

Temperature tolerance and the final preferendum—rapid methods for the assessment of optimum growth temperatures

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The relationship between the temperature requirements of some fish species, using published data for growth optima, final preferences and lethal limits were examined. A good correlation was found and it is suggested that the data established gives a good estimate of the temperature promoting maximum growth. Determinations of final preferenda are easily conducted in the laboratory and could therefore be used to give rapid assessments of optimum growth temperatures of potential culture species. The practical application of such measurements is discussed.

I. INTRODUCTION

Increased use of cooling water by power generating stations and the resultant addition of waste heat to natural waters has stimulated studies into the assessment of environmental effects of thermal effluents. Amongst the most numerous investigations are those defining lethal temperatures for fish (Alabaster & Downing, 1966; Horoszewicz, 1973; Alabaster & Lloyd, 1980), although other workers have investigated the full range of temperature tolerance of selected species (Neill & Magnuson, 1974; Kutty *et al.*, 1980). This increasing body of available information has been used to classify fish into 'thermal guilds', according to their temperature requirements with a view to considering temperature as an ecological resource in a similar manner to food and/or space (Hokanson, 1977; Magnuson *et al.*, 1979; Brandt *et al.*, 1980). With a few notable exceptions, there has been little attempt to study the thermal requirements of fishes in relation to their physiology and behaviour (Brett, 1971; Beitinger & Fitzpatrick, 1979). Brett (1952) determined the preferred temperature for sockeye salmon, *Oncorhynchus nerka*, and subsequent work revealed this temperature to coincide with the temperature optima for swimming speed, metabolic scope and growth (Brett, 1971).

In this paper correlations are sought between the preferred temperature, temperature tolerance, estimated from upper lethal temperatures and physiological optima.

II. THERMAL RELATIONS OF FISHES—DEFINITIONS AND TERMINOLOGY

The temperature responses of fishes are divisible into tolerance, resistance and preference. The thermal responses of a fish relative to acclimation temperature

are summarized in Fig. 1. In order to define the zones of tolerance and resistance, plots of incipient lethal temperatures (tolerance limit) and temperatures at which death is rapid (resistance limit) are made against acclimation temperature. The upper and lower incipient lethal temperatures (UILT and LILT) represent the temperatures at which, theoretically, 50% of the population could survive indefinitely. Outside the tolerance temperatures lies the zone of resistance, within which there is a strong interaction between temperature and exposure time. The upper boundary of the resistance zone is represented by the critical thermal maximum (CTM), which is a measure of thermal resistance determined by increasing the water temperature at a rate of $1^{\circ}\text{C min}^{-1}$ until the fish lose equilibrium. Survival times above CTM are virtually zero.

The UILT, LILT and CTM are dependent upon acclimation temperature and the previous thermal history of the fish (Fig. 1). Figure 1 also shows that the boundaries of the tolerance zone are given by the UILT, LILT and the ultimate upper incipient lethal temperature (UUILT), which is the highest temperature to which the species can be acclimated.

Within the thermal tolerance zone, fish, when given a choice, will spend most time within waters of a certain temperature and these preferred temperatures (acute thermal preferenda) are also dependent upon previous thermal acclimation (Fig. 1). Acute thermal preferenda are usually determined over a short period,

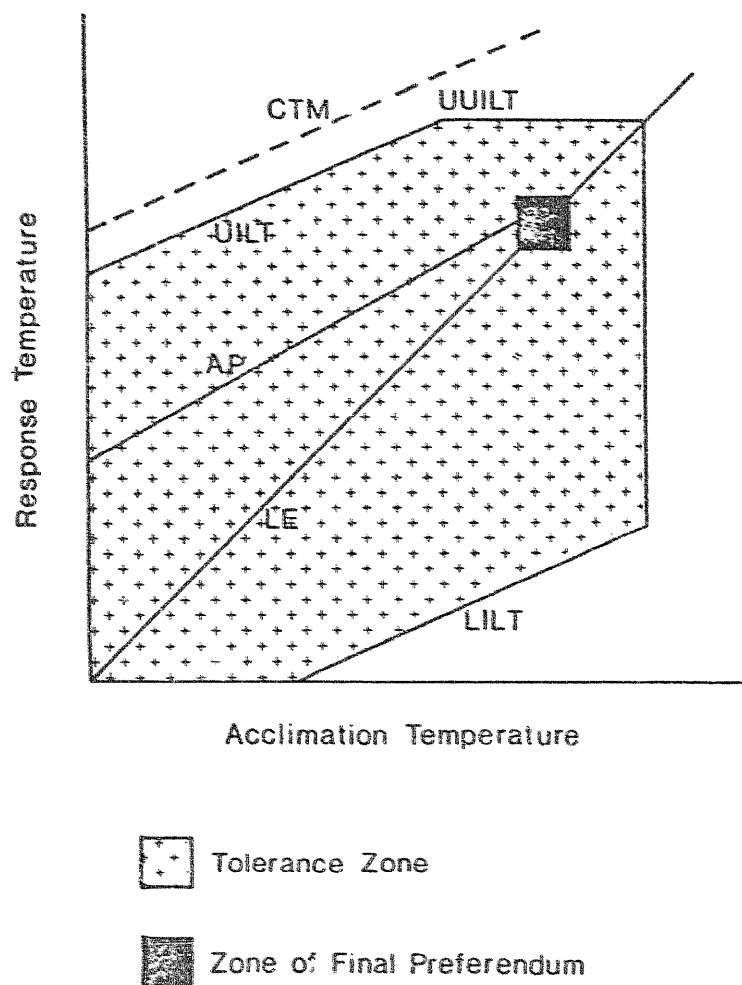


FIG. 1. Diagram showing temperature relations of fish. CTM, Critical thermal maximum; UILT, upper incipient lethal temperature; LILT, lower incipient lethal temperature; UUILT, ultimate upper incipient lethal temperature; AP, acute thermal preferendum; LE, line of equality. For further details see text.

but if fish are left exposed to a temperature gradient for a longer period, they will gradually gravitate towards a given temperature characteristic for the species (final temperature preferendum).

Fry (1947) gave a bipartite definition of the final preferendum as '... a temperature around which all individuals will ultimately congregate, regardless of their thermal experience before being placed in the gradient' and '... that temperature at which the preferred temperature is equal to the acclimation temperature'. This bipartite definition can give rise to two independent methods for the determination of the final preferendum. The first, 'gravitation method', has already been mentioned in that fish are exposed to a temperature gradient for an extended period until they 'gravitate' to the preferred temperature. The alternative method consists of determining acute temperature preferenda for groups of fish acclimated to different temperatures. A line can be plotted through these points and where the line intersects with the 'line of equality' the acclimation temperature is equal to the acute temperature preferendum (Fig. 1). This corresponds to the second part of Fry's (1947) bipartite definition. Both methods of determining final preferenda have been widely used and the methods have been discussed and compared by a number of authors (Badenhuizen, 1967; Richards *et al.*, 1977; Reynolds, 1978; Reynolds & Casterlin, 1979a).

There is increasing evidence that a fish does not move to water of a given temperature within a gradient and then remain there but tends to make 'exploratory movements' into waters of both lower and higher temperature. Therefore, it may be more realistic to consider the final preferendum as a 'zone' rather than a fixed temperature (Fig. 1). Supportive arguments in favour of the 'final preferendum zone', rather than a single temperature, is that the estimate of the final preference has been shown to vary with a number of environmental and other factors (Hutchison & Maness, 1979; McCauley & Huggins, 1979; Reynolds & Casterlin, 1979a). McCauley & Huggins (1979) have also suggested that final preferenda of rainbow trout, *Salmo gairdneri*, may be dependent upon age, the younger stages having higher preferenda than older fish. Definite age effects have not been demonstrated for other species, although there is less data available than for rainbow trout. If future research shows that there are definite ontogenetic variations in temperature preferenda, then the concept of the final preferendum must be revised, but for the purpose of the current paper it will be assumed that this is species-specific, in accord with earlier definitions.

The optimum temperature for growth is defined as the temperature at which growth rate is highest when the fish are reared under conditions of maximum, or excess feeding.

III. MATERIALS AND METHODS

Values for growth optima, final preferenda and temperature tolerance were extracted from the published literature and correlations studied between these indicators of thermal requirements.

Laboratory data of final preferenda using both 'gravitational' and 'acute' methods were included but data of temperature preferenda (other than lethal temperatures) based upon field observations were discarded. Field data was not usually included because the preferred temperature varies with season and the distribution of the fish in the water column may be influenced by factors other than temperature, e.g. light, prey density and

oxygen concentration. As the final preferendum is defined as being species-specific, data referring to all ontogenetic stages have been included. Problems arose with the selection of data relating to upper lethal temperatures. European workers have tended to report lethal temperatures in terms of the CTM, whereas in the U.S.A. and Canada it is more usual to report values of ultimate upper incipient lethal temperatures (UUILT). Figure 1 shows the CTM is dependent on acclimation temperature and so in cases where CTMs have been taken as the assessment of lethal temperature, the value used is the CTM for the fish acclimated to the highest temperature. In some cases, estimates of lethal temperatures taken from field data have also been included. The use of three different estimates of 'lethal temperature' invariably introduces some degree of scatter but the variations were not so great as to mask any general trends. Correlations between the various parameters were sought using least squares linear regression analysis.

IV. RESULTS

The values for growth optima, final preferenda and lethal temperatures for a range of species are listed in Table I. Linear regression analysis showed that there were significant correlations between these three parameters and the respective regression lines are given in Table II. A good correlation was found between the final preferenda and the optimum temperature for growth. When plotted, the points lay about a regression line which was almost equivalent to the line of equality. Hence, the hypothesis that the final preferendum is a good indicator of the optimum temperature for growth (and vice versa) is supported by the available data (Fig. 2).

In cases where two of the parameters had been reported in the literature the equations given in Table II were used to calculate the third temperature. These values are given in Table I and in most cases it can be seen that there is reasonable agreement between the two calculated values.

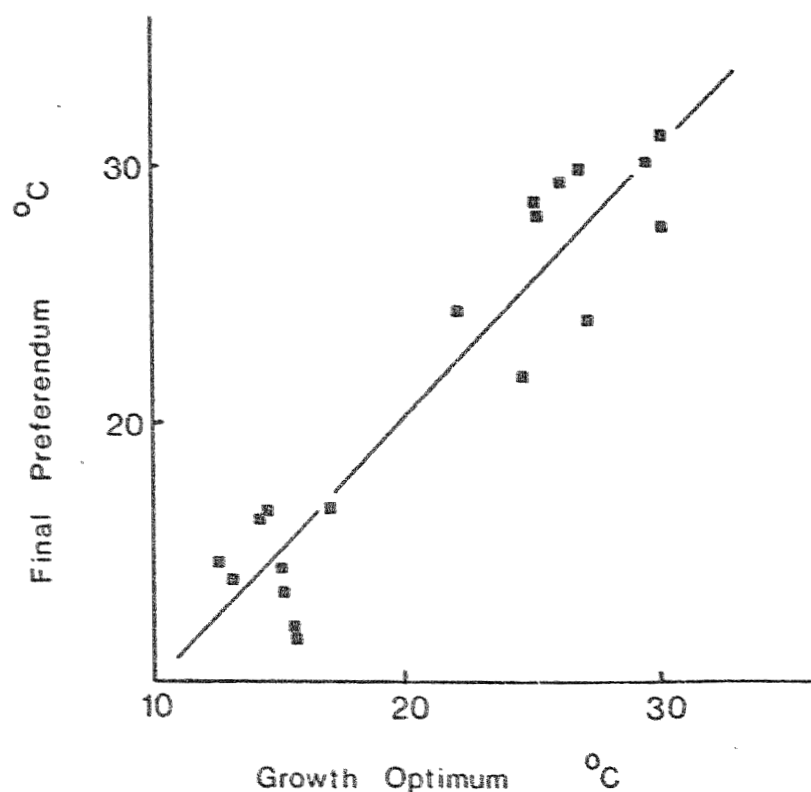


FIG. 2. Relationship between final preferenda and optimum temperatures for growth of various fish species. Points represent means of data given in Table I. $Y = 1.05X - 0.53$; $n = 19$.

TABLE 1. Summary of thermal preference and tolerance data for a number of fish species listed by families						
Species	Optimum growth temperature (° C)		Final preference (° C)		Lethal temperature (° C)	
<i>Petromyzon marinus</i>	15	Farmer <i>et al.</i> (1977)	13.6	Reynolds & Casterlin (1978c)	31	Potter & Beamish (1975)
<i>Oncorhynchus gorbuscha</i>	15.5	Kepshire (1971)	11.7 11.7-12.8	Brett (1952) Hurley & Woodall (1968)	23.9	Brett (1952)
<i>O. kisutch</i>	14.8	Gt. Lakes Fish Lab. (1970)	15/13		25	Brett (1952)
<i>O. tshawytscha</i>	15.5	Banks <i>et al.</i> (1971)	11.7	Brett (1952)	25.1	Brett (1952)
<i>O. nerka</i>	15	Brett <i>et al.</i> (1969)	14.5	Brett (1952)	24.8	Brett (1952)
<i>O. keta</i>	13	Kepshire (1971)	14.1	Brett (1952)	23.7	Brett (1952)
<i>Salvelinus fontinalis</i>	13	Baldwin (1956)	14	Fisher & Elson (1950)	25.3	Fry <i>et al.</i> (1946)
	14	McCormick <i>et al.</i> (1972)	16	Sullivan & Fisher (1953)	20.1	McCormick <i>et al.</i> (1972)
	16.1	Hokanson <i>et al.</i> (1973b)	18	Javaid & Anderson (1967)	24	Cherry <i>et al.</i> (1977)
			16	Peterson (1973)		
			19	Cherry <i>et al.</i> (1975)		
			16	Cherry <i>et al.</i> (1977)		
<i>Salmo gairdneri</i>			18	Müller (1977)		
	17.2	Hokanson <i>et al.</i> (1977)	18	Javaid & Anderson (1967)	26.5	Alabaster & Welcomme (1962)
	16.5	Wurtsbaugh & Davies (1977)	18.5	McCauley & Pond (1971)	26	Bidgood & Berst (1969)
	17	Papoutsoglou & Papaparaskeva-Papoutsoglou (1978)	18	Cherry <i>et al.</i> (1975)	26.3	Charlon <i>et al.</i> (1970)
			19.2	Cherry <i>et al.</i> (1977)	25	Cherry <i>et al.</i> (1977)
			11.3	McCauley <i>et al.</i> (1977)	25	Hokanson <i>et al.</i> (1977)
<i>S. salar</i>			14	McCauley & Huggins (1979)		
	15.1/12.1		14	Fisher & Elson (1950)	23	Bishai (1960)
			18	Javaid & Anderson (1967)		
			14	Peterson & Metcalfe (1979)		

TABLE I. (continued)

Species	Optimum growth temperature (° C)		Final preference (° C)		Lethal temperature (° C)	
<i>S. trutta</i>	10	Pentelow (1939)	17.6	Ferguson (1958)	23	Bishai (1960)
	15.5	Wingfield (1940)	14.3	Cherry <i>et al.</i> (1977)	26.4	Alabaster & Downing (1966)
	12	Swift (1961)	12.2	Reynolds & Casterlin (1979d)	23	Cherry <i>et al.</i> (1977)
<i>Coregonus artedii</i>	12.8	Elliott (1975)				
	18.1	McCormick <i>et al.</i> (1971)	18.5/9.9		19.8	McCormick <i>et al.</i> (1971)
<i>C. clupeaformis</i>					26.2	Edsall & Colby (1970)
	13.5/16.8		12.7	Ferguson (1958)	26.6	Edsall & Rottiers (1976)
<i>Esox lucius</i>			12-16	Hoagman (1974)		
	26	Hokanson <i>et al.</i> (1973a)	23-24	Hokanson (1977)	34	Scott (1964)
	19-21	Casselman (1978)			28.4	Hokanson <i>et al.</i> (1973a)
<i>E. masquinongy</i>					29	Hokanson (1977)
	24/26.6		24	Ferguson (1958)	34	Scott (1964)
<i>Cyprinus carpio</i>			25.1	Reynolds & Casterlin (1979b)		
	30/32		32	Pitt <i>et al.</i> (1956)	35.7	Black (1953)
			31.5	Neill & Magnuson (1974)	38	Meuwis & Heuts (1957)
<i>Carassius auratus</i>			29	Reynolds & Casterlin (1977)	40.6	Horoszewicz (1973)
	25	Audige (1921)	30	Roy & Johansen (1970)	38.6	Fry <i>et al.</i> (1942)
			28	Reynolds <i>et al.</i> (1978)	40	Hoyland <i>et al.</i> (1979)
<i>Campostoma anomalum</i>			28	Reynolds & Casterlin (1979e)		
	26.6/23		28.6	Cherry <i>et al.</i> (1975)	31	Cherry <i>et al.</i> (1977)
<i>Pimephales notatus</i>			26.2	Cherry <i>et al.</i> (1977)		
	27.7/24		29	Cherry <i>et al.</i> (1975)	32	Cherry <i>et al.</i> (1977)
			28.1	Cherry <i>et al.</i> (1977)		

<i>Campostoma anomalum</i>	26.6/23		28.6 26.2	Cherry <i>et al.</i> (1975) Cherry <i>et al.</i> (1977)	31	Cherry <i>et al.</i> (1977)
<i>Pimephales notatus</i>	27.7/24		29 28.1	Cherry <i>et al.</i> (1975) Cherry <i>et al.</i> (1977)	32	Cherry <i>et al.</i> (1977)
<i>P. promelas</i>	26/25.5		23.4 28.5 29 26.6	Jones & Irwin (1965) Opuszynski (1971) Cherry <i>et al.</i> (1975) Cherry <i>et al.</i> (1977)	33.2	Hart (1947)
<i>Notropis rubellus</i>	25.7/25.3		26.8 26	Cherry <i>et al.</i> (1975) Cherry <i>et al.</i> (1977)	33	Cherry <i>et al.</i> (1977)
<i>N. spilopterus</i>	28.6/29.2		29.5 29.4	Cherry <i>et al.</i> (1975) Cherry <i>et al.</i> (1977)	36	Cherry <i>et al.</i> (1977)
<i>N. telescopus</i>	19.6/21.3		20	Cherry <i>et al.</i> (1977)	30	Cherry <i>et al.</i> (1977)
<i>N. atherinoides</i>	27	McCormick & Kleiner (1976)	27.8/25.1		30.7 35.2	Hart (1947) McCormick & Kleiner (1976)
<i>Rhodeus sericeus</i>	24.3/29.9		25	Zahn (1963)	36.5	Horoszewicz (1973)
<i>Hypentelium nigricans</i>	25.8/25.3		26.6	Cherry <i>et al.</i> (1977)	33	Cherry <i>et al.</i> (1977)
<i>Catostomus commersoni</i>	27	McCormick <i>et al.</i> (1977)	24	Reynolds & Casterlin (1978a)	29.3 31.2 30.5	Hart 1947 Brett (1944) McCormick <i>et al.</i> (1977)
<i>Ictalurus punctatus</i>	29 30 28-30	West (1965) Andrews & Stickney (1972) Andrews <i>et al.</i> (1972)	30.5 30	Cherry <i>et al.</i> (1975) Cheetham <i>et al.</i> (1976)	36.1/36.4	
<i>I. nebulosus</i>	28.2/29.9		29-31 27.3	Crawshaw (1975) Richards <i>et al.</i> (1977)	36.5	Brett (1944)
<i>Heteropneustes fossilis</i>	30.7/34.1		31.7	Vasal & Sundararaj (1978)	39.8	Vasal & Sundararaj (1978)
<i>Fundulus heteroclitus</i>	24.3/29.2		25	Garside & Morrison (1977)	36	Garside & Chin-Yuen-Kee (1972)
<i>Lebistes reticulatus</i>	25	Gibson & Hirst (1955)	27.9 29	Ruff & Zippel (1966) Ogilvie & Fryer (1971)	32.8/35.1	
<i>Gambusia affinis</i>	28.6/30.9		28 31	Bacon <i>et al.</i> (1967) Winkler (1979)	37.3	Hart (1952)

TABLE I. (continued)

Species	Optimum growth temperature (° C)		Final preference (° C)		Lethal temperature (° C)
<i>Gasterosteus aculeatus</i>	12·8/19·3		7·5–10 16–18	Røed (1979) Garside <i>et al.</i> (1977)	28·5 Jordan & Garside (1972)
<i>Leuresthes sardina</i>	31/27·9		32	Reynolds & Thomson (1974a)	35 Reynolds & Thomson (1974b)
<i>Perca flavescens</i>	23 28 23–24	Schneider (1973) McCormick (1976) Magnuson <i>et al.</i> (1979)	21 24·2 20·1 23·3 23 21·4 20·2	Ferguson (1958) Ferguson (1958) McCauley & Read (1973) McCauley & Read (1973) Neil & Magnuson (1974) Cherry <i>et al.</i> (1977) Reynolds & Casterlin (1979c)	30·9 29·7 32·3 29·2 33–34 26 Brett (1944) Hart (1947) Hart (1952) Black (1953) McCormick (1976) Cherry <i>et al.</i> (1977)
<i>P. fluviatilis</i>	26	Hokanson (1977)	26·8/23·7		31·4 32 33 Alabaster & Downing (1966) Horoszewicz (1973) Willemsen (1977)
<i>Stizostedion canadense</i>	22	Smith & Koenst (1975)	22·6/21·3		30·5 Smith & Koenst (1975)
<i>Stizostedion vitreum vitreum</i>	22·1	Smith & Koenst (1975)	23/23		31·6 Smith & Koenst (1975)
<i>S. lucioperca</i>	28–30	Hokanson (1977)	30/29		36·3 35·4 Horoszewicz (1973) Willemsen (1977)
<i>Micropterus salmoides</i>	27·5 27 25 26–28	Strawn (1961) Nelson (1974) Niimi & Beamish (1974) Coutant & Cox (1975)	30–32 30 30·2 28·5 29	Ferguson (1958) Neill & Magnuson (1974) Reynolds <i>et al.</i> (1976) Reynolds & Casterlin (1978b) Venables <i>et al.</i> (1978)	36·4 Hart (1952)
<i>M. dolomieu</i>	26	Horning & Pearson (1973)	28 21·2	Ferguson (1958) Cherry <i>et al.</i> (1977)	35 Cherry <i>et al.</i> (1977)

<i>Stizostedion canadense</i>	22	Smith & Koenst (1975)	22.6/21.3	30	Willemssen (1977)
<i>Stizostedion vitreum vitreum</i>	22.1	Smith & Koenst (1975)	23/23	30.5	Smith & Koenst (1975)
<i>S. lucioperca</i>	28-30	Hokanson (1977)	30/29	31.6	Smith & Koenst (1975)
<i>Micropterus salmoides</i>	27.5	Strawn (1961)	30-32	36.3	Horoszewicz (1973)
	27	Nelson (1974)	30	35.4	Willemssen (1977)
	25	Niimi & Beamish (1974)	30.2	36.4	Hart (1952)
	26-28	Coutant & Cox (1975)	28.5		
			29	Ferguson (1958)	
				Neill & Magnuson (1974)	
				Reynolds <i>et al.</i> (1976)	
				Reynolds & Casterlin (1978b)	
				Venables <i>et al.</i> (1978)	
<i>M. dolomieu</i>	26	Horning & Pearson (1973)	28	35	Cherry <i>et al.</i> (1977)
			31.3	Ferguson (1958)	
			30.3	Cherry <i>et al.</i> (1975)	
			28.5	Cherry <i>et al.</i> (1977)	
				Reynolds & Casterlin (1978b)	
<i>M. punctulatus</i>	30.5/29		32.1	36	Cherry <i>et al.</i> (1977)
			30.8	Cherry <i>et al.</i> (1977)	
<i>Ambloplites rupestris</i>	27.7/29		28	36	Cherry <i>et al.</i> (1977)
			29	Neill & Magnuson (1974)	
				Cherry <i>et al.</i> (1977)	
<i>Lepomis gibbosus</i>	30	Pessah & Powles (1974)	31.5	36.6/34.8	
			26	Ferguson (1958)	
			26	Richards <i>et al.</i> (1977)	
				Reynolds & Casterlin (1977)	
<i>L. macrochirus</i>	30.1	Lemke (1977)	32.3	35.5	Hickman & Dewey (1973)
	31	Beitinger & Magnuson (1979)	31.2	37.3	Banner & van Arman (1973)
	29-30	Magnuson <i>et al.</i> (1979)	31	36	Cherry <i>et al.</i> (1977)
			32	Ferguson (1958)	
			30.9	Beitinger (1974)	
			31	Neill & Magnuson (1974)	
				Cherry <i>et al.</i> (1975)	
				Cherry <i>et al.</i> (1977)	
				Reynolds & Casterlin (1979e)	
<i>Sarotherodon mossambica</i>	27.6/34.5		28.5	40	Ananthakrishnan & Srinivasan (1978)
<i>Pomatoschistus minutus</i>	17/22.6		17.3	31	Hesthagen (1979)
<i>Girella nigricans</i>	24/23		23.5	31.4	Duodoroff (1942)
			26	Duodoroff (1942)	
<i>M. punctulatus</i>	14.2	Ursin (1963)	16-17	24.6/27.3	

TABLE II. Linear regression analysis showing relationships between temperature requirements of fishes

Parameters	<i>n</i>	Regression equation	<i>r</i>
Growth optimum (<i>X</i>) Final preference (<i>Y</i>)	19	$Y = 1.05 X - 0.53$	0.937
Growth optimum (<i>X</i>) Lethal temperature (<i>Y</i>)	22	$Y = 0.76 X + 13.81$	0.866
Final preference (<i>Y</i>) Lethal temperature (<i>Y</i>)	38	$Y = 0.66 X + 16.43$	0.880

V. DISCUSSION

It is comparatively easy to determine the final temperature preferences of a fish species using suitably designed electronic shuttleboxes, or temperature gradient apparatus (Richards *et al.*, 1977; Reynolds, 1978). On the other hand, the determination of the optimum temperature for growth is time consuming and involves the use of large numbers of fish acclimated to, and reared at, a wide range of temperatures. The analysis of available data suggests that the final preference gives a good indication of the optimum temperature for growth. Therefore, the determination of the preferenda could be used as a rapid method for the estimation of the temperature required to promote maximum growth of fish. The use of such a method would appear to be particularly valuable in the investigation of ontogenetic changes in temperature requirements (McCauley & Huggins, 1979), an investigation which would be unrealistic using conventional methods for studying interactions between temperature and growth.

A good correlation was also found between lethal temperature and optimum temperature for growth. However, due to the method of assessing lethal temperature, the equation given in Table II is likely to give a less precise estimate of growth optima than the use of the final preferendum-growth optimum relationship. Nevertheless, there is a much wider body of literature referring to 'lethal temperatures' than to preferred temperatures and this information could be used to give an approximation of growth requirements. One of the major difficulties with the use of lethal temperatures is the inconsistency of the methods used. For example, although the CTM is generally considered to be the temperature at which fish lose equilibrium when subjected to water heated at a rate of $1^{\circ}\text{C min}^{-1}$, this has not been universally adopted as a definition. In consequence, various heating rates have been used in the determination of the CTM, leading to considerable variations in values of CTMs for given species. In an evaluation of the methodology, Becker & Genoway (1979) showed that the higher the rate of heating, the higher was the CTM. These authors stressed the need for standardization of technique and concluded that CTM could give a useful means for investigating problems, such as short term changes in temperature tolerances and lethal limits. Thus, values of CTM are likely to be of value in assessing temperature tolerances of fishes subjected to abrupt changes in water temperature induced by periodic thermal discharges. However, such values give little indication of

survival and growth of fish subjected to long term temperature changes. Where information of this nature is required, the determination of the UUILT appears to be more realistic.

Recently, there has been increased interest in the possible use of thermal effluent to promote fish growth (Sylvester, 1975; Aston *et al.*, 1976; Peterson & Seo, 1977; Sadler, 1979) and there are commercial and pilot scale farms using power station cooling water. However, the choice of the culture organisms has not always been made with regard to the physiology and behaviour of the species (Holt & Strawn, 1976, 1977; Branch & Strawn, 1978) and it is proposed that accurate information concerning the optimum temperature for growth and temperature tolerance range would lead to the selection of more suitable species. Preliminary experiments to determine temperature preferenda (growth optima) and UUILTs (tolerance limits) could increase the rate at which potential culture species were 'screened' with a concomitant saving in time and monetary expenditure.

As an illustration, among the major problems faced by culturists of red sea bream, *Chrysophrys major*, in Japan are reduced growth and increased mortality during the summer months (Kitazima, 1969). At this time of the year sea surface temperatures may exceed 30°C and thus approach the UUILT (32°C) of the species (Woo & Fung, 1980). Use of the equations given in Table II provides an estimate of approximately 24°C for optimum growth of red sea bream. Data on temperature tolerance and preference should, therefore, be used when assessing the suitability of sites for culture.

Information relating to the growth of estuary grouper, *Epinephelus salmoides*, has been used to assess the economic feasibility of commercial production (Chua & Teng, 1978, 1979, 1980). The lethal temperature for the species is 39°C (Chua & Teng, 1980), suggesting a growth optimum of about 32°C. A consideration of the hydrographic data given for the experimental cage sites shows that the annual temperature conditions (28–32°C) were close to those promoting maximum growth.

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