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Comparison of the Schoolfield (non-linear Arrhenius) model and the Square Root model for predicting bacterial growth in foods

C. Adair*, D. C. Kilsby and P. T. Whittall†

Microbiology Section, Unilever Research, Colworth House, Sharnbrook, Bedford, MK44 1LQ, UK

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A comparative assessment of eight sets of data demonstrating the effect of temperature on the growth of bacteria in foods was made. For each set of data a Schoolfield model and a Square Root model were constructed. Predictions from both models were compared with the original data to look at the 'goodness of fit'. In every case the Schoolfield model was found to be a more reliable description of the experimental data. The Square Root model was found to deviate significantly from the observed data at the lowest temperatures in all but one case. It is therefore recommended that the Schoolfield model is used to produce predictive models from bacterial growth data.

Introduction

Temperature is a major factor determining the growth rate of bacteria. Increasingly mathematical modelling techniques are being applied to predict the effect of temperature and other factors on bacterial growth rates (Baird-Parker and Kilsby 1987). Various models have been proposed to describe the relationship between temperature and bacterial growth. The original linear Arrhenius equation (Arrhenius 1889) has been applied to microbial growth as well as chemical reactions but it is widely acknowledged that the relationship between the logarithm of the growth curve parameters (for example lag time or generation time) and the inverse of the absolute temperature is non-linear or at least linear over only a portion of the temperature range (Ingraham 1958, Stannard et al. 1985, Mohr and Krawiec 1980, Shaw 1967, Scott 1937 and Ward and Cockson 1972). Ohye and Scott in 1953 showed a non-linear relationship between the logarithm of the lag time of *Clostridium botulinum* and temperature. A non-linear regression of the Arrhenius relationship was proposed by Schoolfield et al. (1981) which has successfully been applied to bacterial growth data by Broughall et al. (1983) and by Broughall and Brown (1984). Another equation which has been proposed is the Square Root relationship of Ratkowsky et al. (1982, 1983). This relates the square root of the growth rate to the temperature of incubation. This model has been applied by various workers, especially in the field of food spoilage (Pooni and Mead 1984, Chandler and McMeekin 1985a,b, Stannard et al. 1985, Gill and Phillips 1985, McMeekin et al. 1987).

* Please address reprint requests to Mrs C. Adair at the above address.
† Present address: Unilever Research, Port Sunlight, Wirral, Merseyside, L63 3JW, UK.

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Other types of models have been used to predict microbial growth such as the quadratic-type response surface (for an example see Gibson et al. 1988).

These polynomial models are not considered further in this paper because the data has to have variation in at least two parameters (neither of which have to be temperature) to be able to construct the model whereas the Schoolfield and Square Root models have temperature variation as their basis and in this paper the data used is of this type.

In this paper we determine if either the Schoolfield or Square Root models are better descriptions of bacterial growth (in terms of lag and generation times) by carrying a direct comparison on eight sets of data covering both the low temperature range (minimum to optimum growth temperatures) and the whole biokinetic growth temperature range (minimum to maximum).

Materials and Methods

Selection of datasets for comparison

Eight sets of bacterial growth data (lag and generation times at varying temperatures) were chosen at random from our extensive database. This database contains over 100 sets of data on the growth of food pathogens and spoilage organisms in various food

Table 1. Summary of the growth parameters investigated.

Dataset number	Organism & food	Inoculum	Lag or generation time model	Whole or lower temperature range studied
1.	Proteolytic *Clostridium botulinum* cooked turkey	Spore cocktail	Lag	Lower
2.	Proteolytic *Clostridium botulinum* cooked turkey	Spore cocktail	Gen	Lower
3.	Gram negative spoilage flora raw beef mince	Indigenous flora	Lag	Lower
4.	*Pseudomonas fluorescens* ice cream mix	Vegetative	Lag	Lower
5.	*Staphylococcus aureus* raw shortcrust pastry	Vegetative	Lag	Whole
6.	*Staphylococcus aureus* raw shortcrust pastry	Vegetative	Gen	Whole
7.	*Bacillus cereus* steak & kideny pie mix	Spore cocktail	Lag	Whole
8.	Gram negative spoilage flora raw fish fillets	Indigenous flora	Gen	Lower

Gen = generation time

products. Data with temperature as the only variable were chosen but the data covers a wide range of organisms (pathogens and spoilage organisms) and foods, and a variety of inoculation techniques (see Table 1 for details).

Strains

The organisms studied (see Table 2) were either (a) indigenous populations of organisms naturally occurring in the food (datasets 3 and 8), (b) inoculated pure cultures of vegetative cells (datasets 4, 5 and 6) or (c) inoculated cocktails of spores (datasets 1, 2 and 7). More details of these organisms are available on request.

Inoculation/sampling

The vegetative cell inocula were stationary phase cultures. The spore inocula were heat shocked before use. No inoculum preparation was necessary in the case of the indigenous flora models. For more details of the inoculum preparation see Table 2.

The foods used as growth menstrua are shown in Table 1. The growth menstrua used in datasets 1, 2, 4, 5, 6 and 7 were not serile but were obtained with very low levels of background flora ($<100\ g^{-1}$). They were each checked for absence of the test organism before use and uninoculated controls were checked throughout the experiments. The foods were dispensed into separate packs, two

Table 2. Details of the inocula used in the experiments.

Dataset number	Organism & food	Number of strains used in inoculum	Suspending medium for inoculum	Inoculum preparation	Final inoculum level per g of food
1.	Proteolytic *Clostridium botulinum* cooked turkey	9 Type A 7 Type B 2 Type F	Sterile distilled water	Heat shock spores 73°C/15 min.	20
2.	Proteolytic *Clostridium botulinum* cooked turkey	←as dataset 1→			
3.	Gram negative spoilage flora (pseudomonads) raw beef mince	Not applicable	None	None	10^4–10^5
4.	*Pseudomonas fluorescens* ice cream mix	8 isolated from ice cream	0·1% peptone water (Evans)	Stationary phase culture (5°C/7 days)	10^3
5.	*Staphylococcus aureus* raw shortcrust pastry	1 (NCTC 10655)	0·1% peptone water (Evans)	Stationary phase culture (37°C/18 hrs)	10^3
6.	*Staphylococcus aureus* raw shortcrust pastry	←as dataset 5→			
7.	*Bacillus cereus* steak & kidney pie mix	4	Sterile distilled water	Heat shock spores 75°C/20 min.	200
8.	Gram negative spoilage flora (pseudomonads) raw fish fillets	Not applicable	None	None	10^5

for each sample time, and each pack inoculated (vegetative and spore inocula) with 10–1000 g^{-1} of the organism/cocktail in 0·1 ml of suspending medium (see Table 2).

All samples were placed in the appropriate incubators or water baths and the temperatures of the incubators and water baths monitored twice daily over the total incubation period to ensure that temperatures were controlled to within 0·5°C of the set temperature.

At each sample time (relevant to the organism/food/temperature combination) two packs of the food were removed from the incubator and then pooled, diluted and counted using the methods shown in Table 3.

Calculation of lag and generation times

Growth curves (logarithm of bacterial counts versus time) were constructed for each organism/food combination at each of the temperatures of incubation. From these growth curves estimates of the lag and generation times were made following the method described by Broughall et al. 1983.

Table 3. Counting methods.

Dataset number	Organism & food	Diluent	Medium for counting organisms	Incubation of plates (time & temperature)
1.	Proteolytic *Clostridium botulinum* cooked turkey	BEM	Tryptone Soya Agar (pour plates)	2 days/30°C anaerobically
2.	Proteolytic *Clostridium botulinum* cooked turkey	←——as dataset 1——→		
3.	Gram negative spoilage flora raw beef mince	0·1% peptone water	Plate Count Agar (pour plates)	2 days/30°C aerobically
4.	*Pseudomonas fluorescens* ice cream mix	0·1% peptone water	Plate Count Agar (spread plates)	2 days/30°C aerobically
5.	*Staphylococcus aureus* raw shortcrust pastry	0·1% peptone water	Baird–Parker Agar (spread plates)	1 day/37°C aerobically
6.	*Staphylococcus aureus* raw shortcrust pastry	←——as dataset 5——→		
7.	*Bacillus cereus* steak & kidney pie mix	0·1% peptone water	*Bacillus cereus* Medium, PEMBA (spread plates)	1 day/37°C aerobically
8.	Gram negative spoilage flora raw fish fillets	0·1% peptone+ 0·5% NaCl	Nutrient Agar +0·5% NaCl (pour plates)	2 days/30°C aerobically

Sources of media:
BEM = Botulinum enrichment medium ref. Hobbs et al. 1982
Tryptone Soya Agar from Oxoid (code CM131)
Peptone water from Evans Medical Ltd.
Plate Count Agar from Difco (code 0479)
Baird–Parker Agar from Oxoid (code CM275)
PEMBA = Polymyxin pyruvate egg yolk mannitol bromothymol blue agar from Oxoid (code CM617)
Nutrient agar from Oxoid (code CM3)

Growth curves at five or more temperatures were used to construct a lower temperature range model (minimum to optimum growth temperatures) and seven or more temperatures for a whole temperature range model (minimum to maximum growth temperatures).

Curve fitting

The two growth curve parameters were then used to construct separate mathematical models – a lag time model describing the effect of temperature on lag and a generation time model describing the effect of temperature on doubling times. The Square Root equation has been used here to model lag times separately from generation times. Most workers in the past have applied this equation to growth rates measured by increases in optical density which does include the lag phase but does not measure it as such. Chandler and McMeekin (1985b) have shown that the same Square Root relationship between the square root of the inverse of the lag time and temperature does apply.

Curve fitting was performed on a VAX 8650 mainframe computer using the non-linear regression (NLIN) procedure of SAS (Statistical Analysis System). The Marquardt iterative method of fitting was used. Details of this procedure are included in the SAS User's Guide (SAS Institute Inc., Cary, North Carolina, USA, 1985).

The original Schoolfield equation (Schoolfield et al. 1981) covering the lower temperature range is as shown below:-

$$\frac{1}{K} = \frac{\rho(25)\frac{T}{298}\exp\left\{\frac{HA}{R}\left(\frac{1}{298} - \frac{1}{T}\right)\right\}}{1 + \exp\left\{\frac{HL}{R}\left(\frac{1}{T1/2L} - \frac{1}{T}\right)\right\}} \quad (1)$$

where K = lag or generation time in days
$\rho(25)$ = growth rate at 25°C
T = temperature in degrees Kelvin
HA = constant describing the enthalpy of activation for microbial growth
R = universal gas constant (1·987 cal mol^{-1} k^{-1})
HL = constant describing the enthalpy of low temperature inactivation of growth
$T1/2L$ = constant describing the temperature for 50% low temperature inactivation of growth

For this paper an alternative form of the equation was developed which has improved numerical stability and increased speed of convergence. Convergence is not as dependent on starting values compared with the original form of the equation. The new form of the equation has some similarities to the equation of Sharpe and DeMichele (1977).

The rewritten form of the Schoolfield equation is:

$$\ln(K) = A + (B/T) - \ln T + \ln(1 + \exp(F + (D/T))) \quad (2)$$

where A, B, D and F can be expressed in terms of HA, HL, $T1/2L$ and $p(25)$ as in Eqn (1) above:

$A = \ln 298 - (HA/(R*298)) - \ln \rho(25)$
$B = HA/R$
$D = -HL/R$
$F = HL/(T1/2L*R)$

and as eqn (1)

K = lag or generation time in days
T = temperature in degrees Kelvin

The Square Root equation for the lower temperature range is:

$$\sqrt{r} = b(T - T_0) \quad (3)$$

where r = growth rate constant (or 1/lag or 1/generation time)
b = regression coefficient
T = temperature in degrees Kelvin
T_0 = conceptual temperature of no metabolic significance (temperature below which the rate of growth is zero or lag time is infinite)

For models covering the entire biokinetic temperature range the following equations were used which include a term to cover high temperature inactivation:

Schoolfield

$$\frac{1}{K} = \frac{\rho(25)\frac{T}{298}\exp\left\{\frac{HA}{R}\left(\frac{1}{298}-\frac{1}{T}\right)\right\}}{1+\exp\left\{\frac{HL}{R}\left(\frac{1}{T1/2L}-\frac{1}{T}\right)\right\}+\exp\left\{\frac{HH}{R}\left(\frac{1}{T1/2H}-\frac{1}{T}\right)\right\}} \quad (4)$$

where K, $\rho(25)$, HA, R, T, HL, $T1/2L$ are as eqn (1)

HH = constant describing the enthalpy of high temperature inactivation of growth

$T1/2H$ = constant describing the temperature for 50% high temperature inactivation of growth

The rewritten form of the Schoolfield equation to cover the entire biokinetic temperature range is:

$$\ln(K) = A + (B/T) - \ln T + \ln(1 + \exp(F + D/T) + \exp(G + H/T)) \quad (5)$$

where A, B, D and F are as eqn (2) and

$G = HH/(R^*T1/2L)$

$H = -HH/R$

Square Root

$$\sqrt{r} = b(T - T\min)\{1 - \exp[c(T - T\max)]\} \quad (6)$$

where r, b, T are as eqn (3)

$T\min$ & $T\max$ = minimum and maximum temperatures, respectively, at which the rate of growth is zero or lag is infinite

c = additional parameter to enable model to fit data for temperatures above the optimal temperature

Results and Discussion

One of the most effective means of comparing the two modelling systems is to compare the predicted values of the two models against the actual observed data points. This is done for the eight chosen examples. Tables 4–7 show the comparisons in detail for datasets 1,3,4 and 5. Table 8 is a summary of all the comparisons. The Figs 1–3 illustrate the same effect for a specific example (dataset 1), each set of predicted and observed data presented on different axes. As a means of quantifying differences between predicted and observed values, a measure of 'goodness of fit', the mean square error (MSE), has been used:

$$\text{MSE} = \Sigma\frac{\{(\text{obs} - \text{pred})^2\}}{n} \quad (6)$$

Table 4. Comparison of the observed data for the growth of Clostridium botulinum (proteolytic) in raw minced turkey with predictions from the Square Root and Schoolfield models (Dataset 1).

	Lag time (h)		
Temperature (°C)	Observed data	Schoolfield prediction	Square Root prediction
15·0	672·0	622·89	387·81
17·5	154·08	184·42	148·01
20·0	74·16	64·92	77·47
25·0	22·22	23·25	32·12
30·0	21·65	21·30	17·47
Mean square error for the fit ⟶ (Number of observations = 5)		683·71	16185·6

Table 5. Comparison of the observed data for the growth of Gram-negative spoilage flora in air packed beef mince with predictions from the Schoolfield and Square Root models (Dataset 3).

	Lag time (h)		
Temperature (°C)	Observed data	Schoolfield prediction	Square Root prediction
−2·0	165·91	158·35	222·58
0·0	98·38	107·08	114·84
2·0	85·37	73·93	69·89
5·0	36·19	44·33	39·53
10·0	20·83	21·50	19·80
13·0	20·74	15·04	14·33
17·0	8·62	10·12	9·96
20·0	7·37	7·88	7·87
25·0	5·54	5·54	5·62
30·0	4·25	4·11	4·20
Mean square error for the fit ⟶ (Number of observations = 10)		36·52	377·51

Table 6. Comparison of the observed data for the growth of Pseudomonas fluorescens in ice cream mix with predictions from the Schoolfield and Square Root models (Dataset 4).

	Lag time (h)		
Temperature (°C)	Observed data	Schoolfield prediction	Square Root prediction
0·8	288·0	247·01	∞
4·0	90·0	128·78	203·28
7·0	78·0	71·40	50·64
10·0	40·8	40·08	22·56
15·0	19·2	15·72	9·26
25·0	2·4	2·66	3·12
Mean square error for the fit ⟶ (Number of observations = 6)		540·05	∞

where obs = observed value of lag or generation time in hours
pred = predicted value of the lag or generation time in h
n = number of observations in the dataset

The residual sum of squares could be used for this comparison, but this is not valid because of the different transformations of the data that are applied by the two modelling techniques (logarithm in the case of the Schoolfield model and square root in the case of the Square Root model). Furthermore, it is useful to compare the values as they are to be used, that is, as values for the lag and generation times of bacteria not as their logarithms or square roots.

The MSE values are shown in Table 8, and it can be seen that the MSE for the Schoolfield model is always smaller than for the Square Root model indicating that the Schoolfield model is producing a better fit to these growth curve paramet-

Table 7. Comparison of the observed data for the growth of Staphylococcus aureus in raw shortcrust pastry with predictions from the Schoolfield and Square Root models (Dataset 5).

Temperature (°C)	Lag time (h) Observed data	Schoolfield prediction	Square Root prediction
10·6	144·0	135·88	260·98
12·7	72·0	82·23	86·50
15·3	48·0	45·33	37·18
20·1	19·0	16·81	13·90
25·2	5·53	7·31	6·96
29·9	7·00	4·33	4·34
30·3	3·31	4·18	4·20
33·3	3·60	3·35	3·34
36·8	2·0	2·78	2·71
36·9	3·0	2·77	2·69
41·5	3·0	2·54	2·59
43·8	3·14	3·42	3·41
45·6	7·01	6·84	6·86
Mean square error for the fit ⟶ (Number of observations = 13)		14·98	1080·58

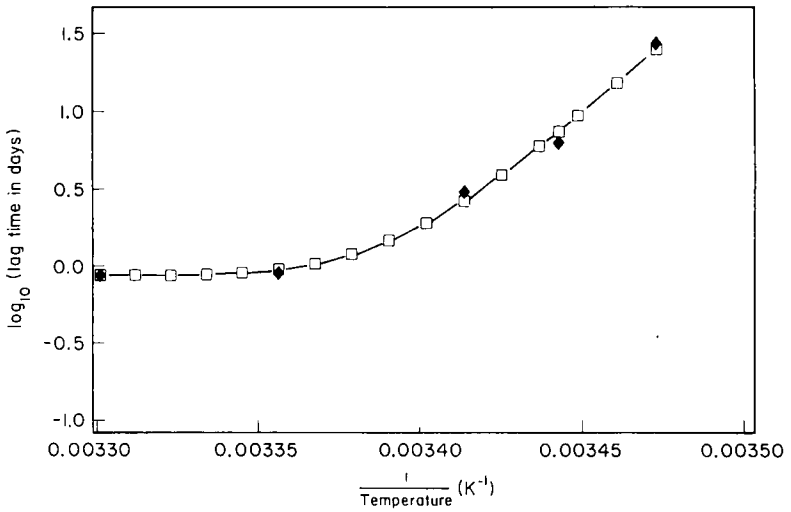

Fig. 1. Observed values for the lag time of *Clostridium botulinum* in turkey meat (dataset 1) and predicted values from the Schoolfield model. ♦ = observed lag; □——□ = predicted lag time.

ers. It might be expected that the model with the greater number of parameters (in this case the Schoolfield model) would produce a slightly better fit but in the cases tested the MSE values for the Schoolfield models are considerably smaller in all cases. For the lower temperature range models, datasets 1–4 and 8, the Schoolfield model produces a very much better fit. This may be explained by the fact that the Square Root equation is, in this case, linear and the data does not fit this relationship well. Even with the whole temperature range models of datasets 5–7, the Schoolfield model produces a better fit than the Square Root

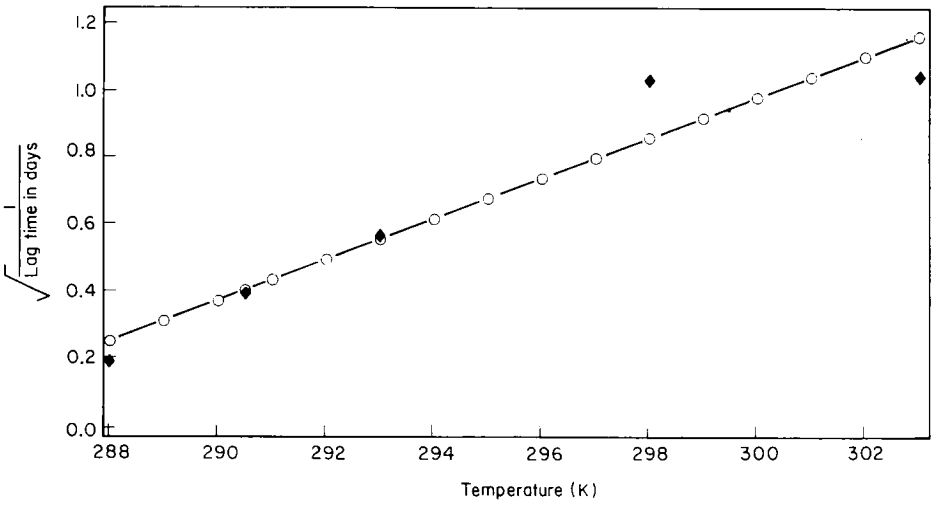

Fig. 2. Observed values for the lag time of *Cl. botulinum* in turkey meat and predicted values from the Square Root model. ♦ = observed lag time; ○——○ = predicted lag time.

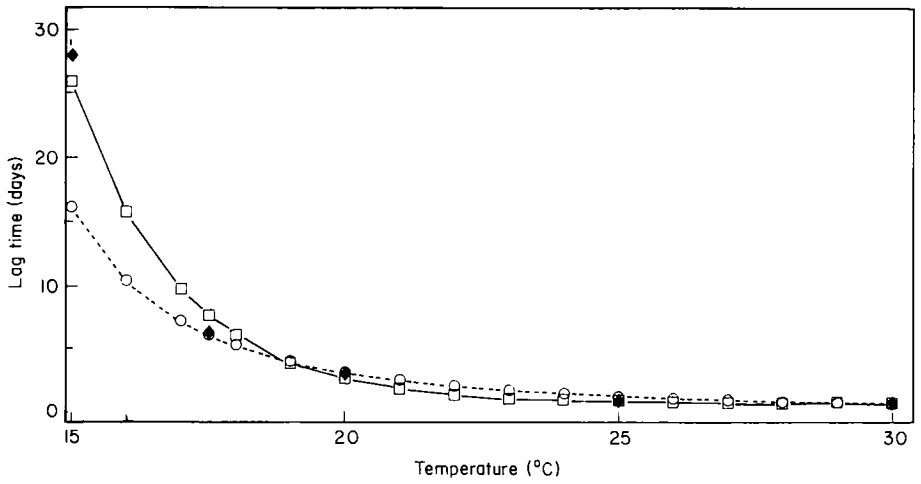

Fig. 3. Comparison of the predicted lag times from the Schoolfield and Square Root models with the observed lag times for dataset 1. ♦ = observed lag time; □——□ = predicted lag time from Schoolfield model; ○— —○ = predicted lag time from Square Root model.

model. For the whole temperature range models the Square Root equation, being non-linear, fits the data well, but not as well as the Schoolfield model.

One apparent reason for the difference in MSEs observed can be seen by reference to the lowest temperature data for the models. With the possible exception of dataset 6, the Square Root model predictions show a systematic divergence from the observed values as the lower temperature limits for growth are approached. This divergence can produce either much higher or much lower predictions when compared to the observed data, the error being in either direction. One of the clearest examples is with dataset 4 (Table 6), where the

Table 8. Summary of the results of the model comparisons.

Dataset number	Organism & commodity	Number of observations	Mean square error for Schoolfield model	Mean square error for Square Root model
1.	Proteolytic *Clostridium botulinum* cooked turkey	5	683·71	16185·6
2.	Proteolytic *Clostridium botulinum* cooked turkey	5	3·80	239·44
3.	Gram negative spoilage flora raw beef mince	10	36·52	377·51
4.	*Pseudomonas fluorescens* ice cream mix	6	540·05	∞
5.	*Staphylococcus aureus* raw shortcrust pastry	13	14·98	1080·58
6.	*Staphylococcus aureus* raw shortcrust pastry	13	1·67	2·53
7.	*Bacillus cereus* steak & kidney pie mix	9	81·22	869·76
8.	Gram negative spoilage flora raw fish fillets	7	6·74	85·65

Square Root model predicts an infinite lag time (no growth) at the lowest temperature (273·76 K) whereas the observed lag time is just 12 days (and Schoolfield prediction is 14·6 days). The predicted square root value at this temperature is actually negative, as it is below the predicted T_0 of 274·01 K, the temperature at which the growth rate is zero.

The real power of the models described here is the ability to combine the growth and lag times, and predict the fate of the modelled organisms in new and untested conditions irrespective of initial contamination levels. this cannot be done with models based upon time to specific levels of increase in counts/absorbance/impedance. As previously described (Broughall et al. 1983) the Verhulst equation can be used by combining lag and generation time predictions to estimate the time to any given level of increase in counts and also the increase in numbers after a given time at a given temperature, as well as allowing predictions of time for growth to begin. One important use of the Schoolfield model is to integrate time and temperature when temperature is fluctuating, and this is likely to be particularly useful at chill temperatures. It is under exactly these conditions

when the Square Root model is likely to make incorrect predictions. It is crucial that the application of these models should be made with confidence, and this can only be done by applying a model such as the Schoolfield which makes realistic predictions of growth over the entire growth range of the bacteria of concern. In this paper we have shown that predictive mathematical models can be built from bacterial growth data.

The two models considered – the Schoolfield and the Square Root – are good for this type of data and are comparable over the majority of the bacterial temperature range.

However, significant errors may result at low (chill) temperatures if the Square Root model is used.

It is therefore proposed that the Schoolfield (non-linear Arrhenius) model is more reliable at low temperatures and should therefore be adopted as the method of producing predictive bacterial growth models.

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