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Tolerance and resistance to thermal stress in juvenile Atlantic salmon, *Salmo salar*

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SUMMARY. 1. The chief objective was to construct a thermal tolerance polygon for juvenile Atlantic salmon, *Salmo salar* L., using fish from four groups and two populations: two age groups from one population (0+, 1+ parr from River Leven), two size groups from the other population (slow and fast growing 1+ parr from River Lune).

2. Fish were acclimated to constant temperatures of 5, 10, 15, 20, 25 and 27°C; then the temperature was raised or lowered at 1°C h^{-1} to determine the upper and lower limits for feeding and survival over 10 min, 100 min, 1000 min and 7 days. As they were not significantly different between the four groups of fish, values at each acclimation temperature were pooled to provide arithmetic means (with SE) for the thermal tolerance polygon.

3. Incipient lethal levels (survival over 7 days) defined a tolerance zone within which salmon lived for a considerable time; upper mean incipient values increased with increasing acclimation temperature to reach a maximum of 27.8±0.2°C, lower mean incipient values were below 0°C and were therefore undetermined at acclimation temperatures <20°C but increased at higher acclimation temperatures to 2.2±0.4°C. Resistance to thermal stress outside the tolerance zone was a function of time; the ultimate lethal level (survival for 10 min) increased with acclimation temperature to a maximum of 33°C whilst the minimum value remained close to 0°C. Temperature limits for feeding increased slightly with acclimation temperature to upper and lower mean values of 22.5±0.3°C and 7.0±0.3°C.

4. In spite of different methodologies, values in the present investigation are similar to those obtained in previous, less comprehensive studies in the laboratory. They also agree with field observations on the temperature limits for feeding and survival. Thermal tolerance polygons are now available for eight species of salmonids and show that the highest temperature limits for feeding and survival are those recorded for juvenile Atlantic salmon.

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Introduction

F. E. J. Fry and his co-workers pioneered the use of thermal tolerance polygons to summarize the temperature limits for fish (see reviews by Fry, 1947, 1967, 1971; Brett, 1956, 1970; Elliott, 1981, 1982). Such polygons provide a useful method for comparisons between species but, unfortunately, the detailed information required to construct such a polygon is lacking for most species. Amongst the salmonids, thermal tolerance polygons are now available for pink, chum, sockeye, coho and chinook salmon (*Oncorhynchus gorbuscha*) (Walbaum), *O. keta* (Walbaum), *O. nerka* (Walbaum), *O. kisutch* (Walbaum), *O. tshawytscha* (Walbaum)) (Brett, 1952, 1956), for American brook trout (*Salvelinus fontinalis* (Mitchill)) (Fry, Hart & Walker, 1946), and for brown trout (*Salmo trutta* L.) (Elliott, 1981). One surprising omission is the Atlantic salmon (*Salmo salar* L.) and, therefore, the chief purpose of the present investigation is to construct a thermal tolerance polygon for juveniles of this species.

Some intraspecific comparisons are also feasible because the young salmon used in the experiments were from two populations (Rivers Leven and Lune), from different age-groups (0+ and 1+ parr) for the Leven population, and from slow and fast-growing groups of 1+ parr for the Lune population. Values obtained in the present investigation are also compared with those obtained in previous, less extensive laboratory experiments and with those observed directly in the field.

Materials and Methods

Salmon were reared from freshly fertilized eggs taken from fish on their spawning migration in the River Leven in South Cumbria and the River Lune in North Lancashire. Eggs were incubated and young fish reared in a hatchery on the shore of Windermere (for methods, see Pickering, Griffiths & Pottinger, 1987; Pickering & Pottinger, 1988). Experiments with Leven salmon were performed in autumn on underyearling fish (0+ parr with a mean length of 5 cm and mean live weight of 1.5 g), and in spring on 1-year-olds (1+ parr with a mean length of 10 cm and mean weight of 11 g). Experiments with Lune salmon were performed in spring on 1-year-olds (1+ parr) that were either slow-growing parr (mean length of 6.0 cm, mean live weight of 1.9 g) or fast-growing parr (mean length of 10.2 cm, mean weight of 11.0 g). The slow-growers were probably salmon that would remain in fresh water for at least 2 years before smoltifying, whilst the fast-growers were probably fish that would smoltify at 1 year old (see review by Thorpe, 1989).

The experiments with Leven salmon were performed in constant-temperature tanks described in detail by Swift (1961). Each tank contained about 100 l of water that was stirred and aerated by compressed air (oxygen concentration in water >85% saturation) and maintained within ±0.1–0.2°C of a constant temperature. The tanks were covered with transparent polyethylene so that there was natural illumination with a light intensity at the water surface of *c.* 100 lux during the day. Experiments with Lune salmon were performed in similar tanks except that water of a constant temperature circulated through all the tanks.

Young salmon of similar size were acclimated to the same constant temperature (either 5, 10, 15, 20, 25 or 27°C) for 2 weeks with one fish in each tank. Water temperature was then raised at about 1°C h^{-1} to a final temperature of either 20, 22, 24, 26, 28, 30, 32 or 34°C. An additional final temperature of 36°C was used for acclimation temperatures of 25°C and 27°C. The rate of temperature increase was similar to mean rates of change in upland salmonid streams but rates as high as 2.2–2.5°C h^{-1} occasionally occur (Macan, 1958; Crisp & Le Cren, 1970; J. M. Elliott, unpublished). Two fish were kept at the acclimation temperature throughout the experiment and served as controls. Freshly killed *Gammarus pulex* L. were fed to the fish.

The survival and feeding rates of the young salmon were recorded every 10 min for the first 100 min, every 100 min for the period 100–1000 min and every 1000 min for the period 1000–10,080 min (7 days). Records were kept of the highest temperature for normal feeding and survival over 10 min, 100 min, 1000 min and 7 days at each acclimation temperature. The experiment was repeated with different fish to provide five (Leven fish) or three (Lune fish) replicates for each size group of salmon at each acclimation temperature.

A similar experimental procedure was used to determine lower temperature limits for feeding and survival. The acclimation temperatures were 5, 10, 15, 20 and 25°C, and the temperature was lowered at about 1°C h^{-1} to final values of 0, 2, 4, 6, 8, 10°C (not 6, 8, 10°C for acclimation temperature of 5°C). It was difficult to maintain

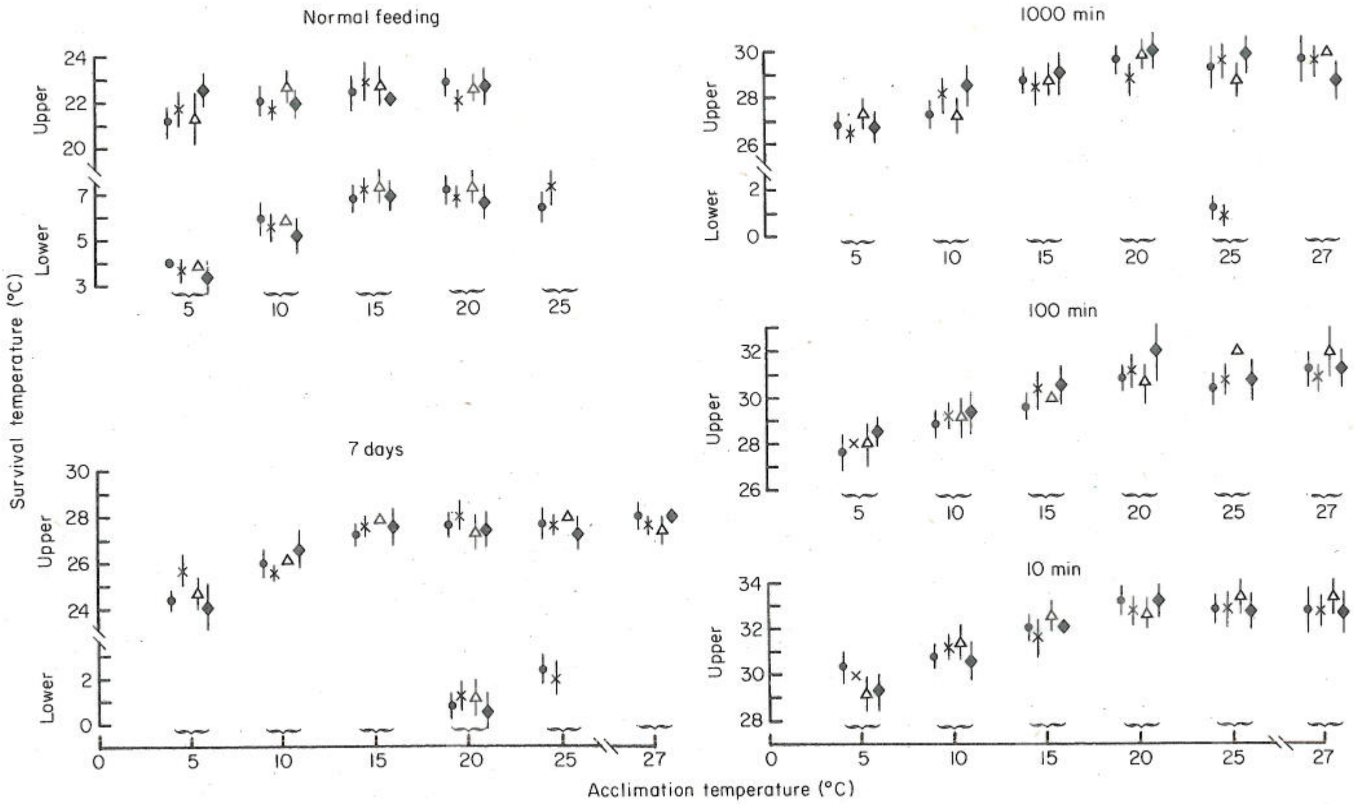

FIG. 1. Comparison of highest and lowest mean temperatures (with SE indicated by vertical bar) for normal feeding of juvenile salmon and their survival over 7 days, 1000 min, 100 min and 10 min; the individual means at each acclimation temperature are for 0+ parr (●) and 1+ parr (x) from River Leven, slow-growing 1+ parr (△) and fast-growing 1+ parr (◆) from River Lune.

the temperature at 2°C or less and iced water had to be added to maintain a temperature near 0°C.

Results

When the young salmon were affected by increasing temperature, their stress response progressed through three phases. The first external indications of abnormal behaviour were a reluctance to feed, sudden bursts of activity with frequent collisions with the tank sides, rolling and pitching, defecation and rapid ventilatory movements. In the second phase, the fish became quiescent with short bursts of weak swimming, it changed colour rapidly and increased its ventilatory movements. Movements were restricted in the third phase to the opercula, pectoral fins and eyes, and finally ceased with death. When fish were transferred to cooler well-oxygenated water, they recovered from the first and second phases but never from phase three. The latter phase was therefore avoided whenever possible to ensure that few fish died during the experiments.

Thermal stress due to decreasing temperature produced a cessation of feeding and sudden bursts of activity followed by a state of coma. Once a fish was in the latter state, it was transferred to slightly warmer water and usually recovered. The stress response was more rapid with decreasing than with increasing temperature.

The highest and lowest temperatures for feeding and survival over 7 days, 1000 min, 100 min and 10 min were expressed as mean values (with SE). As these were not significantly different ($P>0.05$ for all paired *t*-tests) for the four size groups of salmon at each acclimation temperature (Fig. 1), it was concluded that thermal tolerance and resistance did not vary significantly between juvenile salmon from the two populations, between 0+ and 1+ parr from the Leven, and between slow and fast-growing 1+ parr from the Lune. The sixteen values at each acclimation temperature were therefore

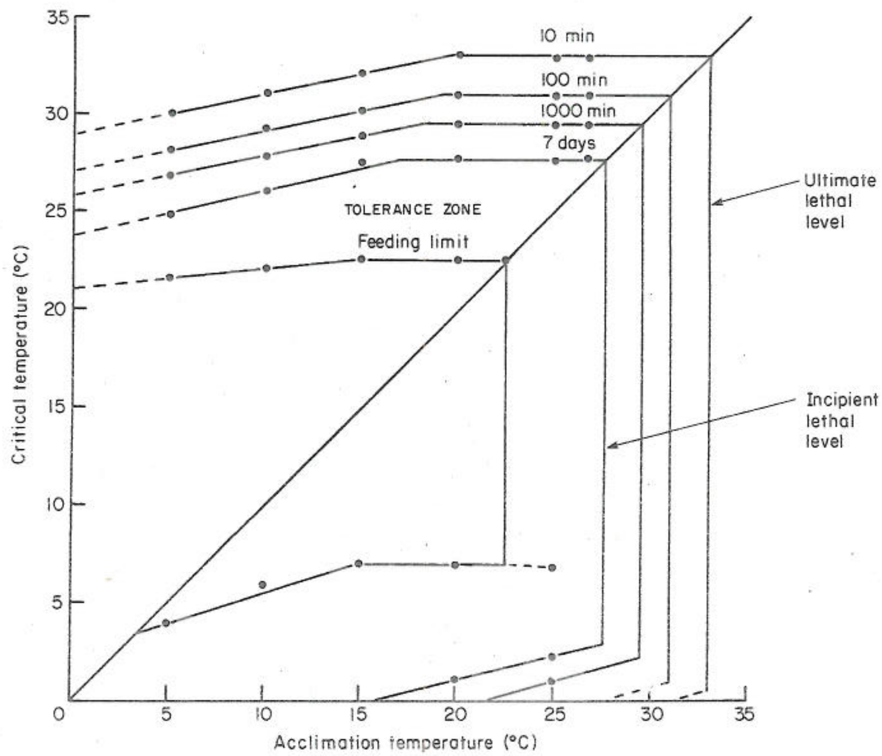

FIG. 2. Thermal tolerance polygon for juvenile Atlantic salmon, showing the feeding zone, tolerance zone, incipient lethal level (survival over 7 days), ultimate lethal level (survival over 10 min) and intermediate levels (survival over 1000 min, 100 min); each point is the arithmetic mean of sixteen values (see Table 1).

combined to provide overall arithmetic means with standard errors (Table 1) and these were used to construct a thermal tolerance polygon (Fig. 2).

Acclimation temperatures markedly affected the mean values for survival (Fig. 2, Table 1). Some salmon that survived for 7 days were kept at the same temperature for up to 1 month and it was therefore concluded that mean temperatures for survival over 7 days were the 'incipient lethal levels' that define the temperature tolerance zone within which the fish can live for a considerable time (all definitions follow the terminology of Fry, 1947, 1971). Upper incipient lethal temperatures increased linearly with increasing acclimation temperature to reach a maximum value of 27.8±0.2°C (Fig. 2, Table 1). The lower incipient lethal temperature could not be determined at acclimation temperatures below 20°C because it was obviously below the freezing point of water. It increased slightly to 1.0±0.3°C and 2.2.±0.4°C at higher acclimation temperatures of 20°C and 25°C, respectively.

Upper mean values for survival over 10 min, 100 min and 1000 min followed a pattern similar to that for the incipient lethal temperatures and were within the 'zone of thermal resistance' outside the tolerance zone and between the incipient and ultimate lethal temperatures (Fig. 2). The latter was estimated by the temperature for survival over 10 min and reached a maximum value of 33°C. The lower ultimate lethal temperature was less than 0°C because all fish survived for at least 10 min and 100 min at 0°C.

The salmon did not feed at acclimation temperatures of 25°C and 27°C. The upper mean temperature for feeding was 22.5±0.3°C, and the lower limit increased from 3.8±0.2°C at an acclimation temperature of 5°C to 7.0±0.3°C at acclimation temperatures of 15°C or higher (Fig. 2). Although fish did not feed initially at 25°C, they commenced feeding as the temperature was reduced to about 10°C and then ceased feeding again between 6 and 8°C. As cessation of feeding will have an important effect on the growth and ultimately the survival of the fish, it must be considered a thermal stress response within the tolerance zone.

The thermal tolerance polygon (Fig. 2) provides a succinct summary of the results of this investigation. As no significant differences could be found between fish from different populations, different age groups and different size groups, the upper and lower temperature limits for feeding and survival are probably applicable to Atlantic salmon parr from other populations.

Discussion

Comparison with previous laboratory studies on thermal tolerance

There are two broad categories of experimental methods used to investigate thermal tolerance in fish. In the first group, a critical thermal maximum is determined by raising the temperature at a constant rate from the acclimation level, then recording the temperature at which the fish first exhibits signs of stress before entering the zone of thermal resistance, and finally recording the lethal maximum at which death occurs. In the second group, the fish are kept at an acclimation temperature and then abruptly transferred to a higher constant temperature, this process being repeated until a critical higher temperature is found. Both groups have their supporters and critics (see Fry, 1947, 1967, 1971; Hutchison, 1976; Becker & Genoway, 1979; Elliott, 1981), and a reconciliation of the two methods is provided by Kilgour & McCauley (1986).

Acclimation temperature is a common variable to both groups, but the effects of rate of change in temperature are included in the first but not the second group. Methods in the second group also have the disadvantage that the fish are subjected to handling stress when they are transferred from the acclimation temperature to the final temperature. The salmon in the present investigation were not subject to the additional stresses of handling and food deprivation because preliminary experiments showed that the young salmon refused to feed for 2–6 days after handling. Differences in experimental technique must therefore be taken into consideration when making comparisons with previous studies.

Four previous studies provide data that can be compared with those for upper temperature limits in the present study (Table 1, note that acclimation temperatures are given in parentheses where they differ slightly from those used in the present study). Bishai (1960) kept salmon alevins at 6°C and then slowly raised the water temperature to critical values that were only slightly lower than those in the present study (Table 1a). Alevins were also acclimated at 10°C and 20°C, then abruptly transferred to higher temperatures to obtain a critical temperature of 23°C that was well below those in the present study, probably because of different experimental techniques (see above).

Using methods similar to those of the present study, Spaas (1960) acclimated salmon alevins, 0+ parr and 1+ parr to 'room temperature' (15–20°C?), then slowly increased the temperature to obtain the lethal values. These are similar to those in the present study (Table 1b) but suggest a slight increase in upper temperature limits with the age of the fish, a conclusion that was not supported for 0+ and 1+ parr in the present study. It is still possible, however, that alevins may have a lower temperature threshold than parr.

Lethal temperatures for salmon smolts in the laboratory (Alabaster, 1967) were lower than those for parr in the present study (Table 1c), perhaps because there are differences in the thermal tolerance of parr and smolts, or because the smolts were suddenly transferred to the test tank at the higher temperature. Finally, values obtained for salmon parr (Garside, 1973) were very similar to those in the present study (Table 1d), even though the fish in the earlier study were subjected to a sudden increase in temperature. It is therefore concluded that, in spite of the problems of different methodologies, values for Atlantic salmon parr in the present investigation are generally similar to those obtained in previous, less comprehensive studies.

As mentioned in the introduction, thermal tolerance polygons provide not only a succinct summary of the temperature requirements of a species, but also a useful method of comparison between species. This is well illustrated by comparing the thermal tolerance of Atlantic salmon parr with that of brown trout and American brook trout (Fig. 3). The temperature tolerance of young salmon is clearly greater than that of the other species with upper temperature limits about 3°C higher than those for brown trout. A useful index of thermal tolerance is provided by the area of the tolerance zone, usually expressed as °C squared. The value of 708°C^2 for young Atlantic salmon is much higher than that recorded for other salmonid species; values being 625°C^2 for *Salvelinus fontinalis* (Fry *et al.*, 1946), 583°C^2 for *Salmo trutta*, (Elliott, 1981) and 450–529°C^2 for five *Oncorhynchus* spp. (Brett, 1952, 1956). Therefore, the highest known temperature limits for feeding and survival in the Family Salmonidae are those recorded for Atlantic salmon parr.

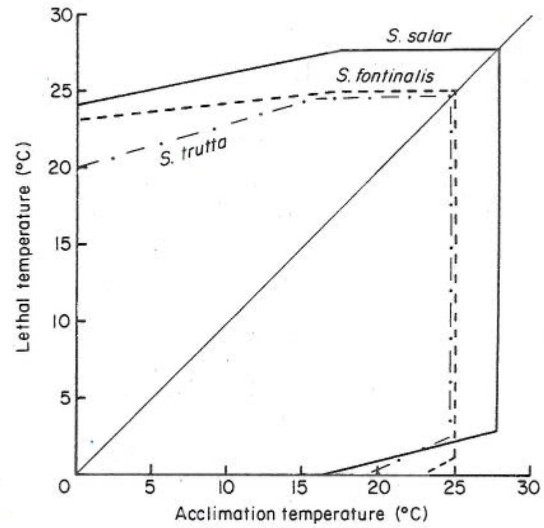

FIG. 3. Comparison of thermal tolerance polygons (only for incipient lethal level) for brown trout, *Salmo trutta* (Elliott, 1981), American brook trout, *Salvelinus fontinalis* (Fry *et al.*, 1946) and Atlantic salmon parr, *Salmo salar* (present study).

Temperature requirements for Atlantic salmon in the field

Little is known about the upper temperature limits for survival of Atlantic salmon in the field. Returning adults migrated through the Thames estuary during August when water temperatures were never lower than 19°C and often exceeded 22°C with occasional values over 25°C (Alabaster & Gough, 1986). Huntsman (1942) found that freshly run grilse in a Canadian river died at 29.5–30.5°C whilst parr died at higher temperatures of 32.9–33.8°C. The latter values are similar to those of the present study in which the ultimate lethal level for salmon parr was 30–33°C and the incipient lethal level was 25–28°C, both levels being about 3°C higher than those of 26–30°C and 22–25°C for brown trout (Elliott, 1981).

More is known about the lower temperature limits for feeding and growth in the field. Allen

(1940, 1941) found that young Atlantic salmon in the Rivers Eden (north-west England) and Thurso (north Scotland) reduced or stopped feeding below 7°C, and he later concluded (Allen, 1969) that juvenile salmon growth was negligible below 7°C. Young salmon in a Scottish stream remained inactive and concealed at temperatures below 6–7°C (Gardiner & Geddes, 1980), but other workers conclude that inactivity occurs below 9°C (Gibson, 1978; Rimmer, Paim & Saunders, 1983). The lower threshold for growth has been given as 7°C (Symons, 1979; Evans, Rice & Chadwick, 1985), 6°C (Power, 1969), 5.6°C (Lee & Power, 1976) and 6.3–7.4°C (Jensen & Johnsen, 1986; Jensen, Johnsen & Saskgard, 1989). An even lower temperature of 0.9°C for feeding has been reported for juveniles in a hatchery (Higgins & Talbot, 1985).

The present investigation has shown that the lower temperature for feeding is usually 7°C but decreases with acclimation temperature. As non-feeding salmon parr will not grow, these values are probably also the lower limits for growth. The value of 7°C agrees with most of the field observations and the slightly lower values in some field studies could be explained by lower acclimation temperatures, as demonstrated in the present study. The lower temperature limits are therefore not constant but decrease with decreasing acclimation temperature from a maximum value of 7°C to a minimum of 4°C. These values are about 3°C higher than the corresponding values for brown trout (Elliott, 1981).

Little is known about the optimum temperatures for growth in young Atlantic salmon in the field, but laboratory studies indicate that they are in the range 16–19°C (e.g. Siginevich, 1967; Dwyer & Piper, 1987; Wankowski & Thorpe, 1979; Peterson & Martin-Robichaud, 1989). This is higher than the optimum range of 13–14°C for brown trout (Elliott, 1975), indicating once again that the temperature requirements for Atlantic salmon are at least 3°C higher than those for brown trout.

The rather limited field data support the general conclusion that amongst the salmonids, Atlantic salmon parr have the highest temperature requirements for survival, feeding and growth. Perhaps the most striking contrast is the 3°C difference between salmon and brown trout because these species are often sympatric in streams and rivers. Brown trout will be less affected by low temperatures because they cease feeding in the range 0–4°C whereas salmon cease feeding in the range 0–7°C depending upon the acclimation temperature. In contrast, higher temperatures will favour Atlantic salmon because they do not cease feeding until 21.6–22.5°C, whereas brown trout cease feeding at about 19°C (Elliott, 1981). Although the lower limits for survival are usually below 0°C for both species, thermal stress commences at a higher temperature for salmon (25–28°C) than for brown trout (22–25°C depending upon acclimation temperature).

These differences indicate that small changes in water temperature due to human activities (e.g. river regulation, afforestation, climate change) could favour one species at the expense of the other. The results of the present investigation on salmon and the previous study on trout therefore have important implications for the conservation and management of both species.

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