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ORIGINAL ARTICLE

Temperature dependence of growth kinetics of food bacteria

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A predictive model is presented that describes the non-Arrhenius behaviour of growth and survival kinetics of food bacteria, in both the growth phase and lag phase of growth as influenced by temperature, in a wide range of foods and media. For independent data spanning 88 years and seven independent researchers, the model gave a very high degree of goodness of fit explaining between 96·1 and 99·9% of the variance accounted for (%V*) in the growth phase, and between 95·6 and 99·5% of the %V in the lag time, with an overall mean of 98·4%V. The model is a* modified *Arrhenius form, formulated from consideration of temperature-dependent chemical rate theory (CRR). This model form has not previously been evaluated for predicting temperature-dependent growth kinetics of bacteria. The model has two terms, namely, 1/*T *and ln*T*, together with three coefficients. The model has fitted all available data without exception. This very good fit of the predictions of the model to primary data compared very well with the established and widely applied, empirical model form of Davey. Both models imply temperature-dependent Arrhenius parameters for the rate of microbial growth and survival. Both appear very useful to describe practically the non-linear dependence of the rate coefficient for growth, and the lag time, which normally prevents the use of the Arrhenius equation.*

Introduction

The food industries are generally a nation's largest manufacturing sector, and one of the most stable (Anon. 1994). Realization of the potential for an improved process design, and the longer-term control and optimization of a large number of food processes, rests on the formulation of adequate models to predict the effect of environmental factors (i.e. temperature, salt concentration (i.e. a_w), pH, etc) on the growth and survival kinetics of bacteria (Davey 1992, 1994, McMeekin et al. 1993). The development of microbial kinetic models and their applications is referred to as 'microbiological process modelling', or more restrictively, 'predictive microbiology' (Davey 1993b). It is desirable that a kinetic model should be robust, parsimonious and be easy to use (McMeekin et al. 1993).

Arrhenius plots of the growth kinetics of bacteria (i.e. a plot of logarithm of the growth rate vs reciprocal of absolute temperature) are widely used in the food industry and elsewhere. However, these plots have been known for some years to be non-linear and to show significant curvature (for substantiated data). That is, they show an apparent change in the Arrhenius parameters (frequency factor and activation energy) with temperature. The magnitude of the activation energy (slope) increases as the value of the reciprocal

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of the absolute temperature increases. See for example the illustrations of Johnson et al. (1974) for both bacteria and fungi. As noted by McMeekin et al. (1993) several investigators have used broken curves, or a series or broken curves, each with a separate value of the activation energy (e.g. Schoolfield et al. 1981), to improve fit of the Arrhenius model to observed data. To overcome this drawback, a continuous model form was proposed by Davey (1989). Subsequently this modified Arrhenius model has been very widely illustrated with a wide range of independent data spanning some 88 years (Davey 1991, 1993a, 1994, Davey and Daughtry 1995). This model has demonstrated a very high degree of goodness of fit to all available data without exception.

We believed that there was a striking similarity between the curvature in the Arrhenius plot for bacteria, and that exhibited by some chemical reactions that also show a non-linearity in an Arrhenius plot. In chemical reactions this can arise if there are two competing reactions with different activation energies, for example, where the same reaction may occur both homogeneously or heterogeneously (Levenspiel 1972). It is perhaps not surprising that the Arrhenius equation is not obeyed by a complex reaction system. This is because the temperature dependence of such a reaction is likely to be a complicated function of the temperature dependencies of many reactions rather than an individual reaction. In this, the growth and survival of a bacterial cell is analogous to the operation of a whole chemical plant, and not a single reaction. Chemical reaction rate (CRR) theory appeared to provide a theoretical justification for a *modified* Arrhenius equation. An investigation was therefore undertaken to test the applicability of this non-linear CRR model to predict the temperature dependence of the growth kinetics of bacteria, and in particular, food bacteria.

We report the fit of the CRR model to both the growth phase and lag phase of growth of food bacteria. A comparison is made with an established empirical predictive model that is widely demonstrated in the literature. The CRR model has not previously been applied to the growth kinetics of food bacteria.

Materials and Methods

Chemical kinetics

To describe chemical reactions van't Hoff proposed an equation that is given by (Buchanan and Fulmer 1930):

$$\frac{d\ln k}{dT} = -\frac{Q}{RT^2} \qquad (1)$$

where k=specific rate of reaction (or rate constant for growth) with dimensions of time^{-1}, Q=heat of chemical reaction, R=gas constant and T=absolute temperature of the reaction.

If the heat of reaction is assumed to be temperature dependent ($Q=a''''+b''''T+c''''T^2\ldots$) then Eqn (1) on integration gives:

$$\ln k = a''' + \frac{b'''}{T} + c'''\ln T + \ldots + I \qquad (2)$$

where I is the integration constant. Van't Hoff pointed out that Eqn (2) has the following approximate form:

$$\frac{d\ln k}{dT} = \frac{a''}{T^2} + b'' \qquad (3)$$

However, Arrhenius found the empirical relation of Eqn (4) below:

$$\frac{d\ln k}{dT} = \frac{E}{T^2} \qquad (4)$$

gave a better fit to observed reaction data such as the hydrolysis of sucrose (Buchanan and Fulmer 1930) than the form of Eqn (3).

The integral of Eqn (4) is the widely familiar form of the empirical Arrhenius equation, namely:

$$k = A\exp(-\frac{E}{RT}) \qquad (5)$$

where E=the activation energy (J mole^{-1}) and A=the frequency, or pre-exponential, factor ($time^{-1}$). A plot of ln$k$ *vs* 1/T (an *Arrhenius plot*) should be linear.

A CRR theory was attempted by Eyring that aimed to give a theoretical basis to the

Arrhenius form. This takes the general mathematical form (Levenspiel 1972):

$$k = A'T^n \exp(-\frac{E'}{RT}) \qquad (6)$$

With n=1 Eqn (6) yields the temperature dependence predicted by the Eyring Transition-state theory, with n=1/2, the equation yields the temperature dependence predicted by collision theory, and with n=zero, the equation reduces to the familiar Arrhenius form of Eqn (5). Readers should note that:

$$E' = E - nRT \qquad (6a)$$

and

$$A' = A(eT)^{-n} \qquad (6b)$$

Equation (6) can be more generally expressed as:

$$\ln k = A'' + B/T + C\ln T \qquad (7)$$

where $A''=\ln A'$, $B=-E'/R$ and $C=n$, are coefficients.

Microbial kinetics

An idealized growth curve for bacteria involves at least four identifiable phases (Stanier et al. 1972, McMeekin et al. 1993) the: lag phase; growth (exponential) phase; stationary phase, and; the death (decline) phase. The idealized curve shows growth starts from a zero rate which accelerates gradually with time to a maximal value, resulting in a lag phase. The lag phase can vary considerably and does not always occur (Stanier 1972). In the growth phase the bacteria divide regularly, with the daughter cells behaving in an identical manner, giving rise to an exponential increase in cell numbers.

Model formulation for bacterial growth kinetics has largely been concerned with the growth, and lag, phases of growth, although we note the work of McKee and Gould (1988) in developing a simple mathematical model of the thermal death of micro-organisms. The growth phase is important to the growth of bacteria (and for defining the growth state of the bacteria), whilst the lag phase is important to the modelling of foodborne pathogens (Zwietering et al. 1992) where delaying the initiation of growth, by maximizing the duration of the lag, is a primary consideration. Of the many environmental factors that affect growth, those considered to be of particular importance are temperature, water activity and pH. Temperature, however, is of primary importance in determining the survival and growth of bacteria (Ross and McMeekin 1991), and model formulation generally starts with temperature effects.

The value of the rate constant for the growth k is obtained from the bacterial growth curve. This can be done by traditional (subjective) methods (Stanier et al. 1972, McMeekin et al. 1993) or by more recent mathematical means, using for example, derivatives of forms of a fit of a logistic equation (Zwietering 1992, Gibson 1988, McMeekin et al. 1993, Davey and Daughtry 1995).

To account for the observed curvature in Arrhenius plots of bacterial growth data, Davey (1989) proposed an empirical and modified *additive* Arrhenius model. This was based initially on a series of observations, and later extensive testing against independent and published data (Davey 1991, 1993a, 1993b, 1994, Davey and Daughtry 1995). Where temperature is the sole environmental factor this model for the growth rate of bacteria in the growth phase is given by:

$$\ln k = C_0 + C_1/T + C_2/T^2 \qquad (8)$$

where C_0–C_2 are coefficients. The model has fitted all published data without exception. It is apparent from Eqn (8) that the model is an Arrhenius form with an additional term $(1/T^2)$ to account for curvature.

For the 'Davey' model the lag time is given by (Davey 1991, 1993a):

$$\ln\left(\frac{1}{\text{lagtime}}\right) = C_0' + C_1'/T + C_2'/T^2 \qquad (9)$$

Readers should note that it is the reciprocal of lag time that is used in Eqns (8) and (9). This is so as to retain consistent dimensions of $time^{-1}$.

For the CRR model a corresponding lag time, based on a similarity with Eqns (8) and (9), could be given by:

$$\ln\left(\frac{1}{\text{lagtime}}\right) = A''' + B'/T + C'\ln T \quad (10)$$

It is noteworthy that the value of the temperature where the first derivative of the CRR model—equations (7) and (10)—and the Davey models—equations (8) and (9)—is zero, namely, T_{opt}, is the value at which the growth rate constant (k) and the reciprocal of the lag time are an optimum. This follows from the structural form of the two models.

Fitting the models to published data

Equations (7) and (8) for the growth phase, and (9) and (10) for the lag phase, were fitted to published and independent data in the literature for a range bacteria using the statistical package GENSTAT (Lane 1987, Digby 1989, Payne 1989).

As a measure of goodness of fit of the models, the per cent variance accounted for (%V) was used (Davey 1993a). The per cent variance accounted for is a measure of the difference between the observed and the predicted values and is given by (Snedecor and Cochran 1969):

$$\%V = \left[1 - \frac{(1 - r^2)(N - 1)}{(N - N_T - 1)}\right] \times 100 \quad (11)$$

where N=number of observations, N_T=number of terms ($1/T$, $\ln T$, $1/T^2$ etc) and r^2=multiple regression coefficient. Because the %V takes into account the number of terms used in a model it is a more stringent and appropriate test than the multiple regression coefficient (r^2). At $N \gg N_T$ the $\%V \sim r^2$. An alternative measure of goodness of fit is the mean square error (MSE). Ratkowsky et al. (1991), however, have criticized the use of MSE as a test for the goodness of fit because bacterial growth responses (generation time and lag time) become more variable as their mean magnitude increases.

Results

Table 1 summarizes the values of the model coefficients, determined from the statistical analyses for a range of independent published data, together with the degree of goodness of fit of both the CRR and Davey models for the growth rate. Also shown in the table is the temperature range of the experimental data, and, the predicted temperature for optimum value of the growth rate determined from the first derivative of the models, Eqns (7) and (8). The derivatives are, respectively, $T_{opt}=B/C$ and $T_{opt}=-2C_2/C_1$ for the CRR and Davey forms.

Substitution of the value of the coefficients into the models gives the value of the growth rate constant in hour^{-1}. For example, for the *Escherichia coli* data of Barber (1908), the CRR rate model for growth is:

$$\ln k_{h-1} = 4505.1 - 2.091 \times 10^5/T - 667.6 \ln T \quad (12)$$

The %V value of 98·7% indicates a very high degree of accurate fit of Eqn (12) to these experimental data. Substitution for a mid-range value of T=30°C yields a value of the growth rate constant of k=1·67 h^{-1}.

In similar fashion, Table 2 summarizes the fit of the models for the lag phase to published and independent data. The lag time is given in hours. For example, the Davey model for the lag time for the *E. coli* data of Smith (1985) is given by:

$$\ln(/\text{lagtime})_h = -403.71 + 2.4792 \times 10^5/T - 3.8083 \times 10^7/T^2 \quad (13)$$

The value of the percent variance accounted for of 99·2% indicates a very high degree of fit of Eqn (13) to these data. Substitution for a mid-range of T=25°C, yields a lag time of 1·84 h.

Tables 3 and 4 are illustrative of the residuals from the models. Table 3 shows the residuals (i.e. observed value–predicted value) from the CRR model fit to the growth rate data of Barber (1908). Table 4 shows the residuals from the Davey model fit to the lag time data of Smith (1985).

Table 1. Summary and comparison of the fit of the chemical reaction-rate[a] and Davey[b] model for the growth rate with temperature as the sole environmental factor

Micro-organism	Model (1) (2)	A'' C_0	B ($\times10^{-5}$) C_1 ($\times10^{-5}$)	C C_2	%V	N	Temperature range (°C)	T_{opt}	Reference
Escherichia coli	(1)	4505·1	−2·091	−667·6	98·7	12	10–40·8	40·2	Barber (1908)
	(2)	−301·5	1·889	$-2{\cdot}979\times10^{7}$	98·8			42·4	
E. coli	(1)	4689·3	−2·187	−694·38	98·9	20	8–46	41·9	Ingraham (1958)
trypticase soy medium	(2)	−310·86	1·9657	$-3{\cdot}1012\times10^{7}$	98·8			42·5	
Pseudomonas aeruginosa	(1)	4849·5	−2·233	−719·73	96·2	10	8–45	37·3	Ingraham (1958)
trypticase soy medium	(2)	−332·87	2·0691	$-3{\cdot}2117\times10^{7}$	96·1			37·5	
Pseudomonad 21–3c	(1)	2576·00	−1·1864	−382·20	98·7	17	0–32	37·4	Ingraham (1958)
trypticase soy medium	(2)	−164·44	1·0263	$-1{\cdot}6001\times10^{7}$	98·8			38·8	
Pseudomonad 1–3b	(1)	1857·80	−0·86077	−275·47	98·8	16	0–32	39·5	Ingraham (1958)
trypticase soy medium	(2)	−116·22	0·73009	$-1{\cdot}147\times10^{7}$	98·8			41·4	
Pseudomonas P-200	(1)	3805·30	−1·7240	−566·46	98·5	16	0–34	31·3	Ingraham (1958)
trypticase soy medium	(2)	−256·09	1·5601	$-2{\cdot}3780\times10^{7}$	98·6			31·9	
E. coli SF grown in	(1)	3930·49	−1·8289	−582·20	98·4	8	8·2–40	41·1	Smith (1985)
minced meat	(2)	−258·685	1·6307	$-2{\cdot}5728\times10^{7}$	98·4			41·9	
Coliforms grown in	(1)	3722·86	−1·7340	−551·01	98·1	8	8·2–40	42·7	Smith (1985)
minced meat	(2)	−241·72	1·5367	$-2{\cdot}4331\times10^{7}$	98·2			43·7	
Salmonella typhimurium	(1)	3685·83	−1·7214	−545·59	98·9	7	10–40	42·5	Smith (1985)
minced meat	(2)	−241·08	1·5307	$-2{\cdot}4215\times10^{7}$	99·0			43·4	
Pseudomonas spp. Strain E5.2	(1)	2282·7	−1·0593	−338·22	99·2	15	4·4–28·1	40·1	Chandler (1988)
media	(2)	−140·80	0·8930	$-1{\cdot}4081\times10^{7}$	99·2			42·4	
Yersinia enterocolitica	(1)	4305·86	−1·9453	−641·65	99·8	10	2·8–24·1	30·2	Adams et al. (1991)
(pH 5·5 with H_2SO_4)	(2)	−286·10	1·726	$-2{\cdot}625\times10^{7}$	99·8			31·2	
Mixed Salmonellae	(1)	9717·7	−4·3921	−1446·52	98·2	5	10–30	30·6	Gibson (pers. comm.)
inoculum[c] tryptone soy broth	(2)	−675·90	4·1023	$-6{\cdot}2288\times10^{7}$	98·2			30·6	
E. coli 0157:H7[d]	(1)	3088·63	−1·4518	−456·78	99·9	13	10–42	44·8	Buchanan (pers. comm.)
brain–heart infusion	(2)	−199·49	1·2733	$-2{\cdot}0306\times10^{7}$	99·8			46·0	

[a] $\ln k = A'' + B/T + C\ln T$; [b] $\ln k = C_0 + C_1/T + C_2/T^2$; [c] NaCl=1·3 wt%/v, pH=5·63. [d] NaCl=5 g/l, pH=6·5, $NaNO_2$=0. k in h^{-1}, T degree absolute.

Table 2. Summary and comparison of the fit of the chemical reaction-rate[a] and Davey[b] models for lag time with temperature as the sole environmental factor

Micro-organism	Model				%V	N	Temperature range (°C)	T_{opt}	Reference
	(1) (2)	A''' C'_0	B' ($\times10^{-5}$) C'_1 ($\times10^{-5}$)	C' C'_2					
Escherichia coli SF grown in minced meat	(1)	5815·18	−2·6547	−864·47	99·2	8	8·2–40	34·0	Smith (1985)
	(2)	−403·71	2·4792	$-3·8083\times10^{7}$	99·2			34·2	
Coliforms grown in minced meat	(1)	4642·18	−2·1463	−688·51	98·8	8	8·2–40	38·7	Smith (1985)
	(2)	−312·0	1·9492	$-3·0428\times10^{7}$	98·9			39·2	
Salmonella typhimurium grown in minced meat	(1)	5584·33	−2·5737	−828·71	95·6	7	10–40	37·6	Smith (1985)
	(2)	−382·85	2·3808	$-3·7001\times10^{7}$	95·9			37·8	
Pseudomonas spp. Strain E5.2	(1)	3036·42	−1·3947	−450·93	99·5	15	4·4–28·1	36·3	Chandler (1988)
	(2)	−195·05	1·2108	$-1·8811\times10^{7}$	99·5			37·7	
Mixed Salmonellae inoculum[c] tryptone soya broth	(1)	6218·03	−2·8253	−925·29	96·6	5	10–30	32·3	Gibson (pers. comm.)
	(2)	−422·22	2·5756	$-3·9394\times10^{7}$	96·5			32·9	
E. coli 0157:H7[d] brain–heart infusion	(1)	4385·12	−2·0329	−650·18	99·1	13	10–42	39·7	Buchanan (pers. comm.)
	(2)	−295·95	1·8506	$-2·8971\times10^{7}$	99·2			40·1	

[a] $\ln\left(\frac{1}{\text{lagtime}}\right) = A''' + B'/T + C'\ln T$

[b] $\ln\left(\frac{1}{\text{lagtime}}\right) = C_0' + C_1'/T + C_2'/T^2$

[c] NaCl=1·3 %wt/v, pH=5·63.
[d] NaCl=5 g/l, pH=6·5, $NaNO_2$=0.
Lagtime in h, T degree absolute.

Fig. 1 illustrates the Arrhenius model (see Eqn 5) fit to the *Yersinia enterocolitica* data (pH 5·5 with the acidulant H_2SO_4) of Adams et al. (1991) over the temperature range 2·8–24·1°C. Two linear portions to the curvature are judged to give the best fit. Each gives rise to a separate activation energy, namely E_1 and E_2. In part (b) of Fig. 1 a comparison of the two Arrhenius activation energies is made with the smooth function of the temperature-dependent CRR activation energy (see Eqn 6a).

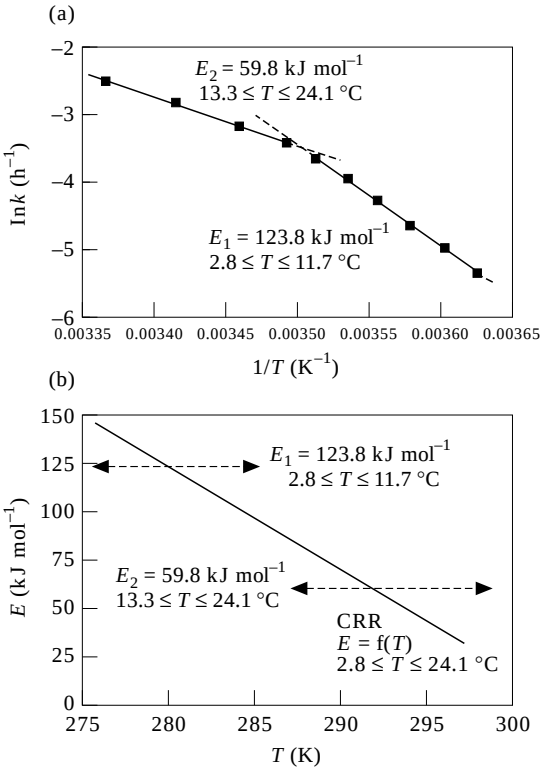

Figure 1. Comparison of the activation energy for both the Arrhenius and CRR models for the *Yersinia enterocolitica* data of Adams et al. (1991). (a) Arrhenius separate activation energies, E_1 and E_2, for best fit to ln$k$ vs 1/T (b) CRR temperature-dependent activation energy, and Arrhenius activation energies as a effected by temperature.

Discussion

It is seen from Tables 1 and 2 that both the CRR and Davey model give a very high degree of fit to independent data for a range of food bacteria. The %V ranges between 96·1 and 99·9% for the growth phase, and, between 95·6 and 99·5% for the lag phase. The overall mean value of the %V is 98·4%. It is apparent that predictions from either model for the growth rate or lag time would be in very good agreement with the observed values. This is borne-out in the values of the residuals illustrated in Tables 3 and 4 and, those for all the data sets of Tables 1 and 2. Because there was no apparent structure in the residuals, it is unlikely that either model form could be reduced to fewer than the two temperature terms used.

Both the CRR and Davey models apply to a wide range of data for food bacteria spanning several independent authors and some 88 years. This apparent universality of the respective model forms is strengthened from

Table 3. Table of residuals (=observed–predicted value) for the CRR predicted rate constant (k) for *Escherichia coli* of the data of Barber (1908)

Temperature (°C)	k (h^{-1})	
	Predicted	Residual
10·0	0·0952	–0·0152
15·4	0·320	0·0522
18·1	0·530	0·108
21·5	0·908	0·0562
23·6	1·205	–0·0379
25·5	1·507	–0·0148
27·6	1·865	–0·221
29·6	2·209	–0·0892
33·6	2·827	–0·427
37·2	3·189	0·054
39·6	3·284	0·246
40·8	3·28	0·206

Table 4. Table of residuals (=observed–predicted value) for the Davey predicted lag time for *Escherichia coli* of the data of Smith (1985)

Temperature (°C)	*Lagtime* (h)	
	Predicted	Residual
8·2	39·7	0·31
10	24·1	2·91
15	7·56	–1·46
20	3·24	–0·044
25	1·84	0·155
30	1·36	0·144
35	1·26	–0·0575
40	1·44	–0·0393

observation of two facts. The first, only the values of the coefficients change for each bacterium (the model form remains constant). Second, the sign on the coefficients of both models for all data of Tables 1 and 2 are consistent. That is, the CRR model has a consistent positive sign on the coefficient A'', and a negative sign on the other model coefficients, B and C; and the coefficients C_0 and C_2 of the Davey form are consistently negative in sign. For the Davey model these signs are consistent with all previous studies (Davey 1989, 1991, 1993a, 1994, Davey and Daughtry 1995).

Despite the very good fit of both models, extrapolation outside the range of experimental data must be done with caution. Neither model predicts a limiting value. Nevertheless, the very good fit obtained suggests limited extrapolation could be done reliably, especially at the lower temperatures.

From Tables 1 and 2 it can be seen that the values of T_{opt}, the temperature at which there is a maximum value of the growth rate constant, or alternatively, the lag time, lies outside the range of experimental data. See for example, the *Y. enterocolitica* data of Adams et al. (1991) in Table 1, and in Table 2, the *Pseudomonas* spp. data of Chandler (1988). It is not known, therefore, whether these are accurate predictions. Confirmation could be readily be obtained with limited experimental work.

Because both the models have an identical number of coefficients (A'', B and C, and C_0–C_2, respectively) and give a very high degree of fit, there appears little advantage in using one over the other. The Davey form might be said to be slightly easier to obtain from the necessary regression analyses of data however. Both models have fitted all available data without exception.

The temperature-dependent activation energy of the CRR model is clearly highlighted through comparison with the two separate activation energies necessary for the Arrhenius model fit to the *Y. enterocolitica* data of Adams et al. (1991), Fig. 1. Arrhenius model fits to these and other data, from Tables 1 and 2, requires that a series of separate portions of the curvature of the Arrhenius plot are defined by separate activation energies. The temperature-dependent activation energy for the CRR model permits a single smooth and continuous function to the curvature. This is advantageous in that it obviates the subjective assessment needed for the Arrhenius model fit to observed curvature.

An interesting feature of the two model forms is the large magnitude of the values of the coefficients. This is most noticeable when comparison is made between the value of the coefficients for bacterial growth kinetics, Tables 1 and 2, and data available for the kinetics of chemical reactions.

Chemical reactions in solution exhibit more curvature in the Arrhenius plot than do reactions in the gas phase. That is, the coefficient C, in the CRR model of equation (7), is greater than that predicted from either collision or transition-state theory. Some reaction examples are (Benson 1982):

$$BrCH_2CO_2^- + S_2O_3^{2-} \rightarrow S_2O_3CH_2CO_2^{2-} + Br^- \quad (14)$$

$$CH_3Br + H_2O \rightarrow CH_3OH + H^+ + Br^- \quad (15)$$

$$CCl_3CO_2H \rightarrow CHCl_3 + CO_2 \quad (16)$$

$$\alpha - glucose \rightarrow \beta - glucose \quad (17)$$

In reaction (14) the non-Arrhenius behaviour is attributed to ion activities, and the effect vanishes at zero ionic strength. When the kinetic data for reactions (15)–(17) are fitted according to the CRR model of Eqn (7) the following values for the model coefficients are obtained, Table 5.

A comparison of the values of these model coefficients with those for example for the

Table 5. CRR model coefficients[a] for reactions (15), (16) and (17)

Reaction	A''	B ($\times 10^{-5}$)	C	Temperature range (°C)
(15)	267·6	–0·08158	–34·30	17–100
(16)	119·0	–0·23513	–10·07	50–100
(17)	97·1	–0·11605	–10·32	0–50

[a]Taken from Benson (1982) and converted to values consistent with Eqn (7) and with the rate constant, k, in hours^{-1}.

CRR model in Table 1, shows that the sign on the model coefficients (*A*", *B* and *C*) for bacterial growth, and that for the chemical reactions, is consistent. The magnitudes, however, for the chemical reactions are significantly less than those values for bacterial growth. One implication of the values of the *B* coefficient shown in Tables 1 and 2 is that food bacteria have large activation energies for growth.

It is apparent that the CRR model could be of immediate practical use for temperature-dependent data that cannot be fitted accurately with the Arrhenius model.

In modelling the kinetic behaviour of bacteria, models that reliably predict the combined effect of a number of environmental factors, e.g. combined T and pH or T and pH & a_w, are of particular interest (Davey, 1989, 1994, McMeekin et al. 1993, Davey and Daughtry 1995, Cerf et al. 1996). The types of these models were categorized by Davey (1989, 1993a) and later, and more extensively, by McMeekin et al. (1993) and Skinner et al. (1994). Model types include the: polynomial; linear and non-linear Arrhenius, and Belehradek (or alternatively titled square-root) forms. The accurate predictions obtained with the CRR form suggests an additional category. Extension of this new category form to predictions for the combined effect of two or more environmental factors is in progress (Davey et al. 1996). The CRR form, however, might not be as easily amenable to this, as for example, are the additive Davey form (Davey, 1989, 1991, 1993a, 1994, Davey and Daughtry 1995) or the square-root form (Adams et al. 1991, Chandler and McMeekin 1989, McMeekin et al. 1993).

Conclusions

(1) A CRR model gives a very high degree of accurate prediction of the rate constant for growth of bacteria in the growth phase, and; the lag time for the lag phase, to independent and published data spanning seven independent researchers and 88 years. These data include a range of bacterial types in food and growth media.

(2) The high degree of accurate prediction of the CRR model compares very well with the established and widely-applied modified Arrhenius model of Davey.

(3) This very good fit of the CRR and Davey model forms to independent data suggest that food bacteria have large, temperature-dependent, activation energies for growth.

(4) Our findings could assist future formulations of mechanistic models of bacterial growth, based on rates of reaction and activation energies.

(5) The CRR model, in addition to the Davey model, is of immediate practical assistance for growth data that cannot be accurately fitted by the use of the Arrhenius equation.

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