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PAPER

Use of response surface models to predict bacterial growth from time/temperature histories

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A program that predicts the number of generations of bacterial growth from time/temperature history data was developed. The program uses response surface models for Listeria monocytogenes, Aeromonas hydrophila, Yersinia enterocolitica *and* Pseudomonoas fragi *to predict growth under fixed conditions of pH, sodium chloride (NaCl) and sodium nitrite ($NaNO_2$) concentrations, and varying temperature. To obtain time/temperature histories, the program can either receive data manually or set up and read time/temperature dataloggers, and store these histories in data files. Published and experimental growth data were compared with growth predicted by the program under both static and fluctuating temperature regimes. To demonstrate a sample use, the growth of each of the species that would occur during 48 hours in two domestic refrigerators was predicted. Copyright © 1996 Elsevier Science Ltd.*

Keywords: response surface models; *Listeria monocytogenes*; *Yersinia enterocolitica*; *Aeromonas hydrophila*; *Pseudomonas fragi*

INTRODUCTION

Predictive microbiology is of increasing interest to the food industry. Its aim is to predict the growth of spoilage and pathogenic bacteria under the various conditions that might be encountered in the 'chill chain'.

Several approaches have been used to predict microbial growth under constant conditions, including the square root model (Ross and McMeekin, 1991) and response surface models (eg Buchanan and Phillips, 1990). The USDA has published software (Pathogen Modelling Program, Version 4.0) that uses response surface models to predict the growth kinetics, time for specified growth and inactivation/survival of a number of pathogenic bacteria.

However, temperature, the main factor affecting the growth of bacteria on food, is likely to vary during the life of a food product. Therefore, models that predict bacterial growth from real-life fluctuating temperature history data would be more useful than those that predict bacterial growth on the basis of constant temperature. Programs exist that will analyse varying temperature data, but they tend to be designed for specific applications. For example, the Meat Industry Research Institute of New Zealand (MIRINZ) has developed a system for assessing the hygienic adequacy of meat plant processes by analysing the temperature histories of carcasses and subsequent cuts through the initial cooling processes until 7°C is reached, at which temperature *Salmonella*

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growth is insignificant (Gill *et al.* 1991). These time/temperature histories are used to predict the number of generations of *Escherichia coli* that could have grown during that time. The number predicted is referred to as the process hygiene index (PHI) (Jones, 1993). Use of PHI values allows meat plants to optimise their processes and these values could be used as a basis for scientifically justified meat hygiene guidelines (Jones, 1993).

MIRINZ has also produced predictive models for cold-tolerant pathogens (Hudson, 1992, 1993, 1994). These models, similar to the ones produced by the USDA, accommodate only fixed values for temperature, pH, NaCl and nitrite concentrations. However, it was felt that these predictive models could be converted to a form that predicted the number of generations from real-life fluctuating temperature histories. This study describes how this was achieved and illustrates the use of this new program in some preliminary analyses.

MATERIALS AND METHODS

Predictive models used

The seven response surface models used were developed in this laboratory. They were: two models for food strains of *Listeria monocytogenes* (strains L70 and L72) (Hudson, 1994); two models for *Aeromonas hydrophila* (modified from Hudson, 1992), (the type strain ATCC 7966 and a food strain JAH4); two models for *Yersinia enterocolitica* (Hudson, 1993), (the type strain ATCC 9610 and a food strain Y3); and one model for a strain of *Pseudomonas fragi* (unpublished data). Aerobic and anaerobic models were used for all organisms except *P. fragi*, which is an aerobe. The models predict the growth kinetics of microorganisms, taking into account the parameters of temperature, pH, NaCl content (% w/v) and nitrite concentration (ppm). Predicted growth kinetics comprises the lag time and specific growth rate.

Program construction

The program was written for use on an IBM or IBM compatible personal computer using TurboPascal version 6.0 (Borland, Scotts Valley, California, USA).

The core of the program is an array of the coefficients for response surface models predicting a lag time or specific growth rate for the specific bacterial strains described above. Even rows of the array contain the coefficients for lag time while the corresponding odd rows contain those for specific growth rate. Where a coefficient is insignificant, a value of zero is used.

The program incorporates a Delphi™ temperature logger (Tru-Test Systems Ltd, Auckland, New Zealand) initiation and reading facility, enabling a logger to be set up using the program. The logger is then used to record a time/temperature history and these data are later transferred via an interface and stored in computer files. The user can also enter time/temperature profiles into the program manually.

The program analyses the time/temperature histories, entered by either procedure, to predict the bacterial growth that would have occurred during either an entire time/temperature history or user-selected segments. The user is required to select the organism and atmosphere (aerobic or anaerobic), and enter the pH, nitrite and NaCl concentrations. The program calculates the growth kinetics, and gives predictions of the number of generations that would have occurred, with an option to include a lag time or to assume the lag phase has been completed.

Lag time is dealt with by assuming that, initially, the organism has 100% of its lag time to be completed at any one temperature. If the storage temperature is changed, the remaining lag time is a proportion of the lag time at the new temperature. This percentage is then decremented until the percentage of remaining lag time reaches zero. For example, if an organism has a lag time of 10 h at 15°C and spends four hours at that temperature, then 40% of its lag time will have expired, leaving 60% to be resolved. If the temperature drops to 10°C and the lag time is, say, 15 h at this temperature then, since 60% of the lag time remains, it will have to be incubated at 10°C for $60/100 \times 15 = 9$ h for the remaining lag time to be resolved. A similar system for calculating remaining lag time is well established (Smith, 1985; Gill and Jones, 1992; Li and Torres, 1993). Once the lag time is fully completed, the program calculates the number of generations that would occur during each temperature-history-sampling interval and accumulates these values. The program samples the time/temperature history from the datalogger every 1.875 min (ie every 1/32 of an hour). Since bacterial growth curves do not instantaneously switch from lag phase to the maximum growth rate, the models described will tend to underestimate total growth where a small number of generations occur.

The lag time used in the program has been subjected to a conversion factor that allows for the fact that the models were produced by measuring the optical density of broth cultures whereas the growth of microorganisms on food is measured using viable counts (Hudson and Mott, 1994). The use of optical density measurements to produce models has been previously discussed (Hudson, 1994; Hudson and Mott, 1994). A number of difficulties have been identified and most can be remedied. Optical density-derived growth data have been applied in automated systems (McClure *et al.*, 1993) and comprise the data used to produce square root models which have good predictive capabilities (Ross and McMeekin, 1991).

Validation of the program

Comparisons of measured growth with predicted growth at constant temperatures

Growth kinetic data obtained in this laboratory, and derived from published data for *L. monocytogenes*, were used to calculate the growth (in generations, ΔG) that occurred over a given time period. These were compared with predictions made by the corresponding model. Since the program does not incorporate a maximum number of generations, comparisons were valid only up to the end of the exponential growth phase. In these comparisons the incubation temperature was constant.

Predictions of ΔG *of* P. fragi *with temperature shifts and cycling*

The time and temperature history data for Figures 7, 8 and 9 of Fu *et al* (1991) were manually entered into the program and analysed using the parameters of pH 6.5, 0 ppm nitrite, and 0.5% NaCl, because the medium used in the original experiments, reconstituted non-fat dried milk, was assumed to be of that composition. The ΔG values predicted by the program were compared with the measured ΔG values estimated from Figures 7, 8 and 9 of Fu *et al.* (1991). The results shown in Figure 7 of Fu *et al.* (1991) were obtained by cycling a culture of *P. fragi* between 4–16°C until it was 100 h old. The results shown in Figure 8 of Fu *et al.* (1991) were obtained by growing a culture of *P. fragi* at 4°C for 50 h, then cycling it between 16–4°C until it was 94 h old. To obtain their Figure 9, Fu *et al.* (1991) cycled a culture of *P. fragi* through a temperature regime described by a sine wave with amplitude of 6°C, mean temperature of 10°C and period of 24 h.

Comparisons of predicted and measured ΔG *values for* Listeria monocytogenes *under shifting temperatures*

Values for ΔG of *L. monocytogenes* strains L70 and L72 were measured under shifting temperature regimes representing cooling, storing and heating cycles (*Table 1*) in broth cultures, and comparisons made with ΔG values predicted by the models.

Table 1 Shifting temperature regimes representing cooling, storing and heating cycles used for *Listeria monocytogenes*. Time (hours) spent moving to or holding at specified temperatures

Time (h) taken to cool from 40°C to 4°C	Time (h) held at 4°C	Time taken (h) to heat from 4°C to 20°C[a]
1	24	2
1	24	4
4	24	2
4	24	4
1	168	2
1	168	4
4	168	2
4	168	4

[a]For all trials the temperatures at the start and end were 40°C and 20°C respectively.

The medium used was Brain Heart Infusion (BHI, Difco, Detroit, Michigan, USA) containing 10 g/l morpholinopropane sulphonic acid (Serva, Heidelberg, Germany) buffer. Sodium chloride (NaCl) was added where required, and the pH of the medium was adjusted using HCl or NaOH. The medium was dispensed in 15 ml volumes in Hungate Tubes and autoclaved at 121°C for 15 min. Filter-sterilized $NaNO_2$ was added aseptically after autoclaving and just prior to use, where required.

The inocula were incubated in BHI at 30°C for 16 h. Serial ten-fold dilutions of each culture were prepared in 0.85% saline solution, and 0.1 ml volumes of appropriate dilutions were added to the experimental media in tempered Hungate tubes. The Hungate tubes were incubated in Julabo waterbaths (Seelbath, Germany), with the temperature controlled using a Julabo-Programmer PRG (Seelbach, Germany). The waterbaths were equipped with both heating and cooling coils capable of maintaining precise temperature control. The temperature of each waterbath was recorded every 1.875 min using a Delphi temperature logger with the probe inserted into a Hungate tube containing 15 ml of distilled water and sealed with Silaflex RTV (Fosroc Expandite Ltd., Petone, New Zealand), a silicone sealant.

Viable counts at the start and end of each trial were obtained by preparing serial ten-fold dilutions of samples taken from the experimental tubes in dilution fluid (0.85% NaCl + 0.1% peptone) and spreadplating 0.1 ml volumes of appropriate dilutions in duplicate onto half plates of Plate Count Agar (Difco). The plates were incubated at 25°C for 48 h. The number of organisms (cfu/ml) at the start and the end of each experiment was subjected to a logarithmic transformation before any further calculations. Results reported for each trial are the means of triplicate experiments.

Data from the temperature loggers were downloaded using the program and subsequently analysed to give predicted ΔG values for both strains of *L. monocytogenes* under aerobic conditions.

Sample application of the program – predicting growth in refrigerators

Dataloggers were used to record time/temperature histories of two domestic refrigerators. A 48 h section of each time/temperature history was selected and the program was used to predict the growth of the three pathogens and *P. fragi* over that period in each refrigerator.

RESULTS

Practical considerations of the program

An easy-to-use pop-up and pull down menu system is used to access modules for controlling the set-up and downloading of loggers, entry and storage of data and data analysis, including the conditions of the analyses.

Time/temperature histories recorded by temperature loggers can be downloaded, stored and the data analysed after selection of the relevant portion of the temperature record and definition of the growth conditions. Previously stored time/temperature histories may be re-analysed if required.

Comparisons of measured ΔG *values with predicted* ΔG *values at constant temperatures*

Graphs of data interpreted in terms of ΔG values plotted against predicted values are shown in *Figures 1, 2* and *3* for *L. monocytogenes* strains L70 (aerobic), L72 (aerobic) and L70 (anaerobic), respectively. The equations describing the linear regressions of the data in these graphs are:

$$\text{Predicted } \Delta G = 0.930 + 0.950 \times \text{measured } \Delta G \quad (\textit{Figure 1})$$

$$\text{Predicted } \Delta G = 0.857 + 0.747 \times \text{measured } \Delta G \quad (\textit{Figure 2})$$

$$\text{Predicted } \Delta G = 0.562 + 0.686 \times \text{measured } \Delta G \quad (\textit{Figure 3})$$

for the three models respectively. For a perfect fit the equations should read:

$$\text{Predicted } \Delta G = 0 + 1 \times \text{measured } \Delta G$$

The aerobic models for *L. monocytogenes* strains L70 and L72 both performed reasonably well, predicting accurately the amount of growth that would occur under the given conditions. Under anaerobic conditions the model predicted less growth than actually occurred.

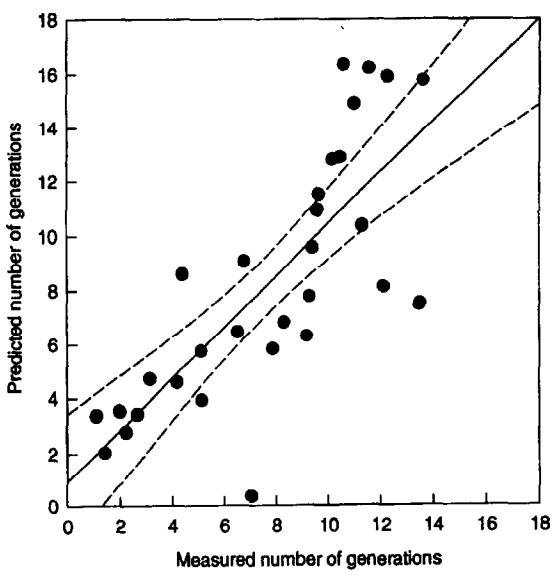

Figure 1 Comparison of measured and predicted growth (in generations) for *L. monocytogenes* L70 under aerobic conditions - - - is 95% confidence interval. ——— is regression line. Measured data were collected in this laboratory (Gill and Reichel, 1989; Hudson and Mott, 1993a, 1993b and 1993c; Hudson and Avery, 1994) in addition to being derived from Wimpfheimer *et al.* (1990), Harmayani *et al.* (1993), Varabioff *et al.* (1992), and Grau and Vanderlinde (1993)

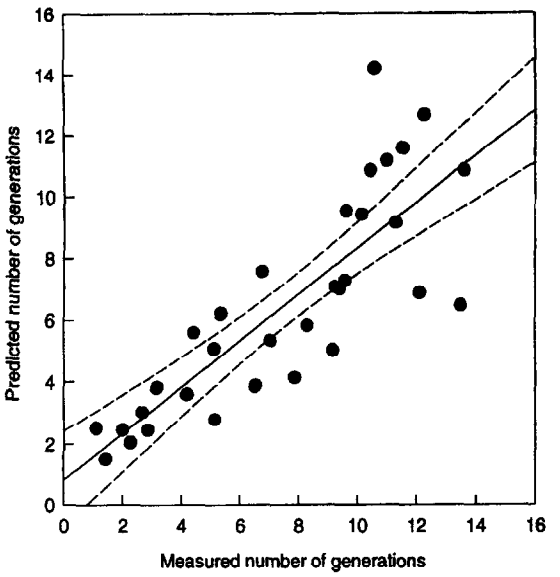

Figure 2 Comparison of measured and predicted growth (in generations) for *L. monocytogenes* L72 under aerobic conditions - - - is 95% confidence interval. ——— is regression line. Measured data were collected in this laboratory (Gill and Reichel, 1989; Hudson and Mott, 1993a, 1993b and 1993c; Hudson and Avery, 1994) in addition to being derived from Wimpfheimer *et al.* (1990), Harmayani *et al.* (1993), Varabioff *et al.* (1992), and Grau and Vanderlinde (1993)

Predictions of ΔG *of* P. fragi *with temperature shifts and cycling*

Data given in Figures 7, 8 and 9 in the paper of Fu *et al.* (1991) were interpreted in this study in terms of ΔG values over the measured growth of *P. fragi* up to the end of the exponential phase. ΔG values estimated from Figures 7, 8 and 9 of Fu *et al.* (1991) and ΔG values calculated by the program are shown in *Table 2*. For all three figures the ΔG values

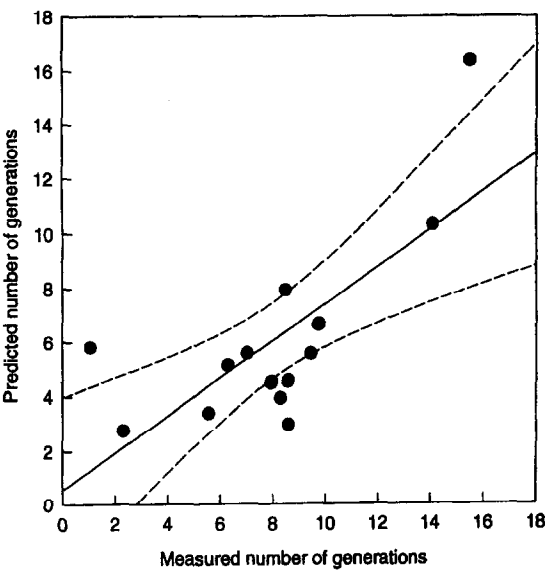

Figure 3 Comparison of measured and predicted growth (in generations) for *L. monocytogenes* L70 under anaerobic conditions - - - is 95% confidence interval. ——— is regression line. Measured data were collected in this laboratory (Gill and Reichel, 1989; Hudson and Mott, 1993b and 1993c; Avery *et al.*, 1994; Hudson and Avery, 1994) and derived from Varabioff *et al.* (1992)

Table 2 Comparison of measured and predicted ΔG values of *Pseudomonas fragi* under temperature shifts and cycling

Data from Fu *et al.* (1991)	Measured ΔG values	Predicted ΔG values
Figure 7	14.7	14.9
Figure 8	13.3	15.0
Figure 9	13.3	16.5

predicted by the program were similar to those estimated from the figures.

Comparisons of predicted and measured ΔG *values for* Listeria monocytogenes *under shifting temperatures*

Graphs of measured ΔG with shifting temperatures using *L. monocytogenes* strains L70 and L72 are shown in *Figures 4* and *5*. The equations describing the linear regressions of the data in these graphs are:

$$\text{Predicted } \Delta G = 0.897 + 0.567 \times \text{measured } \Delta G \quad (\textit{Figure 4})$$

$$\text{Predicted } \Delta G = 0.892 + 0.457 \times \text{measured } \Delta G \quad (\textit{Figure 5})$$

for models using L70 and L72 respectively. Both models predicted less growth than was measured by bacterial counts.

Sample application of the program – predicting growth in refrigerators

Figure 6 shows a typical 48 h time/temperature curve for refrigerator B, indicating the cyclic nature of temperatures in domestic refrigerators. Refrigerator A maintained a cooler internal temperature than refrigerator B, with minimum temperatures of 3.25°C and 5°C and maximum temperatures of 9°C and 13°C, respectively.

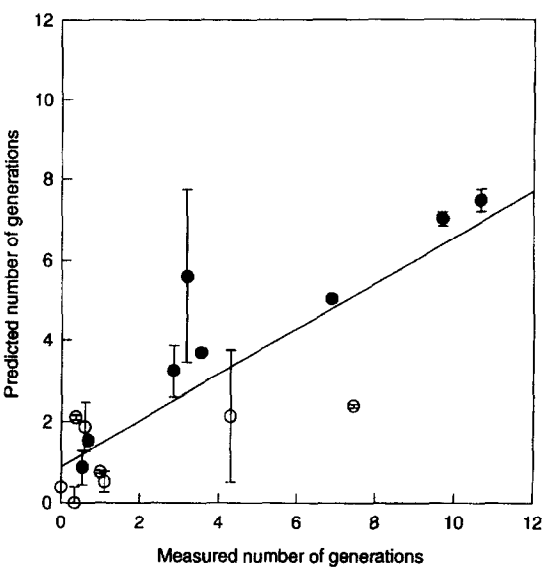

Figure 4 Comparison of measured growth (in generations) for *L. monocytogenes* L70 under aerobic conditions with predicted growth. • pH 7, 0 ppm nitrite and 0.5% NaCl; ○, pH 6, 30 ppm nitrite and 3.0% NaCl. Vertical bars show the standard deviation, ——— is regression line

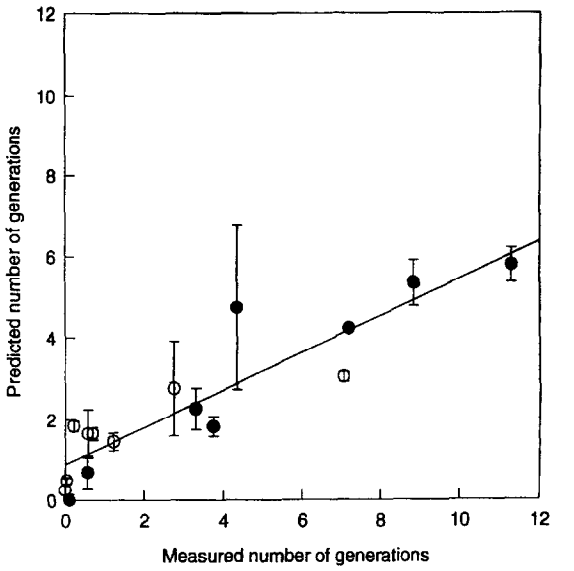

Figure 5 Comparison of measured growth (in generations) for *L. monocytogenes* L72 under anaerobic conditions with predicted growth. • pH 7, 0 ppm nitrite and 0.5% NaCl; ○, pH 6, 30 ppm nitrite and 3.0% NaCl. Vertical bars show the standard deviation, ——— is regression line

Program analyses for potential growth of the bacterial included in the program under aerobic conditions are shown in *Table 3*. *Pseudomonas fragi* was predicted to grow most of all the organisms whereas *Y. enterocolitica* was, in general, predicted to grow most among the pathogens.

DISCUSSION

To date, response surface models only take into account the effects of constant temperature, among other parameters, on bacterial growth kinetics. In reality, temperature is likely to be a major factor in

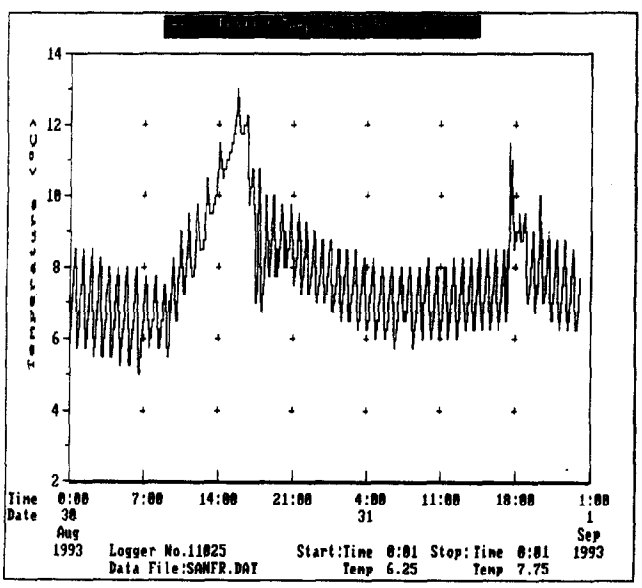

Figure 6 Time/temperature curve over 48 h for refrigerator B

Table 3 Microbial growth predicted from time/temperature histories of two domestic refrigerators recorded over 48 h

		ΔG values (log increases) including lag time				ΔG values (log increases) excluding lag time			
		pH 5.5		pH 6.1		pH 5.5		pH 6.1	
Species	Strain	Fridge A	Fridge B	Fridge A	Fridge B	Fridge A	Fridge B	Fridge A	Fridge B
Pseudomonas fragi	P1	2.6 (0.8)	7.6 (2.3)	4.9 (1.5)	11.4 (3.4)	3.6 (1.1)	9.5 (2.9)	6.3 (1.9)	13.3 (4.0)
Listeria monocytogenes	L70	0.5 (0.2)	1.3 (0.4)	0.8 (0.2)	2.3 (0.7)	0.7 (0.2)	1.6 (0.5)	1.2 (0.4)	2.9 (0.9)
	L72	0.2 (0.1)	0.8 (0.2)	0.3 (0.1)	1.4 (0.4)	0.6 (0.2)	1.4 (0.4)	1.2 (0.4)	2.9 (0.9)
Aeromonas hydrophila	TS	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.7 (0.2)	1.3 (0.4)	3.6 (1.1)	2.0 (0.6)	5.4 (1.6)
	JAH4	1.6 (0.5)	4.1 (1.2)	3.2 (1.0)	7.1 (2.1)	3.3 (1.0)	6.0 (1.8)	5.0 (1.5)	9.2 (2.8)
Yersinia enterocolitica	TS	1.8 (0.5)	3.7 (1.1)	2.9 (0.9)	5.9 (1.8)	2.9 (0.9)	5.9 (1.8)	4.5 (1.4)	7.6 (2.3)
	Y3	2.8 (0.8)	4.8 (1.4)	4.2 (1.3)	7.4 (2.2)	3.5 (1.1)	5.8 (1.7)	5.5 (1.7)	9.1 (2.7)

TS = Type Strain. Fridge A; Maximum 9°C, minimum 3.25°C. Fridge B; Maximum 13°C, minimum 5°C. pH 5.5 was selected to represent fresh beef, and pH 6.1 to represent roast beef. ΔG = increase in the number of generations.

determining the growth kinetics of bacteria, but it is also likely to be the most widely fluctuating of the parameters modelled. Therefore, predictions of bacterial growth kinetics under fluctuating temperatures are more desirable than predictions that do not take temperature variations into account. Two factors determine the accuracy of predictions of bacterial growth under fluctuating temperatures, as described in this study. The first is the accuracy of the response surface models used to make predictions of bacterial growth kinetics. The second is the accuracy of predictions of the effects of fluctuating temperatures on the bacterial growth kinetics.

In this study, the program predicted ΔG with reasonable accuracy under most of the conditions. At constant temperatures, the predictions of ΔG for *L. monocytogenes* compared very well with the values measured from published data and with data obtained in this laboratory. However, under fluctuating temperatures the program gave fewer accurate predictions of ΔG for *L. monocytogenes*. This may have been due to the low temperature (4°C for most of the experiment) used in the experiments where the temperature was fluctuating. It is reasonable to expect that predictions at temperatures close to the extremities of the range of data from which the models were constructed will be less accurate than for conditions near the 'centre' of the data set. Buchanan and Phillips (1990) noted this 'tapering effect'. Predictions of ΔG for *P. fragi* under fluctuating temperatures mostly higher than 4°C were very close to those actually measured from published data.

Response surface models produced with axenic cultures in laboratory media, such as those used in the program described in this study, have been developed for a number of bacteria. Such models have been described as giving good 'first estimates' of growth kinetics (Buchanan and Phillips, 1990). These authors presented a table of comparative data between predicted and measured growth of *L. monocytogenes* to illustrate this.

However, bacterial growth on foods is influenced by many unmodelled factors including nutrient availability, the occurrence of antimicrobial agents, the type of acidulants and humectants used and the presence of competing species of bacteria. For example, *Yersinia enterocolitica* competes poorly with spoilage bacteria on meat substrates (Fukushima and Gomyoda, 1986; Kleinlein and Untermann, 1990) and the growth of *L. monocytogenes* was inhibited in co-culture with *Y. enterocolitica* in whole milk (Budu-Amoako *et al.*, 1993), but was enhanced in co-culture with *Pseudomonas* in milk (Marshall and Schmidt, 1988; Farrang and Marth, 1989). Jeppesen and Huss (1993) showed that two strains of lactic acid bacteria inhibited the growth of both *L. monocytogenes* and *Y. enterocolitica* in a model fish substrate. Such factors are not accounted for in the models currently available, thus reducing their predictive accuracy, and hence also reducing the predictive accuracy of the program described in this study, which was developed using those models.

Much of the literature data used in this study on the growth kinetics of the organisms did not contain information on one or more of the parameters required by the program. These parameters (for example pH and NaCl content) had to be estimated, introducing inherent inaccuracies in the modelling.

The program described in this study assumes no transition time will be needed for an organism growing exponentially at one temperature to adapt to another (ie there is no 'history' effect). This approach agrees with recent findings by Zwietering *et al.* (1994), who found that temperature shifts while the organism (*Lactobacillus plantarum*) was in the exponential phase did not result in an equilibration period before the new growth rate was attained for most (but not all) growth curves obtained in their study. In another recent study, Mitchell *et al.* (1994) also found that the growth of exponential cultures of *Salmonella typhimurium* exposed to sinusoidally cycling temperatures could be predicted by a simple growth model that did not include any lag time modelling. However, some reports (eg Fu *et al.*, 1991) do describe history effects. The temperature changes leading to such observations were abrupt, eg almost instantaneous 12°C temperature shifts. Bacteria on

food will be buffered from such abrupt changes and hence we have inclined to accept the conclusions of Zwietering *et al.* (1994) and Mitchell *et al.* (1994).

Response surface models should not be applied beyond the boundaries of the experimental variables that were used in their construction. For example, the growth of an organism at pH 8.5 cannot be predicted by a model if that model was not constructed using a pH of at least 8.5. For some models, a tapering effect at the limits of the models' construction has been noted (Buchanan and Phillips, 1990), creating inherent inaccuracies in predictions at these values.

The program described in this paper does not allow for the maximum population being reached. If the maximum number is reached and incubation continues, the program assumes continued exponential growth and returns large values for ΔG. The maximum likely ΔG to be encountered would be in the order of 26.6, assuming an increase of 10^2 to $>10^{10}$ bacteria/g. Interpretation of data, therefore, requires some care.

The program described in this study uses response surface models to predict microbial growth from real time/temperature histories. Such programs offer greater flexibility than those that estimate microbial growth from a single set temperature, and hence may be more useful in the manufacturing and distribution chains of food industries. The ability of food manufacturers and distributors to predict the amount of microbial growth in foods offers multiple benefits, including cost savings and the ability to monitor the effects of 'out of specification temperatures'. The most important benefit, though, will be increased consumer safety through more accurate predictions of the growth of food-borne pathogens from real time/temperature histories taken from foods.

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