

A COMPARISON OF THERMAL POLYGONS FOR BRITISH FRESHWATER TELEOSTS

ALEX ELLIOTT

(*J. A. Elliott, 51312 Muirhead House, University of Stirling,
Stirling FK9 4LG, Scotland.*)

Introduction

Almost all fish are obligate poikilotherms (literally meaning "obliged to have many temperatures"), the few exceptions being the sharks of the family Lamnidae and some tunas of the family Scombridae. Temperature defines the lethal limits to life, controls the rate of growth, establishes the limits of metabolic rate within which a fish can respire and influences movements to new environmental conditions. It is the high specific heat of water, which efficiently buffers its aquatic inhabitants against the extremes of aerial conditions, that has chained the gill-respiring vertebrate to a poikilothermic life. Although the gills act as an active heat exchanger, they account for only 10-30% of the total heat exchange, the rest being conducted through the body wall. Fish possess little or no control over this heat exchange and therefore the body temperature of all freshwater teleosts is intrinsically linked to the ambient temperature of their surrounding environment. This association means that it is important to understand at what temperatures fish can no longer survive, i.e. the thermal limits of the species.

In 1942, the Canadian team of Fry, Brett and Clawson published the first comprehensive quantitative study on the thermal limits of a freshwater teleost, the goldfish *Carassius auratus*. Fry put forward a graphical way to demonstrate an individual species' thermal requirements by creating temperature polygons, a paradigm that will be discussed later. This initial study was repeated, using similar methods, for numerous North American fish, the work finally being compared in an excellent review by Brett (1956). In Britain, Fry's temperature polygons have been constructed by Cocking (1959) for the roach *Rutilus rutilus* and, in recent years, for the brown trout *Salmo trutta* (Elliott 1981), Atlantic salmon *Salmo salar* (Elliott 1991), Arctic charr *Salvelinus alpinus* (Baroudy & Elliott 1994), stone loach *Barbatula barbatula* (formerly *Noemacheilus barbatulus*) (Elliott et al. 1994) and the bullhead *Cottus gobio* (Elliott & Elliott 1995a). With the completion of these last few papers, it now seems an ideal moment to compare the results of this work on these British freshwater fish, with particular reference to the Fry temperature polygons which provide the most complete information on the thermal requirements of a fish species.

Upper and lower thermal limits

The types of behaviour that a fish exhibits at different temperatures can be classified into one of three groups: *resistance*, *tolerance* and *preference*. This review shall concern itself only with the former two types. Over the years, workers on thermal stress have devised many different methods to evaluate the extent of temperature tolerance and resistance and, out of these many methods, two types have emerged. The first method is that of slowly changing, at a constant rate, the temperature of the medium from the acclimation level until the animal first exhibits signs of stress, usually in the form of exaggerated swimming (Elliott 1981; Kilgour & McCauley 1986). This temperature is recorded as the incipient lethal temperature and represents the behavioural transition between tolerance and resistance. The experiment is often continued until restricted movements of the operculum are observed, this point being recorded as the lethal maximum or ultimate lethal temperature, as death would follow within 2 to 5 minutes of this observation. The fish are therefore removed before death occurs and recover rapidly when transferred to more suitable temperatures. In the second method, the fish are kept at an acclimation temperature as in the first method but are then transferred rapidly to a higher, or lower, constant temperature, the procedure being repeated until a critical value is reached (Fry 1947, 1967, 1971; Brett 1956; Cocking 1959).

Both methods have their critics as, for example, the first method has the extra variable of rate of temperature change and the second has the extra stress induced by handling and thermal shock. These factors must be considered when comparing values derived from either of the two methods, although attempts have been made to reconcile the different methods (Kilgour & McCauley 1986). The effect of the rate of temperature change on the lethal levels ascertained using the first method has been investigated for the stone loach (Elliott et al. 1994), bullhead (Elliott & Elliott 1995a), brown trout and salmon (Elliott & Elliott 1995b), using nine different rates from 0.5°C per 48 hours to 18°C per hour. For all four species, the highest rates of temperature change which gave the greatest level of precision (i.e. the lowest variability) were 1 and 2°C per hour, these being used in the later experiments.

Both methods acknowledge the importance of acclimation temperature in determining the lethal limits, i.e. fish held for an extended period at lower temperatures are more cold-tolerant and more heat-sensitive than fish held in warmer water. Therefore it is important, in order to obtain a complete picture, to measure the lethal limits of fish acclimated to a wide range of constant temperatures. The resulting diagram showing these limits was first proposed by Fry et al. (1942) and has now come to be known as a Fry thermal tolerance polygon (Fig. 1). As the latter is not easy to understand, an explanation is provided below.

The boundary between the zone of tolerance and that of resistance is defined by the inner polygon describing the incipient lethal level (Fig. 1). The rising

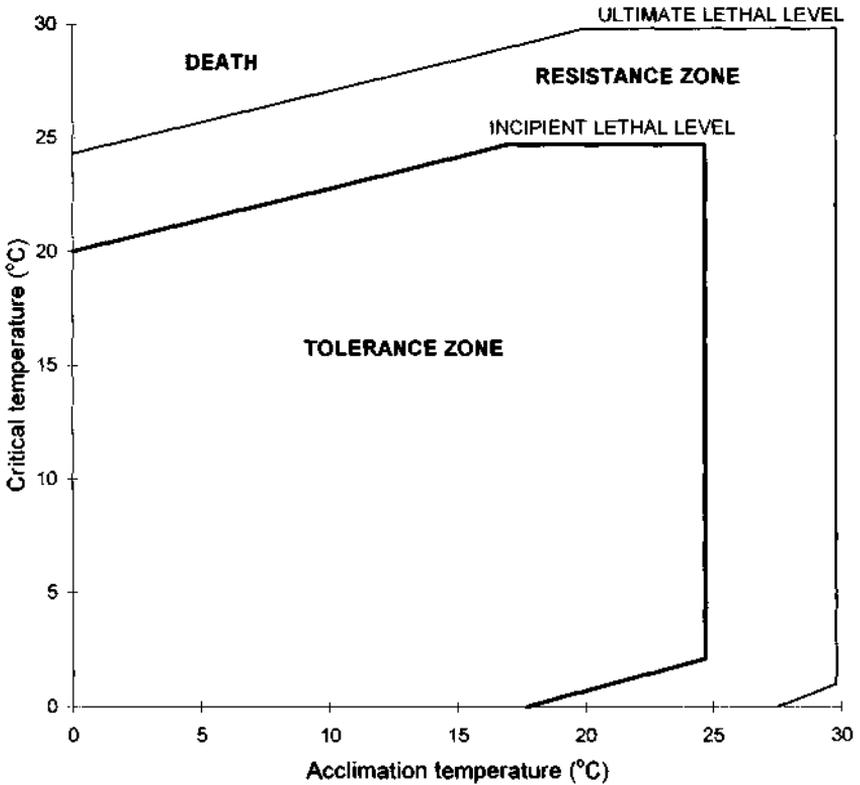


Fig. 1. Thermal tolerance diagram for brown trout *Salmo trutta*, illustrating the tolerance and resistance zone, and polygons of the incipient and ultimate lethal levels (after Elliott 1981).

sections for both the upper and lower temperature relationships of the boundary represent the regions where lethal temperature increases proportionally to increasing acclimation temperature. The horizontal or plateau portion of the line defines the temperature beyond which an increase in acclimation temperature fails to produce an increase in lethal temperature. The vertical line simply reaffirms this point as, clearly, fish by definition cannot survive at acclimation temperatures above the incipient lethal limit. The second (outer) polygon demarcates the ultimate lethal limit beyond which the fish cannot survive for even a short time (usually 10 minutes) and is not

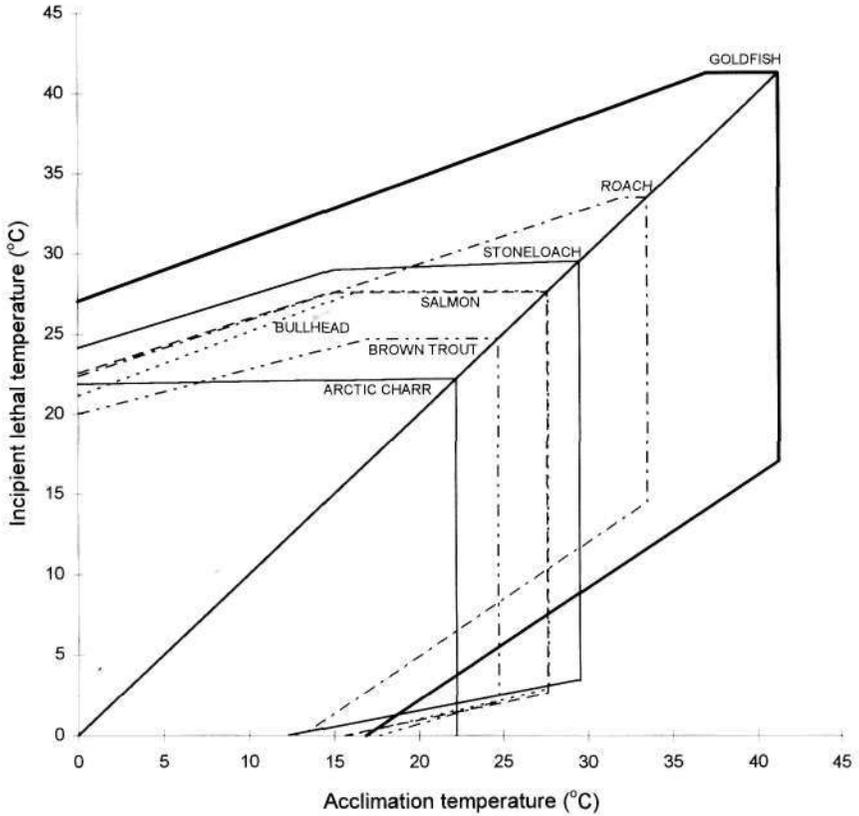


Fig. 2. Polygons of the incipient lethal levels for seven British freshwater species of fish: Arctic charr (Baroudy & Elliott 1994), brown trout (Elliott 1981), Atlantic salmon (Elliott 1991), bullhead (Elliott & Elliott 1995a), stone loach (Elliott et al. 1994), roach (Cocking 1959) and goldfish (Fry et al. 1942).

always given by experimentalists. Its ecological value is also questionable as it is difficult to foresee a natural situation where a fish would be suddenly subjected to such an extreme temperature for a short period, except by an accidental thermal discharge. Even then, the incipient and ultimate values are usually so close that it probably would not matter unless the temperature of the discharge was exactly within the two limits. For these reasons, the incipient lethal polygons are used in the next section to illustrate any differences between the thermal requirements of the freshwater species

considered here, particularly as the fish were subjected to the critical experimental temperature for a longer period (usually 7 days) and therefore the incipient lethal limit has greater ecological significance.

A comparison of incipient lethal polygons

The thermal tolerance polygons from various studies have been presented in the same figure (Fig. 2) in order to aid comparison. A simple index of thermal tolerance is the area enclosed by the incipient limits, expressed in units of $^{\circ}\text{C}^2$, and this is known for all seven teleosts included in Fig. 2. The Arctic charr, being a cold-water lake species in Britain, shows the least resistance to high temperatures with a maximum lethal limit of 22.7°C , but has the best resistance to cold temperatures (Baroudy & Elliott 1994). This was confirmed by experiments in sea water on older charr, giving an ultimate lower lethal temperature of -0.99°C ; values for other species were as follows: -0.81°C for *S. trutta* and -0.75°C for *S. salar* (Saunders 1986; Fletcher et al. 1988). Of course these temperatures would normally not occur in fresh water. This tolerance by charr to very low temperatures and a relatively low tolerance to high temperatures agrees well with their comparative geographical distribution and their low tolerance index of 461°C^2 . It should be noted that the Arctic charr appears to differ from the other species in that its response to temperature increase is not greatly influenced by the previous short-term thermal history in the range 0°C to 22.7°C , in stark contrast to the other teleosts, especially the goldfish.

The other two species of salmonids considered here are the brown trout and Atlantic salmon. The former has a maximum incipient value of 24.7°C and an index of 583°C^2 (Elliott 1981), and the latter has a value of 27.7°C and an index of 708°C^2 (Elliott 1991), clearly showing that, of the three salmonids, the salmon is the most tolerant at higher temperatures and over the greatest range. The bullhead, in the family Cottidae, is also a stream-dweller and has almost an identical polygon to the salmon, with a lethal limit of 27.6°C and an index of 701°C^2 (Elliott & Elliott 1995a), and the stone loach, in the family Cobitidae, has the greatest tolerance of the four stream-dwelling species, with a limit of 29.5°C and 782°C^2 (Elliott et al. 1994). The ecological significance of this may be that in times of drought, when stream water levels are low and what little water remains is found in pools, water temperatures may be quite high, and the stone loach will survive and suffer the least thermally induced stress. In British rivers the brown trout would be most susceptible, followed by salmon and bullhead. Of course, other factors such as the cessation of feeding have to be taken into account when making these generalisations and only a few studies have investigated this factor (Elliott 1981, 1991; Elliott et al. 1994; Elliott & Elliott 1995a). The roach (Cocking 1959) and goldfish (Fry et al. 1942), both cyprinids and predominantly found in lakes or slow-moving water, are the

most temperature-tolerant of the British freshwater fish studied to date, with incipient values of 35.5°C and 41.3°C, and tolerance indices of 770°C² and 1220°C², respectively. It should be noted that although the roach has a higher incipient lethal limit than the stone loach (Fig. 2), the latter has a greater tolerance area and therefore is more thermally tolerant. Despite this, it is interesting to note that the goldfish also had the highest incipient lethal temperature and thermal tolerance area of all the North American fish (23 in total) that Brett (1956) reviewed, and maybe this high tolerance is a relic from its oriental past. It is little wonder, therefore, that goldfish survive in little plastic bags at fairgrounds!

Conclusions

Despite the sparsity of detailed research into the thermal tolerance of British freshwater teleosts, some broad conclusions may be drawn. It would appear that the cyprinids are the most tolerant and the salmonids the least tolerant of the families studied. The Arctic charr is the most resistant to cold temperatures and the goldfish is the most tolerant to high temperatures. The stone loach is the most resistant of the stream-dwelling species, which may give it an advantage in times of drought. These are general statements, which take no account of the species' feeding habits at different temperatures or their tolerances during various life-stages from egg to adult. Very few workers have investigated all these factors and there is a need for a great deal more research in this neglected branch of ichthyology.

References

- Baroudy, E. & Elliott, J. M. (1994). The critical thermal limits for juvenile Arctic charr, *Salvelinus alpinus*. *Journal of Fish Biology*, 45, 1041-1053.
- Brett, J. R. (1956). Some principles in the thermal requirements of fishes. *Quarterly Review of Biology*, 31, 75-87.
- Cocking, A. W. (1959). The effects of high temperatures on roach (*Rutilus rutilus*). I. The effects of constant high temperatures. *Journal of Experimental Biology*, 36, 203-216.
- Elliott, J. M. (1981). Some aspects of thermal stress on freshwater teleosts. In *Stress and Fish* (ed. A. D. Pickering), pp. 209-245. Academic Press, London.
- Elliott, J. M. (1991) Tolerance and resistance to thermal stress in juvenile Atlantic salmon, *Salmo salar*. *Freshwater Biology*, 25, 61-70.
- Elliott, J. M., Elliott, J. A. & Allonby, J. D. (1994). The critical thermal limits for the stone loach, *Noemacheilus barbatulus*, from three populations in northwest England. *Freshwater Biology*, 32, 593-601.
- Elliott, J. M. & Elliott, J. A. (1995a). The critical thermal limits for the bullhead, *Cottus gobio*, from three populations in northwest England. *Freshwater Biology*, 33, 411-418.

- Elliott, J. M. & Elliott, J. A. (1995b). The effect of the rate of temperature increase on the critical thermal maximum for parr of Atlantic salmon, *Salmo salar*, and brown trout, *Salmo trutta*. *Journal of Fish Biology*, in press.
- Fletcher, G. L., Kao, M. H. & Dempson, J. B. (1988). Lethal freezing temperatures of Arctic charr and other salmonids in the presence of ice. *Aquaculture*, 71, 369-378.
- Fry, F. E. J. (1947). Effects of the environment on animal activity. *University of Toronto Studies in Biology Series 55, Publications of the Ontario Fisheries Research Laboratory*, 68, 5-62.
- Fry, F. E. J. (1967). Responses of vertebrate poikilotherms to temperature. *Thermobiology* (ed. A. H. Rose), pp. 375-409. Academic Press, London.
- Fry, F. E. J. (1971). The effect of environmental factors on the physiology of fish. *Fish Physiology, Vol. VI* (eds W. S. Hoar & D. J. Randall), pp. 1-98. Academic Press, London.
- Fry, F. E. J., Brett, J. R. & Clawson, G. H. (1942). Lethal limits of temperature for young goldfish. *Revue Canadienne de Biologie*, 1, 50-56.
- Kilgour, D. M. & McCauley, R. W. (1986). Reconciling the two methods of measuring upper lethal temperatures in fishes. *Environmental Biology of Fishes*, 17, 281-290.
- Saunders, R. L. (1986). The thermal biology of Atlantic salmon: influence of temperature on salmon culture with particular reference to constraints imposed by low temperature. *Report of the Institute of Freshwater Research, Drottningholm*, 63, 77-90.