Temperature tolerances of North American freshwater fishes exposed to dynamic changes in temperature

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Synopsis

Traditionally lower and upper temperature tolerances of fishes have been quantified in the laboratory via three different experimental approaches: the Fry or incipient lethal temperature (ILT), critical thermal (CTM) and chronic lethal (CLM) methodologies. Although these three experimental laboratory approaches generate endpoints which are quantitatively expressed as a temperature, are determined experimentally with random samples of fish acclimated to specific temperatures, and involve both time and temperature as major test variables, they do not quantify the same response. All three approaches generate valuable, albeit different, information concerning the temperature tolerance of a species. In this review we have summarized published research concerning the tolerance of North American freshwater fishes to dynamic changes in temperature, i.e., tolerance is tested by methods that gradually change temperatures until biological stress is observed. We found more than 450 individual temperature tolerances listed in 80 publications which present original dynamic temperature tolerance data for 116 species, 7 subspecies and 7 hybrids from 19 families of North American freshwater fishes. This total represents about 1/3 of the families and 1/6 of the known North American freshwater species. Temperature tolerance data were partitioned by experimental approach, i.e., critical thermal method (CTM) and chronic lethal method (CLM), and direction of temperature change. Although both CTM and CLM expose fish to dynamic changes in water temperature, these two methods differ in temperature change rates and test endpoints, and hence measure different aspects of thermal stress. A majority of the 80 studies employed CTM to assess temperature tolerance, in particular determination of CTmaxima. One or more CTmaxima has been reported for 108 fishes. Twenty-two fishes have reported highest CTmaxima of 40°C or higher. Several species in the family Cyprinodontidae have generated some of the highest CTmaxima reported for any ectothermic vertebrate. For a variety of reasons, data concerning tolerance of low temperatures are less plentiful. Low temperature tolerance quantified as either CTminima or CLminima were found for a total of 37 fishes. Acclimation temperature exerts a major effect on the temperature tolerance of most North American fish species and it is usually strongly linearly related to both CTmaxima and CTminima. Although we uncovered dynamic temperature tolerance data for 130 fishes, only a single dynamic, temperature tolerance polygon has been published, that for the sheepshead minnow, *Cyprinodon variegatus*.

Introduction

Importance of temperature in the life of fishes

A vast literature documents the importance of temperature in the life of fishes. Although early studies of temperature and fishes date to the 1800s, much of our contemporary knowledge concerning the role of temperature on fishes can be attributed to research of 'the father of fish environmental physiology', F.E.J. Fry, and his students at the University of Toronto, including J.R. Brett. Their work and that of other researchers

can be found in several now classic reviews (Fry 1947, 1964, 1967, 1971, Brett 1956, 1970, 1971). From this research Brett (1971) identified temperature as the abiotic master factor for fishes. In 1956 he developed the thermal primacy paradigm, 'because of the all pervading nature of environmental temperature, the fundamental thermal requirement of fishes is an external environment most suitable to their internal temperature'.

Body temperatures of fishes

The body temperatures of most of the over 20 000 described species of fishes are a direct function of water temperature. A combination of several environmental, anatomical and physiological factors, e.g., high specific heat of water, relatively low metabolic rate, lack of insulation and countercurrent lamellar blood–water flow, cause the body temperature of most fishes to conform to water temperatures, i.e., most fishes are classic ectotherms. The relation between fish body temperatures and water temperatures has been a subject of study for more than 150 years (see Morrow & Mauro 1950). Many of these early studies involved fish captured in the field where body temperatures were measured relatively crudely, water temperatures from which fish were taken were assumed to equal surface temperatures and fish were taken by angling after varying lengths of capture time. More recent controlled laboratory experiments have shown that the rate of change of fish body temperatures follows Newton's Law of cooling and can be accurately modelled (Stevens & Fry 1970, Spigarelli et al. 1974, Weller et al. 1984). At temperature equilibrium, the body temperature of a fish is usually about 0.1 to 1°C above water temperature (Clausen 1934, Gunn 1942, Fry 1967, Stevens & Fry 1970, 1974, Dean 1976, Spigarelli et al. 1977). This difference between water and body temperatures, termed an excess temperature (Stevens & Fry 1970), is a result of thermal inertia (Neill & Stevens 1974) and dependent upon fish size (Stevens & Fry 1974, Spigarelli et al. 1977, Beitinger et al. 1977). Studies by Stevens & Sutterlin (1976) and Beitinger et al. (1977) estimated that conduction through the body surface accounts for a majority (ca. 80%) of total heat transfer responsible for bringing the body temperature of a fish into equilibrium with water temperature. Dean (1976) found that forced exercise in the rainbow trout, Oncorhynchus mykiss, did not increase excess temperatures even of muscles. In fact, the more vigorous the exercise, the quicker muscle temperatures

equaled water temperature. This suggests an enhanced heat transfer through the gills when a fish exercises.

Exceptions to thermal conformity between water and fish body temperatures include some tunas and lamnid sharks which possess anatomical heat conservers to retain metabolically generated heat (see Carey & Teal 1966, 1969a,b, Carey et al. 1971 and several others). Although exciting from an environmental physiology perspective, these 'warm bodied' fishes represent only a small minority of fish species.

Effects of environmental temperature

Temperature affects virtually all biochemical, physiological and life history activities of fishes. Temperature can be viewed as an environmental resource (Magnuson et al. 1979) and fish will compete for favorable temperatures (Beitinger & Magnuson 1975, Medvick et al. 1981). An abiotic environmental factor such as temperature should be viewed in the context of its multiple effects on fishes. Fry (1947) delineated five major effects of temperature: controlling (setting the pace of development and metabolism), masking (affecting the expression of other environmental factors), limiting (influencing locomotory activity and hence distribution), directing (stimulating an orientation response), and finally, as a lethal agent, i.e., too much or too little can destroy the integrity of a fish causing its death. This latter effect of temperature is the topic of this review.

Temperature tolerance of fishes

Probably the most dramatic effect of temperature is to act as a lethal agent (Fry 1947). Owing to the large number of species and their key role in freshwater and marine ecosystems, a vast literature reports temperature tolerances of fishes. Many of the earliest reports of fish involved temperature tolerance, e.g., Heath (1884), Day (1885), Carter (1887), Vernon (1899) and Wells (1914). Some recent reviews which give some fish thermal tolerance data include Hutchison (1976), Spotila et al. (1979), Houston (1982), and Lutterschmidt & Hutchison (1997b).

Temperature-induced fish kills in nature

Most laboratory temperature tolerance estimates for fishes involve high temperatures, whereas most fish

kills in nature are caused by exposure to low temperatures. Although we could find only a few examples of fish kills directly attributed to heat death (Huntsman 1942, 1946, Bailey 1955, Coulton 1959, Matthews et al. 1982, Mundahl 1990), the literature contains numerous reports of death due to low temperatures (Willcox 1887, Bangs 1895, Verril 1901, Fitch 1917, Agersbork 1930, Storey & Gudger 1936, Storey 1937, Miller 1940, Galloway 1941, Gunther 1941, 1947, 1952, Gunther & Hildebrandt 1951, Simpson 1953, Wells et al. 1961, Tabb & Manning 1961, Tabb et al. 1962, Dahlberg & Smith 1970, Overstreet 1974, Moore 1976, Holt & Holt 1983, Bennett & Judd 1992).

Several observations may help explain the disparity between the number of reports of 'cold' and heat deaths. First, fish are able to increase their tolerance of high temperatures, i.e., gain of heat tolerance, more quickly than they can increase their tolerance of low temperatures, i.e., gain 'cold' tolerance (Doudoroff 1942, Brett 1946, Davies 1973). Second, fish lose heat tolerance relatively slowly (Davenport & Castle 1895, Loeb & Wasteneys 1912, Hathaway 1927). Third, high temperatures induce frantic activity which assists fish to flee from high temperatures, whereas cold induces lethargy which prevents fish from escaping low temperatures. Fourth, upper temperature tolerances of most North American fishes are well above ambient temperatures in their natural habitats (Mundahl 1990). These observations suggest that fishes are better adapted to withstand sudden exposures to temperatures near upper lethal than lower lethal levels. Furthermore, a majority of low temperature death reports occurred in marine environments when cold fronts caused rapid decreases in inshore temperatures and dramatic mortalities of game and commercially important species. In contrast, most reported heat deaths occurred in shallow, sometimes intermittent freshwater. The latter are both less dramatic and obvious to humans than the former.

A majority of the recorded fish kills were the result of the vagaries of weather. However, 70 years ago Belding (1928) concluded that human activities such as deforestation, cultivation and industrial operations had increased the temperature of inland waters to the detriment of valuable cold-water species of fish. In 1930, Agersborg reported the death of large numbers of freshwater fishes attracted to the warm-water discharge of a corn products industry in winter. A decrease in plant operations resulted in a sharp decline in water temperature which was responsible for these mortalities.

In the 1960s and 1970s, the proliferation of once-through cooling systems of steam electric power stations along the shores of many major bodies of water generated wide spread concern for the potentially adverse effects of 'waste heat' (Alabaster 1963, Cairns 1968, Clark 1969). The first wave of thermal effects research related to water quality regulations after the Federal National Pollution Contract Act in 1965 established the requirement for temperature standards. The United States Federal Water Pollution Control Act of 1972 targeted heat as a pollutant and Section 301 of the Act prohibited the discharge of pollutants (including heat) into navigable waters. Variance to these regulations is possible through Section 316(a) which applied only to heat, and it authorized on a case-by-case basis, an easing of thermal limitations that are more stringent than necessary 'to assure the protection and propagation of a balanced, indigenous population of shellfish, fish and wildlife in the receiving waters'. Probably more than any other single event, Section 316(a) stimulated thermal research and forced industry to finance many of the tremendous number of fish-temperature studies which proliferated in the 1970s. Concerns over the potential adverse effects of thermal pollution fueled numerous conferences including two sponsored by the United States Atomic Energy Commission (later the Energy Research Development Agency, ERDA) which resulted in two excellent published proceedings edited by Gibbons & Sharitz (1974) and Esch & McFarlane (1976). A major outcome of the wealth of fish-temperature research during this time is the observation that fishes possess acute temperature discrimination powers and use behavior to avoid or rapidly escape thermally hostile areas, if thermally favorable environments are available (Neill & Magnuson 1974, Coutant 1975, Richards et al. 1977). Thermal effluents from once-through cooling systems were shown to influence the distribution of fishes (Neill & Magnuson 1974, Spigarelli et al. 1974, Coutant 1975, Kelso 1976). Surprisingly, there are few published reports of fish kills from exposure to excessive heat at power stations (Young & Gibson 1973). However, Coutant (1977) cites several examples where fish attracted to warm water discharges were killed via cold shock due to changes in plant operation or cooling water conditions. In general, adverse environmental effects have been minimized by prudent design and location of intake and discharge structures at many electric generating facilities.

During the 1960s and 1970s the primary effects of excessive 'waste' heat were considered site specific. In contrast today, with an awareness of the increasing greenhouse gases in the atmosphere concerns

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have become global in scope. The United States National Research Council (1983) proposed that global mean air temperatures may increase by 1.5 to 4.5°C in the next half century. Since 1981 when Coutant (op. cit.) wrote about potential CO_2-induced climate changes on freshwater, numerous investigators have addressed the potential effects of global warming on various levels of biological organization. These studies included entire fish communities in the Great Lakes (Meisner et al. 1987, Magnuson et al. 1990), and the southern plains and southwest (Matthews & Zimmerman 1990), individual species, e.g., coastal striped bass, *Morone saxatilis* (Coutant 1990), brook charr *Salvelinus fontinalis* (Meisner 1990), physiological processes such as growth of largemouth bass, *Micropterus salmoides* (McCauley & Kilgour 1990), and the commercial culture of channel catfish, *Ictalurus punctatus* (McCauley & Beitinger 1992). In their introduction to a symposium on the effects of climate change on fish held in Toronto during 1988, Regier et al. (1990) stated, 'On a global basis, climate change will likely trigger major catastrophes and major opportunities, both on regional scales'. The potential effects of global warming make continued efforts to define temperature tolerance of fishes an important area of research.

Estimation of thermal tolerances of fishes

Field observations

One approach to estimate thermal tolerance is to measure water temperatures during or following fish kills from exposure to extreme temperatures. Although only occasionally used (Storey 1937, Gunther & Hildebrand 1951, Holt & Holt 1983), this technique neither lends a determination of accurate lethal temperatures nor assures that fishes were directly killed by temperature rather than other biotic or abiotic factors.

Determining minimum and maximum water temperatures within a species natural distribution is another approach to estimate thermal tolerance. Brett (1956) concluded that this method may not reflect accurate tolerance limits, because most fishes can survive temperatures which they do not voluntarily occupy in nature. A contemporary version of this approach to estimate upper temperature tolerances is provided by Eaton et al. (1995). Their technique is based upon Biesinger et al. (1979) who generated a large database consisting of spatial and temporal records of stream temperatures and fish collections. Field temperatures and fish collection data were matched. The Fish Temperature

Database Matching System (FTDMS) was then used to estimate temperature regimes of freshwater fishes in the United States. From a larger and modified version of the FTDMS, Eaton et al. (1995) estimated maximum temperature tolerances from a minimum of 50 warmest weekly mean temperature values for 30 species of stream dwelling fishes. The 95th percentile estimated upper temperature tolerances estimates were consistently less (range 0.8 to 6.7°C) than reported laboratory derived upper lethal temperatures for all 30 species investigated. A problem with this approach is the assumption that water in nature is homeothermal. In most, if not all aquatic ecosystems, environmental heterogeneity offers fish microhabitats which differ in temperature.

Laboratory studies

Quantitative laboratory studies of temperature tolerance of fishes date from Loeb & Wasteneys (1912), Britton (1924), Huntsmen & Sparks (1924), Hathaway (1927) and Sumner & Doudoroff (1938) and escalated during the 1940s and early 1950s with numerous publications by Brett (1941, 1944, 1946, 1952), Fry et al. (1942, 1946), Doudoroff (1942, 1945) and Hart (1947, 1952). In each case, an effort was made to provide a statistically valid index, usually expressed as the mean or median temperature tolerated by a random sample of fish exposed to a predetermined interval of time (Brett 1956). From these early attempts, two universally accepted laboratory approaches have evolved to quantify temperature tolerance in fishes: the Fry or incipient lethal temperature (ILT) technique and the critical thermal method (CTM). Both of these techniques have been employed in numerous studies to estimate the temperature tolerance abilities of fishes.

Fry or incipient lethal temperature technique

In the Fry, plunge, static or incipient lethal temperature (ILT) technique which was developed from the dose–reponse research of Bliss (1937), a temperature lethal to 50% of a fish sample is determined by plunging groups of fish from a variety of acclimation temperatures into a series of constant test temperatures near the estimated upper and lower temperature limits of a species (Fry 1947). Mortality is the endpoint and is recorded over time. An estimate of the temperature tolerated by 50% of a sample for various exposure time intervals, e.g., 12, 24, 48, 96 h, is made from a regression of percentage mortality on test temperature. Since thermal resistance usually is not linear with respect to time, data are often

transformed as probits and plotted against the logarithm of time. Results are reported as incipient lower and incipient upper lethal temperatures, i.e., ILLT and IULT, for a specified exposure time.

This experimental technique separates temperature tolerance and resistance. The latter represents the time to death at a particular lethal temperature. Fry et al. (1946) introduced the concept of mortification rates which equals the reciprocal of mean or median survival times from results of short-term resistance experiments. These were included in the National Academy of Sciences' Water Quality Criteria in 1972 and used in evaluations of thermal effects of power plants (see Coutant 1972). In 1985, Kilgour et al. developed a model incorporating mortification rates to estimate IULT for results of short-term thermal resistance experiments. Application of their model to data for 12 species of North American fishes predicted IULTs within 1°C of observed IULT values. When ILLT and IULT are determined over the temperature tolerance range of a species, i.e., the range of temperatures to which a fish can be acclimated, a temperature tolerance polygon can be generated. Calculating the area of the temperature tolerance polygon yields a single number in °C^2 units, which represents the degree of eurythermicity of a species. Since the first temperature tolerance polygon for goldfish, *Carassius auratus*, reported by Fry et al. (1942), temperature tolerance polygons have been published for probably fewer than 40 North American fish species.

Critical thermal methodology
The critical thermal methodology (CTM) is a second laboratory approach to characterize temperature tolerances, particularly relative or comparative tolerance of fishes. In a departure from Becker & Genoway (1979) who have referred to the CTM as both a method and a parameter, we choose to use the designation CTM to refer to the general method and the specific terms CTminimum and CTmaximum to refer to the measured endpoints. In the CTM, a random sample of fish, usually acclimated to specific temperature(s), are subjected to a constant linear increase or decrease in temperature until a predefined sublethal but near lethal, endpoint is reached (Figure 1). The endpoint (critical thermal maxima or minima, CTmaximum and CTminimum, respectively) is defined as pre-death thermal point at which locomotory movements become disorganized and a fish loses the ability to escape from conditions which may ultimately lead to its death. In this approach lethal temperatures are estimated without actually killing fish.
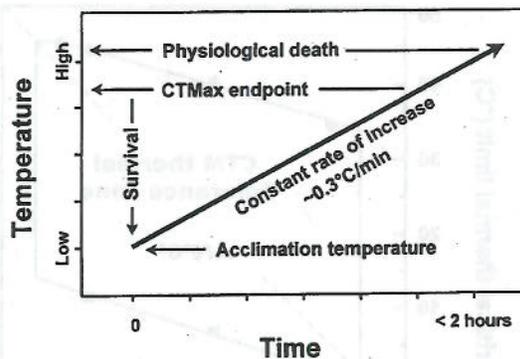
Figure 1. Determination of the critical thermal maximum (CTmaximum). Fish are exposed to a constant linear increase in water temperature until the selected sublethal endpoint is reached. Once this endpoint is reached, the fish is quickly returned to its pretest acclimation temperature and checked for survival. The endpoint temperature equals the CTmaximum which occurs prior to physiological death. CTmaximum data obtained for a sample are usually described via the mean and standard deviation.

The CTmaximum and CTminimum are calculated as the arithmetic mean of the collective thermal points at which the endpoint was reached by individuals of a random sample of fish (Lowe & Vance 1955). If rescued and returned to the pretrial acclimation temperature, fish reaching the specified endpoint should survive. In fact, the heat shock experienced by animals during CTmaximum trials has been reported to produce heat hardening, i.e., a transitory increase in CTmaximum following exposure to near lethal temperatures (Hutchison 1961, Hutchison & Maness 1979, Maness & Hutchison 1980).

Huntsman & Sparks (1924) appear to be first to use a modified CTM when they recorded the death point of numerous species of marine fishes and invertebrates exposed to temperature increases of 0.2°C min⁻¹. Sumner & Doudoroff (1938) combined dynamic temperature changes (0.05°C min⁻¹) with a sublethal endpoint (cessation of respiratory movements) to measure 'lethal' temperatures in the longjaw mudsucker, *Gillichthys mirabilis*. These authors noted that this endpoint did not necessarily represent death since many of the fish recovered when returned to cooler water. Nevertheless, Cowles & Bogert (1944) are given credit for originating this methodology and coining the terms CTmaximum and CTminima (although they determined no CTminimum) in their classic monograph concerning thermal relations of desert reptiles. Of note, Cowles & Bogert (op. cit.) developed the

Figure 2. Temperature tolerance polygon generated from CTmaxima and CTminima data for the sheepshead minnow. This temperature tolerance polygon is based on 60 data points.
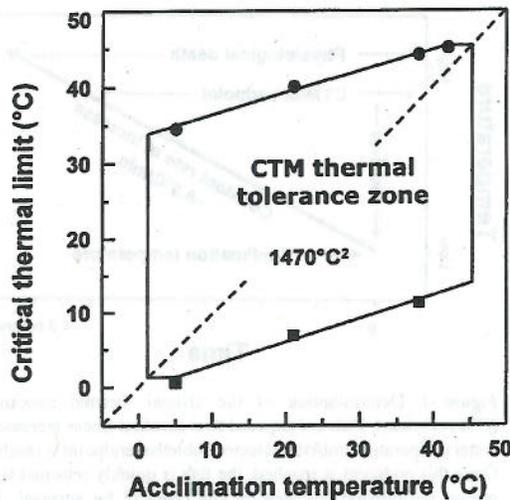
CTM approach at about the same time that Fry and his coworkers were generating the ILT protocol for fishes. Although several studies have employed CTM to quantify temperature tolerances in numerous species of reptiles (Larson 1961, Kour & Hutchison 1970, Spellerberg 1973) and amphibians (Zweifel 1957, Hutchison 1961, Brattstrom 1968), research by (Heath 1963, Heath 1967 and Lowe & Heath 1969) appear to be the first published uses of CTM with fishes. Bennett & Beitinger (1997) generated a CTM temperature tolerance polygon for the sheepshead minnow, *Cyprinodon variegatus* (Figure 2). Previous reviews of the CTM in fish research are provided by (Hutchison 1976, Becker & Genoway 1979, Paladino et al. 1980, Beitinger & McCauley 1990, Lutterschmidt & Hutchison 1997b).

Elliott's hybrid temperature tolerance methodology

A hybrid of the CTM and ILT techniques has been used by Elliott (1981, 1991) to characterize upper and lower temperature tolerances of some salmonids. Instead of instantaneously plunging fish into test temperatures as is done in the ILT technique, Elliott exposed fish, acclimated to a large range of temperatures, to temperature change rates of $1°C\,h^{-1}$ until a series (about 5) of final constant temperatures were reached at which fish were held and observed for mortality. Death was

recorded over a period of 10 080 min (7 days). This technique combines dynamic temperature changes of the CTM with constant test temperatures and death as an endpoint characteristics of the ILT technique. Elliott used this approach to generate a 7-d thermal tolerance polygon for parr of the Atlantic salmon, *Salmo salar*.

Comparison of ILT and CTM approaches

Although both CTM and ILT techniques generate endpoints which are quantitatively expressed as a temperature, are determined experimentally with random samples of fish acclimated to specific temperatures and involve both time and temperature as major test variables, the two methods do not quantify the same response. The CTM requires a constant, linear change of temperature upward or downward from acclimation temperature until physical disorganization occurs. Conversely, the ILT method requires an abrupt transfer to temperatures either above or below acclimation and exposure until lethality occurs. Either loss of equilibrium or the onset of muscle spasms is the usual endpoint for dynamic tests, whereas, death is the endpoint for ILT tests. This is an important distinction since CTM allows testing temperature tolerance of fishes without lethality. The combination of a nonlethal endpoint with the observation that CTM does not require the large number of fish needed in ILT measurements, indicates that the CTM can be used to estimate the thermal tolerances of endangered or threatened species of fishes (Gelbach et al. 1978) or in cases where only a small sample of fish are available (Bennett et al. 1997). It has been used extensively as a comparative method for quantifying differences in thermal tolerances between species or within a species.

A valid criticism pointed out by Coutant (1970) and Hutchison (1976) is that the two major independent variables, temperature and time, are changing during a CTM. This confuses interpretation of CTM data, particularly when different rates of temperature change and endpoint criteria are used. It is best used as a relative and not absolute measure of temperature tolerance, since the changing temperature during a CTM trial typically overshoots the temperature at which physiological disorganization occurs. However, the CTM approximates natural conditions better than static methods (Bennett & Judd 1992). As long ago as 1946, Fry et al. concluded that ILT data have little or no direct application in the field. Any thermal death in nature is almost certain to be brought about by changing temperature conditions. Since fishes lack a means

of maintaining independent body temperatures, they may be a victim of rapid internal temperature change caused by sudden fluctuations in environmental temperature (Brett 1956). The CTM provides a lethal index since fishes in nature may encounter such temperatures either temporally or spatially as fluctuations outside of their tolerance limits (Hutchinson 1976).

Finally, the statistical manipulations required to determine the ILT and CTM of fish acclimated to the same temperature are considerably different. ILTs are determined from an approach (LC-50) of Bliss (1937) to characterize dose–response data. To obtain an ILT for a single acclimation temperature, samples of ten or so fish acclimated to a series of temperatures are usually plunged into a series (usually five) constant temperature baths and times to death (resistance times) are recorded. Resistance times are usually linearized as probits and a single LC-50 is estimated for a particular time, e.g, 24 h. Conversely, in the CTM each individual fish generates a datum. Following Lowe & Heath (1969), most investigators numerically characterize CTmaximum and CTminimum with simple parametric descriptive statistics, i.e., mean and standard deviations as measures of central tendency and variation, respectively. Consequently, CTM data are easy to calculate and can be easily compared via independent t and ANOVA hypothesis tests. In the majority of studies where temperature tolerance is used to bioassay the effects of various environmental stressors, the CTM is the method of choice (see Beitinger & McCauley 1990). Both methods yield valuable information concerning temperature tolerances of fishes.

Few studies have measured temperature tolerances via both CTM and ILT approaches in fish of the same species acclimated to similar temperatures; however, comparisons of literature values suggest that at similar acclimation temperatures, CTmaxima generally exceed the IULTs and the CTminima will be lower than ILLTs measures by approximately 1 to 4°C for a species. This is expected since a time lag occurs before LOE is observed. During the time lag, the temperature is changing causing the CTM to 'overshoot' the ILT estimate. In a study that measured both CTM and ILT in a species (sheepshead minnow, *Cyprinodon variegatus*) acclimated over the same range of temperatures (5 to 38°C), Bennett & Beitinger (1997) found that the thermal tolerance polygon from the CTM was about 5% larger ($70°C^2$, 1450 versus $1380°C^2$) than that of 12-h thermal tolerance polygons of the ILT technique (see Figure 4).

Theoretically, it is possible to predict CTM values from resistance data generated by ILT trials. This was first discussed by Fry et al. (1946) and again in 1947 and 1971, and by other researchers including Brett (1956), Becker & Genoway (1979), Kilgour & McCauley (1986) and Bennett & Beitinger (1997). From ILT resistance data, minute mortification rates are calculated as the reciprocal of the median lethal exposure time which represent percentage mortality per hour at each of several test (plunge) temperatures. The predicted CTM value for each acclimation temperature is taken as the point at which the fractions of dying at the various plunge temperatures equal one (see Fry et al. 1946). Although several investigators have discussed this approach, few examples have been provided. Bennett & Beitinger (1997) used this approach to predict both CTmaxima and CTminima for sheepshead minnows at acclimation temperatures of 5, 21 and 38°C (Table 1). CTmaxima predicted from the ILT data underestimated empirically derived CTmaxima by 1.7. 0.0 and 0.2°C at these three acclimation temperatures, respectively. The accuracy (within 5%) of these predicted CTmaxima is reasonable considering the dissimilar endpoints and large range of acclimation temperatures over which these estimates were made. In contrast, poor agreement occurred between predicted and empirically derived CTminima in sheepshead minnows; and the difference between predicted and measured CTminima became progressively greater as acclimation temperature increased from 5 to 38°C (Table 1). Since the model used to predict CTminima assumes a linear mortality rate relative to time (Fry 1947), it appears reasonable to conclude that the inability of ILLT data to accurately predict CTminima in sheepshead minnow is related to a violation of this assumption. Nonlinear lower thermal tolerance responses have been observed

Table 1. Comparison of measured CTmaxima and CTminima (°C) and those predicted from resistance data of ILT trials for sheepshead minnow acclimated to 5, 21, and 38°C (from Bennett & Beitinger 1997).

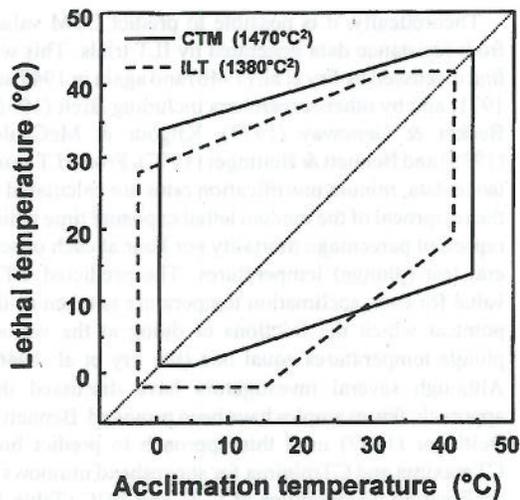| Parameter	Acclimation temperature, °C		
	5	21	38
Predicted CTmaxima, °C	36.3	40.1	44.0
Measured CTmaxima, °C	34.6	40.1	44.2
Difference, °C	1.7	0.0	0.2
Predicted CTminima, °C	−1.6	0.8	3.3
Measured CTminima, °C	0.6	6.9	11.3
Difference, °C	2.2	6.1	8.0

Figure 3. Temperature tolerance polygons via the CT and ILT methods for the shepshead minnow. Note that the areas of tolerance are different and somewhat offset.

in many fishes and are often attributed to differing mechanisms of death at low temperatures (Brett 1956, Fry 1971, Schmidt-Nielsen 1994). At lower temperatures, metabolism slows and longer exposure times are needed to elicit physiological effects such as death. Consequently, time becomes a major factor affecting death at low temperatures. During ILLT trials, relatively short exposure time can depress measured ILLT values in fish at low acclimation extremes, widening the physiological temperature tolerance zone. This phenomenon is apparent in ILLT data for sheepshead minnow and apparently explains why ILLT data are poor predictors of CTminima in this fish. Although the lower boundary of the CTM temperature tolerance polygon is linear, the slope of the ILLT boundary shifts as the major factor determining death changes from acclimation temperature to exposure time. When the shift occurs, the ILLTs of fish acclimated at temperatures nearer to the lower limit begin to approach and eventually fall below the CTminimum (see Figure 3).

Further considerations concerning CTM

Two concerns in CTM trials are (1) rates of temperature change and (2) the selected endpoint. The rate of temperature change (ΔT) during a CTM trial should be constant and linear. An early criticism of the CTM approach (Fry 1971) is that it confounds time and temperature since both are changing simultaneously.

Consequently, if temperature change rates are not constant during a CTM trial or if different rates of temperature change are applied to fish acclimated to similar pretest conditions, measured CTM values will vary. This criticism was warranted in early studies (Vernon 1899, Huntsman & Sparks 1924) where temperature change rates during tolerance trials were inconsistent. Cocking (1959) was the first to expose a fish (roach, *Rutilus rutilus*), to five consistent rates of temperature change ranging between $0.05°C\,h^{-1}$ ($0.00083°C\,min^{-1}$) and $0.8°C\,h^{-1}$ ($0.013°C\,min^{-1}$) and record temperature at death. Over this range of temperature changes, mean temperatures at death of roach ranged between 31.4 and 32.9°C. Since Cocking's study, several investigators have examined the influence of different rates of temperature change during CTM trials including Burton et al. (1972), Cox (1974), McFarlane et al. (1976), Becker et al. (1977), Becker & Genoway (1979) and Lutterschmidt & Hutchison (1997a). According to the CTM definition, the rate of temperature change must be slow enough so that a fish's core temperatures do not significantly lag behind water temperatures, and rapid enough so test fish do not have time to thermally reacclimate during a trial. Of note, if the rate of temperature change is either too rapid or too slow, the measured CTM values will be biased towards higher temperatures. The CTM literature contains rates as slow as $1°C\,h^{-1}$ (Becker et al. 1977) and as fast as $1°C\,min^{-1}$ (Hoss et al. 1972, Cox 1974, Copeland et al. 1974, Holland et al. 1974, Smith & Scott 1975, Cheetham et al. 1976, Hassem & Spotila 1976, McFarlane et al. 1976). From an extensive review of the literature and their own data, Becker & Genoway (1979) recommend a $0.3°C\,min^{-1}$ rate of temperature change for CTM research with fishes. They found that pumpkinseed sunfish, *Lepomis gibbosus*, exposed to $1°C\,h^{-1}$ ($= 0.016°C\,min^{-1}$) gained temperature tolerance as the test progressed. Conversely, a change of $1°C\,min^{-1}$ in water temperature was too rapid for deep body temperature to track water temperature without a significant time lag. The faster rates of temperature change also amplify the importance of fish size, since body temperature change is a function of fish size (Stevens & Fry 1974, Spigarelli et al. 1977). At a ΔT of approximately $0.3°C\,min^{-1}$, core temperatures of smaller fish closely track changes in water temperature. An exception to this rate occurs in CTminimum determinations, especially when exposure temperatures near 0°C are required. Due to the greater difficulty in achieving linearity during 'extreme' cooling, rates between 0.1 and $0.15°C\,min^{-1}$ have been used

(Ward et al. 1993, Bennett & Beitinger 1997, Bennett et al. 1997).

It is important to mention that the ILT technique also involves both time and temperature as major variables, yet during trials temperatures are constant. However, choice of exposure time will alter measured ILT values. In contrast to the CTM approach where 0.3°C has been proposed as the standard rate of temperature change, there is not an accepted exposure time in ILT approach. In research on temperature tolerance in the goldfish, Fry et al. (1942) followed Hathaway (1927) and employed a 14-hour exposure time. At that time, Fry et al. concluded, 'Fourteen hours can be equivalent to infinity for all practical purposes as far as the direct lethal effects of temperature are concerned'. Nevertheless subsequent researchers have used a variety of exposure times in ILT research on fishes: 12 h (Brett 1946), 24 h (Black 1953), 48 h (Brett 1952), 8000 min (Hart 1947, 1952), 7 days (Otto 1974, Kaya 1978) and 20 000 min (Allen & Strawn 1967). By 1971, Fry reconsidered his 1942 statement and concluded, '... it must always be realized that there is no finality to the ILT short of maintaining a test throughout the whole life of the organism'. In a comprehensive study of the temperature tolerance of sheepshead minnow, *Cyprinodon variegatus*, Bennett & Beitinger (1997) found an expected inverse relationship between exposure time (12, 24 and 48 h) and areas of ILT tolerance polygons 1380, 1251 and 1118°C², respectively (Figure 4). Use of different exposure times in ILT studies, like different ΔTs in CTM research can affect measured temperature tolerance.

Whereas there has been little debate concerning the choice of appropriate rates of temperature change during CTM research, controversy has arisen over the choice of the most appropriate endpoint criterion (Hutchison 1976, Becker & Genoway 1979, Bonin 1981, Bennett & Beitinger 1997, Lutterschmidt & Hutchison 1997a). Cowles & Bogert (1944) originally defined the critical thermal minimum for reptiles as 'the temperature that causes a cold narcosis and effectively prevents locomotion. At this temperature, the animals are helpless to escape enemies or to remedy their thermal impasses if they have not already sought sanctuary'. Similarly, they defined the critical thermal maximum as 'the thermal point at which locomotory activity becomes disorganized and the animal loses its ability to escape from conditions that will promptly lead to its death'. Recovery from this incapacitation is the criterion for determining whether or not the animal has been exposed to unnecessarily high temperatures. From the ecological viewpoint, it is the lethal
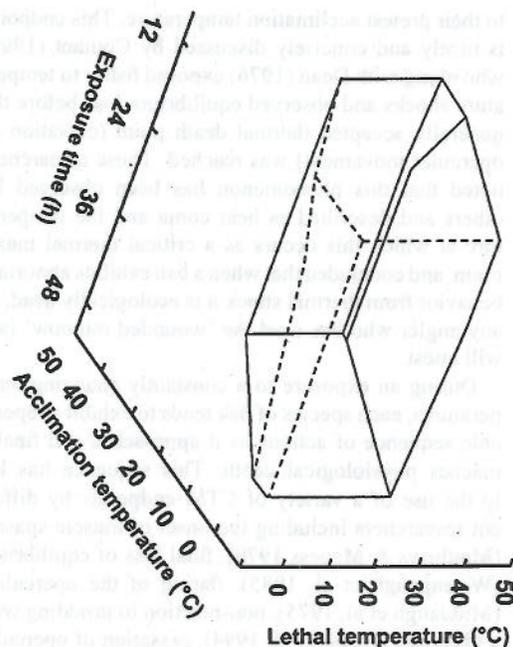
Figure 4. Three dimensional representation to the incipient lethal temperature tolerance 'volume' in the sheepshead minnow exposed to lethal temperatures. The incipient lethal temperatures are a function of both acclimation temperature and exposure time.

temperature (Cowles & Bogert 1944). These original definitions were slightly modified by Lowe & Vance (1955) and Hutchison (1961) and finally, Cox who offered the following definition in 1974, 'The critical thermal maximum or minimum is the arithmetic mean of the collective thermal points at which locomotory activity becomes disorganized and the animal loses its ability to escape from conditions that will promptly lead to its death when heated (or cooled) from, a previous acclimation temperature at a constant rate just fast enough to allow deep body temperature to follow environmental test temperatures without a significant time lag'. This is the definition cited in a majority of contemporary publications employing the CTM with fishes. It is noteworthy that exact criteria for identifying the point of locomotory disorganization are unspecified.

Relative to these definitions, the key aspects are that the CTM endpoint is a sublethal but near lethal temperature, that locomotion becomes disorganized, and survival occurs if test fish are immediately returned

to their pretest acclimation temperature. This endpoint is nicely and concisely discussed by Coutant (1969) who along with Dean (1976) exposed fishes to temperature shocks and observed equilibrium loss before the generally accepted thermal death point (cessation of opercular movement) was reached. These researchers noted that this phenomenon has been observed by others and described as heat coma and the temperature at which this occurs as a critical thermal maximum, and concluded that when a fish exhibits abnormal behavior from thermal shock it is ecologically dead, as any angler who has used the 'wounded minnow' lure will attest.

During an exposure to a constantly changing temperatures, each species of fish tends to exhibit a repeatable sequence of actions as it approaches and finally reaches physiological death. This sequence has led to the use of a variety of CTM endpoints by different researchers including the onset of muscle spasms (Matthews & Maness 1979), final loss of equilibrium (Watenpaugh et al. 1985), flaring of the operculars (Middaugh et al. 1975), non-reaction to prodding with a glass rod (Heath et al. 1994), cessation of opercular movements (Bettoli et al. 1985), and even combinations of the above (Hassam & Spotila 1976, Bonin & Spotila 1978). One liability of OS is that they are not observed in fish during CTminima trials.

Loss of equilibrium (LOE) and the onset of muscle spasms (OS) are the most commonly reported CTM endpoints, as both represent systematic disorganization that prevent fishes from escaping conditions that promptly result in death.

A statistical defense of LOE as an appropriate CTM endpoint has also been generated by numerous studies, involving a variety of researchers and fish species. Standard deviations for CTmaxima are often less than 1°C. In Sylvester's (1975) study of temperature tolerance in three species of Hawaiian estuarine fishes acclimated to five temperatures, only one of the 15 species-acclimation temperature combinations had a CTmaximum standard deviation of more than 1.0°C. Ten CTmaximum standard deviations measured in five species of trout and charr acclimated to two temperatures ranged from 0.19 to 0.67°C (Lee & Rinne 1980). Bulger (1984) reported a range in CTmaximum standard deviations of 0.25 to 0.59°C in *Fundulus heteroclitus* held under different temperature and photoperiod combinations and tested at various times during the day; Bulger reported standard deviations for 20 trials. King et al. (1985) reported a CTmaximum standard deviation range of 0.94 to 0.41°C for red shiners, *Cyprinella lutrensis*, collected from five sites in the Brazos River, Texas. Green sunfish, *Lepomis cyanellus*, acclimated to 20°C and tested after 1, 5 and 10 days of holding had CTmaximum standard deviations from 0.40 to 0.69°C (Carrier & Beitinger 1988). Control rainbow trout, *Oncorhynchus mykiss*, studied by Strange et al. (1993) had a CTmaximum standard deviation of 0.59°C. CTmaximum standard deviations of control fathead minnows, *Pimephales promelas*, acclimated to four different temperatures ranged from 0.24 to 0.95°C (Richards & Beitinger 1995). Finally, Bennett et al. (1998) reported CTmaximum standard deviations of 0.25 to 0.66°C for channel catfish, *Ictalurus punctatus*, acclimated to 10, 20, 30 and 35°C. The precision indicated by the small variation in CTmaximum determined via LOE in these and many other studies, demonstrate that LOE is an appropriate endpoint for CTM research.

Finally, in a few studies in which fish were exposed to constant changes in temperature, investigators have reported the death point (DP) in addition to or in place of a typical CTM endpoint, e.g., OS or LOE. Since the DP is easily determined by simply continuing to heat (or cool) test fish beyond CTM temperatures, it allows the generation of both a sublethal and lethal estimate of temperature tolerance for each fish. Examples of this approach include Holland et al. (1974), Cheetham et al. (1976), McFarlane et al. (1976) and Becker & Wolford (1980). Becker & Genoway (1979) proposed the terms, 'lethal thermal maximum' and 'lethal thermal minimum' for temperatures corresponding to death during dynamic temperature exposures. Nevertheless, use of death as an endpoint is justified when the typical CTM endpoints are neither obvious nor consistent among test fish exposed to changing temperatures. For example, owing to the excitable behavior of grass, *Ctenopharyngodon idellus* and bighead carp, *Hypophthalmichthys nobilis*, Bettoli et al. (1985) found that cessation of respiratory movement and loss of response to touch (death), yielded a more precise endpoint.

Only CTM values determined using similar endpoints can be directly compared and there is probably not a single CTM endpoint that is best for all fish species. Although LOE has been used in far more studies than OS, the choice of an appropriate endpoint, as long as it represents a consistent, observable systematic disorganization consistent with the CTM definition, should be chosen by the investigator. The endpoint needs to be clearly described in the methods section of a manuscript. The comparative value of CTM data are influenced by the ΔT and endpoint used.

Chronic lethal maxima and minima

A few investigators have measured temperature tolerance by exposing fishes to dynamic temperature increases (Hickman & Dewey 1973, Alcorn 1976, Guest 1985, Fields et al. 1987, Grande & Andersen 1991) or decreases (Shafland & Pestrak 1982, Zale & Gregory 1989) of $1°C\,d^{-1}$ or slower, and have employed death as the endpoint. This approach differs from the CTM in two ways. First, the rate of temperature change will permit fish to reacclimate during trials and second, death is used as the test endpoint. In Fields et al. (1987) the upper temperature tolerance of four groups of largemouth bass, *Micropterus salmoides*, acclimated to 32°C were investigated at temperature increase rates of $0.2°C\,min^{-1}$ and $1.0°C\,d^{-1}$. The mean upper lethal values in the four groups of largemouth bass heated at $1°C\,d^{-1}$ were 1.8 to 3.6°C lower than those measured at $0.2°C\,min^{-1}$. These results suggest that slow heating allows longer time at each temperature for reacclimation to occur; however, simultaneously, it permits more time for heat to exert its lethal effects. At least in largemouth bass, the latter effect was more important than the former. To distinguish between these two techniques and following the recommendation of Becker & Genoway (1979), we would refer to the slow heating trials with death as the endpoint as chronic lethal methodology, i.e., CLM. Comparing the chronic lethal values and critical maxima to published IULT for largemouth bass at the same acclimation temperature (Currie et al. 1997) indicate the following sequence: IULT < CLmaximum < CTmaximum.

Review of published tolerance data

The temperature tolerance zone of a species represents the thermal 'arena' within which individuals of a species can survive. Because of its critical importance, defining the limits and factors effecting the limits of this zone for fish have been the subject of numerous studies. This review is restricted to studies of fishes exposed to constantly decreasing or increasing temperatures during temperature tolerance trials, i.e., dynamic temperature changes. We partitioned dynamic temperature tolerance studies into two distinct categories: critical thermal methodology which exposes fish to relatively rapid temperature changes and employs a sublethal endpoint, and chronic lethal methodology which incorporates slow changes in temperature and a lethal test endpoint. To avoid confusion in abbreviations, we use the designation CTM (critical thermal

method) to refer to the experimental method and the terms CTmaximum and CTminimum as the procedurally and statistically defined endpoints for CTM trials. Similarly, CLM (chronic lethal method) yields the endpoints, CLmaximum and CLminimum. Previous reviews of CTM include Fry (1967), Hutchison (1976), Becker & Genoway (1979), Paladino et al. (1980), Beitinger & McCauley (1990) and Lutterschmidt & Hutchison (1997b), and reviews containing lists of CTmaxima and CTminima for fishes are provided by Spotila et al. (1979) and Houston (1980).

In this review dynamic temperature tolerance data are presented by experimental method in Tables 2 (CTmaxima), 3 (CTminima), 4 (CLmaxima) and 5 (CLminima). These tables list more than 450 individual measures of dynamic temperature tolerance for 130 North American freshwater fishes. In addition to simple statistics, i.e., mean, standard deviation and sample size describing temperature tolerance, each listing includes pretest acclimation temperature, rate of temperature change, endpoint criterion and source.

Number of studies

We focused our review on native North American freshwater fishes; however, we have included temperature tolerance information on exotic species that have been observed in North America. An extensive literature search uncovered 80 studies which provide original temperature tolerance data measured by either critical thermal or chronic lethal methods for North American freshwater fishes, beginning with Heath's (1963) study of the effect of diel thermoperiods on upper temperature tolerance in cutthroat trout, *Oncorhynchus clarkii clarkii*, the first use of CTM with fishes. Figure 5 illustrates the number of dynamic temperature tolerance publications each five year interval beginning in 1960. Concerns of the negative effects of thermal pollution in aquatic environments stimulated the surge in these studies during the 1970's, and the contemporary concern of global warming continues to make this research area important as we enter the next millennium. Interestingly, 47 (59%) of these 80 studies concerned only one fish species, and 70 studies (88%) involve three or fewer species. In contrast, studies by Kowalski et al. (1978), Shafland & Pestrask (1982), Lutterschmidt & Hutchison (1997a) and Smale & Rabeni (1995) report original dynamic temperature tolerance data for 13, 14, 24 and 34 species, respectively. Although a large number of species was examined in these four studies, in

Table 2. Critical thermal maxima (CTmaxima) for North American freshwater fishes by family. Each entry includes pretest acclimation temperature, rate of temperature increase during CTmaximum trial and reported test endpoint (OS = onset of muscular spasms, LOE = loss of equilibrium, PGR = prodding with glass rod, DP = death point). Acclimation temperatures (second column) are from constant laboratory conditions unless otherwise indicated. CTmaxima (°C) data (column 5) estimated from published figures are indicated by the superscript a. Standard deviations calculated from standard errors or 95% confidence limits are indicated by superscript b. Superscript c indicates that standard deviations were calculated from plots giving either standard errors or 95% confidence limits. Question marks indicate information not reported. Regression models were either published or calculated from published mean CTmaxima values, T_a = acclimation temperature.

Species	$T_{acclimation}$ °C	ΔT °C min^{-1}	Test endpoint	CTmaxima, °C		n	Reference
				mean	SD		
Family Atherinidae							
Labidesthes sicculus	26	0.017	LOE	36.0	0.44	8	Smale & Rabeni (1995)
Menidia beryllina	10	1.0	OS[1]	31.6	1.84	20	Lutterschmidt & Hutchinson (1997a)
Family Catostomidae							
Carpiodes cyprinus	24 (field)	0.5–0.8	LOE	38.8	0.8	6	Mundahl (1990)
Catostomus commersoni	26	0.017	LOE	34.9	0.25	5	Smale & Rabeni (1995)
Catostomus snyderi	20	0.3	LOE	32.6	—	1	Castelberry & Cech (1992)
Chasmistes brevirostris	20	0.3	LOE	32.7	0.32[b]	10	Castelberry & Cech (1992)
Hypentelium nigricans	15	1.0	OS	30.8	0.86[c]	4	Kowalski et al. (1978)
Ictiobus bubalus	10	1.0	OS[1]	31.3	—	1	Lutterschmidt & Hutchison (1997a)
Family Centrarchidae							
Lepomis cyanellus	20 (day 1)	0.3	LOE	35.8	0.69	9	Carrier & Beitinger (1988a)
	20 (day 5)	0.3	LOE	35.8	0.40	11	Carrier & Beitinger (1988a)
	20 (day 10)	0.3	LOE	35.9	0.56	9	Carrier & Beitinger (1988a)
	26	0.017	LOE	37.9	0.75	8	Smale & Rabeni (1995)
	10	1.0	OS[1]	34.2	2.06	15	Lutterschmidt & Hutchison (1997a)
Lepomis gibbosus	10	0.3[2]	LOE[3]	30.1	0.77[c]	24	Becker & Genoway (1979)
	20	0.3[2]	LOE[3]	35.1	0.95[c]	24	Becker & Genoway (1979)
Lepomis gulosus	10	1.0	OS[1]	32.9	0.22	4	Lutterschmidt & Hutchison (1997a)
Lepomis humilis	26	0.017	LOE	36.4	0.55	9	Smale & Rabeni (1995)
Lepomis macrochirus	25 (4 Collection sites)	1.0	LOE[3]	36.3–37.0	—	13–36	Holland et al. (1974)
	30 (4 Collection sites)	1.0	LOE[3]	37.4–39.6	—	16–36	Holland et al. (1974)
	35 (4 Collection sites)	1.0	LOE[3]	40.4–41.4	—	6–31	Holland et al. (1974)
	26	0.1	LOE[3]	36.6	?	30	Cox (1974)
	26	0.5	LOE[3]	37.5	?	30	Cox (1974)
	26	1.0	LOE[3]	37.9	?	30	Cox (1974)
	16 (Pond C)	1.0	LOE	31.5	—	9	Murphy et al. (1976)

Species / Acclimation temp	Rate	Method	CTMax	Rate	n	Reference
16 (Par Pond)	1.0	LOE	31.4	—	8	Murphy et al. (1976)
24 (Pond C)	1.0	LOE	37.5	—	10	Murphy et al. (1976)
24 (Par Pond)	1.0	LOE	35.6	—	10	Murphy et al. (1976)
32 (Pond C)	1.0	LOE	41.4	—	10	Murphy et al. (1976)
32 (Par Pond)	1.0	LOE	38.5	—	10	Murphy et al. (1976)
26	0.017	LOE	37.9	0.68	8	Smale & Rabeni (1995)
10	1.0	OS[1]	33.6	1.20	84	Lutterschmidt & Hutchison (1997a)
Lepomis megalotis 26	0.017	LOE	37.8	0.84	12	Smale & Rabeni (1995)
10	1.0	OS[1]	34.1	1.99	59	Lutterschmidt & Hutchison (1997a)
Lepomis microlophus 10	1.0	OS[1]	34.1	0.87	3	Lutterschmidt & Hutchison (1997a)
Micropterus dolomieu 26	0.017	LOE	36.9	0.31	8	Smale & Rabeni (1995)
10	1.0	OS[1]	34.8	—	1	Lutterschmidt & Hutchison (1997a)
Micropterus punctatus 10	1.0	OS[1]	34.2	0.57	5	Lutterschmidt & Hutchison (1997a)
Micropterus salmoides 20	1.0	LOE	36.7	0.76[b]	40	Smith & Scott (1975)
28	1.0	LOE	40.1	1.33[b]	40	Smith & Scott (1975)
26	0.017	LOE	36.3	0.60	10	Smale & Rabeni (1995)
10	1.0	OS[1]	33.4	1.90	17	Lutterschmidt & Hutchison (1997a)
M. salmoides salmoides (northern largemouth bass: NLMB) 8	0.2	DP	29.2	1.36	10	Fields et al. (1987)
16	0.2	DP	33.6	0.87	10	Fields et al. (1987)
24	0.2	DP	36.5	0.51	10	Fields et al. (1987)
32	0.2	DP	40.9	0.40	10	Fields et al. (1987)
				$CTMax = 25.55 + 0.475\,T_a$		
20	0.3	LOE	35.4	0.47	20	Currie et al. (1998)
25	0.3	LOE	36.7	0.59	20	Currie et al. (1998)
30	0.3	LOE	38.5	0.34	20	Currie et al. (1998)
				$CTMax = 28.92 + 0.32\,T_a$		
M. salmoides floridanus (Florida largemouth bass: FLMB) 8	0.2	DP	30.4	0.97	10	Fields et al. (1987)
16	0.2	DP	34.1	0.48	10	Fields et al. (1987)
24	0.2	DP	37.5	0.64	10	Fields et al. (1987)
32	0.2	DP	41.8	0.38	10	Fields et al. (1987)
				$CTMax = 26.55 + 0.47\,T_a$		
NLMB ♀ × FLMB ♂ 8	0.2	DP	30.1	0.48	10	Fields et al. (1987)
16	0.2	DP	34.0	0.98	10	Fields et al. (1987)
24	0.2	DP	37.0	0.53	10	Fields et al. (1987)
32	0.2	DP	41.6	0.62	10	Fields et al. (1987)
				$CTMax = 26.30 + 0.47\,T_a$		

Table 2. (Continued)

Species	$T_{acclimation}$ °C	ΔT°C min^{-1}	Test endpoint	CTmaxima, °C mean	SD	n	Reference
NLMB ♂ × FLMB ♀	8	0.2	DP	30.8	0.76	10	Fields et al. (1987)
	16	0.2	DP	34.4	0.47	10	Fields et al. (1987)
	24	0.2	DP	37.9	0.49	10	Fields et al. (1987)
	32	0.2	DP	41.9	0.51	10	Fields et al. (1987)
				CTMax = 27.05 + 0.46 T_a			Fields et al. (1987)
Family Cichlidae							
Oreochromis niloticus	10	1.0	OS^1	33.6	1.40	25	Lutterschmidt & Hutchison (1997a)
Family Clupeidae							
Alosa pseudoharengus	5–25 (adult)	0.3	LOE	CTMax = 24.6 + 0.4 T_a		85	Otto et al. (1976)
	5–25 (y-o-y)	0.3	LOE	CTMax = 21.9 + 0.5 T_a		90	Otto et al. (1976)
Family Cottidae							
Cottus bairdi	15	1.0	OS	30.9	0.27^c	9	Kowalski et al. (1978)
Cottus cognatus gracilia	5 (1972 & 1973)	0.5	LOE	22.7 & 24.0	—	5, 5	Otto & O'Hara Rice (1977)
	10 (1972 & 1973)	0.5	LOE	24.8 & 25.1	—	5, 5	Otto & O'Hara Rice (1977)
	15 (1972 & 1973)	0.5	LOE	26.3 & 27.3	—	5, 5	Otto & O'Hara Rice (1977)
	20 (1972)	0.5	LOE	29.4		5	Otto & O'Hara Rice (1977)
				CTMax = 21.2 + 0.387 T_a			Otto & O'Hara Rice (1977)
Family Cyprinidae							
Campostoma anomalum	7.5	1.0	LOE	28.8	0.74^c	10	Chagnon & Hlohowskyj (1989)
	23	1.0	LOE	35.8	?	8	Chagnon & Hlohowskyj (1989)
	24 (field)	0.5–0.8	LOE	37.7	0.8	6	Mundahl (1990)
	26	0.017	LOE	37.2	0.33	13	Smale & Rabeni (1995)
	10	1.0	OS^1	31.8	0.62	18	Lutterschmidt & Hutchison (1997a)
Carrassius auratus	10	1.0	OS^1	35.8	0.29	11	Lutterschmidt & Hutchison (1997a)
Ctenopharyngodon idella	23	0.5	DP	39.3	0.53^a	18	Bettoli et al. (1985)
Hypophthalmichthyes nobilis	23	0.5	DP	38.8	0.44^a	18	Bettoli et al. (1985)
F_1 hybrid of above two species	23	0.5	DP	40.3	0.41^a	18	Bettoli et al. (1985)
Cyprinella lutrensis	25	1.0	OS	39.0	0.16	10	Matthews & Maness (1979)
	15	1.0	OS	32.0^a	1.04^c	82	Maness & Hutchison (1980)
	22	0.3	LOE	36.2	0.49	12	Takle et al. (1983)

Species	Acclimation	Rate	Method	Temp	Value	n	Reference
	25 (5 collection sites)	0.3	LOE	36.5–38.0	0.41–0.94	48–66	King et al. (1985)
	20 (day 1)	0.3	LOE	35.0	1.23[a]	11	Carrier & Beitinger (1988b)
	20 (day 5)	0.3	LOE	34.5	0.46[a]	11	Carrier & Beitinger (1988b)
	20 (day 10)	0.3	LOE	34.1	1.15[a]	10	Carrier & Beitinger (1988b)
	30	0.33	LOE	39.6	0.23	10	Rutledge & Beitinger (1989)
	26	0.017	LOE	38.1	0.42	11	Smale & Rabeni (1995)
	10	1.0	OS[1]	34.0	0.89	20	Lutterschmidt & Hutchison (1997a)
Ericymba buccata	24 (field)	0.5–0.8	LOE	37.0	0.9	10	Mundahl (1990)
Gila bicolor	20	0.3	LOE	33.2	0.63[b]	10	Castleberry & Cech (1992)
Gila bicolor mohavensis	18	0.14	LOE	33.5	range 33.0–33.7	5	McClanahan et al. (1986)
	24	0.14	LOE	34.9	range 34.7–35.2	5	McClanahan et al. (1986)
	30	0.14	LOE	36.2	range 35.8–36.5	5	McClanahan et al. (1986)
Gila coerulea	20	0.3	LOE	31.5	1.26[b]	10	Castleberry & Cech (1992)
Hybognathus placitus	25	1.0	OS	40.0	0.07	2	Matthews & Maness (1979)
	10	1.0	OS[1]	31.8	0.88	26	Lutterschmidt & Hutchison (1997a)
Hybopsis amblops	10	1.0	OS[1]	31.7	—	1	Lutterschmidt & Hutchison (1997a)
Luxilus chrysocephalus	26	0.017	LOE	36.2	0.48	8	Smale & Rabeni (1995)
Luxilus cornutus	26	0.017	LOE	35.7	0.39	18	Smale & Rabeni (1995)
Luxilus zonatus	26	0.017	LOE	35.3	0.50	8	Smale & Rabeni (1995)
Lythurus umbratilis	26	0.017	LOE	36.2	0.54	12	Smale & Rabeni (1995)
Nocomis micropogon	26	0.017	LOE	35.6	0.55	8	Smale & Rabeni (1995)
	15	1.0	OS	30.9	0.53[c]	15	Kowalski et al. (1978)
Notemigonus crysoleucas	26	0.017	LOE	36.8	0.37	8	Smale & Rabeni (1995)
	10	1.0	OS[1]	33.4	0.73	28	Lutterschmidt & Hutchison (1997a)
Notropis atherinoides	25	1.0	OS	37.6	0.40	10	Matthews & Maness (1979)
	10	1.0	OS[1]	34.1	0.65	8	Lutterschmidt & Hutchison (1997a)
Notropis chrysocephalus	24 (field)	0.5–0.8	LOE	36.2	1.0	6	Mundahl (1990)
	11 (Field)	1.0	LOE	30.8	1.8	8	Hockett & Mundahl (1988)
Notropis cornutus	15	1.0	OS	31.9	0.48[c]	8	Schubauer et al. (1980)
	15 (Dec)	1.0	OS	30.6	0.97[c]	10	Kowalski et al. (1978)
	15 (Mar)	1.0	OS	32.0	0.54[c]	16	Kowalski et al. (1978)
Notropis cummingsae	8	1.0	LOE[3]	29.0	1.3	?	McFarlane et al. (1976)
	8	0.1	LOE[3]	28.0	1.1	?	McFarlane et al. (1976)
Notropis dorsalis	26	0.017	LOE	36.6	0.49	9	Smale & Rabeni (1995)
Notropis girardi	25	1.0	OS	38.6	0.32	10	Matthews & Maness (1979)
Notropis lutipinnis	13	1.0	LOE[3]	30.0	1.2	?	McFarlane et al. (1976)
	13	0.1	LOE[3]	29.0	0.7	?	McFarlane et al. (1976)
Notropis nubilus	26	0.017	LOE	36.2	0.62	9	Smale & Rabeni (1995)
Notropis rubellus	15	1.0	OS	31.8	0.51[c]	5	Kowalski et al. (1978)
	26	0.017	LOE	35.3	0.23	7	Smale & Rabeni (1995)

Table 2. *(Continued)*

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Species	$T_{acclimation}$ °C	ΔT°C min^{-1}	Test endpoint	CTmaxima °C mean	SD	n	Reference
Notropis spilopterus	11(field)	1.0	LOE	31.8	1.8	26	Hockett & Mundahl (1988)
Notropis stramineus	15(4 seasons)	1.0	OS	32.3–33.0	0.45–0.68	10–18	Kowalski et al. (1978)
Phenacobius mirabilis	26	0.017	LOE	37.0	0.27	6	Smale & Rabeni (1995)
	10	1.0	OS[1]	33.4	0.63	2	Lutterschmidt & Hutchison (1997a)
Phoxinus erythrogaster	26	0.017	LOE	35.9	0.42	12	Smale & Rabeni (1995)
Pimephales notatus	15	1.0	OS	31.9	0.55[c]	9	Kowalski et al. (1978)
	11 (field)	1.0	LOE	31.3	1.1	9	Hockett & Mundahl (1988)
	24 (field)	0.5–0.8	LOE	37.9	0.5	10	Mundahl (1990)
	26	0.017	LOE	36.6	0.48	16	Smale & Rabeni (1995)
	10	1.0	OS[1]	33.7	0.48	29	Lutterschmidt & Hutchison (1997a)
Pimephales promelas	14.5[3] (diel min.,2200)	0.22	LOE	32.4	1.72	33	Spieler et al. (1977)
	14.5[3] (diel max.,1400 & 0200)	0.22	LOE	34.0	1.13, 1.17	32, 34	Spieler et al. (1977)
	15	1.0	OS	33.2[a]	0.57[c]	79	Maness & Hutchison (1980)
	21	0.3	LOE	35.1	1.15	20	Watenpaugh & Beitinger (1985)
	20 (day 1)	0.3	LOE	34.8	0.73[a]	12	Carrier & Beitinger (1988b)
	20 (day 5)	0.3	LOE	34.9	0.61[a]	12	Carrier & Beitinger (1988b)
	20 (day 10)	0.3	LOE	34.8	0.65[a]	12	Carrier & Beitinger (1988b)
	20	0.3	LOE	33.1	0.63[b]	10	Castleberry & Cech (1992)
	24 ♀ (nonspawn)	0.3	LOE	36.9	0.86	18	Pyron & Beitinger (1993)
	24 ♀ (postspawn)	0.3	LOE	36.8	1.40	13	Pyron & Beitinger (1993)
	24 ♂ (nonspawn)	0.3	LOE	36.2	1.22	12	Pyron & Beitinger (1993)
	24 ♂ (postspawn)	0.3	LOE	36.7	1.38	13	Pyron & Beitinger (1993)
	22.5 (larvae)	0.3	LOE	Median = 34.4, Q_1, Q_3 = 33.8, 35.0		30	Heath et al. (1994)
	5	0.3	LOE	28.6	0.80	10	Richards & Beitinger (1995)
	12	0.3	LOE	30.7	1.0	10	Richards & Beitinger (1995)
	22	0.3	LOE	36.4	0.75	10	Richards & Beitinger (1995)
	32	0.3	LOE	40.4	0.25	10	Richards & Beitinger (1995)
				CTMax = 25.9 + 0.457 T_a			
Pimephales vigilax	26	0.017	LOE	36.5	0.50	8	Smale & Rabeni (1995)
Rhinichthys atratulus	30	0.33	LOE	39.3	0.25	10	Rutledge & Beitinger (1989)
	15	1.0	OS	31.9	0.89[c]	17	Kowalski et al. (1978)
Rhinichthys cataractae	15	1.0	OS	31.4	0.64[c]	12	Kowalski et al. (1978)
Rhinichthys osculus	20	0.3	LOE	32.4	1.90[b]	10	Castleberry & Cech (1992)

Species	Acclimation temp	Rate	Endpoint	CTMax	Value	N	Reference
R. o. thermalis	24	0.45	LOE	34.5	0.71	12	Kaya et al. (1992)
	27	0.45	LOE	34.6	0.67	14	Kaya et al. (1992)
R. o. yarrowi	24	0.45	LOE	33.9	0.77	13	Kaya et al. (1992)
	27	0.45	LOE	34.9	0.84	13	Kaya et al. (1992)
Semotilus atromaculatus	26	0.017	LOE	35.7	0.44	9	Smale & Rabeni (1995)
Family Cyprinodontidae							
Cyprinodon sp.	5 (0‰ salinity)	0.3	LOE	27.2	2.80	5	Otto & Gerking (1973)
	5 (15‰)	0.3	LOE	36.1	1.70	5	Otto & Gerking (1973)
	15 (0‰)	0.3	LOE	39.2	0.35	5	Otto & Gerking (1973)
	15 (15‰)	0.3	LOE	40.8	0.31	5	Otto & Gerking (1973)
	15 (30‰)	0.3	LOE	41.3	0.34	5	Otto & Gerking (1973)
	25 (0‰)	0.3	LOE	40.7	0.39	5	Otto & Gerking (1973)
	25 (15‰)	0.3	LOE	41.7	0.18	5	Otto & Gerking (1973)
	25 (30‰)	0.3	LOE	41.7	0.19	5	Otto & Gerking (1973)
	25 (45‰)	0.3	LOE	41.4	0.17	5	Otto & Gerking (1973)
	35 (0‰)	0.3	LOE	43.1	0.39	5	Otto & Gerking (1973)
	35 (15‰)	0.3	LOE	43.6	0.04	5	Otto & Gerking (1973)
	35 (30‰)	0.3	LOE	43.4	0.20	5	Otto & Gerking (1973)
	35 (45‰)	0.3	LOE	43.6	0.22	5	Otto & Gerking (1973)
				$CTMax = 27.71 + 0.49\,T_a$ (0‰)			
Cyprinodon artifons	30	0.3	LOE[2]	43.7[a]	0.31[c]	7	Heath et al. (1993)
	26–40 (diel cycle)	0.3	LOE[2]	45.4[a]	0.19[e]	8	Heath et al. (1993)
Cyprinodon elegans	20 ♂	0.5–1.0	LOE	40.1	0.25[b]	8	Gelbach et al. (1978)
	20 ♀	0.5–1.0	LOE	40.5	0.34[b]	8	Gelbach et al. (1978)
Cyprinodon macularius	30 (day 7)	0.5	LOE	42.0	0.30[b]	19	Lowe & Heath (1969)
	32 (day 7)	0.5	LOE	42.5	0.29[b]	17	Lowe & Heath (1969)
	34 (day 7)	0.5	LOE	43.2	0.24[b]	12	Lowe & Heath (1969)
	field maximum	0.5	LOE	44.6	0.50[b]	30	Lowe & Heath (1969)
Cyprinodon nevadensis	15	0.033	DP	40.1[a]	2.36[c]	17	Feldmuth et al. (1974)
	15	0.033	DP	40.2[a]	2.24[c]	18	Feldmuth et al. (1974)
	25	0.033	DP	41.7[a]	0.69[c]	20	Feldmuth et al. (1974)
	25	0.033	DP	41.7	0.94[c]	20	Feldmuth et al. (1974)
	35	0.033	DP	43.3[a]	0.59[c]	20	Feldmuth et al. (1974)
	35	0.033	DP	42.3[a]	0.42[c]	18	Feldmuth et al. (1974)
				$CTMax = 38.23 + 0.132\,T_a$			
Cyprinodon variegatus	5	0.1	LOE	34.6	1.95	20	Bennett & Beitinger (1997)
	21	0.1	LOE	40.1	0.90	30	Bennett & Beitinger (1997)
	38	0.1	LOE	44.2	0.29	20	Bennett & Beitinger (1997)
				$CTMax = 33.43 + 0.29\,T_a$			
	37–42 (diel cycle)	0.3	LOE	45.1	0.38	20	Bennett & Beitinger (1997)

Table 2. (Continued)

Species	$T_{acclimation}$ °C	ΔT°C min^{-1}	Test endpoint	CTmaxima, °C mean	SD	n	Reference
Floridichthys carpio	30 (diel cycle)	0.3	LOE[3]	42.2[a]	0.16[c]	8	Heath et al. (1993)
	26–40 (diel cycle)	0.3	LOE[3]	43.6[a]	0.27[c]	5	Heath et al. (1993)
Fundulus heteroclitus	12 (diel min., 1600 h)	0.3	LOE	34.3	0.46	20	Bulger (1984)
	12 (diel max., 1200 h)	0.3	LOE	36.2	0.38	20	Bulger (1984)
	27 (diel min., 0700 h)	0.3	LOE	41.0	0.25	20	Bulger (1984)
	27 (diel max., 1200 h)	0.3	LOE	42.4	0.40	20	Bulger (1984)
	30 (tested only at 1200 h)	0.3	LOE	43.1	0.24	20	Bulger (1984)
	36 (tested only at 1200 h)	0.3	LOE	44.1	0.14	20	Bulger (1984)
	7	0.3	LOE	32.2	0.59	20	Bulger & Tremaine (1985)
	12	0.3	LOE	36.2	0.38	20	Bulger & Tremaine (1985)
	20	0.3	LOE	38.5	0.33	33	Bulger & Tremaine (1985)
	22	0.3	LOE	39.0	0.54	18	Bulger & Tremaine (1985)
	24	0.3	LOE	40.5	0.29	20	Bulger & Tremaine (1985)
	27	0.3	LOE	42.4	0.40	20	Bulger & Tremaine (1985)
	30	0.3	LOE	43.1	0.24	22	Bulger & Tremaine (1985)
	34	0.3	LOE	43.6	0.20	29	Bulger & Tremaine (1985)
	36	0.3	LOE	44.1	0.14	18	Bulger & Tremaine (1985)
				$CTMax = 30.5 + 0.40\,T_a$			
Fundulus notatus	30	0.33	LOE	41.6	0.21	10	Rutledge & Beitinger (1989)
Fundulus olivaceus	26	0.017	LOE	38.3	0.67	7	Smale & Rabeni (1995)
Fundulus sciadicus	26	0.017	LOE	38.8	0.59	7	Smale & Rabeni (1995)
	26	0.017	LOE	37.0	0.30	3	Smale & Rabeni (1995)
Family Esocidae							
Esox masquinongy	7 (1–31 d post hatch)	1.0	body bends	27.2–34.0	0.23–0.98[c]	11 trials, n = 4–6	Hassam & Spotila (1976)
	15 (1–31 d post hatch)	1.0	bends & LOE	29.8–34.4	0.22–1.09[c]	13 trials, n = 3–6	Hassam & Spotila (1976)
	25 (1–19 d post hatch)	1.0	LOE	33.2–36.1	0.41–1.28[c]	10 trials, n = 6	Hassam & Spotila (1976)
	15 (2–15 d post hatch)	1.0	variable	30.5–34.0	0.63–1.54[c]	8 trials, n = 6	Paladino & Spotila (1976)
Esox masquinony ♀ ×	16–22 (varying) 53 d	1.0	OS & PGR	29.9–35.6	0.22–1.06[c]	19 trials, n = 10	Bonin & Spotila (1978)
Esox lucius ♂ hybrid	16–22 (varying) 53 d	1.0	OS & PGR	30.9–36.0	0.22–0.62[c]	19 trials, n = 10	Bonin & Spotila (1978)

Family Gasterosteidae							
Gasterosteus aculeatus	8.0	DP	0.25	30.5	0.73[e]	10	Feldmuth & Baskin (1976)
williamsoni	13.0	DP	0.25	32.5[a]	0.73[e]	10	Feldmuth & Baskin (1976)
	15.6	DP	0.25	33.5[a]	0.32[e]	10	Feldmuth & Baskin (1976)
	18.6 (0.18 g)	DP	0.25	33.5	0.22[e]	8	Feldmuth & Baskin (1976)
	18.6 (1.39 g)	DP	0.25	33.6	0.19	8	Feldmuth & Baskin (1976)
	22.7	DP	0.25	34.6	0.73[e]	10	Feldmuth & Baskin (1976)
				$CTMax = 28.74 + 0.27\,T_a$			
Family Ictaluridae							
Ameiurus melas	26	LOE	0.017	38.1	0.39	7	Smale & Rabeni (1995)
Ameiurus natalis	26	LOE	0.017	37.9	0.44	7	Smale & Rabeni (1995)
Ictalurus punctatus	12	LOE	1.0	34.5[a]	0.53[e]	12	Cheetham et al. (1976)
	16	LOE	1.0	34.2[a]	0.74[e]	12	Cheetham et al. (1976)
	20	LOE	1.0	35.5[a]	0.38[e]	12	Cheetham et al. (1976)
	24	LOE	1.0	37.5[a]	0.52[e]	12	Cheetham et al. (1976)
	28	LOE	1.0	39.2[a]	0.58[e]	12	Cheetham et al. (1976)
	32	LOE	1.0	41.0[a]	0.31[e]	12	Cheetham et al. (1976)
				$CTMax = 29.2 + 0.35\,T_a$			Watenpaugh et al. (1985)
	20	LOE	0.3	38.0	0.39	20	Currie et al. (1998)
	20	LOE	0.3	36.4	0.25	20	Currie et al. (1998)
	25	LOE	0.3	38.7	0.36	20	Currie et al. (1998)
	30	LOE	0.3	40.3	0.29	20	Currie et al. (1998)
				$CTMax = 28.6 + 0.40\,T_a$			
	10	LOE	0.15	30.9	0.61	30	Bennett et al. (1998)
	20	LOE	0.15	35.8	0.47	30	Bennett et al. (1998)
	30	LOE	0.15	40.1	0.66	30	Bennett et al. (1998)
	35	LOE	0.15	42.1	0.25	30	Bennett et al. (1998)
				$CTMax = 26.6 + 0.45\,T_a$			
Noturus exilis	10	OS[1]	1.0	33.3	0.54	20	Lutterschmidt & Hutchison (1997a)
	26	LOE	0.017	36.5	0.24	8	Smale & Rabeni (1995)
Family Percichthyidae							
Morone saxatilis	10	OS[1]	1.0	31.6	0.53	3	Lutterschmidt & Hutchison (1997a)
Morone saxatilis ♀ x	6.5	LOE	0.3	28.0	0.1	4–5	Woiwade & Adelman (1992)
M. chrysop ♂ hybrid	12.2	LOE	0.3	31.0	0.2	4–5	Woiwade & Adelman (1992)
	18.0	LOE	0.3	33.4	< 0.1	4–5	Woiwade & Adelman (1992)

Table 2. (Continued)

Species	$T_{acclimation}$ °C	ΔT°C min^{-1}	Test endpoint	CTmaxima, °C mean	SD	n	Reference
	23.0	0.3	LOE	36.2	0.2	4–5	Woiwade & Adelman (1992)
	27.0	0.3	LOE	38.3	0.2	4–5	Woiwade & Adelman (1992)
	29.2	0.3	LOE	39.1	0.1	4–5	Woiwade & Adelman (1992)
	31.0	0.3	LOE	39.2	< 0.1	4–5	Woiwade & Adelman (1992)
	33.1	0.3	LOE	40.5	0.1	4–5	Lohr et al. (1996)
	6.5–33.1 (sated)	0.3	LOE	$CTMax = 25.04 + 0.478\,T_a$			Lohr et al. (1996)
	6.5–33.1 (starved)	0.3	LOE	$CTMax = 24.58 + 0.485\,T_a$			Woiwade & Adelman (1992)
Family Percidae							
Etheostoma blennioides	15	1.0	OS	32.2	0.83[e]	9	Kowalski et al. (1978)
	0–25 (field)	1.0	LOE	$CTMax = 27.42 + 0.25\,T_f$			Hlohowskyj & Wissing (1985)
	10 (4 seasons)	1.0	LOE	28.8–33.5[2]	—	8–20	Hlohowskyj & Wissing (1985)
	20 (4 seasons)	1.0	LOE	32.2–34.5[2]	—	10–17	Hlohowskyj & Wissing (1985)
Etheostoma caeruleum	15	1.0	OS	32.1	0.78[e]	10	Kowalski et al. (1978)
	0–25 (field)	1.0	LOE	$CTMax = 27.99 + 0.31\,T_f$			Hlohowskyj & Wissing (1985)
	10 (4 seasons)	1.0	LOE	29.8–32.0[2]	—	10–27	Hlohowskyj & Wissing (1985)
	20 (4 seasons)	1.0	LOE	32.8–34.0[2]	—	8–39	Hlohowskyj & Wissing (1985)
	26	0.017	LOE	35.6	0.59	11	Smale & Rabeni (1995)
Etheostoma cragini	20–30	0.5	LOE	35.0–38.4	—	60	Smith & Fausch (1997)
Etheostoma flabellare	15	1.0	OS	32.1	0.63[e]	14	Kowalski et al. (1978)
	15 (winter)	1.0	OS	31.1	0.79[2]	11	Ingersall & Claussen (1984)
	15 (summer)	1.0	OS	31.3	0.67[2]	10	Ingersoll & Claussen (1984)
	0–25 (field)	1.0	LOE	$CTMax = 30.41 + 0.22\,T_f$			Hlohowskyj & Wissing (1985)
	10 (3 seasons)	1.0	LOE	31.1–34.0[2]	—	5–12	Hlohowskyj & Wissing (1985)
	20 (4 seasons)	1.0	LOE	32.9–35.0[2]	—	5–15	Hlohowskyj & Wissing (1985)
	20	1.0	LOE	~33[a]	—	5	Lydy & Wissing (1988)
	24 (field)	0.5–0.8	LOE	37.7	0.5	10	Mundahl (1990)
	26	0.017	LOE	36.0	0.54	9	Smale & Rabeni (1995)
Etheostoma nigrum	15 (3 Seasons)	1.0	OS	30.1–31.3	0.16–0.40[e]	4–7	Kowalski et al. (1978)
	15 (winter)	1.0	OS	30.9	1.12[2]	10	Ingersoll & Claussen (1984)
	15 (summer)	1.0	OS	30.5	0.39[2]	11	Ingersoll & Claussen (1984)
	20	1.0	LOE	~33	—	5	Lydy & Wissing (1988)
	20–30	0.5	LOE	34.0–37.4	—	57	Smith & Fausch (1997)
	26	0.017	LOE	36.4	0.45	7	Smale & Rabeni (1995)

Etheostoma spectabile (4 populations)						
29 (field)	1.0	LOE	37.9	0.74	15	Matthews et al. (1982)
20 (Cummings Spring)	1.0	LOE[5]	32.2	1.0[a]	25	Feminella & Matthews (1984)
20 (Pennington Creek)	1.0	LOE[5]	32.8	0.80[a]	25	Feminella & Matthews (1984)
20 (Byrd's Mill Creek)	1.0	LOE[5]	34.0	1.10[a]	20	Feminella & Matthews (1984)
20 (Brier Creek)	1.0	LOE[5]	34.4	1.11[a]	25	Feminella & Matthews (1984)
26	0.017	LOE	36.5	0.15	8	Smale & Rabeni (1995)
10	1.0	OS[1]	31.5	0.64	19	Lutterschmidt & Hutchison (1997a)
Stizostedion vitreum						
23 (Iowa)	1.0	LOE[5]	34.8	0.3	15	Peterson (1993)
23 (Mississippi)	1.0	LOE[5]	35.0	0.6	15	Peterson (1993)
Family Poeciliidae						
Gambusia affinis Utah and Arizona populations						
5 (Utah)	0.3	LOE	32.5[a]	?	10	Otto (1973)
5 (Ariz.)	0.3	LOE	33.7[a]	?	10	Otto (1973)
10 (Utah)	0.3	LOE	33.5[a]	?	10	Otto (1973)
10 (Ariz.)	0.3	LOE	35.0[a]	?	10	Otto (1973)
15 (Utah)	0.3	LOE	34.8[a]	?	10	Otto (1973)
15 (Ariz.)	0.3	LOE	35.6[a]	?	10	Otto (1973)
20 (Utah)	0.3	LOE	37.4[a]	?	10	Otto (1973)
20 (Ariz.)	0.3	LOE	37.4[a]	?	10	Otto (1973)
25 (Utah)	0.3	LOE	38.8[a]	?	10	Otto (1973)
25 (Ariz.)	0.3	LOE	39.5[a]	?	10	Otto (1973)
30 (Utah)	0.3	LOE	41.4	?	10	Otto (1973)
30 (Ariz.)	0.3	LOE	42.3	?	10	Otto (1973)
35 (Utah)	0.3	LOE	42.1	?	10	Otto (1973)
35 (Ariz.)	0.3	LOE	43.5	?	10	Otto (1973)
			$CTMax = 30.3 + 0.35\,T_a$ (Utah)			
			$CTMax = 31.3 + 0.34\,T_a$ (Arizona)			
25	0.3	LOE	38.0	0.40	10	Otto (1974)
30	0.3	LOE	41.0	0.30	10	Otto (1974)
35	0.3	LOE	42.3	0.40	10	Otto (1974)
			$CTMax = 27.53 + 0.43\,T_a$			
34–41.5 (diel cycle)[6]	0.3	LOE	43.7	0.4	10	Otto (1974)
18.5[7] (♀ diel min., 2200–2359)	0.3	LOE[3]	34.9	0.62[b]	32	Johnson (1976)
18.5[7] (♀ diel max., 1200–1359)	0.3	LOE[3]	36.9	0.37[b]	45	Johnson (1976)
18.5[7] (♂ diel min., 0200–0359)	0.3	LOE[3]	33.2	0.66[b]	103	Johnson (1976)

Table 2. (Continued)

Species	$T_{acclimation}$ °C	ΔT°C min^{-1}	Test endpoint	CTmaxima, °C mean	SD	n	Reference
	18.5[1] (♂ diel min., 1000–1159)	0.3	LOE[3]	36.6	0.62[b]	48	Johnson (1976)
	18.5[1] (gravid ♀)	0.3	DP	37.9	0.68[b]	46	Johnson (1976)
	18.5[1] (nongravid ♀)	0.3	DP	38.0	0.50[b]	40	Johnson (1976)
	10	1.0	OS[1]	38.5	0.74	20	Lutterschmidt & Hutchison (1997a)
Gambusia holbrooki	25 (ambient pond)	0.4	LOE[3]	39.8[a]	0.39[c]	41	Meffe et al. (1995)
	25 (Pond C)	0.4	LOE[3]	40.1[a]	0.38[c]	39	Meffe et al. (1995)
Gambusia nobilis	20♀	0.5–1.0	LOE	39.3	0.48[b]	8	Gehlback et al. (1978)
	20♂	0.5–1.0	LOE	38.1	0.42[b]	8	Gehlback et al. (1978)
Gambusia yucatana	30	0.3	LOE[3]	42.2[a]	0.27[b]	8	Heath et al. (1993)
	26–40 (diel cycle)	0.3	LOE[3]	42.4[a]	0.92[c]	7	Heath et al. (1993)
Family Polyodontidae							
Polyodon spathula	21 (5 days old)	0.2	DP	33.4	1.18[4]	30	Kurten & Hutson (1992)
	21 (25 days old)	0.2	DP	33.5	0.41[4]	30	Kurten & Hutson (1992)
	21 (80 days old)	0.2	DP	35.2	0.30[4]	30	Kurten & Hutson (1992)
Family Salmonidae							
Oncorhynchus kisutch	5	0.3[1]	LOE[3]	27.5	0.44[c]	16	Becker & Genoway (1979)
	15	0.3[1]	LOE[3]	29.7	0.38[c]	16	Becker & Genoway (1979)
	15	0.1	LOE[3]	28.7	0.30	20	Becker & Wolford (1980)
	11.5 (field)	0.33	LOE	28.2	0.54	28	Konecki et al. (1995)
	14.6 (field)	0.33	LOE	29.2	0.29	43	Konecki et al. (1995)
	16.6 (field)	0.33	LOE	29.1	0.31	42	Konecki et al. (1995)
	11.1	0.33	LOE	27.6	0.95	47	Konecki et al. (1995)
	11.1	0.33	LOE[3]	27.9	0.62	45	Konecki et al. (1995)
Oncorhynchus mykiss	8	0.1	LOE[3]	26.9	0.89	56	Becker & Wolford (1980)
	10	0.02	LOE	28.4	0.28	5	Lee & Rinne (1980)
	20	0.02	LOE	29.4	0.19	5	Lee & Rinne (1980)
	15	0.3	LOE	29.4	0.59[b]	55	Strange et al. (1993)
	10	0.3	LOE	28.0	0.36	20	Currie et al. (1998)
	15	0.3	LOE	29.1	0.27	20	Currie et al. (1998)
	20	0.3	LOE	29.8	0.36	20	Currie et al. (1998)
				CTMax = 26.2 + 0.18T_a			Currie et al. (1998)
Oncorhynchus apache	10	0.02	LOE	28.5	0.35	5	Lee & Rinne (1980)
	20	0.02	LOE	29.4	0.21	5	Lee & Rinne (1980)
Oncorhynchus clarkii clarkii	10	0.4	LOE	27.6	0.43[b]	29	Heath (1963)

Species	Acclimation temp	Rate	Endpoint	CTMax	Value	n	Reference
	15	0.4	LOE	29.1	0.47[b]	90	Heath (1963)
	20	0.4	LOE	29.9	0.72[b]	64	Heath (1963)
					CTMax = 25.5 + 0.225 T_a		Heath (1963)
Oncorhynchus gilae	10–20 (diel cycle)[7]	0.4	LOE	29.8	0.32	65	Heath (1963)
	10	0.02	LOE	28.2	0.22	5	Lee & Rinne (1980)
	20	0.02	LOE	29.6	0.31	5	Lee & Rinne (1980)
Salmo salar	15 0+ year	0.033[9]	LOE	32.9	1.26	10	Elliott & Elliott (1995)
	15 1+ year	0.033[9]	LOE	32.6	1.19	10	Elliott & Elliott (1995)
	20 0+ year	0.033[9]	LOE	32.8	1.19	10	Elliott & Elliott (1995)
	20 1+ year	0.033[9]	LOE	32.7	1.41	10	Elliott & Elliott (1995)
Salmo trutta	10	0.02	LOE	29.0	0.41	5	Lee & Rinne (1980)
	20	0.02	LOE	29.8	0.58	5	Lee & Rinne (1980)
	15	0.033[9]	LOE	29.9	1.10	10	Elliott & Elliott (1995)
	20	0.033[9]	LOE	30.0	1.76	10	Elliott & Elliott (1995)
Salvelinus fontalinis	10	0.02	LOE	28.7	0.67	5	Lee & Rinne (1980)
	20	0.02	LOE	29.8	0.35	5	Lee & Rinne (1980)
Thymallus arcticus	5	?	DP	24.8	1.5	?	McLeay et al. (1983)
	5	?	DP	24.9	1.4	?	McLeay et al. (1983)
	15	?	DP	27.9	0.1	?	McLeay et al. (1983)
	15	?	DP	27.7	0.1	?	McLeay et al. (1983)
	15	?	DP	27.7	0.1	?	McLeay et al. (1983)
	15	?	DP	27.5	0.1	?	McLeay et al. (1983)
	8.4	0.4	LOE	26.4	0.8	20	Lohr et al. (1996)
	16	0.4	LOE	28.5	0.4	18	Lohr et al. (1996)
	20	0.4	LOE	29.3	0.3	17	Lohr et al. (1996)
					CTMax = 24.3 + 0.25 T_a		

[1] Loss of righting response also listed.
[2] Four additional rates of temperature change were used.
[3] Death point (DP) temperatures also were listed.
[4] Pimephales were tested 6 times in 24 h.
[5] Temperature at onset of spasms (OS) also were given.
[6] Eleven other diel cycles were tested.
[7] Gambusia were tested each 2 h for 24 h.
[8] Oncorhynchus clarkii were tested at four other cycles.
[9] Salmo salar and S. trutta were tested at 9 different rates of temperature change.

Table 3. Critical thermal minima (CTminima) for North American freshwater fishes by family. Each entry indicates pretest acclimation temperature, rate of temperature decrease during CTminimum trials and reported test endpoint (OS = onset of muscular spasms; LOE = loss of equilibrium, PGR = lack of responses for prodding with a glass rod. Acclimation temperatures (second column) are from constant laboratory conditions unless otherwise indicated. CTminima data (column 5) estimated from published figures are indicated by the superscript a. Standard deviations (SD) calculated from published standard errors or 95% confidence limits are denoted by the superscript b. The superscript c indicates that listed standard deviations were calculated from estimates of plots giving either standard errors or 95% confidence limits. Regression models were either published or calculated from published mean CTminima values, T_a = acclimation temperature.

Species	$T_{acclimation}$ °C	ΔT °C min^{-1}	Test endpoint	CTminima, °C mean	SD	n	Reference
Family Centrarchidae							
Lepomis gibbosus	15	0.3[1]	LE-50[2]	1.7	—	20	Becker et al. (1977)
	20	0.3[1]	LE-50[2]	4.1	—	20	Becker et al. (1977)
	25	0.3[1]	LE-50[2]	8.7	—	20	Becker et al. (1977)
	30	0.3[1]	LE-50[2]	12.1	—	20	Becker et al. (1977)
				CTMin $= -9.46 + 0.716\,T_a$			Becker et al. (1977)
Micropterus salmoides	20	0.3	LOE	3.2	0.27	20	Currie et al. (1998)
salmoides	25	0.3	LOE	7.3	0.52	20	Currie et al. (1998)
	30	0.3	LOE	10.7	0.61	20	Currie et al. (1998)
				CTMin $= -11.87 + 0.76\,T_a$			Currie et al. (1998)
Family Characidae							
Pygocentrus natteri	10	0.15	LOE	10.0	0.15	10	Bennett et al. (1997)
	15	0.15	LOE	10.5	0.44	10	Bennett et al. (1997)
	20.5	0.15	LOE	12.1	0.31	20	Bennett et al. (1997)
	25	0.15	LOE	13.7	0.61	10	Bennett et al. (1997)
	30	0.15	LOE	16.3	0.55	9	Bennett et al. (1997)
	35	0.15	LOE	19.7	1.18	9	Bennett et al. (1997)
				CTMin $= 11.15 - 0.26\,T_a + 0.014\,T_a^2$			Bennett et al. (1997)
Family Cichlidae							
Tilapia melanotheron	21 (5‰salinity)	0.017	LOE	9.4	0.27	9	Jennings (1991)
	21 (15‰salinity)	0.017	LOE	9.7	0.09	9	Jennings (1991)
	21 (35‰salinity)	0.017	LOE	9.6	0.31	9	Jennings (1991)
Family Cyprinidae							
Gila bicolor mohavensis	18	0.14	LOE	2.8	range 2.6–3.2	5	McClanahan et al. (1986)
	24	0.14	LOE	4.8	range 4.6–5.1	5	McClanahan et al. (1986)
	30	0.14	LOE	7.2	range 7.0–7.7	5	McClanahan et al. (1986)
				CTMin $= -3.9 + 0.37\,T_a$			McClanahan et al. (1986)
Notropis chrysocephalus	22	0.5	LOE	4.5	0.7	2	Hockett & Mundahl (1988)
Notropis spilopterus	22	0.5	LOE	4.5	1.0	25	Hockett & Mundahl (1988)
Pimephales notatus	22	0.5	LOE	6.4	1.2	5	Hockett & Mundahl (1988)

Species	Temp (°C)	Rate	Endpoint	Mean	SD	n	Reference
Pimephales promelas	22.5 (larvae)	0.3	PGR	Median = 5.9, Q_1, Q_3 5.4, 7.4		30	Heath et al. (1994)
Rhinichthys osculus thermalis	28	0.75[3]	LOE	6.7	0.25	9	Kaya et al. (1992)
R. o. yarrowi	28	0.75[3]	LOE	6.6	0.30	9	Kaya et al. (1992)
Family Cyprinodontidae							
Cyprinodon nevadensis	15	0.033	LOE	0.6[c]	1.5[c]	16	Feldmuth et al. (1974)
	15	0.033	LOE	0.8[a]	0.4[c]	11	Feldmuth et al. (1974)
	25	0.033	LOE	2.2[a]	0.4[c]	19	Feldmuth et al. (1974)
	25	0.033	LOE	2.2[a]	0.6[c]	13	Feldmuth et al. (1974)
	35	0.033	LOE	4.3[a]	1.33[c]	27	Feldmuth et al. (1974)
	35	0.033	LOE	3.9[a]	0.9[a]	25	Feldmuth et al. (1974)
				$CTMin = -1.92 + 0.17T_a$			
Cyprinodon variegatus	15–35 diel cycle	0.033	LOE	2.5[a]	1.0[a]	17	Feldmuth et al. (1974)
	5	0.1	LOE	0.6	1.31	20	Bennett & Beitinger (1997)
	21	0.1	LOE	6.9	1.97	30	Bennett & Beitinger (1997)
	38	0.1	LOE	11.3	0.52	20	Bennett & Beitinger (1997)
				$CTMin = -0.63 + 0.32T_a$			
Family Ictaluridae							
Ictalurus punctatus	20	0.3	LOE	2.7	0.41	20	Currie et al. (1998)
	25	0.3	LOE	6.5	0.40	20	Currie et al. (1998)
	30	0.3	LOE	9.8	0.41	20	Currie et al. (1998)
				$CTMin = -11.3 + 0.70T_a$			
Family Poeciliidae							
Poeciliopsis lucida	25	0.0035	LOE	6.4	0.91	128	Bulger & Schultz (1979)
Poeciliopsis monacha	25	0.0035	LOE	6.8	1.06	53	Bulger & Schultz (1979)
Poeciliopsis occidentalis	25	0.0335	LOE	4.8	1.14	26	Bulger & Schultz (1982)
P. lucida × P. monacha	25	0.0035	LOE	5.2	0.90	127	Bulger & Schultz (1979)
P. monacha × P. occidentalis	25	0.0035	LOE	5.2	1.13	39	Bulger & Schultz (1982)
P. monacha × P. lucida	25	0.0035	LOE	6.9	1.08	83	Bulger & Schultz (1982)
Family Salmonidae							
Oncorhynchus mykiss	10	0.3[1]	LE-50[2]	< 0.0	—	20	Becker et al. (1977)
	15	0.3[1]	LE-50[2]	0.7	—	20	Becker et al. (1977)
	20	0.3[1]	LE-50[2]	2.1	—	20	Becker et al. (1977)
	10	0.3	LOE	< 0.0	—	20	Currie et al. (1998)
	15	0.3	LOE	0.2	0.16	20	Currie et al. (1998)
	20	0.3	LOE	2.0	0.16	20	Currie et al. (1998)
				$CTMin = -5.31 + 0.36T_a$			

[1] Four other rates of temperature decrease were used.
[2] LE-50 = point where 50% of fish lost equilibrium.
[3] Mean decrease, however ΔT during trials was curvilinear.

Table 4. Chronic lethal maxima for North American freshwater fishes by family. Each entry includes pretest acclimation temperature and rate of temperature increase during trials. Acclimation temperature (second column) are from constant laboratory conditions unless otherwise indicated. Standard deviations (SD) calculated from published standard errors or 95% confidence limits are denoted by the superscript b.

Species	$T_{acclimation}$ °C	ΔT°C day^{-1}	Test endpoint	Chronic lethal maxima, °C mean	SD	n	Reference
Family Centrarchidae							
Lepomis macrochirus	21.5	2	DP	median = 35.5	Q_1, Q_3 = 33.9, 37.5	10	Hickman & Dewey (1973)
Micropterus salmoides	30 (0.50 g)	1	DP	39.8	0.31[b]	10	Guest (1985)
salmoides	30 (5.6 g)	1	DP	38.9	0.28[b]	8	Guest (1985)
	30 (218 g)	1	DP	39.1	0.26[b]	7	Guest (1985)
	36 (0.4 g)	1	DP	39.3	0.63[b]	10	Guest (1985)
	32	1	DP	37.3	0.60	10	Fields et al. (1987)
Micropterus salmoides	30 (0.5 g)	1	DP	39.4	0.63[b]	10	Guest (1985)
floridans	30 (9.1 g)	1	DP	38.2	0.85[b]	8	Guest (1985)
	30 (200 g)	1	DP	38.8	0.56[b]	8	Guest (1985)
	36 (0.4 g)	1	DP	39.1	0.63[b]	10	Guest (1985)
	32	1	DP	39.1	0.97	10	Fields et al. (1987)
M. s. salmoides ♀× *M. s. floridans* ♂	32	1	DP	40.1	0.64	10	Fields et al. (1987)
M. s. salmoides ♂× *M. s. floridans* ♀	32	1	DP	39.2	0.64	10	Fields et al. (1987)
Family Cyprinidae							
Notropis pilsbryi	21.5	2	DP	median = 32.3	Q_1, Q_3 = 31.9, 33.0	10	Hickman & Dewey (1973)
Family Salmonidae							
Oncorhynchus mykiss	17	0.67	DP	median = 26.3	—	10	Grande & Andersen (1991)
Oncorhynchus apache	13–15	2–3°C in 2 days	DP	range = 22.0–24.0	—	20	Alcorn (1976)
Salmo salar	17	0.67	DP	median = 28.7	—	10	Grande & Andersen (1991)
	17	1.5	DP	median = 29.2	—	10	Grande & Andersen (1991)
Salmo trutta	17	1.5	DP	median = 27.8	—	10	Grande & Andersen (1991)
Salvelinus fontinalis	17	0.67	DP	median = 26.2	—	10	Grande & Andersen (1991)
	17	1.5	DP	median = 27.2	—	10	Grande & Andersen (1991)
Salvelinus namaycush	17	1.5	DP	median = 25.9	—	10	Grande & Andersen (1991)

Table 5. Chronic lethal minima for North American freshwater fishes by family. Each entry includes pretest acclimation temperature and rate of temperature decrease during trials. Acclimation temperatures (second column) are from laboratory conditions unless otherwise indicated. DP = death point, i.e., temperature at which death occured.

Species	$T_{acclimation}$ °C	ΔT°C day^{-1}	Test endpoint	Chronic lethal minima, °C mean	SD	n	Reference
Family Centrarchidae							
Micropterus salmoides salmoides	10 (0.04 g) summer	1	DP[1]	1.3	0.95	10	Guest (1985)
salmoides	10 (7.3 g) summer	1	DP[1]	< 1.0	—	8	Guest (1985)
	10 (725 g) summer	1	DP[1]	3.0	1.56	5	Guest (1985)
	10 (682 g) winter	1	DP[1]	< 1.0	—	8	Guest (1985)
Micropterus salmoides floridanus	10 (0.3 g) summer	1	DP[1]	3.1	2.53	10	Guest (1985)
	10 (10.6 g) summer	1	DP[1]	4.0	0.85	8	Guest (1985)
	10 (470 g) summer	1	DP[1]	3.4	1.22	6	Guest (1985)
	10 (624 g) winter	1	DP[1]	< 1.0	—	5	Guest (1985)
Family Cichlidae							
Astronotus ocellatus	28	1	DP[1]	12.9	0.4	23	Shafland & Pestrak (1982)
Cichlasoma bimaculatum	21	1	DP[1]	8.9	0.9	13	Shafland & Pestrak (1982)
Cichlasoma cyanoguttatum	30	1	DP[1]	5.0	0.0	6	Shafland & Pestrak (1982)
Cichlasoma meeki	25	1	DP[1]	10.3	0.5	9	Shafland & Pestrak (1982)
Cichlasoma octofasciatum	20	1	DP[1]	8.0	0.0	6	Shafland & Pestrak (1982)
Cichlasoma trimaculatum	22	1	DP[1]	10.9	0.4	19	Shafland & Pestrak (1982)
Hemichromis bimaculatus	21	1	DP[1]	9.5	0.5	9	Shafland & Pestrak (1982)
Oreochromis aureus	28	1	DP[1]	6.2	0.4	20	Shafland & Pestrak (1982)
	20 (salinity = 0‰)	1	DP[1]	median = 6	—	2 trials of 12	Zale & Gregory (1989)
	20 (5‰)	1	DP[1]	median = 5	—	2 trials of 12	Zale & Gregory (1989)
	20 (11.6‰)	1	DP[1]	median = 5	—	2 trials of 12	Zale & Gregory (1989)
	20 (20‰)	1	DP[1]	median = 7	—	2 trials of 12	Zale & Gregory (1989)
	20 (35‰)	1	DP[1]	median = 9	—	2 trials of 12	Zale & Gregory (1989)
Tilapia mariae	25	1	DP[1]	11.2	0.7	9	Shafland & Pestrak (1982)
Tilapia melanotheron	25	1	DP[1]	10.3	0.5	9	Shafland & Pestrak (1982)
Tilapia mossambica	28	1	DP[1]	9.5	0.5	6	Shafland & Pestrak (1982)
Family Clariidae							
Clarias batracus	29	1	DP[1]	9.8	0.4	6	Shafland & Pestrak (1982)
Family Loricariidae							
Hypostomus sp.	25	1	DP[1]	11.2	0.4	6	Shafland & Pestrak (1982)
Family Poeciliidae							
Belonesox belizanus	24	1	DP[1]	9.7	0.6	11	Shafland & Pestrak (1982)

[1]In addition to death, LOE and cessation of feeding were reported.
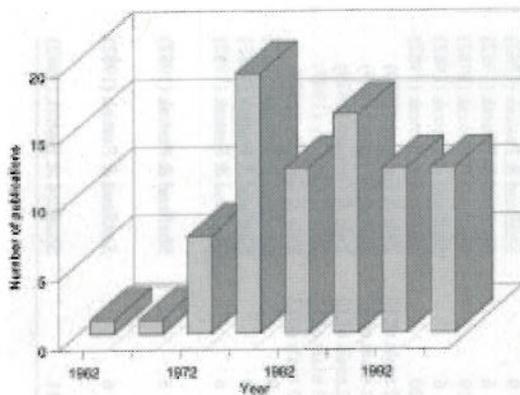
Figure 5. Number of publications reporting original dynamic temperature tolerance data for fishes by five-year intervals since 1960, n = 80.

each only a single temperature tolerance value at one acclimation temperature was reported for each species.

Coverage by family and species

In their Atlas of North American Fishes, Lee et al. (1980) list 56 families containing 775 species of fishes extant in North America. Mexico was excluded from their coverage. Dynamic temperature tolerance data were found for 19 or about 1/3 of the families and 116 species, 7 subspecies and 7 hybrids (130 fishes), or approximately 1/6 of North American freshwater fish species. For eight of the 19 families (Table 6) dynamic temperature tolerance data are published for only one or two species. Not surprisingly, for the most species – rich North American fish family, Cypinidae (minnows), we found the most dynamic temperature tolerance data: 37 species, 3 subspecies and 1 hybrid which represents about 1/5 of the total number of North American cyprinids. In five other families (Centrarchidae, Cichlidae, Cyprinodontidae, Poeciliidae and Salmonidae), temperature tolerance data have been published for 10 or more fishes.

Investigators have concentrated their research efforts on (i) a few key game fish species, e.g., largemouth bass, *Micropterus salmoides* (6 studies), bluegill, *Lepomis macrochirus* (6 studies), channel catfish, *Ictalurus punctatus* (5 studies), and rainbow trout, *Oncorhynchus mykiss* (6 studies); (ii) smaller fishes such as minnows (family Cyprinidae), in particular the red shiner, *Cyprinella lutrensis* (8 studies) and the

fathead minnow, *Pimephales promelas*, a United States Environmental Protection Agency recommended test species which has been the subject of 8 studies, (iii) the genera *Etheostoma* (10 studies) and *Gambusia* (7 studies), and (iv) fishes with large thermal tolerances, in particular the family Cyprinodontidae (10 studies). In contrast, we found no dynamic temperature tolerance data for fishes in some of the most primitive fish families, e.g., Petromyzontidae, Lepisosteidae, Amiidae and Acipenseridae. Similarly, published dynamic temperature data were not discovered for numerous game species including white bass, *Morone chysops*, white and black crappies, *Pomoxis annularis* and *P. nigromaculatus*, and yellow perch, *Perca flavescens*. Surprisingly, only a single CTmaximum exists for goldfish, *Carassius auratus*, which was the subject of the original ILT study of Fry et al. (1942) and, is the first species for which an ILT temperature tolerance polygon was developed.

Coverage by experimental method

This review summarizes 74 papers containing published CTmaxima for 108 fishes (96 species, 7 subspecies and 5 hybrids) representing 16 families and CTminima for 21 fishes (15 species, 3 subspecies and 3 hybrids) from 8 families (Tables 2, 3 and 6). Sixty-one papers reported only CTmaxima, 5 contained only CTminima and 7 papers gave both CTmaxima and CTminima (Table 7). The large disparity between the number of reported CTmaxima and CTminima can be explained by several observations. First, CTmaxima are easier to experimentally measure than CTminima. Difficulties arise in achieving a constant linear rate of temperature decrease as water temperatures approach 0°C and in identifying a clear-cut test endpoint as fish are cooled during CTminima determinations, mentioned by numerous investigators including Otto (1973), Beitinger & McCauley (1990) and Bennett & Judd (1992). Second, the ultimate lower temperature tolerance of most North American fishes approaches 0°C, whereas upper temperature tolerances are more interspecifically variable. Third, the prevailing perception is that high environmental temperatures are more likely to limit fishes than low temperatures. Nevertheless, CTminima are important since more fish kills in nature are caused by exposure to rapidly decreasing temperatures than rapidly increasing temperatures.

We found CLmaxima (Table 4) for 11 fishes (7 species, 2 subspecies and 2 hybrids) from 3 families

Table 6. Summary of dynamic temperature tolerance data of North American freshwater fishes. Values listed within the tables are the numbers of species, subspecies and hybrids, respectively, for each family.

Family	Temperature tolerance method				Total species, subspecies, hybrids
	CTmaxima	CTminima	CLmaxima	CLminima	
Atherinidae	2	0	0	0	2
Catostomidae	6	0	0	0	6
Centrarchidae	10, 2, 2	2	1, 2, 2	0, 2	14
Characidae	0	1	0	0	1
Cichlidae	1	1	0	11	12
Clariidae	0	0	0	1	1
Clupeidae	1	0	0	0	1
Cottidae	1, 1	0	0	0	2
Cyprinidae	37, 3, 1	4, 3	1	0	42
Cyprinodontidae	11	2	0	0	11
Esocidae	1, 0, 1	0	0	0	2
Gasterosteidae	1	0	0	0	1
Ictaluridae	4	1	0	0	4
Loricariidae	0	0	0	1	1
Percichthyidae	1, 0, 1	0	0	0	2
Precidae	7	0	0	0	7
Poeciliidae	4	3, 0, 3	0	3	10
Polyodontidae	1	0	0	0	1
Salmonidae	8, 1	1	5	0	10
Total families	16	8	3	5	19
Total species	96	15	7	14	116
Total subspecies	7	3	2	2	7
Total hybrids	5	3	2	0	7
Total fishes	108	21	11	16	130

Table 7. Number of publications containing original dynamic temperature tolerance data for fishes (species, subspecies and hybrids) by experimental methods and direction of temperature change, n = 80.

CTmaximum only	CTminimum only	Both	CLmaximum only	CLminimum only	Both	CTmaximum & CLmaximum
61	5	7	3	2	1	1

and CLminima (Table 5) for 16 fishes distributed among 5 families, reported in a total of 7 publications (Table 7). Fourteen of the 16 CLminima were measured by Shafland & Pestrak (1982) in species of the families Cichlidae, Clariidae, Poeciliidae and Loricariidae, exotics which have been introduced into the State of Florida.

Comparison of CTM and CLM

Although both the CT and CL methodologies expose fish to changes in temperature during tolerance trials, i.e., temperature dynamic methods (versus the ILT where test temperature are static), these two dynamic temperature tolerance methods differ in both endpoint and ΔT.

Slower temperature change rates (1 to $2°C\,d^{-1}$, Tables 4 and 5) and hence, longer exposure times, characteristic of the CLM may allow the temperature tolerance acclimation state of a fish to change during a trial. This approach may generate a better estimate of the ultimate upper and lower temperature tolerances of a species and may allow tolerance to be independent of the pretest acclimation temperature; however, it simultaneously allows more time for heat to exert its lethal effects at any particular temperature. The

former would be expected to increase, whereas the latter would be expected to decrease temperature tolerance limits. Comparison of CTM and CLM endpoints for a species would indicate which of the above competing processes predominates. Unfortunately, relatively few species have been tested by both methods. We found only five cases where both CT and CL methods were applied to the same species. The CTminimum of 9.4°C (Jenning 1991) and CLminimum of 10.3°C (Shafland & Pestrak 1982) for blackchin tilapia, *Tilapia melanotheron*, are similar especially when considering tilapia were acclimated to 21°C in the former and 25°C in the latter study. Although the lower lethal temperatures for the northern subspecies of largemouth bass, *Micropterus salmoides salmoides*, were measured both as CLminimum (Guest 1985) and CTminimum (Currie et al. 1998), the large difference in acclimation temperatures preclude direct comparisons of these data. A single CLmaximum (median = 35.5°C) for bluegill, *Lepomis macrochirus*, acclimated to 21.5°C by Hickman & Dewey (1973) fits nicely between CTmaxima of 31.5 and 37.5°C for bluegill acclimated to 16 and 24°C, respectively (Murphy et al. 1976). In contrast to the examples listed above, there are two cases where CTmaxima are larger than CLmaxima for the same species. Grande & Andersen (1991)

reported a CLmaximum of 26.3°C for rainbow trout, *Oncorhynchus mykiss*, acclimated to 17°C which is approximately 3°C less than CTmaxima reported by both Strange et al. (1993) and Currie et al. (1998) for rainbow trout acclimated to 15°C. Similar results were reported by Fields et al. (1987) which is the only study where both CTmaxima and CLmaxima were measured in a fish acclimated to the same temperature. The CTmaxima for the northern and Florida subspecies of largemouth bass acclimated to 32°C were 3.6 and 2.7°C higher, respectively, than CLmaxima for these subspecies. Although not conclusive, results of these latter studies suggest that any gain in temperature tolerance acclimation occurring during the slower temperature change rates of CLM trials is offset by the increased thermal stress owing to the increased amount of exposure time at each test temperature. When acclimated to the same temperature, we predict that the CTminimum would be lower than the CLminimum and the CTmaximum would exceed the CLmaximum for a species.

High temperature tolerance

Highest CTmaximum for each species in each of the 16 families (Figure 6) fall out as expected. The

Family	No. of fishes
Cottidae	2
Salmonidae	9
Cichlidae	1
Clupeidae	1
Polyodontidae	1
Atherinidae	2
Esocidae	2
Catostomidae	6
Percidae	7
Cyprinidae	41
Gasterosteidae	1
Centrarchidae	14
Ictaluridae	4
Percichthyidae	2
Poeciliidae	4
Cyprinodontidae	11
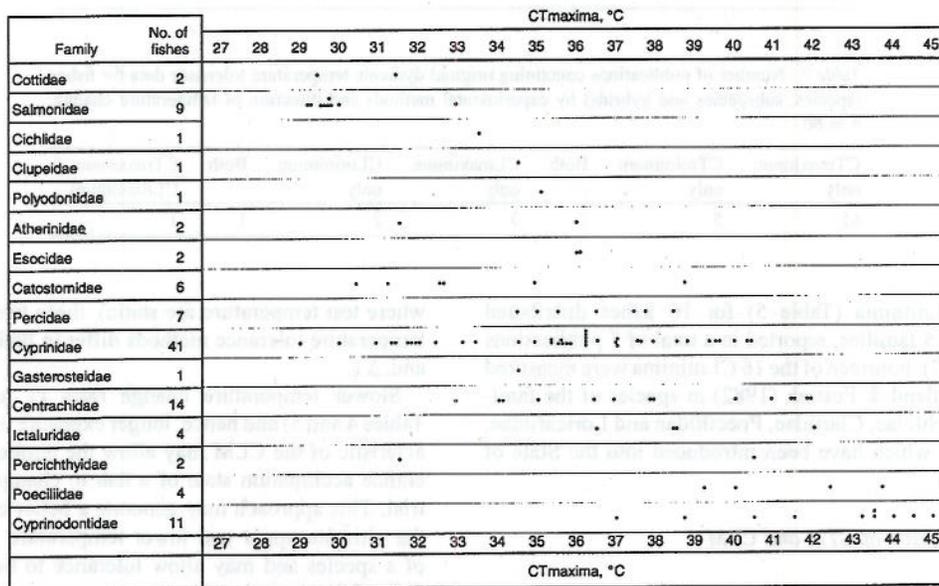
Figure 6. Highest reported mean or median CTmaximum (°C) for 108 fishes (species, subspecies, hybrids) grouped by family (from Table 4).

Salmonidae, along with the Cottidae, had the lowest tolerance of high temperatures and also had the least variation in highest CTmaxima. Eight of the nine salmonids have highest CTmaxima between 29.2 and 30.0°C. This finding suggests that upper temperature tolerance in this group is phylogentically conservative. These CTmaxima are about 4 to 5°C higher than reported ILUTs for these species which again demonstrate the overshoot inherent in the CTM. The highest tolerance of high temperatures occur in the families Poeciliidae and Cyprinodontidae.

Twenty-two fishes have a highest reported CTmaxima of 40°C or higher (Table 8). These fishes belong to six families: Centrarchidae, Cyprinidae, Ictaluridae, Percichthyidae, Poeciliidae and Cyprinodontidae. Nine of the 11 listed cyprinodontids are in this group, including the four highest CTmaxima reported. Three belonged to the genus *Cyprinodon*, the Balizian pupfish *C. artifons* 45.4°C (Heath et al. 1993), the sheepshead minnow *C. variegatus* 45.1°C (Bennett & Beitinger 1997) and the desert pupfish *C. macularius* 44.6°C (Lowe & Heath 1969); the fourth is the mummichog, *Fundulus heteroclitus* 44.1°C (Bulger 1984, Bulger &

Tremaine 1985). These extreme upper temperature tolerances apparently establish the upper biokinetic limit for aquatic ectothermic vertebrates (Brock 1985). The only cyprinodontid species to have sub 40°C CTmaxima are *Fundulus olilvaceus* and *F. sciadicus*; however, both species were tested only at an acclimation temperature of 26°C. If acclimated to higher temperatures, it is likely that both of these species would have CTmaxima exceeding 40°C.

In contrast, 9 species had highest reported CTmaxima less than 30°C. This group included one cottid, *Cottus cognatus gracilis*, one cyprinid, *Notropis cummingsae* which was tested at an acclimation temperature of only 8°C, and 7 of the 9 salmonid tested. Consequently, the highest reported CTmaxima of the majority of fishes (67 of 130 or 51%) extend between 30.0 and 39.9°C.

These data are limited by the acclimation temperatures used in these studies. Few studies have attempted to determine the highest CTmaximum for a species (for exceptions see Otto 1974, Bulger & Tremaine 1985, Heath et al. 1993, Bennett & Beitinger 1997). Recent research indicate that in CTmaximum trials

Table 8. Fish with reported highest CTmaximum °C equaling or exceeding 40°C.

Family	Species	Highest CTmaximum, °C	Reference
Cyprinodontidae	*Cyprinondon artifons*	45.4	Heath et al. (1993)
Cyprinodontidae	*Cyprinondon variegatus*	45.1	Bennett & Beitinger (1997)
Cyprinodontidae	*Cyprinondon macularius*	44.6	Lowe & Heath (1969)
Cyprinodontidae	*Fundulus heteroclitus*	44.1	Bulger (1984), Bulger & Tremaine (1985)
Poeciliidae	*Gambusia affinis*	43.7	Otto (1973)
Cyprinodontidae	*Floridichthys carpio*	43.6	Heath et al. (1993)
Cyprinodontidae	*Cyprinondon* sp.	43.6	Otto & Gerking (1973)
Cyprinodontidae	*Cyprinondon nevadensis*	43.3	Feldmuth et al. (1974)
Poeciliidae	*Gambusia yucatana*	42.4	Heath et al. (1993)
Ictaluridae	*Ictalurus punctatus*	42.1	Bennett et al. (1998)
Centrachidae	♂*M.s. salmoides* × ♀*M.s. floridans*	41.9	Fields et al. (1987)
Centrachidae	*Micropterus salmoides floridans*	41.8	Fields et al. (1987)
Centrachidae	♀*M.s. salmoides* × ♂*M.s. floridans*	41.6	Fields et al. (1987)
Cyprinodontidae	*Fundulus notatus*	41.6	Rutledge & Beitinger (1989)
Centrachidae	*Lepomis macrochirus*	41.4	Holland et al. (1974), Murphy et al. (1976)
Centrachidae	*M. salmoides salmoides*	40.9	Fields et al. (1987)
Percichthyidae	*Morone saxatilis* × *M. chrysops*	40.5	Woiwade & Adelman (1992)
Cyprinodontidae	*Cyprinodon elegans*	40.5	Gelbach et al. (1978)
Cyprinidae	*Pimephales promelas*	40.4	Richards & Beitinger (1995)
Cyprinidae	*Hypophthalmichthys nobilis* × *Ctenopharyngodon idella*	40.3	Bettoli et al. (1985)
Poeciliidae	*Gambusia holbrooki*	40.1	Meffe et al. (1995)
Cyprinidae	*Hybognatus placitus*	40.0	Matthews & Maness (1979)

loss of righting response (LLR) was exhibited before onset of muscle spasms in all 24 fish species tested by Lutterschmidt & Hutchison (1997a). The mean onset of muscle spasms occurred at temperatures 3.2°C higher than LLR. Use of higher acclimation temperatures, i.e., ≥ 30°C and onset of muscle spasms instead of loss of equilibrium as an endpoint would substantially increase the number of North American freshwater fish species with CTmaximum exceeding 40°C.

Low temperature tolerance

For reasons discussed earlier, data concerning tolerance of fishes to low temperatures are far more limited. Tables 3 and 5 contain CTminima and CLminima data for 21 and 16 fishes, respectively. Reported low temperature tolerances range from 0.0 (*Oncorhynchus mykiss*) to 12.9°C (*Astronotus acellatus*). Whereas the majority of published CTminima were measured in native North American fishes and are generally 5°C or less, 14 of the 16 reported CLminima were measured in exotic species found in Florida. CLminima in these fishes (11 Cichlids, and 1 each of the families Clariidae, Loricariidae and Poeciliidae) average 9.4±2.2 (SD)°C. Information concerning low temperature tolerance is necessary to estimate whether or not these species can overwinter in the United States and to predict possible distribution throughout North America.

Acclimation temperature

Among the myriad of biotic, chemical and physical factors influencing temperature tolerance (see Hutchison 1976), acclimation temperature is probably the most critical. In a majority of the fishes listed in Tables 5 through 7, only a single temperature tolerance value at one acclimation temperature was reported. Some of these are bioassay studies where controls yield a single CTmaximum or CTminimum for a species (Watenpaugh et al. 1985, Strange et al. 1993, Heath et al. 1993), whereas others survey a relatively large number of species at a single acclimation temperature (Kowalski et al. 1978, Smale & Rabeni 1995, Lutterschmidt & Hutchison 1997a).

In the few species that have been tested over a range of acclimation temperatures, a 10°C or more change is seen in both CTminima, e.g. *Cyprinodon variegatus*, *Lepomis gibbosus* and *Pygocentrus natteri* and CTmaxima, e.g., *Fundulus heteroclitus*, *Pimephales promelas* and *Gambusia affinis*. In studies in which three or more acclimation temperatures were

employed, regression models were either taken from the text or calculated from mean temperature tolerance values reported at each acclimation temperature. Both CTminima and CTmaxima are strongly linearly related to acclimation temperature for nearly all species. Linearity may be an outcome of the observation that CTmaxima and CTminima were measured mainly at acclimation temperatures that are within the middle of the temperature tolerance zone of each species, e.g., 10 to 30°C for warm-water species. If acclimated to temperatures either above or below this range, it is possible that the linear relationship between acclimation and CTM tolerance temperatures will not hold.

The effect of acclimation on temperature tolerance is reflected mathematically by the magnitude of the slopes relating these two variables. The slope reflects the change in temperature tolerance for each 1°C change in acclimation temperature. As acclimation temperature is increased, both CTmaxima and CTminima increase. The former represents a gain in heat tolerance and the latter, a loss of 'cold' tolerance. The pupfish, *Cyprinodon nevadensis*, appears to possess the most unusual relationship between acclimation and tolerance temperatures. It has the smallest slopes for both CTminima, 0.17, and CTmaxima, 0.13, of all species summarized. Although this cyprinodontid species possesses a wide tolerance of temperature, the magnitude of these slopes suggest that temperature tolerance is not strongly effected by acclimation temperature. Over an acclimation temperature range of 30°C, CTminima and CTmaxima of the desert pupfish change by only 3.9 and 5.1°C, respectively.

Although few species were acclimated to temperatures low enough to produce CTminima close to 0°C, we used CTminima-acclimation temperature regression models to estimate (extrapolate) an acclimation temperature which would be equivalent to a CTminimum of 0°C for six species (Table 9). This manipulation assumes that the ultimate CTminimum, i.e., absolute lowest temperature that could be tolerated, equals 0°C in these species. Estimated acclimation temperature for these six species ranged from 10.5 to 16.1°C. If these extrapolations hold, they suggest that these species have a large amount of protection against temperature decreases. For example, if subjected to CTM-like temperature decreases, the pumpkinseed sunfish, *Lepomis gibbosus*, would need to have a temperature tolerance acclimation state in excess of 13.2°C before an endpoint is reached.

Eliminating data for *Cyprinodon nevadensis* (already discussed) and the three species (*Etheostoma*

Table 9. Estimated (extrapolated) acclimation temperatures equivalent to CTminimum = 0°C from linear regression models relating acclimation temperature to CTminima (See Table 6).

Species	Range of acclimation temperature, °C	Estimated acclimation temperature where CTminimum = 0°C	Reference
Lepomis gibbosus	15–30	13.2	Becker et al. (1977)
Micropterus salmoides salmoides	20–30	15.6	Currie et al. (1998)
Gila bicolor mohavensis	18–30	10.5	McClanhan et al. (1986)
Cyprinodon nevadensis	15–30	11.3	Feldmuth et al. (1974)
Ictalurus punctatus	20–30	16.1	Currie et al. (1998)
Oncorhynchus mykiss	20–30	14.8	Currie et al. (1998)

blennoides, E. caeruleum and *E. fabellare*) measured only under field temperatures, yield surprisingly similar slopes relating CTmaxima and acclimation temperature for the remaining 20 species. Slopes for these species which represent 9 distinct families, range from 0.27 to 0.50 with a mean±SD of 0.41±0.07°C.

Although dynamic temperature data were found for 130 fishes, only a single dynamic, tolerance polygon has been published for a species, the sheepshead minnow, *Cyprinodon variegatus* (Bennett & Beitinger 1997). Over an acclimation range of 5 to 38°C, this eurythermal species has a CTM temperature tolerance polygon of 1470°C^2 which is 5% larger than the tolerance polygon measured by ILT methods for this species. With the above exception, no single study has measured both CTminima and CTmaxima over a wide enough range of acclimation temperatures to generate CTM tolerance polygons. However, enough data are available for at least a few species, e.g., largemouth bass, channel catfish, desert pupfish and rainbow trout, to creatively estimate CTM temperature tolerance polygons.

Summary

Studies of temperature tolerance of fishes have more than a 100 year history and have resulted in the evolution of two generally accepted techniques to quantify temperature tolerance of fishes: the incipient lethal temperature (ILT) and critical thermal method (CTM). Although the ILT and CTM are quantitatively expressed as a temperature, determined with fishes acclimated to known temperatures and involve both time and temperature as major test variables, these two methods do not quantify the same response. Both methods generate valuable information concerning temperature tolerance of fishes.

In the CTM approach, test fish are either heated or cooled at a constant linear rate from a pretest acclimation temperature until an obvious sublethal but near lethal, incapacitation occurs, usually either loss of equilibrium (LOE) or the onset of muscular spasms (OS). The water temperature at this endpoint is the CTmaximum or CTminimum. If fish at this point are quickly returned to their pretest acclimation temperature, 100% survival is expected. CTmaximum or CTminimum are usually summarized as the mean of a trial. The rate of temperature change during a trial needs to be constant, linear and fast enough to prevent tolerance from being gained during the trial and slow enough to allow the fish's body temperature to closely track water temperature. Empirical findings indicate a constant, linear temperature change of 0.3°C min^{-1} meets these criteria. Although some controversy exists concerning the most appropriate CTM endpoint, particularly OS versus LOE, we believe that the chosen endpoint, as long as it satisfies CTM endpoint criteria, should be selected by the investigator relative to the responses of the test species during temperature change exposures.

Acknowledgements

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