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Review article

Heat Resistance in Liquids of *Enterococcus* spp., *Listeria* spp., *Escherichia coli, Yersinia enterocolitica, Salmonella* spp. and *Campylobacter* spp.

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Sörqvist S: Heat resistance in liquids of *Enterococcus* spp., *Listeria* spp., *Escherichia coli, Yersinia enterocolitica, Salmonella* spp. and *Campylobacter* spp. Acta vet. scand. 2003, 44, 1-19. – The aim of the work was to collect, evaluate, summarize and compare heat resistance data reported for *Campylobacter, Enterococcus, Escherichia, Listeria, Salmonella* and *Yersinia* spp. The work was limited to resistance in liquids with pH values 6-8. Results obtained under similar experimental conditions were sought. Thermal destruction lines for the various bacterial groups studied were constructed using $\log_{10} D$ values and treatment temperatures. There was a good linear relationship between $\log_{10} D$ and temperature with *Escherichia coli,* listerias and salmonellas. For campylobacters, enterococci and yersinias the relationships were weaker but, nevertheless, present. Using the slopes of the lines and their 95% confidence limits, *z* values and their 95% confidence limits were calculated. *z* values were compared with *z* values obtained from reports. The equations for the lines were also used for calculation of predicted means of *D* values at various treatment temperatures. 95% confidence limits on predicted means of *D* values and on predicted individual *D* values were also calculated. Lines and values are shown in figures and tables. Differences in heat resistance noted between and within the bacterial groups studied are discussed.

Campylobacter jejuni/coli; Enterococcus faecalis; Enterococcus faecium; Escherichia coli; Listeria innocua; Listeria ivanovii; Listeria monocytogenes; Listeria seeligeri; Listeria welshimeri; Salmonella; Yersinia enterocolitica; thermal resistance; influencing factors; methods of determination; differences between species; differences between strains.

Introduction

Microbiologists now and then need heat resistance data for various microorganisms. In the literature, data of this kind are frequently based on reports from few investigations. To collect the data required, however, may be a laborious and time-consuming task for the individual user. The literature is generally extensive and many factors that may have influenced the results reported must be taken into consideration (for general information on influencing factors, see e.g. *Hansen & Riemann* 1963, *Stumbo* 1973, *Pflug & Holcomb* 1983). Furthermore, the presentations of results often differ essentially.

The aim of the present work was to collect, summarize, evaluate and compare heat resis-

tance data reported for *Campylobacter, Enterococcus, Escherichia, Listeria, Salmonella* and *Yersinia* spp. As it was well known that considerably more heat resistance results were published from investigations with liquids than from those with other heating menstrua, it was considered appropriate to base the work on results obtained in liquids. Moreover, results of this kind could be expected to reflect the inherent heat resistance of the bacteria investigated better than those obtained in more complex heating menstrua.

Reports published until 2000 were studied. Data produced under experimental conditions as similar as possible were sought. This meant that results from some kinds of experiments were excluded. The various types of excluded data are given below under the different subheadings in Experimental conditions. It should be mentioned here that extensive reviews of heat resistance data reported for *Escherichia coli* O157:H7, *Listeria monocytogenes* and *Salmonella* spp. have been published recently by *Stringer et al.* (2000), *Doyle et al.* (2001) and *Doyle & Mazzotta* (2000), respectively. However, the aims and the selections and analyses of data in these reviews differ from those in the present work.

Bacteria

The work deals with the following bacteria: *Campylobacter jejuni/coli, Enterococcus faecalis, Enterococcus faecium, Escherichia coli, Listeria innocua, Listeria ivanovii, Listeria monocytogenes, Listeria seeligeri, Listeria welshimeri, Salmonella* spp. and *Yersinia enterocolitica.* Some of these bacteria are well-known food-associated human pathogens, others are utilized - enterococci and *E. coli* - or proposed - *L. innocua* (*Foegeding & Stanley* 1991, *Fairchild & Foegeding* 1993) - as indicators. Some types of *E. coli* also appear as food-linked human pathogens (*Morgan et al.* 1988, *Murano & Pierson* 1992, 1993, *Clavero & Beuchat* 1995, *Clementi et al.* 1995, *Jackson et al.* 1996, *Blackburn et al.* 1997, *Williams & Ingham* 1997, *George & Peck* 1998, *Kaur et al.* 1998) and enterococci have recently emerged as one of the leading causes of nosocomial, non-food-associated, infections (*Kearns et al.* 1995).

Experimental conditions

Growth of test bacteria

In most cases the bacteria were grown in conventional media. In some investigations the growth media were milk, liquid egg products or clarified cabbage juice. The pH values of the media were given in some cases. The values varied from 5.6 to 7.4. Enterococci, *E. coli,* listerias and salmonellas were incubated aerobically at 30-37 °C and *Y. enterocolitica* aerobically at 25-37 °C. Campylobacters were grown microaerobically at 35-43 °C. In the great majority of cases the bacteria were incubated for 12-48 h, i.e. they could be considered to have reached the late logarithmic or stationary growth phase. At stationary growth phase, bacterial heat resistance is at a maximum (*Elliker & Frazier* 1938, *White* 1953, *Krishna Iyengar et al.* 1957, *Lemcke & White* 1959, *Beuchat & Lechowich* 1968, *Ng et al.* 1969, *Humphrey et al.* 1990, *Jackson et al.* 1996, *Lou & Yousef* 1996, *Kaur et al.* 1998, *Pagán et al.* 1998, 1999).

Heat resistance results obtained for bacteria grown under carbon, glucose or nitrogen starvation or other stress conditions (see e.g. *Ng et al.* 1969, *Jenkins et al.* 1988, *Lou & Yousef* 1996) were not used in the present work.

Conditions between growth and heat treatment

Results recorded for bacteria subjected to stress conditions prior to heat treatment were not used: sublethal heat shock (see e.g. *Mackey & Derrick* 1986, 1987b, 1990, *Bunning et al.*

1990, 1992, *Murano & Pierson* 1992, 1993, *Boutibonnes et al.* 1993, *Humphrey et al.* 1993a, *Flahaut et al.* 1996, 1997, *Shenoy & Murano* 1996, alkaline stress (*Humphrey et al.* 1991, 1993b), acid stress (*Farber & Pagotto* 1992, *Leyer & Johnson* 1993, *Williams & Ingham* 1998), osmotic stress (*Jørgensen et al.* 1995) or other types of stress (see e.g. *Boutibonnes et al.* 1993, *Flahaut et al.* 1996, 1997).

Heating menstrua

Heating menstrua used were milk and liquid milk products, broths, physiological saline and other salt solutions, liquid egg products, diluted soups, scalding waters used at chicken or pig slaughter, and some other liquids. Heat resistance results obtained in menstrua with pH values of approx. 6-8 were used in the present work, as the bacterial species investigated are known to have their maximum heat resistances in this pH range (see e.g. *Anellis et al.* 1954, *Krishna Iyengar et al.* 1957, *White* 1963, *Garibaldi et al.* 1969a, *Humphrey et al.* 1981, *Sanz Pérez et al.* 1982, *Okrend et al.* 1986, *Blackburn et al.* 1997, *Pagán et al.* 1998, 1999). Results from experiments where salts, fats, carbohydrates, proteins or other substances were added to the heating menstrua with the aim of influencing the heat resistance of the test bacteria were excluded (see e.g. *Lategan & Vaughn* 1964, *Calhoun & Frazier* 1966, *Baird-Parker et al.* 1970, *Goepfert et al.* 1970, *Vrchlabski & Leistner* 1970, *Corry* 1974, *Anderson et al.* 1991, *Palumbo et al.* 1995, *Blackburn et al.* 1997, *Knight et al.* 1999).

Heat treatment

Various methods of heat treatment were applied, e.g. heating in water baths using glass capillary tubes, sealed glass tubes, glass ampoules or polythene pouches completely immersed in the water, test tubes placed with the water level to the bases of the test tube plugs, flasks or cups placed with the menstruum levels under the water level and in some cases shaken, and heating using pasteurizers, two-phase slug flow heat exchangers (*Bradshaw et al.* 1985, *Bunning et al.* 1986, 1988, 1992, *Konvincic et al.* 1991, *Clementi et al.* 1995), submerged-coil heating apparatuses (*Anderson et al.* 1991, *Jørgensen et al.* 1995, 1996, *Blackburn et al.* 1997, *Juneja et al.* 1998), thermoresistometers (*Read et al.* 1968, *Pagán et al.* 1998, 1999) and an "attemperated dilution blank method" (*Magnus et al.* 1986, 1988).

Results from experiments using rising heating temperatures (*Tsuchido et al.* 1974, *Mackey & Derrick* 1987a, *Quintavalla et al.* 1988, *Stephens et al.* 1994) were excluded.

Recovery of heat-treated bacteria

In the great majority of cases the recovery of heat-treated bacteria was performed on agar plates. Enterococci and *E. coli* were incubated aerobically at 30-37 °C for 24 h-7 days, listerias, salmonellas and *Y. enterocolitica* aerobically at 25-37 °C for 24 h-7 days and campylobacters microaerobically at 37-43 °C for 24-72 h. In some studies anaerobic recovery was used: *L. monocytogenes* (*Knabel et al.* 1990, *George et al.* 1998), *E. coli* (*Murano & Pierson* 1992, 1993, *Gadzella & Ingham* 1994, *Blackburn et al.* 1997, *George et al.* 1998, *George & Peck* 1998) and salmonellas (*Xavier & Ingham* 1993, *Blackburn et al.* 1997, *George et al.* 1998). Most Probable Number (MPN) techniques were applied in some investigations. Procedures for repair of heat-injured bacteria were studied by *Ahmad et al.* (1978), *Northolt et al.* (1988), *Meyer & Donnelly* (1992), *Sörqvist* (1993, 1994) and *George et al.* (1998).

Results from experiments where heat-treated bacteria were recovered on selective or other media known to inhibit growth of heat-injured cells were excluded.

Table 1. *z* values reported from investigations where the experimental conditions laid down in this study were fulfilled.

Bacterium/ Bacterial group	*z** values (°C)			References
	Range	Mean ± SD	No. of values	
Enterococcus faecium	3.63-12.82	8.4 ± 2.5	14	*Sanz Pérez et al.* (1982), *Magnus et al.* (1986), *Quintavalla et al.* (1988), *Gordon & Ahmad* (1991), *Simpson et al.* (1994), *Mulak et al.* (1995)
Enterococcus faecalis	2.24-9.06	6.0 ± 2.5	10	*Gardner & Patton* (1975), *Sanz Pérez et al.* (1982), *Magnus et al.* (1986), *Quintavalla et al.* (1988)
Listeria innocua	4.65-6.9	5.8 ± 0.8	8	*Quintavalla & Barbuti* (1989), *Foegeding & Stanley* (1991), *Fairchild & Foegeding* (1993), *Palumbo et al.* (1995)
Listeria monocytogenes	4.30-11.45	6.1 ± 1.2	85	*Bradshaw et al.* (1985, 1987b, 1991), *Beuchat et al.* (1986), *Bunning et al.* (1986, 1988), *Donnelly & Briggs* (1986), *El-Shenawy et al.* (1989), *Lemaire et al.* (1989), *Quintavalla & Barbuti* (1989), *Foegeding & Leasor* (1990), *Linton et al.* (1990), *Foegeding & Stanley* (1991), *Quintavalla & Campanini* (1991), *Fairchild & Foegeding* (1993), *Sörqvist* (1993, 1994), *Bartlett & Hawke* (1995), *Palumbo et al.* (1995), *Muriana et al.* (1996), *Schuman & Sheldon* (1997), *Casadei et al.* (1998), *Pagán et al.* (1998), *Rowan & Anderson* (1998), *Knight et al.* (1999)
Listeria ivanovii	6.3-6.6	6.5 ± 0.2	2	*Bradshaw et al.* (1991)
Listeria seeligeri	6.4-6.9	6.7 ± 0.3	2	*Bradshaw et al.* (1991)
Listeria welshimeri	6.1-6.9	6.5 ± 0.5	2	*Bradshaw et al.* (1991)
Escherichia coli	3.4-6.0	5.1 ± 0.8	11	*Read et al.* (1961), *Dega et al.* (1972), *Morgan et al.* (1988), *Clementi et al.* (1995), *Blackburn et al.* (1997), *Williams & Ingham* (1998)
Yersinia enterocolitica	4.0-5.78	4.8 ± 0.6	10	*Lovett et al.* (1982), *Sörqvist* (1989), *Sörqvist & Danielsson-Tham* (1990), *Pagán et al.* (1999)
Salmonella spp. (except *Salm. senftenberg* 775W)	3.24-9.5	5.5 ± 1.7	36	*Anellis et al.* (1954), *Garibaldi et al.* (1969b), *Dega et al.* (1972), *Gibson* (1973), *Bradshaw et al.* (1987a), *Sörqvist & Danielsson-Tham* (1990), *Shah et al.* (1991), *Xavier & Ingham* (1993), *Wolfson & Sumner* (1994) *Palumbo et al.* (1995), *Blackburn et al.* (1997), *Schuman & Sheldon* (1997), *Humpheson et al.* (1998), *Michalski et al.* (1999)
Salm. senftenberg 775W	5.3-6.8	6.0 ± 0.4	13	*Anellis et al.* (1954), *Thomas et al.* (1966), *Baird-Parker* et al. (1970), Gibson (1973)
Campylobacter jejuni/coli	2.8-5.81	4.8 ± 0.7	14	*Blankenship & Craven* (1982), *Waterman* (1982), *Sörqvist* (1989), *Sörqvist & Danielsson-Tham* (1990)

* The *z* value is the number of degrees of temperature change needed to change the *D* value by a factor of 10 (The term *D* value, see Table 3).

Table 2. *z* values obtained using the slopes of thermal destruction lines constructed in the study and their 95% confidence limits and, for comparison, summaries of reported and calculated *z* values.

Bacterium/ Bacterial group	*z* values (°C)*			
	Obtained value and its 95% confidence interval	Reported and calculated** values		
		Range	Mean ± SD	No. of values
Enterococcus faecium	9.6 (8.8 - 10.5)	3.63 - 14.3	10.2 ± 3.3	24
Enterococcus faecalis	9.5 (8.5 - 10.8)	2.24 - 14.2	8.1 ± 3.2	36
Listeria innocua	5.0 (4.5 - 5.6)	4.65 - 7.3	6.0 ± 0.9	9
Listeria monocytogenes	5.7 (5.6 - 5.9)	4.30 - 11.45	6.3 ± 1.3	103
Listeria ivanovii, L.seeligeri, L. welshimeri †	6.4 (6.1 - 6.7)	6.1 - 6.9	6.5 ± 0.3	6
Escherichia coli	6.0 (5.9 - 6.1)	3.2 - 9.1	5.4 ± 1.5	33
Yersinia enterocolitica	6.7 (6.0 - 7.7)	4.0 - 13.7	6.6 ± 2.7	20
Salmonella spp. (except *Salm. senftenberg* 775W)	5.2 (5.1 - 5.3)	3.24 - 9.5	5.1 ± 1.6	63
Salmonella senftenberg 775W	5.8 (5.4 - 6.4)	4.5 - 9.1	6.2 ± 1.1	16
Campylobacter jejuni/coli	6.4 (5.8 - 7.0)	2.8 - 8.0	5.5 ± 1.1	24

** Calculated *z* values were figured out from reported or calculated *D* values (see Types of collected data and statistical analysis) and reported treatment temperatures.
† *Listeria ivanovii, L. seeligeri* and *L. welshimeri* are taken together.

Types of collected data and statistical analysis

D and *z* values were collected from the studied literature. The *D* value is the time of heat treatment required at a certain temperature to destroy 90% of the bacterial cells, and the *z* value is the number of degrees of temperature change needed to change the *D* value by a factor of 10 (*Stumbo* 1973). When not reported, *D* values were, where possible, calculated from bacterial counts and periods of time of heat treatment given in texts, tables or figures. Some *z* values were worked out from reported or calculated *D* values and reported treatment temperatures.

For each of the bacterial species/groups studied, the $\log_{10}$ of *D* values recorded were plotted *vs* temperature and a thermal destruction line (*Stumbo* 1973) was fitted using the method of least squares (*Colton* 1974). The equation for the line is $\log_{10} D = a - bt$, where *D* is the decimal reduction time in s, *a* the intercept, *-b* the slope and *t* the treatment temperature in °C. The degree of linear relationship between the temperatures used and the logarithms of *D* values recorded was expressed by the coefficient of correlation, *r* (*Colton* 1974). Using the absolute and inverse values of the slope and its 95% confidence limits, the *z* value and its 95% confidence limits were calculated (*Stumbo* 1973, *Colton* 1974).

95% confidence limits on predicted means (*Colton* 1974) of *D* values were calculated (the predicted mean is the same as *D* in the equation). 95% confidence limits on predicted individual *D* values (*Colton* 1974) were also figured out (From a practical point of view it may be more interesting to know these limits than those on predicted means).

Figure 1

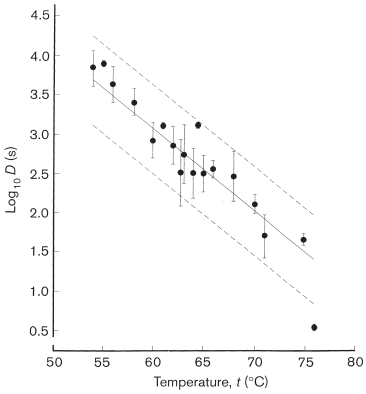

Figure 2

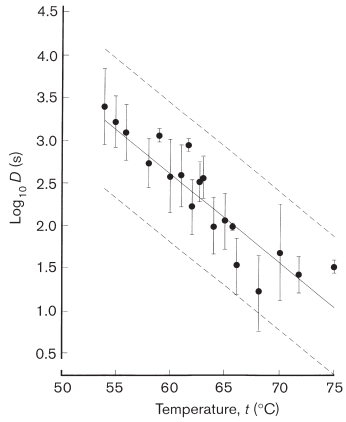

Figure 3

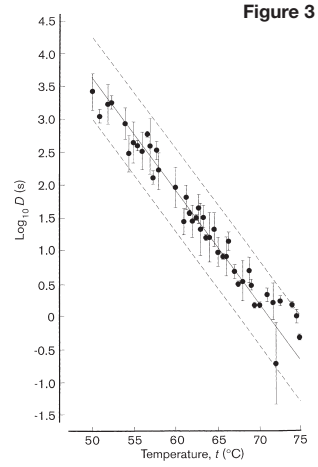

Figure 4

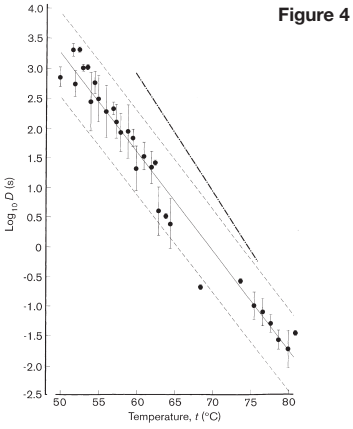

Figure 5

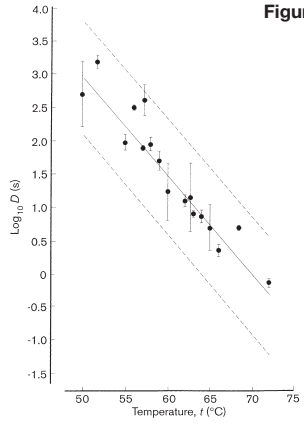

Figure 6

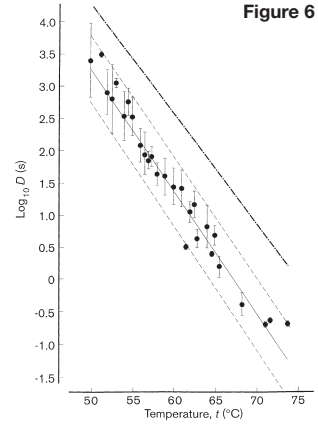

Figure 7

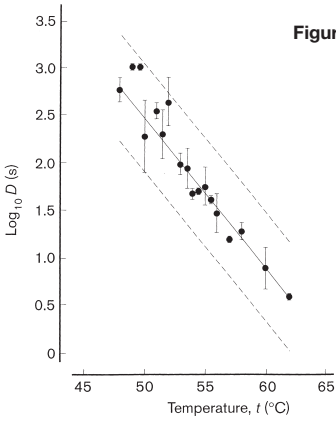

Figure 1. Heat resistance data (Mean ± SD) recorded at the different treatment temperatures used and fitted thermal destruction line (-) for *Enterococcus faecium.* The equation for the line is $\log_{10} D = 9.3080 - 0.10412t$ ($r = -0.84748$; total number of $\log_{10} D$ values = 195). The 95% confidence limits on predicted individual $\log_{10} D$ values are shown by (- -). The figure is based on data from: *Greenberg & Silliker* (1961), *Zivanovic et al.* (1965), *Ienistea et al.* (1970), *Vrchlabsky & Leistner* (1970), *Sanz Pérez et al.* (1982), *Magnus et al.* (1986, 1988), *Quintavalla et al.* (1988), *Gordon & Ahmad* (1991), *Kornacki & Marth* (1992), *Patel & Wilbey* (1994), *Simpson et al.* (1994), *Kearns et al.* (1995), *Mulak et al.* (1995), *Renner & Peters* (1999).

Figure 2. Heat resistance data (Mean ± SD) recorded at the different treatment temperatures used and fitted thermal destruction line (-) for *Enterococcus faecalis.* The equation for the line is $\log_{10} D = 8.9359 - 0.10531t$ ($r = -0.72968$; total number of $\log_{10} D$ values = 244). The 95% confidence limits on predicted individual $\log_{10} D$ values are shown by (- -). The figure is based on data from: *Richards & White* (1949), *White* (1953), *Krishna Iyengar et al.* (1957), *White* (1963), *Zivanovic et al.* (1965), *Beuchat & Lechowich* (1968), *Clark et al.* (1968), *Ienistea et al.* (1970), *Shannon et al.* (1970), *Vrchlabsky & Leistner* 1970), *Dabbah et al.* (1971a, c), *Gardner & Patton* (1975), *Sanz Pérez et al.* (1982), *Magnus et al.* (1986, 1988), *Quintavalla et al.* (1988), *Boutibonnes et al.* (1993), *Kearns et al.* (1995), *Flahaut et al.* (1996, 1997).

Figure 3. Heat resistance data (Mean ± SD) recorded at the different treatment temperatures used and fitted thermal destruction line (-) for *Listeria monocytogenes.* The equation for the line is $\log_{10} D = 12.3787 - 0.17401t$ ($r = -0.95631$; total number of $\log_{10} D$ values = 474). The 95% confidence limits on predicted individual $\log_{10} D$ values are shown by (- -). The figure is based on data from: *Bradshaw et al.* (1985), *Beuchat et al.* (1986), *Bunning et al.* (1986), *Donnelly & Briggs* (1986), *Bradshaw et al.* (1987b), *Donnelly et al.* (1987), *Fernández Garayzabal et al.* (1987), *Bunning et al.* (1988), *Farber et al.* (1988), *Golden et al.* (1988), *Northolt et al.* (1988), *Steinmeyer* (1988), *El-Shenawy et al.* (1989), *Fedio & Jackson* (1989), *Lemaire et al.* (1989), *Quintavalla & Barbuti* (1989), *Suárez Fernández et al.* (1989), *Boyle et al.* (1990), *Bunning et al.* (1990), *Foegeding & Leasor* (1990), *Knabel et al.* (1990), *Linton et al.* (1990), *Mackey et al.* (1990), *Anderson et al.* (1991), *Bradshaw et al.* (1991), *Foegeding & Stanley* (1991), *Konvincic et al.* (1991), *McKenna et al.* (1991), *Quintavalla & Campanini* (1991), *Bunning et al.* (1992), *Farber & Pagotto* (1992), *Holsinger et al.* (1992), *Meyer & Donnelly* (1992), *Fairchild & Foegeding* (1993), *Sörqvist* (1993, 1994), *Stephens et al.* (1994), *Bartlett & Hawke* (1995), *Jørgensen et al.* (1995, 1996), *Palumbo et al.* (1995, 1996), *Lou & Yousef* (1996), *Muriana et al.* (1996), *Patchett et al.* (1996), *Schuman & Sheldon* (1997), *Casadei et al.* (1998), *George et al.* (1998), *Juneja et al.* (1998), *Pagán et al.* (1998), *Rowan & Anderson* (1998), *Knight et al.* (1999).

Figure 4. Heat resistance data (Mean ± SD) recorded at the different treatment temperatures used and fitted thermal destruction line (-) for *Escherichia coli.* The equation for the line is $\log_{10} D = 11.6471 - 0.16768t$ ($r = -0.97349$; total number of $\log_{10} D$ values = 332). The 95% confidence limits on predicted individual $\log_{10} D$ values are shown by (- -). Data used are from: *Elliker & Frazier* (1938), *Katzin et al.* (1943), *Solowey et al.* (1948), *Chambers et al.* (1957). *Read et al.* (1957), *Lemcke & White* (1959), *Read et al.* (1961), *Calhoun & Frazier* (1966), *Evans et al.* (1970), *Goepfert et al.* (1970), *Dabbah et al.* (1971c), *Dega et al.* (1972), *Tsuchido et al.* (1974), *Ahmad et al.* (1978), *Katsui et al.* (1981), *Yamamori & Yura* (1982), *D´Aoust et al.* (1988), *Jenkins et al.* (1988), *Morgan et al.* (1988), *Murano & Pierson* (1992, 1993), *Gadzella & Ingham* (1994), *Ahmed & Conner* (1995), *Clavero & Beuchat* (1995, 1996), *Clementi et al.* (1995), *Jackson et al.* (1996), *Teo et al.* (1996), *Blackburn et al.* (1997), *Williams & Ingham* (1997, 1998), *George et al.* (1998), *George & Peck* (1998), *Kaur et al.* (1998), *Semanchek & Golde*n (1998).
Thermal destruction line for an unusually heat-resistant strain of *E. coli* reported by *Holland & Dahlberg* (1940) is also shown (- · -).

Figure 5. Heat resistance data (Mean ± SD) recorded at the different treatment temperatures used and fitted thermal destruction line (-) for *Yersinia enterocolitica.* The equation for the line is $\log_{10} D = 10.4176 - 0.14896t$ ($r = -0.86082$; total number of $\log_{10} D$ values = 88). The 95% confidence limits on predicted individual $\log_{10} D$ values are shown by (- -). The figure is based on data from: *Hanna et al.* (1977), *Francis et al.* (1980), *Norberg* (1981), *Lovett et al.* (1982), *D´Aoust et al.* (1988), *Sörqvist* (1989), *Sörqvist & Danielsson-Tham* (1990), *Toora et al.* (1992), *Shenoy & Murano* (1996), *Pagán et al.* (1999).

Figure 6. Heat resistance data (Mean ± SD) recorded at the different treatment temperatures used and fitted thermal destruction line (-) for *Salmonella* spp. The equation for the line is $\log_{10} D = 12.9511 - 0.19282t$ ($r = -0.92147$; total number of $\log_{10} D$ values = 647). The 95% confidence limits on predicted individual $\log_{10} D$ values are shown by (- -). Data used are from: *Solowey et al.* (1948), *Anellis et al.* (1954), *Osborne et al.* (1954), *Lategan & Vaughn* (1964), *Davidson et al.* (1966), *Ng* (1966), *Thomas et al.* (1966), *Corry & Barnes* (1968), *Read et al.* (1968), *Garibaldi et al.* (1969a, b), *Ng et al.* (1969), *Baird-Parker et al.* (1970), *Evans et al.* (1970), *Goepfert et al.* (1970), *Rossebø* (1970), *Dabbah et al.* (1971a, b), *Moats et al.* (1971), *Dega et al.* (1972), *Gibson* (1973), *Corry* (1974), *Thompson et al.* (1979), *Humphrey* (1981), *Humphrey et al.* (1981), *Mackey & Derrick* (1986), *Okrend et al.* (1986), *Bradshaw et al.* (1987a), *D´Aoust et al.* (1987), *Mackey & Derrick* (1987a, b), *Baker* (1990), *Bunning et al.* (1990), *Humphrey et al.* (1990), *Humphrey* (1990), *Mackey & Derrick* (1990), *Sörqvist & Danielsson-Tham* (1990), *Humphrey et al.* (1991), *Shah et al.* (1991), *Humphrey et al.* (1993a, b), *Leyer & Johnson* (1993), *Xavier & Ingham* (1993), *Wolfson & Sumner* (1994), *Humphrey et al.* (1995), *Palumbo et al.* (1995, 1996), *Muriana et al.* (1996), *Teo et al.* (1996), *Blackburn et al.* (1997), *Schuman & Sheldon* (1997), *George et al.* (1998), *Humpheson et al.* (1998), *Michalski et al.* (1999).
Thermal destruction line for the extremely heat-resistant *Salm. senftenberg* 775W is also shown (- · -) ; for references, see text.

Figure 7. Heat resistance data (Mean ± SD) recorded at the different treatment temperatures used and fitted thermal destruction line (-) for *Campylobacter jejuni/coli.* The equation for the line is $\log_{10} D = 10.3432 - 0.15717t$ ($r = -0.89853$; total number of $\log_{10} D$ values = 112). The 95% confidence limits on predicted individual $\log_{10} D$ values are shown by (- -). The figure is based on data from: *Doyle & Roman* (1981), *Gill et al.* (1981), *Blankenship & Craven* (1982), *Christopher et al.* (1982), *Waterman* (1982), *Oosterom et al.* (1983), *Humphrey & Cruickshank* (1985), *Okrend et al.* (1986), *Humphrey & Lanning* (1987), *D´Aoust et al.* (1988), *Sörqvist* (1989), *Sörqvist & Danielsson-Tham* (1990).

Table 3. Heat resistance values at 4 temperatures for bacteria studied in the work. The values are based on results reported from investigations where the experimental conditions laid down in the work were fulfilled.

Bacterium/ Bacterial group**	Temperature (°C)	*D** values (s)		
		Mean	95% confidence interval	
			For the mean	For a predicted individual value
Enterococcus faecium	55	3813	3095-4697	1041-13969
	60	1150	1017-1300	317-4166
	65	347	315-381	96-1254
	72	65	53-79	18-237
Enteroccus faecalis	55	1393	1089-1783	220-8816
	60	415	361-476	66-2593
	65	123	108-141	20-771
	72	23	17-30	3.5-144
Listeria innocua	55	1635	1050-2549	474-5644
	60	162	127-207	50-529
	65	16	13-20	5.0-52
	72	0.6 †	0.4-1.0	0.2-2.2
Listeria monocytogenes	55	643	577-715	150-2754
	60	87	81-93	20-371
	65	12	11-13	2.7-50
	72	0.7	0.6-0.8	0.2-3.0
Escherichia coli	55	266	239-297	53-1338
	60	39	35-42	8-194
	65	5.6	5.1-6.2	1.1-28
	72	0.4	0.3-0.5	0.1-1.9
Yersinia enterocolitica	55	168	124-227	23-1244
	60	30	24-37	4.1-221
	65	5.4	4.0-7.4	0.7-40
	72	0.5	0.3-0.9	0.1-3.9
Salmonella spp. (except *Salm. senftenberg* 775W)	55	222	208-237	64-771
	60	24	23-26	7.0-84
	65	2.6	2.3-2.9	0.8-9.1
	72	0.1	0.1-0.2	0.1-0.4
Campylobacter jejuni/coli	55	50	44-57	13-190
	60	8.2	6.5-10	2.1-32
	65	1.3 †	0.9-2.0	0.3-5.4
	72	0.1 †	0.1-0.2	0.1-0.5

* The *D* value is the time of heat treatment required at a certain temperature to destroy 90% of the bacterial cells.
** The bacteria are arranged according to their mean heat resistances at 60 and 65°C.
† Extrapolated value.

Summaries of data

Reported *z* values are summarized in Table 1. Reported and calculated *z* values taken together are given in Table 2, where *z* values figured out in the work by means of the equation mentioned, etc. are also shown. Thermal destruction lines for the bacteria studied, except those for *L. innocua, L. ivanovii, L. seeligeri* and *L. welshimeri,* are depicted in Figures 1-7, where 95% confidence limits on predicted individual $\log_{10} D$ values are also illustrated graphically. In Table 3, some *D* values at these limits are shown for the seven bacterial groups and also for *L. innocua.* Equations for the thermal destruction line of *L. innocua* and that of *L. ivanovii, L. seeligeri* and *L. welshimeri* taken together, are given below under the headings *Listeria innocua* and *Listeria ivanovii, L. seeligeri* and *L. welshimeri,* respectively.

Comments and further information

D and r values

The order of death of bacteria subjected to heat at a constant lethal temperature is often logarithmic (*Hansen & Riemann* 1963, *Stumbo* 1973, *Pflug & Holcomb* 1983), i.e. when the logarithm of survivors is plotted against the time of heating, the curve obtained, the survivor curve, is a straight line. The *D* value can then easily be calculated using the slope of the line. Deviations from the logarithmic order of death, however, are rather frequent and non-logarithmic survivor curves of some different types are obtained (*Hansen & Riemann* 1963, *Stumbo* 1973, *Pflug & Holcomb* 1983). Deviations of this kind often make determinations of *D* values difficult.

The *r* values, varying from -0.92147 to -0.99405, obtained for *Salmonella* spp., *E. coli* and the 3 *Listeria* groups indicate very good linear relationships (*Colton* 1974) between the $\log_{10} D$ values recorded and the treatment temperatures used. The *r* values, varying from -0.72968 to -0.89853, recorded for *Ent. faecalis, Ent. faecium, Y. enterocolitica* and *Camp. jejuni/coli* indicate weaker but, nevertheless, good linear relationships (*Colton* 1974). The following should be noted here: The number of *Y. enterocolitica* strains investigated is low. The results reported, however, indicate that great variation in heat resistance exists between strains of this species. As to enterococci, non-logarithmic survivor curves were reported in several works (*Zivanovic et al.* 1965, *Dabbah et al.* 1971a,c, *Sanz Pérez et al.* 1982, *Magnus et al.* 1986, *Gordon & Ahmad* 1991, *Boutibonnes et al.* 1993).

Listeria monocytogenes

Mackey & Bratchell (1989) published a similar review of the heat resistance of *L. monocytogenes.* Equations were given for heat treatments in: (a) various menstrua and (b) milk. The treatments in (b) had been performed by a sealed tube method (b1) or a slug flow heat exchanger (b2). The equations for (a), (b1) and (b2) were $\log_{10} D = 10.888 - 0.14519t$, $\log_{10} D = 11.931 - 0.1635t$ and $\log_{10} D = 10.126 - 0.1348t$ (*D* is in s in the equations). The means of *D* values obtained by the 3 equations for 55, 60, 65 and 72 °C are shown in Table 4. The means in (a), (b1) and (b2) except that in (b2) for 55 °C are higher than the corresponding ones (c) recorded for *L. monocytogenes* in the present work (Table 3). The differences between (a) and (c) may, at least to some extent, be explained by the fact that some of the heating menstrua in (a) were solids. The differences between (b1) or (b2) and (c) are therefore of greater interest, as all data for these 3 groups were obtained in liquids. A probable explanation of these differences is that heat resistance data for several "new" strains have been published later than the review by *Mackey & Bratchell* (1989) and have thus been included in the present work. Furthermore, the methods of determining the heat

Table 4. *D* values for *Listeria monocytogenes* according to the review by *Mackey & Bratchell* (1989).

Heating menstruum(-a)/ Treatment method(s)	*D*** value (s)			
	55°C	60°C	65°C	72°C
(a) Various/Various	799*	150*	28*	2.7*
(b1) Milk/ST	868	132	20	1.4†
(b2) Milk/SF	515‡	109	23	2.6

** The *D* value is the time of heat treatment required at a certain temperature to destroy 90% of the bacterial cells. ST, sealed tubes; SF, slug flow heat exchanger.
*, †, ‡ Value calculated using the equation given by the authors for (a), (b1) and (b2) respectively.

resistance of bacteria have been widely discussed in recent years and some improvements or new procedures have been introduced. Factors of this kind may also have contributed to the differences.

Listeria innocua

The non-pathogenic *L. innocua* is of special interest as it has, as mentioned, been proposed to be used as an indicator organism to evaluate thermal processes for lethality to *L. monocytogenes.* To function satisfactorily in this respect it is desirable that the indicator has heat resistance equal to or greater than the average heat resistance of *L. monocytogenes* or, more desirably, has heat resistance equal to that of the most resistant strains of this species. In the present work, heat resistance results for *L. innocua* were found in 5 reports (*Quintavalla & Barbuti* 1989, *Mackey et al.* 1990, *Foegeding & Stanley* 1991, *Fairchild & Foegeding* 1993, *Palumbo et al.* 1995). The equation for the thermal destruction line constructed was $\log_{10} D$ (*D* in s) = 14.2559 - 0.20077*t* (*r* = -0.95519). The average heat resistance values at 55, 60 and 65 °C calculated for *L. innocua* were greater than those for *L. monocytogenes* (Table 3), but none of analysed differences between means of *D* values were statistically significant. As to *L. innocua,* however, only 36 *D* values were reported totally and the *D* values obtained at the individual treatment temperatures used were few, 1-4. The most heat-resistant strain of the *L. innocua* strains investigated was reported by *Quintavalla & Barbuti* (1989). *D* values determined at 58, 60, 63 and 65 °C using a culture medium as heating menstruum were 2.7 to 5.4 times greater than the average *D* values found in the present work for *L. monocytogenes* at these temperatures. *Foegeding & Stanley* (1991) tested *L. innocua* strain ATCC 33091 in buffer and in skim milk at 56, 60 and 66 °C. In buffer, the *D* values were lower at 56 and 60 but higher at 66 °C than the corresponding average values for *L. monocytogenes.* When *L. innocua* PFEI (strain ATCC 33091 containing a plasmid which did not alter its heat resistance) was tested in skim milk, all *D* values obtained at these temperatures were higher, 1.5 to 2.1 times, than the values mentioned for *L. monocytogenes. Palumbo et al.* (1995) determined *D* values for a *L. innocua* strain isolated from raw egg. The tests were performed in egg yolk. *D* values obtained at 61.1, 63.3 and 64.4 °C were 2.5 to 2.9 times longer than the corresponding average values for *L. monocytogenes.* The results reported indicate that *L. innocua* may have greater average heat resistance than *L. monocytogenes.* However, as mentioned, only few heat resistance results are reported for *L. innocua* and more research on this matter is required.

Listeria ivanovii, L. seeligeri and L. welshimeri

Bradshaw et al. (1991) studied the heat resistance of *L. ivanovii, L. seeligeri* and *L. welshimeri.* One strain of each species was tested in milk at 52.2, 57.8, 63.3 and 68.9 °C. The equation for the 3 species taken together is $\log_{10} D$ (*D* in s) = 11.3419 - 0.15713*t* ; *r* = -0.99405. All means of *D* values obtained for the 4 treatment temperatures were lower than the corresponding means noted in the present work for *L. monocytogenes.* The differences be-

tween the means were statistically significant for the values obtained at 52.2 and 57.8 °C ($p < 0.05$ and < 0.001) but not for those obtained at 63.3 and 68.9 °C. In view of the low number of *D* values, 24, reported for *L. ivanovii, L. seeligeri* and *L. welshimeri* and the fact that only one strain of each of these species was tested, no conclusion, however, should be drawn about differences in average heat resistance between these species and *L. monocytogenes.*

Salmonella

Ng (1966) studied the heat resistance of 300 *Salmonella* isolates and gave $D_{57°C}$ values for 123 strains. The well-known extremely heat-resistant *Salm. senftenberg* 775W and 19 other strains of *Salm. senftenberg* were among the tested isolates. The resistance of the 19 strains was similar to that of the majority of isolates. Ng concluded that strains of salmonellae as resistant to heat as *Salm. senftenberg* 775W are rare. A similar conclusion was drawn by *Rossebø* (1970) who compared the heat resistance of *Salm. senftenberg* 775W with that of 20 strains of *Salm. senftenberg* isolated from herring meal.

The heat resistance of *Salm. senftenberg* 775W was also tested by *Anellis et al.* (1954), *Osborne et al.* (1954), *Davidson et al.* (1966), *Thomas et al.* (1966), *Corry & Barnes* (1968), *Read et al.* (1968), *Garibaldi et al.* (1969a), *Ng et al.* (1969), *Baird-Parker et al.* (1970), *Goepfert et al.* (1970), *Dabbah et al.* (1971a, b), *Gibson* (1973), *Corry* (1974), *Humphrey et al.* (1990) and *Blackburn et al.* (1997). The thermal destruction line fitted to the data (number of *D* values = 54) reported by the investigators mentioned is shown in Fig. 6. The equation for the line is $\log_{10} D$ (*D* in s) = 12.8001 - 0.17111*t* (*r* = -0.94992).

In a screening of 221 *Salmonella* isolates, *Baird-Parker et al.* (1970) found that 2 strains, one of *Salm. senftenberg* tested earlier by *Davidson et al.* (1966) and one of *Salm. bedford,* had $D_{60°C}$ values similar to that of *Salm. senftenberg* 775W. *Baird-Parker et al.* considered it possible, although unlikely, that the *Salm. senftenberg* strain was identical to *Salm. senftenberg* 775W (the strain was isolated from home-killed meat in the United Kingdom and *Salm. senftenberg* 775W from dried eggs in the United States). The authors determined *D* values in heart infusion broth for the *Salm. bedford* strain and for *Salm. senftenberg* 775W. *D* values obtained at 50, 55 and 60 °C were 350, 18.8 and 4.3 min for the *Salm. bedford* strain and 268, 36.2 and 6.3 min for *Salm. senftenberg* 775W. For comparison, it may be mentioned that the *D* values obtained for *Salm. senftenberg* 775W using the equation constructed in the present study are 293, 40.8 and 5.7 min at these temperatures.

Escherichia coli

Holland & Dahlberg (1940) investigated an *E. coli* strain noted for its heat resistance. Tests were performed in milk. The thermal destruction line based on the data (number of *D* values = 22) reported by Holland and Dahlberg is shown in Fig. 4. The equation for the line is $\log_{10} D$ (*D* in s) = 14.7478 - 0.19777*t* (*r* = -0.99403). The *z* value is 5.1 °C. The author of the present work is unaware of whether this *E. coli* strain has been subjected to further heat resistance studies.

Concluding remarks

The design of the present study required that some differences in composition, etc. of heating menstrua used and in methods used for heat treatment and for recovery of heat-treated bacteria had to be accepted when heat resistance data were collected from the literature. This meant that experimental factors of varying character might have influenced the magnitude of heat resistance values used in the work. Sta-

tistical analyses of the results of these fairly numerous influences could not be achieved on the basis of available information. Scrutiny of heat resistance values chosen according to the stipulations laid down in the study, however, indicated that value differences probably caused by differences in experimental conditions were, in most cases, small or moderate.

The summary heat resistance values recorded - especially those for *L. monocytogenes, E. coli* and salmonellas which are based on large numbers of data - may give useful information on what is at present known about the heat resistance that the bacteria reviewed show in liquid heating menstrua with pH values of approx. 6-8. It should, however, be emphasized that they may, and often do, show heat resistance of different magnitude in other types of heating menstrua.

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Sammanfattning

Värmeresistens i vätskor hos Enterococcus-, Listeria-, Escherichia-, Yersinia- , Salmonella- and Campylobacter-arter.

Syftet med arbetet var att samla in, utvärdera, sammanfatta och jämföra värmeresistensdata som rapporterats för *Campylobacter, Enterococcus, Escherichia, Listeria, Salmonella* and *Yersinia* spp. Resultat erhållna under så likartade experimentella förhållanden som möjligt eftersträvades. Noterade värmeresistensvärden, $\log_{10}$ *D*-värden, och rapporterade behandlingstemperaturer användes för upprättande av temperatur-avdödningslinjer för de olika bakteriegrupperna (*D*-värdet är den tid som krävs vid en viss behandlingstemperatur för att 90% av bakterierna skall inaktiveras). Med användning av lutningen hos respektive linje och lutningens 95%-konfidensintervall beräknades *z*-värdet och dess 95%-konfidensgränser (*z*-värdet är den temperaturändring som erfordras för att *D*-värdet skall öka eller minska med en 10-potens). Beräknade *z*-värden jämfördes med *z*-värden som erhållits från litteraturen. Linjernas ekvationer användes också för uträkning av *D*-värdesmedeltal och dessas 95%-konfidensgränser vid olika behandlingstemperaturer. 95%-konfidensgränser för "predicted" ("förutspådda") individuella *D*-värden räknades också ut. Linjer och värden visas i figurer och tabeller. Vissa noterade skillnader i värmeresistens mellan och inom bakteriegrupperna diskuteras i artikeln.

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