0]	54	4.84	–	–	Temperature, monolaurin	Oh and Marshall (1993)
	3 [4.4;7.0]	3	4.06	–	–	–	Brocklehurst et al. (1995b)
	3 [5.4;5.8]	45	5.12	–	–	Acid, strain	Vasseur et al. (1999)
	[4.6;7.4]	–	3.84	–	9.82	–	Wijtzes et al. (1993)
	–	–	4.62	–	–	Temperature, strain	George et al. (1988)
	–	–	4.3	–	–	–	Farber et al. (1989)
	–	–	4.25	–	–	a_w	McClure et al. (1989)
	–	–	4.5	–	–	Temperature, acid, strain	Sorrells et al. (1989)
	–	–	4.53	–	–	–	Cole et al. (1990)
	–	–	4.5	–	–	Acid	Conner et al. (1990)
	–	–	5	–	–	Temperature, a_w, nitrite	McClure et al. (1991)
a_w	19 [0.886;0.994]	19	0.951	–	–	Solute, sodium lactate	Chen and Shelef (1992)
	15 [0.893;0.929]	16	0.916	–	–	Solute	Nolan et al. (1992)
	11 [0.924;0.997]	19	0.902	–	–	Solute	Robinson et al. (1998)
	7 [0.87;0.99]	17	0.90	–	–	Solute	Miller (1992)
	4 [0.960;0.993]	53	0.862	–	–	pH	Duffy et al. (1994a)
	3 [0.977;0.997]	18	0.931	–	–	Temperature	Robinson et al. (1998)
	3 [0.946;0.973]	15	0.864	–	–	Strain	Vasseur et al. (1999)
	[0.950;0.997]	–	0.916	–	–	–	Wijtzes et al. (1993)
	–	–	0.90	–	–	–	Petran and Zottola (1989)
	–	–	0.91	–	–	Temperature, solute, strain, inoculum	Tapia de Daza et al. (1991)
	–	–	0.91	–	–	–	Farber et al. (1992)

that optimal growth rates were obtained for temperatures around 35–37°C. The T_{opt}-value was then set at 37°C.

For the pH, the median pH_{min}-, pH_{opt}-, and pH_{max}-values were respectively 4.55, 7.10, and 9.61 (Table 2).

The water activity of culture broths ranges from 0.995 to 0.997 (Tapia de Daza et al., 1991; Nolan et al., 1992), the $a_{w,opt}$-value was then arbitrarily set at 0.997. The median $a_{w,min}$-value was 0.910 (Table 2).

6.2. Estimation of minimal inhibitory concentrations

The square root type model generally described satisfactorily the decrease of $\mu_{max}^{0.5}$ with increasing concentration of inhibitor (Fig. 2a–e). This was previously observed by Dalgaard (1995) with the effect of CO_2. Even if this decrease sometimes did not seem linear (Fig. 2f), and that models with shape parameters as proposed by Levenspiel (1980), Luong (1985) or Houtsma et al. (1994) should be prefered, the parsimonious square root type model was used to model the effects of all inhibitory substances used in the published studies.

Organic acids exert their inhibitory activity by decreasing the cell pH (Booth, 1985) and by a specific effect of the acid on the metabolic activities of microbial cells (Ita and Hutkins, 1991). Because the most potent effect of weak organic acids is mediated through the undissociated form, their minimal inhibitory concentrations (MIC) were calculated for undissociated concentrations (Presser et al., 1997). MICs of undissociated acetic, lactic, and citric acids are reported in Table 3. When sodium salt of lactic acid was used, the MIC of lactic acid was corrected as being the MIC of sodium lactate multiplied by the molar mass ratio, 90/112. The median *MIC*-values obtained for undissociated acetic, lactic, and citric acid were respectively 20.1, 5.4, and 1.6 mM. The *MIC*-values obtained for undissociated sodium benzoate and potassium sorbate (Table 3) were, respectively, 0.7 and 5.1 mM.

The median *MIC*-value obtained for undissociated form of sodium nitrite which seems also to be the most inhibitory form (Duffy et al., 1994a) was 11.4 μM (Table 3).

The inhibitory activity of glycerol monolaurate, a monoester of lauric acid, has been extensively studied. The median *MIC*-value obtained from seven studies (Table 3) was 18.5 $\mu g.ml^{-1}$.

The median *MIC*-values obtained for butylated hydroxyanisole and tertiary butylhydroquinone were, respectively, 254 and 48.7 $\mu g.ml^{-1}$ (Table 3). The MIC of butylated hydroxytoluene was 1400 $\mu g.ml^{-1}$.

The theoretical median *MIC*-value obtained from 5 studies (Table 3) was a CO_2 proportion of 1.64 (called theoretical because it is greater than 1).

Results concerning the effect of vacuum-packaging are conflicting. Some studies seemed to show that vacuum led to a decrease of μ_{max} (Manu-Tawiah et al., 1993) and that vacuum was equivalent to an atmosphere composed of 30% CO_2 and 70% N_2 (Beumer et al., 1996), and conversely, others showed that *L. monocytogenes* growth was similar under vacuum-packaged and aerobic conditions (Hudson and Mott, 1993a,b). Because the effect of vacuum-packaging was not significant on growth data included in the database ($P>0.51$), it was not taken into account.

The MIC of caffeine was 10.8 $g.l^{-1}$ (Table 3).

The *MIC*-value obtained for phenol from the study of Membré et al. (1997) was 12.5 ppm (Table 3).

6.3. Effects of qualitative factors

Only qualitative factors for which a significant effet on μ_{max} was observed were taken into account in the model.

Agitation of fluid media has a variable effect on growth rate according to the growth medium used (Jones et al., 1995) but generally it led to an increase of μ_{max}. The median *k*-value obtained for agitation was 1.08 (Table 4).

Conflicting results have been obtained for anaerobic conditions, in some studies there was no significant effect (Buchanan et al., 1989; Buchanan and Phillips, 1990; Jones et al., 1995), in others there was a stimulating effect (Buchanan and Klawitter, 1990), and conversely, in others an inhibitory effect was observed (George and Lund, 1992). This factor was then not taken into account.

The presence of *Pseudomonas* spp. in the growth medium seemed to enhance the growth rate of *L. monocytogenes* (Marshall and Schmidt, 1988). The median *k*-value obtained for *Pseudomonas* spp. was 1.28 (Table 4).

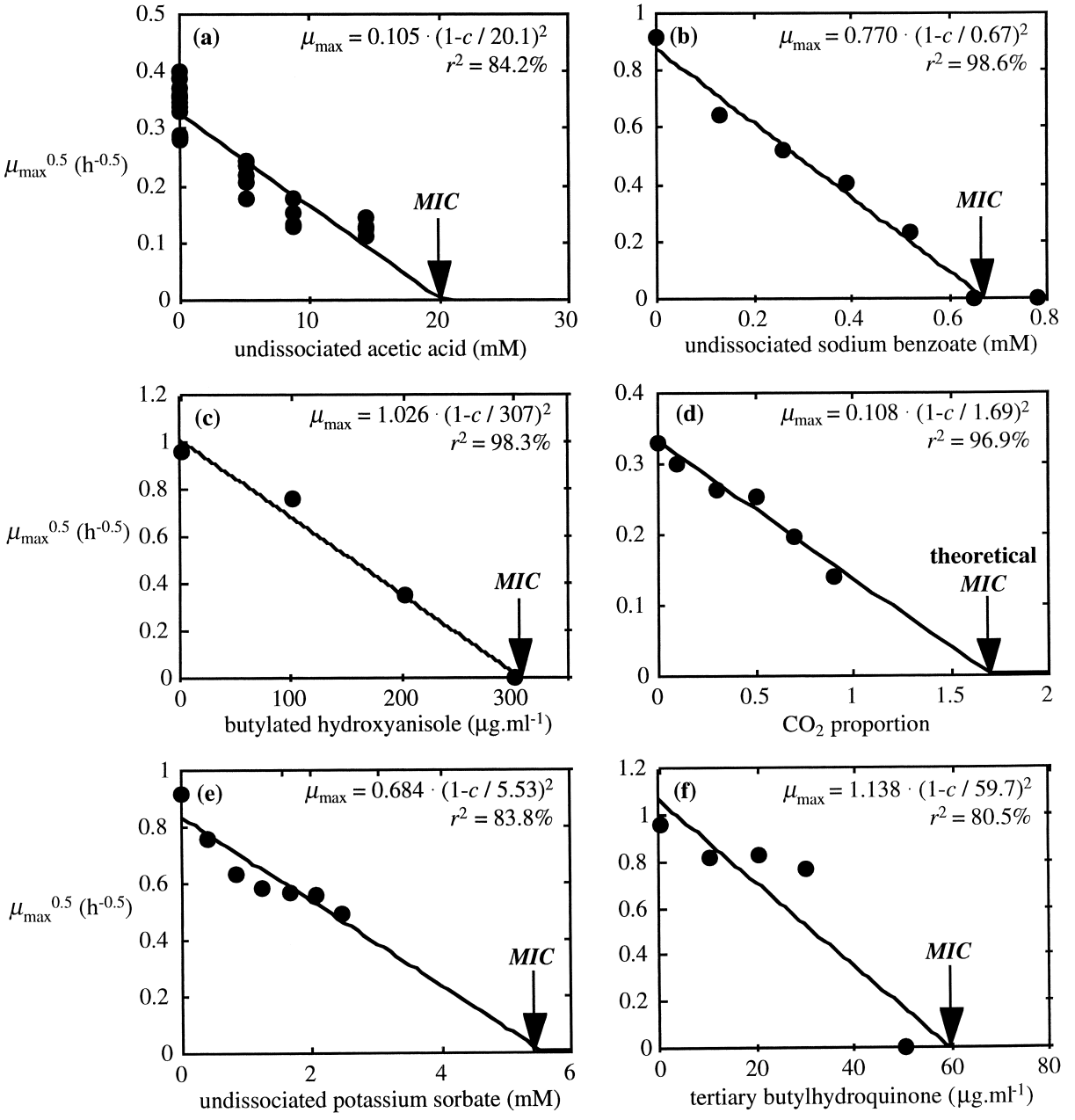

Fig. 2. Effect of the concentrations of (a) undissociated acetic acid, (b) undissociated sodium benzoate, (c) butylated hydroxyanisole, (d) CO_2, (e) undissociated potassium sorbate, and (f) tertiary butylhydroquinone on the maximum specific growth rate of *L. monocytogenes*. MIC are the minimal inhibitory concentrations and the lines represent the fitted square root type model on observed data (●). Data from: (a) Vasseur et al. (1999), (b) El-Shenawy and Marth (1988a), (c) Yousef et al. (1991), (d) Farber et al. (1996), (e) El-Shenawy and Marth (1988b) and (f) Yousef et al. (1991).

The presence of lactic acid bacteria in the growth medium seemed to reduce the growth rate of *L. monocytogenes* (McKellar et al., 1994; Schmidt, 1995; Beumer et al., 1996). The median *k*-value obtained for the presence of 1 to 10^2 cfu.g^{-1} of *Lactobacillus curvatus* was 0.81 (Table 4).

Table 3
Minimal inhibitory concentrations (MIC) for growth of *L. monocytogenes*

Inhibitor (unit)	No. levels [range]	No. points	MIC	Concomitant variables	Ref
Undissociated acetic	6 [0;132]	23	25.0	pH	Young and Foegeding (1993)
acid (mM)	4 [0;21.3]	32	6.2	Temperature, pH	Ahamad and Marth (1989)
	4 [0;14.3]	30	20.1	pH, strain	Vasseur et al. (1999)
Undissociated lactic	6 [0;29.7]	23	5.4	pH	Young and Foegeding (1993)
acid (mM)	4 [0;1.2]	7	1.1	a_w	Chen and Shelef (1992)
	4 [0;2.4]	30	5.6	pH, strain	Vasseur et al. (1999)
Undissociated citric	5 [0;2.6]	19	3.0	pH	Young and Foegeding (1993)
acid (mM)	4 [0;0.5]	32	0.1	Temperature, pH	Ahamad and Marth (1989)
Undissociated sodium benzoate (mM)	7 [0;2.8]	56	0.7	Temperature, pH	El-Shenawy and Marth (1988a)
Undissociated potassium sorbate (mM)	7 [0;7.2]	56	5.1	Temperature, pH	El-Shenawy and Marth (1988b)
Undissociated sodium	5 [0;33.9]	160	14.4	Temperature, pH, atmosphere	Buchanan et al. (1989)
nitrite (μM)	5 [0;322]	378	8.4	Temperature, pH, a_w	McClure et al. (1991)
Monolaurin ($\mu g.ml^{-1}$)	6 [0;9]	54	26.6	Temperature, pH	Oh and Marshall (1993)
	4 [0;5]	14	7.55	Temperature, pH, additives	Wang and Johnson (1997)
	–	–	8	–	Oh and Marshall (1992)
	–	–	20	–	Wang and Johnson (1992)
	–	–	96	–	Razavi-Rohani and Griffiths (1994)
	–	–	16	–	Bal'a and Marshall (1996a)
	–	–	18.5	Temperature, strain, substrate, inoculum	Bal'a and Marshall (1996b)
BHA[a] ($\mu g.ml^{-1}$)	4 [0;300]	4	308	–	Yousef et al. (1991)
	2 [0;100]	4	199	Monolaurin	Wang and Johnson (1997)
BHT[b] ($\mu g.ml^{-1}$)	4 [0;700]	4	1400	–	Yousef et al. (1991)
TBHQ[c] ($\mu g.ml^{-1}$)	5 [0;50]	5	59.7	–	Yousef et al. (1991)
	2 [0;30]	4	37.7	Monolaurin	Wang and Johnson (1997)
CO_2 proportion	6 [0;0.9]	38	1.64	Temperature, pH	Farber et al. (1996)
	4 [0.25;1]	4	1.42	–	Fernández et al. (1997)
	3 [0;0.8]	9	10	Temperature	Marshall et al. (1991)
	3 [0;0.4]	4	1.56	–	Manu-Tawiah et al. (1993)
	2 [0;0.099]	14	5.14	Temperature	Katoh (1989)
Caffeine ($g.l^{-1}$)	3 [0;10]	12	10.8	Substrate	Pearson and Marth (1990c)
Phenol (ppm)	–	–	12.5	Temperature, a_w	Membré et al. (1997)

[a] BHA, butylated hydroxyanisole.
[b] BHT, butylated hydroxytoluene.
[c] TBHQ, tertiary butylhydroquinone.

The presence of *Penicillium camemberti* in whey enhanced significantly the growth rate of *L. monocytogenes*, the *k*-value for this factor was 1.74 (Table 4).

The enumeration medium used in growth kinectics experiments did not seemed to have a significant effect (Stillmunkes et al., 1993; Palumbo and Williams, 1994).

Table 4
Effect of qualitative factors on maximum specific growth rate of *L. monocytogenes*

Factor	$k^{0.5}$	No. points	Concomitant variables	Refs.
Agitation	1.08	12	Cocoa	Pearson and Marth (1990a)
	0.96	22	Cocoa	Pearson and Marth (1990b)
	1.04	5	Substrate	Jones et al. (1995)
Pseudomonas fragi	1.07	5	Substrate	Marshall and Schmidt (1988)
P. fluorescens P26	1.13	3	Substrate	
P. fluorescens T25	1.13	3	Substrate	
P. fluorescens B52	1.28	3	Substrate	
Lactobacillus curvatus	0.95	1	–	Beumer et al. (1996)
L. curvatus	0.9	1	–	
L. curvatus	0.89	1	–	
Penicillium camemberti	1.32	12	pH, strain	Ryser and Marth (1988)
Nonfat dry milk/milk	0.96	8	Temperature, strain	Donnelly and Briggs (1986)
	0.95	5	*Pseudomonas* spp.	Marshall and Schmidt (1988)
Cream/milk	1.04	14	Temperature, strain	Rosenow and Marth (1987a)
	1.26	3	Temperature	Murphy et al. (1996)
Retentate/milk	1.08	12	Temperature, strain	El-Gazzar et al. (1991)
Permeate/milk	0.92	12	Temperature, strain	El-Gazzar et al. (1991)
Semi-skim milk/TSBYE	0.95	3	–	Denis and Ramet (1989)

6.4. Effect of the growth medium on μ_{max}

No significant differences ($P>0.17$) were observed between growth rates obtained in skim and whole milk (Donnelly and Briggs, 1986; Rosenow and Marth, 1987a; Marshall and Schmidt, 1988). Growth rates obtained in reconstitued nonfat dry milk were lower than those obtained in milk (Donnelly and Briggs, 1986; Marshall and Schmidt, 1988), the median *k*-value was 0.91 with milk set at level 0 (Table 4). Growth rates were higher in cream than in milk (Rosenow and Marth, 1987a; Murphy et al., 1996), the median *k*-value was 1.32 (Table 4). El-Gazzar et al. (1991) obtained growth rates significantly higher ($P=5.9\times10^{-3}$) and lower ($P=3.5\times10^{-2}$) in, respectively, retentate and permeate from ultrafiltered skim milk than in skim milk. The *k*-values were, respectively, 1.17 and 0.85 (Table 4).

A significant effect ($P=4.1\times10^{-6}$) of the nutritional properties of culture broths was observed by George and Lund (1992) who obtained higher growth rates in tryptone soya broth with yeast extract and glucose than in tryptose phosphate broth. Results obtained from the database did not show systematic deviation of μ_{opt} between nutritionaly ''rich'' culture broths and ''poor'' broths. For example, the median of $\mu_{opt}^{0.5}$ for tryptone soya broth (68 data) and tryptone soya with yeast extract broth (215 data) were respectively 0.960 and 0.950. We have then considered that nutritional properties have no significant effect on the growth rate and we calculated a joint median for all culture broths. μ_{opt} were estimated for each growth medium from all non nil values of μ_{max} using the model described by the Eq. (6) with previously estimated parameters (Fig. 3).

Denis and Ramet (1989) obtained growth rates significantly lower ($P=3.2\times10^{-2}$) in semi-skim milk than in tryptone soya with yeast extract broth. Similar results were observed for μ_{opt} in milk and in culture broth (Fig. 3). Differences were also observed between the median μ_{opt} obtained for culture broths, meats and liquid eggs (Fig. 3). The following

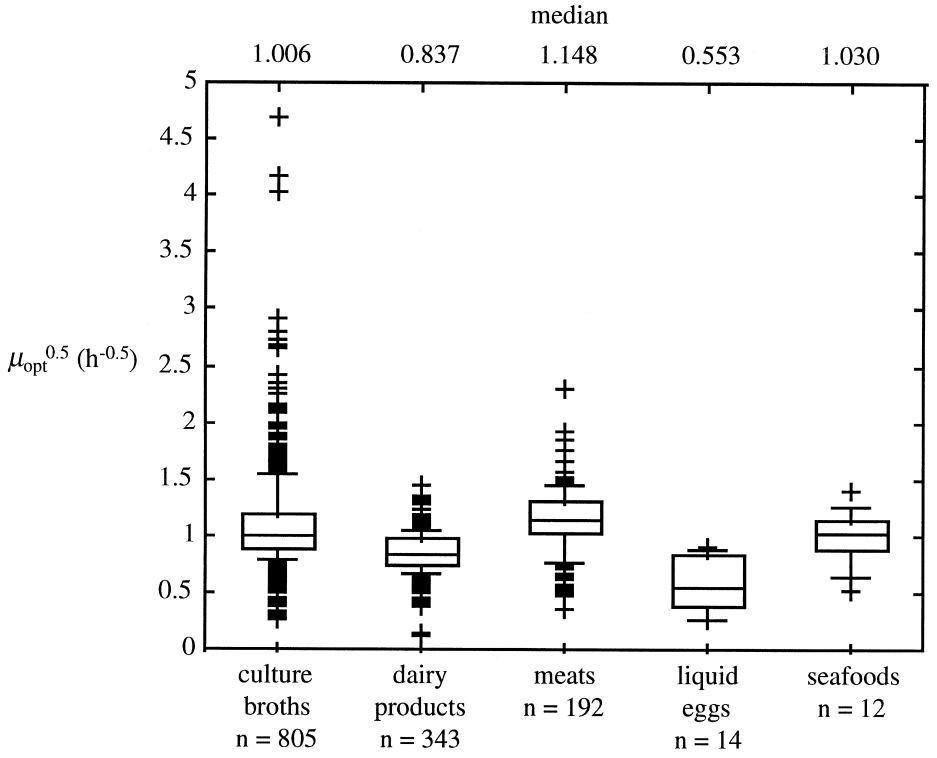

Fig. 3. Effect of the nature of the substrate on estimated μ_{opt}-values for *L. monocytogenes* (box plots displaying the 10th, 25th, 50th, 75th, and 90th percentiles of the square root of the growth rate, *n* is the number of data points).

k-values were then used to take into account the effect of the nature of the substrate: 0.69, 1.30, 0.30, and 1.00 for, respectively, milk, meats, liquid eggs, and seafoods. The level 0 was set for culture broth medium. Given the low number of data for seafoods (12 data) and the closeness of medians obtained, no difference was considered between seafoods and culture broths.

6.5. Estimation of μ_{opt}

μ_{opt} were estimated from the non nil values of μ_{max} included in the database using the Eq. (6) with previously estimated parameters. The μ_{opt}-values obtained correspond then to the maximum specific growth rates of *L. monocytogenes* in the following growth conditions: pure culture in a culture broth (pH 7.1, a_w 0.997) without agitation, without inhibitory substances, at 37°C. The median μ_{opt}-value obtained was 1.016 h^{-1}.

6.6. Estimation of lag/Tg

If the ratio *lag*/*Tg* is constant, a linear correlation should be observed between ln(*lag*) and ln(*Tg*) and the slope of the regression line should be equal to 1. A reasonable linear correlation ($\rho = 0.84$) was effectively observed between ln(*lag*) and ln(*Tg*) and the slope of the regression line was close to 1.0 (Fig. 4). The logarithm of ratios *lag*/*Tg* were then calculated and the median value obtained for ln(*lag*/*Tg*) was 1.128 (Fig. 5) so the parameter *K* of the Eq. (7) is equal to exp(1.128) = 3.09.

7. Performance evaluation of the model

7.1. μ_{max} Modelling

Calculated μ_{max} with the global model (Eq. (6)) with the 35 parameters previously described are

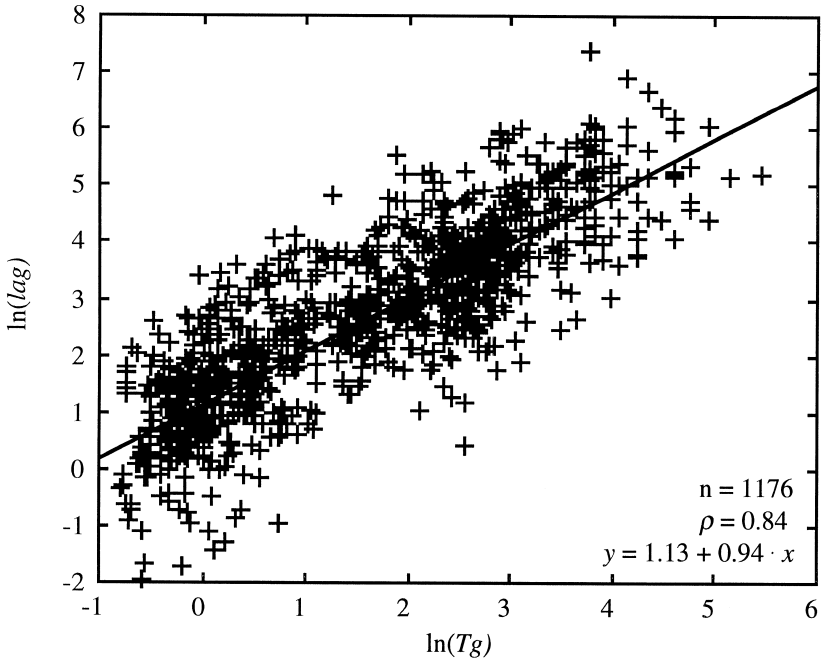

Fig. 4. Plots and regression line of observed ln(*lag*) against observed ln(*Tg*) for *L. monocytogenes*.

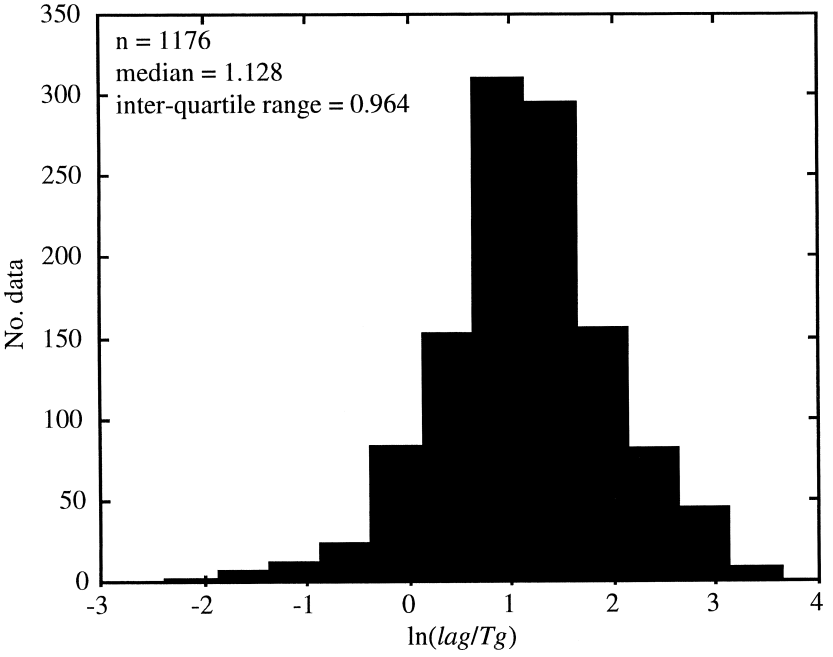

Fig. 5. Distribution of the ratios *lag*/*Tg* for *L. monocytogenes*.

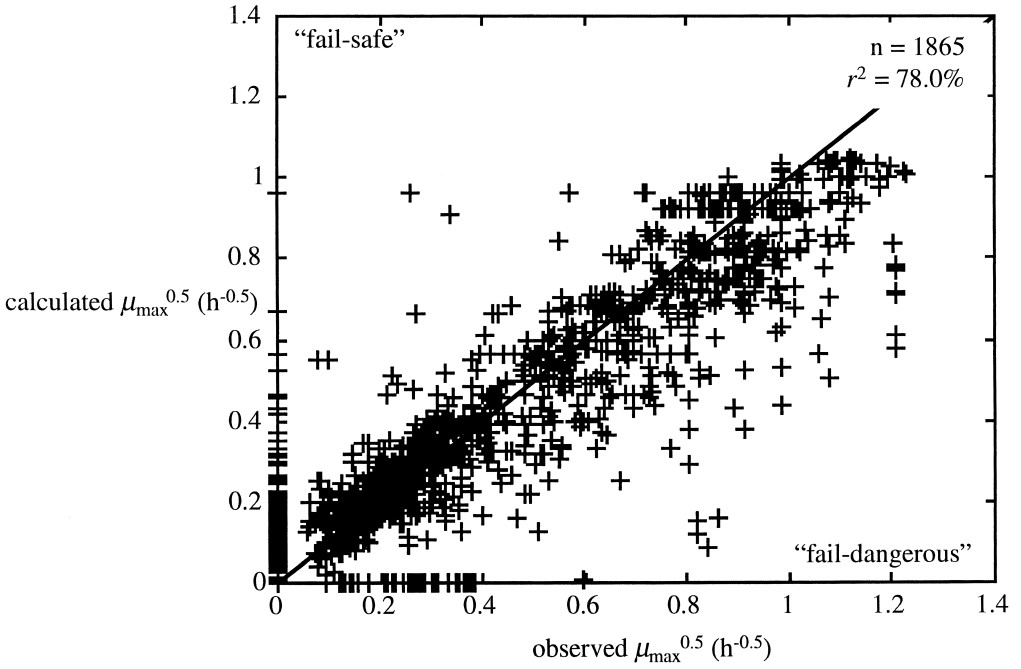

Fig. 6. Plots of calculated maximum specific growth rates according to the global model against observed maximum specific growth rates for *L. monocytogenes*.

shown in Fig. 6. The model explains 78.0% of the variability of $\mu_{max}^{0.5}$.

The accuracy factor is frequently used to estimate the average error in growth parameter estimates from models (Baranyi and Roberts, 1995; Baranyi et al., 1996, 1999; Ross, 1996; Fernández et al., 1997). This accuracy factor was defined by Baranyi et al. (1999) by the formula: $A_f = \exp\sqrt{(E(\ln x_{fitted} - \ln x_{observed})^2)}$ where $E(.)$ is the expected value (the mean) of the argument in parenthesis, and x is the growth parameter. A_f corresponds to the average error and can then be strongly influenced by a few predictions which deviate widely from the observed ones. As the database contains growth parameters possibly inaccurate because estimated with only a few cell counts, we used also the median error defined by the following formula to evaluate the accuracy of the model: $\exp\sqrt{(\text{median}(\ln x_{fitted} - \ln x_{observed})^2)}$.

Accuracy of the model was estimated by calculating the mean and median per cent discrepancies for the generation time (Baranyi and Roberts, 1995; Baranyi et al., 1996, 1999; Fernández et al., 1997) then the no growth data could not be included which was disappointing, as pointed out by Buchanan and Phillips (1990). The observed generation times (or maximum specific growth rates) differ from the calculated by 90% by using the mean error and by 32% by using the median error. By assuming independent errors, and as the measurement error of the generation time is approximately 10% (Baranyi and Roberts, 1995; Bégot et al., 1996) and the error linked to the correction for the growth model used was approximately 10%, the model function mean and median errors are, respectively, 70 and 12%. Baranyi et al. (1996) observed that, for 3 variables models (temperature, pH, and water activity), the accuracy was limited to no better than ~15% and Fernández et al. (1997) obtained, for a 4 variables model (temperature, pH, NaCl and CO_2 concentrations) an error of prediction of about 24%. The accuracy for a 28 variables model seems then satisfactory.

The bias factor is also used to evaluate if a model over- or under-estimates the growth parameters (Ross, 1996; Baranyi et al., 1999). This bias factor was defined by Baranyi et al. (1999) by the formula: $B_f = \exp(E(\ln x_{fitted} - \ln x_{observed}))$. As the accuracy

factor, this mean bias can be strongly influenced by a few outliers, we have then also used the median bias defined by: $\exp(\text{median}(\ln x_{\text{fitted}} - \ln x_{\text{observed}}))$. The mean per cent bias between the fitted and observed generation times is 3%, this indicates the presence of absurd large estimations because the median per cent bias is 0%.

For full evaluation of the performance of the model, we have to deal with no growth data which were deleted above. Among the 1579 growth conditions for which growth is predicted, growth was not observed 213 times, i.e. 13.5% of fail-safe growth predicted, and among the 286 remaining conditions for which growth is not predicted, growth was observed 46 times, i.e. 16.1% of fail-dangerous no growth predicted. The high rate of fail-dangerous no growth predicted can be due to an over-estimation of minimal cardinal values, but if smaller values were used, the rate of fail-safe growth predicted would increase. The fit of the model seems then poor near the limits of growth of *L. monocytogenes*.

This poor fit can be due to the hypothesis of multiplicative effects of growth conditions on the growth rate. A contour plot of $\mu_{\max}$ was built (Fig. 7) by calculating $\mu_{\max}$ with Eq. (6), with T and pH as independent variables. The combinations of T and pH for which no growth occurs correspond to the dark area. We can observe that the growth/no growth interface is questionable because it is independent of the growth conditions but depends only on $T_{\min}$ and $pH_{\min}$ which are independent of other growth conditions.

7.2. lag Modelling

Lag times were calculated using the Eq. (7) with Tg obtained from $\mu_{\max}$ previously estimated. The model explains 70.1% of the variability of ln(*lag*) (Fig. 8).

Accuracy of calculated lag times was estimated by calculating the mean and median errors for lag time. These errors are, respectively, 133 and 61%. As the measurement error of the lag time is approximately 20% (Bégot et al., 1996) and the correction for the growth model error was approximately 15%, the model function mean and median errors are, respectively, 98 and 26%. The model is then two times less accurate for lag time than for generation time.

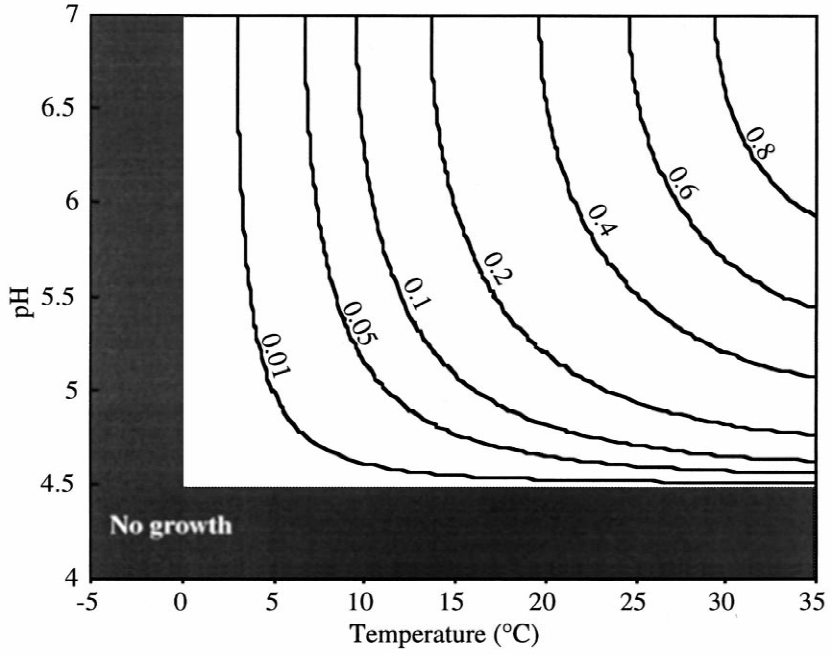

Fig. 7. Contour plot of maximum specific growth rate according to temperature and pH without interaction. The axes represent temperature and pH, and the lines represent the same level for maximum specific growth rate. $\mu_{\max}$ are calculated with Eq. (6) with T and pH as independent variables and with the following parameters: $\mu_{\text{opt(T,pH)}} = 1\ \text{h}^{-1}$, $T_{\min} = 0°\text{C}$, $T_{\text{opt}} = 35°\text{C}$, $pH_{\min} = 4.5$, and $pH_{\text{opt}} = 7.0$.

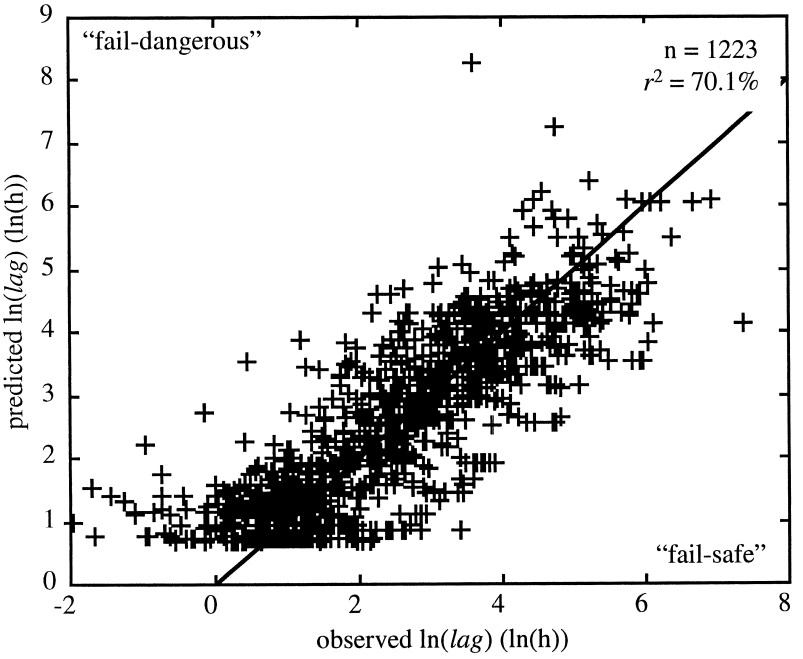

Fig. 8. Plots of calculated lag times according to the global model against observed lag times for *L. monocytogenes*.

The mean and median per cent bias are equal to 3% indicating an over-estimation of the lag time by the model. This bias is perhaps due to the fact that lag times were estimated for 1223 growth conditions whereas K was estimated with only 1176 values of *lag* and *Tg*.

The considerable scatter in the plots of ln(*lag*) against ln(*Tg*) and the resulting large spread of the ln(*lag*/*Tg*) distribution (Figs. 4 and 5) implied that the initial hypothesis: cells in the same initial state and no significant effect of growth conditions on the ratio *lag*/*Tg*, are over-simplifications which could explain the worst accuracy of estimated lag times in comparison with generation times.

It has been observed that temperature could sometimes have a significant effect on the ratio *lag*/*Tg* (Delignette-Muller, 1998; Robinson et al., 1998). In this case, the ratio generally decreased with increasing temperature (Delignette-Muller, 1998) which means logically that the amount of work needed to prepare for growth would decrease when growth temperature approaches the optimal one. However, Robinson et al. (1998) observed a different behavior, the ratio decreased with increasing temperature from 5 to 37°C but unexpected very high ratios were systematically observed at 20 and 25°C. For pH, it seemed also that the ratio was higher near the minimal pH for growth and that it decreased with increasing pH near the optimal one (Delignette-Muller, 1998; Robinson et al., 1998). The same observations were done with the water activity but the effect seemed solute dependent (Robinson et al., 1998).

The effect of inhibitory substances on the ratio *lag*/*Tg* was varying. Generally, an increase of the ratio with increasing inhibitor concentration was observed. A highly significant effect ($P = 5.4 \times 10^{-10}$) was observed with monolaurin (Fig. 9a) by Oh and Marshall (1993) who explained these observations by assuming that cells may detoxify the inhibitory substance before growth occurs, which corresponds to an increasing work needed before growth. However, with other inhibitory substances, the opposite phenomenon occured. We observed a significant ($P = 1.4 \times 10^{-2}$) unexpected decrease of the ratio with increasing sodium benzoate concentration (Fig. 9b).

The extension of lag phase when physical injuries are applied has been frequently observed (Kaufman et al., 1959; Jackson and Woodbine, 1963; Mackey

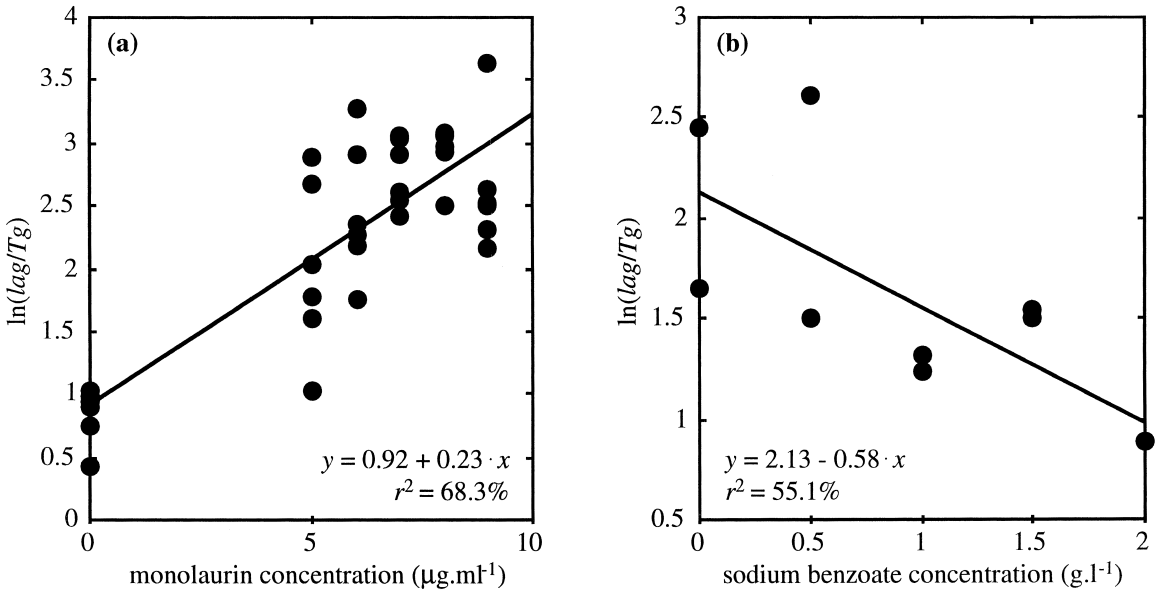

Fig. 9. Effect of (a) the monolaurin concentration and (b) the sodium benzoate concentration on the ratio *lag*/*Tg* for *L. monocytogenes*. Data from: (a) Oh and Marshall (1993), (b) El-Shenawy and Marth (1988a).

and Derrick, 1982, 1984; Grant et al., 1993). This effectively corresponds to an increase of the work needed before growth when injuries are applied to initial cells. Models describing the effect of heat injury on subsequent lag time before regrowth have been recently published for *L. monocytogenes* (Bréand et al., 1997, 1999; McKellar et al., 1997).

The pre-incubation conditions can also influence the duration of the lag time. It has been frequently observed that the temperature history had a significant effect on the lag phase duration (Walker et al., 1990; Buchanan and Klawitter, 1991; Wang and Shelef, 1992; Hudson, 1993; Beumer et al., 1996; Gay et al., 1996; Dufrenne et al., 1997; Membré et al., 1999). The lag time before regrowth at low temperature has been observed shorter with low than with high pre-incubation temperatures. Buchanan and Klawitter (1991) have shown that the increase of lag time with increasing pre-incubation temperature was not continuous and that there was probably a cut-off pre-incubation temperature beyond which the lag time increases (Fig. 10a). They also observed differences between *lag* obtained in aerobic and anaerobic conditions, and with the nature of substrate used. Gay et al. (1996) observed a decrease of lag time when cells were pre-incubated at 14°C instead of 30°C only with a previous cold storage at 4°C and with a low inoculum size. Furthermore, the increase in lag time seemed to depend on the temperature of incubation. Hudson (1993) observed with *Aeromonas hydrophila* that the lag phase duration was the shortest when the pre-incubation temperature matched the incubation temperature. From the data of Walker et al. (1990), a decrease of the ratio of *lag*/*Tg* between pre-incubations at 30 and 4°C could be observed when incubation temperature increased (Fig. 10b).

The same effect could exist with pH since Johansen et al. (1994) reported an elimination of the lag phase when, before growth in a pH 5.5 medium, the inoculum was prepared at pH 5.5.

The history of the inoculum can then significantly influence the duration of the lag phase but the relation seems is depend on numerous factors and today no models have been published to describe this effect.

Although some studies have shown that inoculum size does not have a significant influence on the lag time of *L. monocytogenes* (Denis and Ramet, 1989; Buchanan and Phillips, 1990; Duffy et al., 1994b), Gay et al. (1996) have recently observed that in some conditions the use of a low initial bacterial

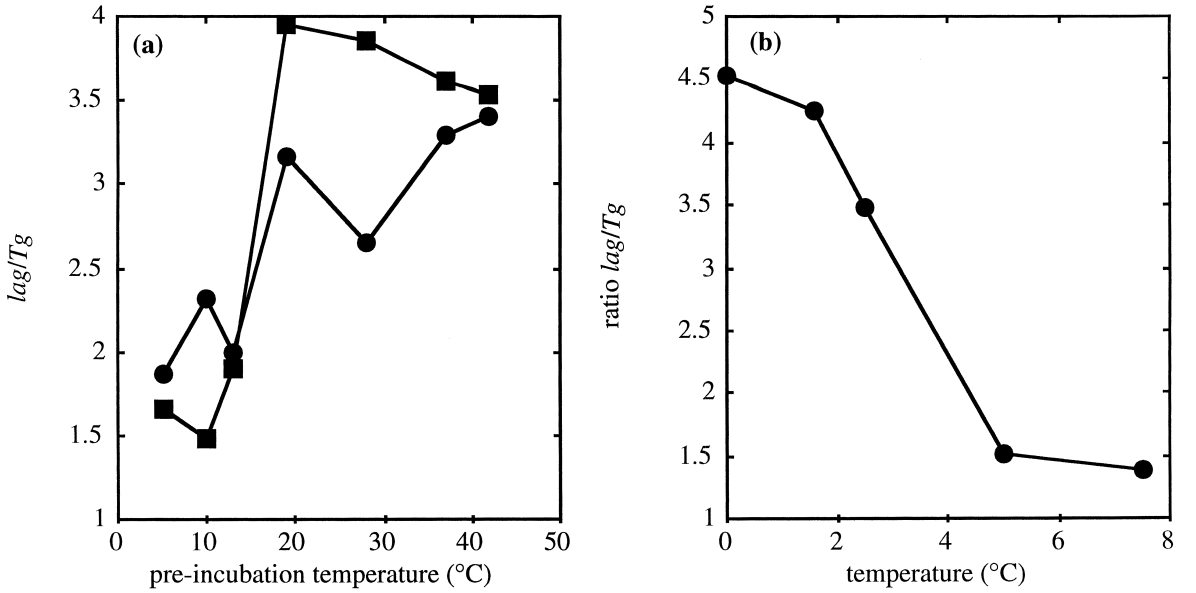

Fig. 10. Effect of (a) pre-incubation temperature on *lag/Tg* and of (b) the incubation temperature on the pre-incubation dependent increase of *lag/Tg* for *L. monocytogenes*. In (a), (●) are ratios obtained in aerobic conditions and (■) are ratios obtained in anaerobic conditions. Ratios plotted in (b) are *lag/Tg* obtained for a pre-incubation at 30°C divided by those obtained for a pre-incubation at 4°C. Data from: (a) Buchanan and Klawitter (1991), (b) Walker et al. (1990).

concentration could widely increase the lag phase duration.

7. Conclusion

The use of existing predictive models allows to explain the main variability of the growth rate of *L. monocytogenes* in different environmental conditions but the hypothesis of multiplicative effects of environmental factors on μ_{max} leads to a poor fit near the limits of growth of the pathogen which are conditions met in agro-food industry. Furthermore, a great dispersion was observed for some parameter estimations. The coefficients of variation for T_{min}, pH_{min}, $a_{w,min}$, monolaurin and CO_2 MICs, and μ_{opt} were, respectively, 1.66, 0.08, 0.03, 1.12, 0.94, and 26.98. The high values obtained for T_{min}, monolaurin and CO_2 MICs, and μ_{opt} can be due to absurd outliers or to effects of environmental factors not taken into account by the model, i.e. interactions, or to a strain effect.

The model used is also two times less accurate to describe the effect of environmental factors on the lag time of *L. monocytogenes*. New models must then be proposed for lag time, particularly to model the effect of ecological conditions encountered by cells during agro-food processes on subsequent lag time of the pathogen in foods.

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