

# using science to create a better place

## The thermal biology of brown trout and Atlantic salmon

Science Report

The Environment Agency is the leading public body protecting and improving the environment in England and Wales.

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# Science at the Environment Agency

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- **Delivering information, advice, tools and techniques**, by making appropriate products available to our policy and operations staff.



Steve Killeen

**Head of Science**

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# 1 Introduction

“Among gill-respiring vertebrates there is no escape from environmental temperature”.

Brett J R (1956) *Some principles of the thermal requirements of fishes.*

## 1.1 Background

The impetus for this report comes from an earlier study that looked at anthropogenic influences on the temperature of water along the Hampshire Avon (Solomon 2005). This earlier work attempted to link aspects of river temperature regime with the fortunes of salmon at different stages of their life cycle. A lack of readily-accessible information on the thermal biology of salmonids was noted, and a review was recommended. The increasing awareness of, and concern over, the impacts of climate change on the distribution and well-being of native biota have also increased the need for such a review.

Fish have very little control over their body temperature. If the temperature of their immediate environment is uncomfortable, unsuitable or even harmful, they may be able to migrate or seek thermal refuges locally. However, in general terms, water temperature has a fundamental impact upon the distribution, migration, survival, physiology, feeding, growth, reproduction, ecology and behaviour of all fish species.

It is clear, therefore, that any change in a water body's temperature regime is likely to have an effect on its fish populations, although the impact may be much more subtle than an increase in the frequency of directly lethal conditions: *“it is interesting to note that speckled trout are not usually found at temperatures exceeding 19°C, which is the upper limit of their preferred range, although considerably below the upper lethal level.”* (Brett 1956).

This project summarises what is already known about the effect of temperature on salmonids native to the streams and rivers of England and Wales. This work is important in our attempts to understand the impact of climate change upon stocks of salmonids in England and Wales.

The project covers Atlantic salmon (*Salmo salar*) and the brown and sea trout (*Salmo trutta*) at various stages of their life history. Reference is also made to related species from North America and elsewhere, where appropriate.

The majority of observations on the effect of temperature on salmonids come from carefully-controlled laboratory or hatchery experiments where all other variables except temperature are kept constant so that the direct effect of temperature changes can be examined. These are valuable observations and are reviewed here. However, in practice, and especially at high temperatures, other associated factors may have a major effect, such as lowered dissolved oxygen, reduced streamflow or interactions with a predator or pathogen.

Some field observations do exist and these are considered most carefully within this report to assess what they can add to the laboratory results. Wherever possible, field observations are discussed in the context of associated conditions that the fish are likely to be encountering.

It is possible that some aspects of thermal biology may vary between populations of the same species. Care is taken in this report to give details of the origin of the fish used in experimental studies, wherever this information is available from the original publication.

## 1.2 Life histories and terminology

### 1.2.1 Salmon

The length and timing of each stage in the life history of salmonids varies with latitude and their opportunity for growth. The ranges discussed below are those that occur in England and Wales.

Salmon and trout spawn in the late autumn and winter. The eggs are laid in depressions in riverbed gravel which are created by the female fish energetically flapping her tail while swimming on her side. After the eggs are laid and fertilised the female covers them with more gravel from upstream; the whole gravel spawning structure is called a redd.

The eggs are around 5 mm in diameter and the rate of the embryo development is temperature dependent. The eggs hatch in the spring, and the emerging young fish, called alevins, live for some time on their yolk sac. After a few more weeks they emerge from the gravel and start feeding, dispersing from the redd area. For the next few months the young fish are termed fry, and later, parr. The exact distinction between fry and parr is vague and varies between areas; in Scotland the fish are considered to be fry until about a year after they hatch, whereas in the southern England, where growth is faster, the fry stage is deemed to last only a few months.

After a duration of one to three (or sometimes more) years in fresh water, salmon parr develop into the smolt stage and migrate to sea, generally in the spring (March to early June in England and Wales). They return to the river to spawn after one to four years in the sea. Those returning after just one year are termed grilse or one sea-winter fish (1 SW), and enter the river from June onwards. Older fish (2 SW, 3 SW etc) may enter the river during any season. Those doing so before about June are termed spring salmon, those doing so in June to August summer salmon, and later fish are autumn salmon.

The adult salmon do not feed in fresh water and thus may fast for many months before spawning. The time of spawning ranges from November to February, varying with temperature, so that the resultant fry eventually emerge from the gravel at the appropriate time in the spring; fish in the north and those spawning at high altitudes spawn earlier than those in the south and at low altitudes. Most salmon die after spawning, though some females (perhaps 5 per cent) survive to return to sea and return for a second time.

### 1.2.2 Trout

Trout have a more varied life cycle. Brown trout do not leave the river, but may redistribute widely within fresh water. Sea trout develop into smolts and migrate to sea in a similar manner to salmon, but may return to spawn within a few months or after an absence of between one and three years. Once they return to spawn for the first time they continue to do so each year; survival is quite high (typically 30 per cent or more) and large fish may have spawned several times.

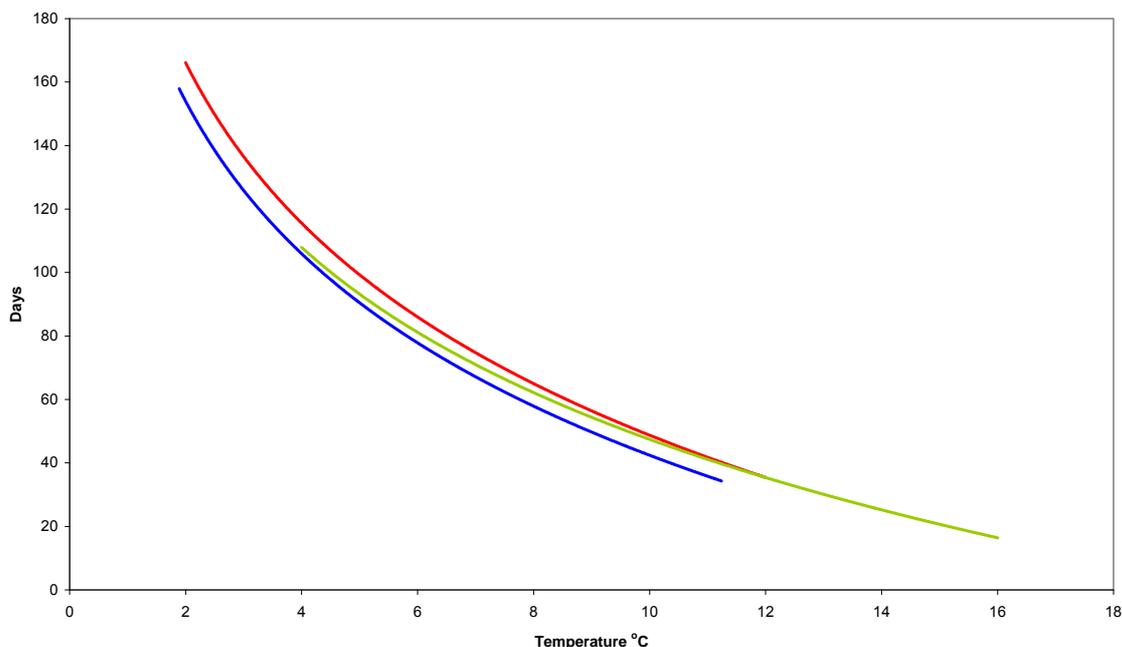
## 2 Eggs from spawning to hatching

### 2.1 Incubation period

As early as 1859 Stephen Ainsworth produced a table of how the hatching time of trout was dependent upon the temperature of the water (Embody 1934). It is widely believed that the time between spawning and hatching of eggs for all salmonids is temperature-dependent, and that local stocks are adapted to spawn at a particular time so that the fry start to feed under appropriate conditions in the spring.

Fish-farmers use the concept of “degree-days”, based upon observations over a range of water temperatures, to calculate incubation times. This approach was reported as early as 1870 (Embody 1934). Although the degree-day concept provides a useful rule of thumb, especially where temperatures are changing during the incubation period, the true relationship between temperature and incubation time is more complex than this simple rule suggests. Gunnes (1979), for example, noted that the total number of degree-days to hatching in Atlantic salmon was significantly less at 12°C than at 8 or 10°C; these eggs were derived from a “single Norwegian strain”.

Embody (1934) measured the duration of incubation from fertilization of the eggs to hatching (median time, i.e. for 50 per cent hatch) in four species of trout, including brown trout. The results for brown trout are shown in Figure 2.1. The origin of the fish was not stated. Jungwirth and Winkler (1984) undertook a similar investigation on three salmonids (including brown trout) and grayling; again the results for brown trout are shown in Figure 2.1. The eggs were derived from a wild stock in Austria.



**Figure 2.1. Relationship between incubation temperature and the duration of incubation in brown trout as determined by Embod (1934, blue line) and Jungwirth and Winkler (1984, green line) and for Atlantic salmon by Kane (1988, red line)**

The authors provided the following formula:

$$Y = 746 / (X - 0.5323)^{1.2233} \quad Y = \text{days to median hatch, } X = \text{temperature.}$$

The relationship between temperature and time to first feeding for Atlantic salmon was investigated by Kane (1988) but he also recorded the time it took for 50 per cent of the eggs to hatch. The relationship is included in Figure 2.1. Kane gave the formula:

$$\text{Log}_e Y = 5.483 e^{-0.0347 X} \quad Y = \text{days to median hatch, } X = \text{temperature.}$$

Jensen *et al* (1991) modelled hatching date and date of first-feeding based on spawning time and water temperature regimes for a wide range of natural stocks of brown trout and Atlantic salmon in rivers in Norway. They found that the point of initial feeding correlated with temperature; initial feeding was avoided in all rivers before the water temperature reached 8°C. This important issue is discussed later in this report (see “spawning”, Section 9).

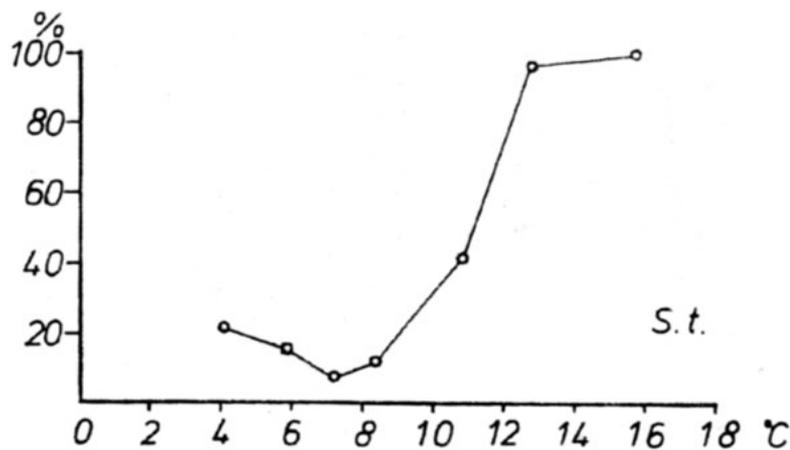
## 2.2 Survival

A study on the incubation of brown trout eggs by Jungwirth and Winkler (1984) indicated that survival was highest when the incubation temperature was around 8°C, with almost total mortality above 12°C (Figure 2.2). Frost and Brown (1967) state that trout eggs hatch well within the range of 5-13°C, but mortality increases markedly outside this range.

Ojanguren *et al* (1999) reared eggs of Atlantic salmon (derived from a stock in northern Spain) at temperatures ranging from 4 to 22°C. They observed an upper thermal limit

for successful incubation of 16°C. Poor survival has been observed at lower maximum temperatures by other workers, however. Gunnes (1979) reared Atlantic salmon eggs at 8, 10 and 12°C, and noted high mortality at the highest temperature (66.1 per cent mortality, fertilization to hatching) compared to the lower two temperatures which were associated with a mean mortality rate of 14.25 per cent). Peterson *et al* (1977) also noted increased mortality of salmon eggs at 12°C compared to lower temperatures, perhaps partly due to fungal infections. They suggested that if a single temperature were to be selected for hatchery incubation, 6°C would be optimal; rearing at 2°C would produce the largest alevins, and initial incubation at 6°C to the eyed stage (ie the time that eyes were visible in the developing embryo) followed by an increase to 12°C would be optimal for fastest hatching.

Gunnes (1979) noted that mortality at 12°C in his study was higher than that observed at the same temperature by Peterson *et al* (1977); he suggested that his eggs were derived from stock that may have been genetically adapted to breed in cooler water. Some support for the hypothesis that Atlantic salmon may be genetically adapted to different incubation temperature ranges comes from the results of Ojanguren *et al* (1999), whose observations of a rather higher temperature tolerance of eggs (discussed above) was based on a stock from the southern edge of the species' distribution range, in Spain.



**Figure 2.2. Mortality of eggs of brown trout incubated at a range of temperatures (From Jungwirth and Winkler, 1984).**

### 2.3 Other temperature effects on incubation

A number of developmental effects induced by incubation temperature have been observed; these effects may account for the changes in survival that have been reported.

Frost and Brown (1967) report that brown trout alevins are smaller when hatching from eggs incubated outside the range 7-12°C. Ojanguren *et al* (1999) observed that salmon embryos incubated at higher temperatures had a lower body weight at hatching and at first exogenous feeding. The emerging alevins from the 12°C group in the study by Gunnes (1979) averaged little more than half the weight of those incubated at 8 and

10°C. Ørnsrud *et al* (2004) noted a number of effects of incubation temperature including higher levels of retinol and increased amounts of notochord tissue in embryos reared at 14°C compared to 8°C. Embryos incubated at 5.6 to 10°C have fewer abdominal myomeres than those incubated at 1.3 to 1.9°C (Pavlov 1985).

Takle *et al* (2004) investigated the causal mechanisms of deformities of skeletal structures, the heart and other organs associated with elevated egg incubation temperature that have been observed by the salmon farming industry. They identified five genes that were temperature sensitive. Matschak *et al* (1997) reared eggs of Atlantic salmon at 5 and 10°C and noted that rearing temperature affected muscle fibre number and cross-section area. Fibre numbers at 100 per cent air saturation levels of oxygen were 17 per cent lower at the higher temperature. However, when the egg case was removed, the temperature effect was nullified, suggesting that it may be a temperature-mediated availability of oxygen that is the causal mechanism.

# 3 Alevins from hatching to first feeding

## 3.1 Influence of temperature on the duration of this phase

After hatching, the alevins remain within the gravel around the redd, subsisting on their yolk sacs. They begin feeding on exogenous material while still within the gravel, but emerge soon after that. Water temperature has a similar effect on the duration of the phase between hatching and first feeding as it does on incubation time to hatching. Kane (1988) noted that, over the range of water temperatures from 4 to 8°C, the time to hatching averaged 58.3 per cent of the overall time from fertilization to first feeding in Atlantic salmon.

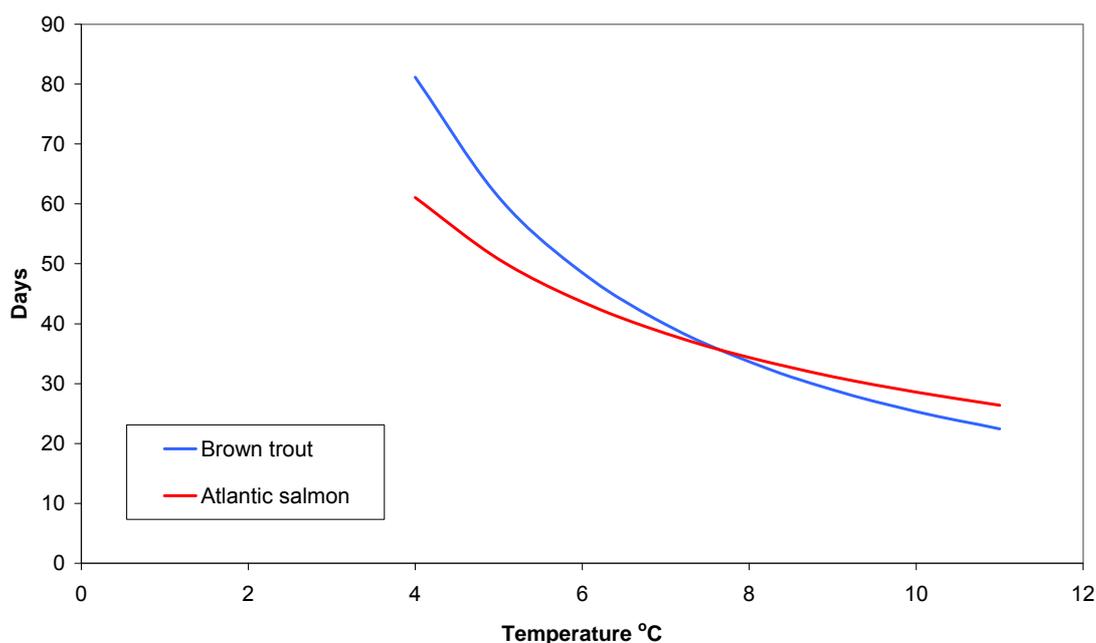
Jensen *et al* (1989) recorded the time between hatching and 50 per cent feeding in both brown trout and salmon over the temperature range 4 to 11°C. They used the results to produce the formulae:

$$Y = 472 X^{-1.27} \quad r^2 = 0.956 \quad \text{for Atlantic salmon}$$

$$Y = 193 X^{-0.83} \quad r^2 = 0.970 \quad \text{for brown trout}$$

Where Y = number of days and X = temperature.

The relationships are shown graphically in Figure 3.1. The relationship is similar at about 7.5°C, but below this temperature the Atlantic salmon develops more slowly, and above this temperature, more rapidly, than brown trout. The eggs were all derived from wild stocks in the River Vefsna, Norway.



**Figure 3.1. Influence of temperature on time between hatching and 50 per cent feeding for brown trout and Atlantic salmon, using the formulae derived by Jensen *et al* (1989). See text for further information.**

## 3.2 Survival

It is clear that the hatched alevins of salmonids are able to survive at significantly higher temperatures than the pre-hatching stages. The study by Ojanguren *et al* (1999) reported total mortality of Atlantic salmon eggs at 16°C and above, but hatched larvae survived at temperatures up to 22°C. Siemien and Carline (1991) fed first-feeding fry of Atlantic salmon to satiation at 10, 14, 18 and 22°C, and observed that growth was greatest at 18°C.

# 4 Brown trout, fry to adult

## 4.1 General

A wide range of temperature effects on juvenile and adult salmonids have been studied, including lethal temperatures, feeding and growth, and preferred/selected temperatures. Trout of all sizes appear to respond in a similar way to changes in water temperature and are thus dealt with together in this report; size (or age) differences are highlighted where they are known to exist. Atlantic salmon are covered in a separate section (Section 5).

Brett (1956) discussed general principles of the thermal requirements of fish and devised a “thermal tolerance” graph which has been further developed by other authors (e.g. Elliott, 1994) to include the temperature envelopes for feeding and growth. Such graphs for Atlantic salmon and brown trout are presented in Figure 4.1.

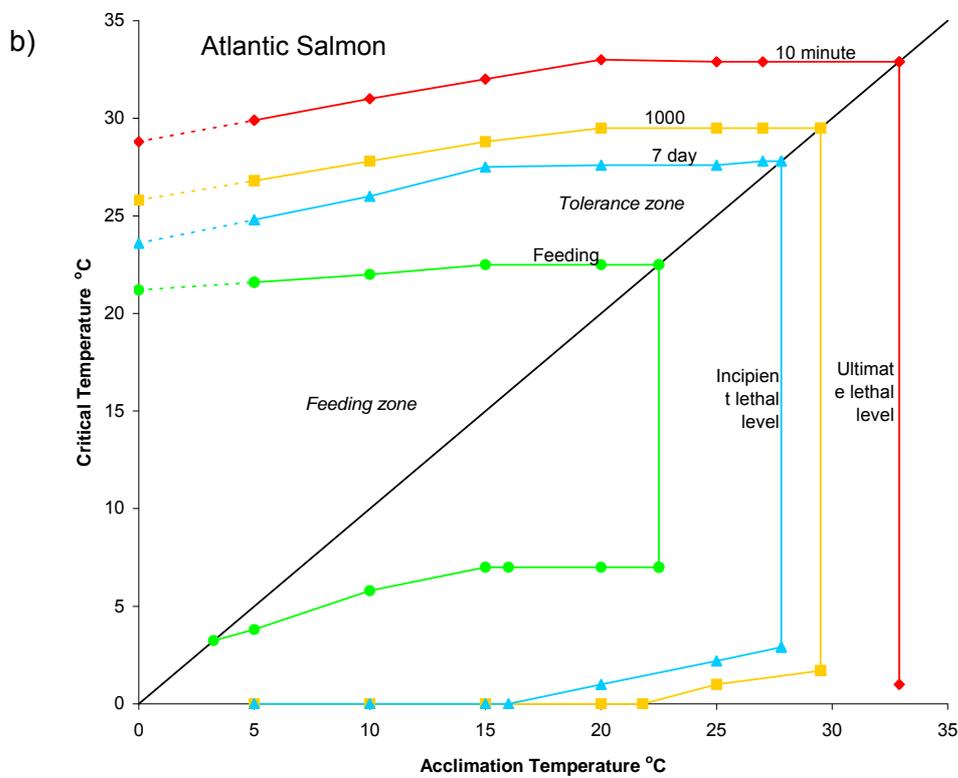
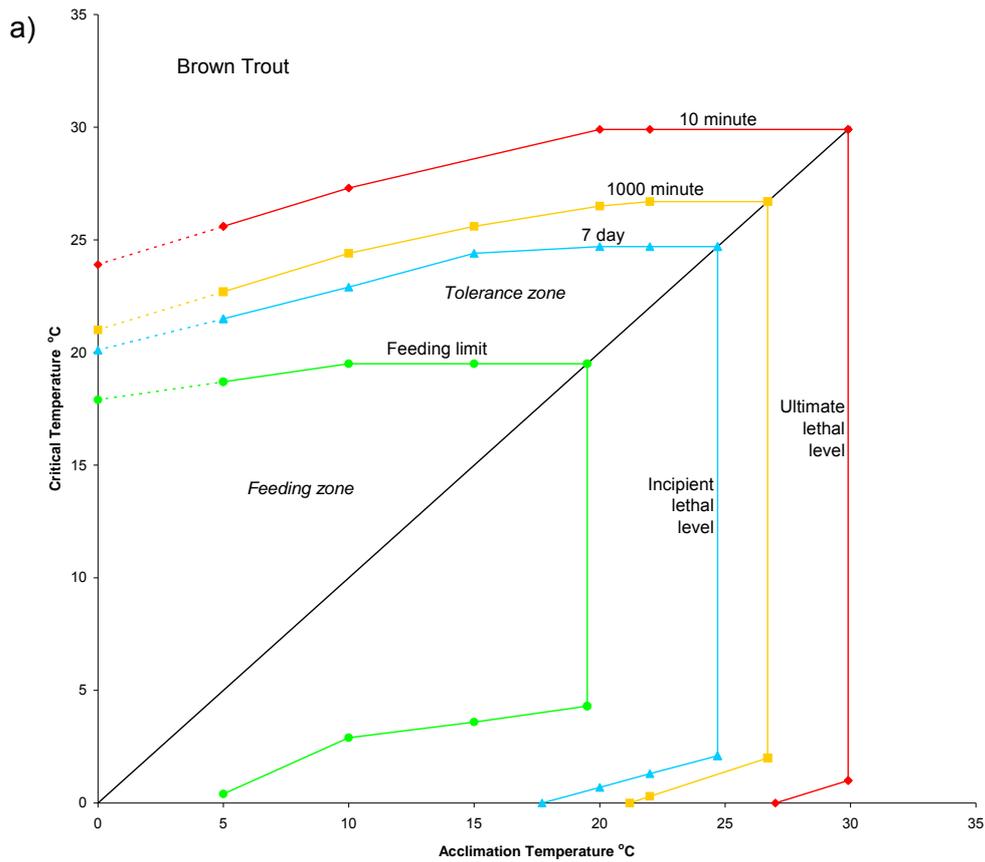
An important principle is that of acclimation (or acclimatisation); the value of critical temperatures (e.g. for survival) is influenced by the recent experience of the fish. Extreme temperatures are likely to be approached gradually in nature – when a fish is subjected to a temperature of 25°C, for example, it has probably been experiencing warm water temperatures during the preceding hours or days. The time allocated to acclimation varies between studies; Elliott (1981) used a period of two weeks in the study to establish the lethal temperatures for brown trout presented in Figure 4.1.

## 4.2 Lethal temperatures

For a given species there is a range of temperatures within which the species can survive, but there are a number of ways of defining the lower and upper limits. These limits vary, mainly in the length of time that fish survive at the extremes, and the extent to which the fish are acclimated to temperatures close to the extreme (Elliott 1981).

For brown trout, these variations are illustrated clearly in the thermal tolerance graph in Figure 4.1. The ultimate upper lethal temperature (i.e. the temperature at which the fish can survive for 10 minutes) is probably of little more than academic interest, but the 1000 minute (i.e. about 17 hours) is more meaningful, as this might approximate to the period of high temperature on a very hot day. With acclimation to warm water, the 1000 minute lethal temperature is about 26.7°C, and the seven-day value about 24.7°C. The fish used by Elliott in this study were of hatchery origin. While there is likely to be some variation in the lethal temperatures between stocks and extremes of the geographic range of each species, remarkably similar results are provided by a range of studies in different countries.

Thermal refuges may be crucial for the survival and well-being of salmonids. Elliott (2000) described the situation on a small Lake District stream, the Wilfin Beck. In non-drought years trout remained in five pools on the experimental stretch, and temperatures at the deepest point of each were similar (range 12-18°C) as were dissolved oxygen levels (7.8-9.8 mg/l). However, in drought years conditions deteriorated as flows decreased, and conditions in the two smallest pools were outside the limits for trout, with temperatures of 24-29°C and dissolved oxygen levels of 1.2-2.5 mg/l; trout were absent from these pools under such conditions.



**Figure 4.1. Thermal polygons for brown trout (a) and Atlantic salmon (b), using data from Elliott 1981 and 1994. See text for explanation.**

However, conditions in the two largest pools were much more benign (20-25°C, 3.6-4.8 mg/l) and trout of all ages were present. These “large” pools were, in reality, quite small: one was 24 m<sup>2</sup> in surface area, with a maximum depth during drought of 1.55 m; the second was 12 m<sup>2</sup> in area, with a maximum drought depth of 1.4 m.

A similar situation exists in small sea trout nursery streams in the New Forest, where water surface temperatures may reach 30°C on very hot days (T E Langford, personal communication). These observations highlight the importance of temporary thermal refugia in streams.

### 4.3 Feeding and growth

Frost and Brown (1967) summarised a number of early studies on the effect of water temperature on feeding and growth in brown trout (reproduced in Table 4.1).

**Table 4.1. Summary of findings of early studies on the effect of temperature on feeding and growth in brown trout.**

Author	Fish age (months)	Growth optimum temperature (°C)	Feeding optimum temperature (°C)
Brown 1951	0 - 6	12 better than 10	
Brown 1946	24 - 36	7-9 better than 16-19	10 – 19
Gerrish 1935	All ages?		5 - 13 and 16 – 19
Hewitt 1943	All ages?	15 - 19	
Myers 1946	0 - 12		7-15
Pentelow 1939	6 - 18	10 - 15	10
Swift 1955	36 - 48	8 - 12 and 15 - 16	
Swift 1961	12 - 24	12	
Wingfield 1940	6 - 18	10 - 15	

The most comprehensive series of studies are those conducted by Malcolm Elliott and his colleagues (Elliott 1975; Elliott *et al.* 1995). They developed a model for trout growth at maximum rations and demonstrated that temperature and fish size were the dominant variables. Based upon two series of experiments they produced the growth formula:

$$G_w = cW_t^{-b} (T - T_{lim}) / (T_M - T)$$

Where:

G is the specific growth rate in weight (per cent per day)

W is the weight of the fish

T is the temperature (°C)

c is a constant with a value of 2.308, equivalent to the growth rate of 1 g fish at the optimal temperature of 13.11°C

b is a constant with a value of 0.308

T<sub>M</sub> is the optimal growth temperature with a value of 13.11°C

T<sub>lim</sub> is the limiting temperature i.e. the temperature at which growth is zero (for a value of T of less than T<sub>M</sub> use T<sub>L</sub>, and for a value of T of more than T<sub>M</sub> use T<sub>U</sub>)

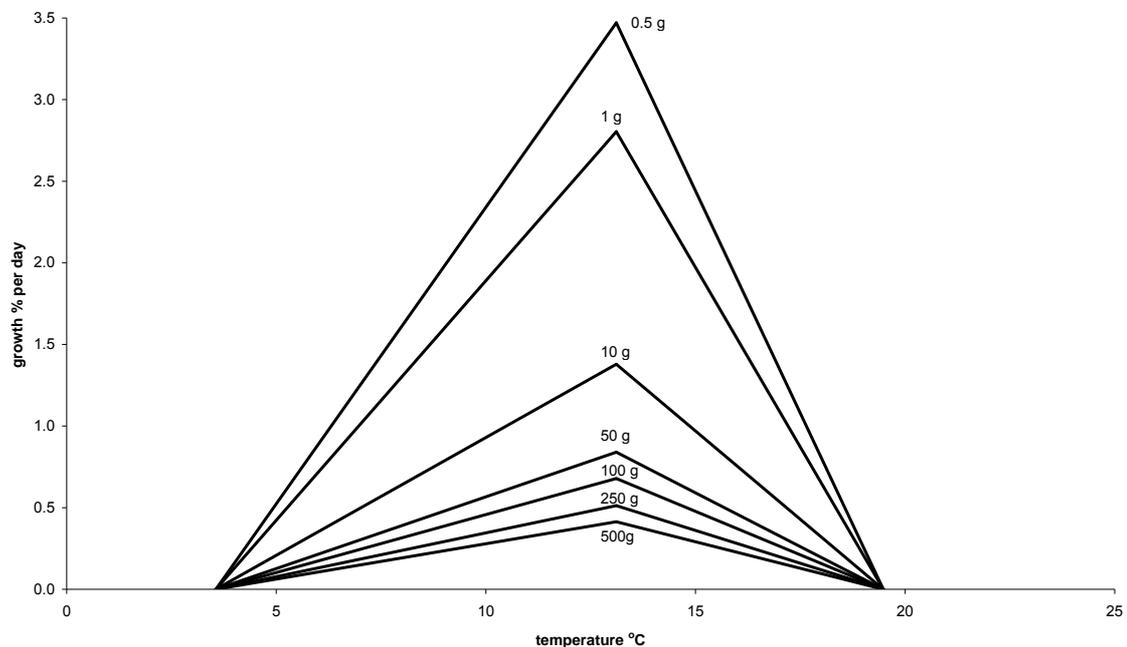
T<sub>L</sub> is 3.56°C

T<sub>U</sub> is 19.48°C

The growth curves for a range of fish sizes are shown in Figure 4.2.

“Maximum rations” means that the fish were fed all the food they would eat, such that intake would not limit growth. In other studies the terms “fed to satiation” and “fed *ad libitum*” have been used. These have essentially the same meaning.

Elliott’s model suggests that even with maximum rations there is zero growth at 3.56°C and 19.48°C, and that the fish would lose weight at lower and higher temperatures. The optimal temperature for growth for all sizes of fish is 13.11°C. The output from this model is in fair agreement with the earlier study findings in Table 4.1, though this thorough investigation found no evidence of the bimodal peaks in growth reported by some other authors. The fish used in this study were derived from eggs taken from wild sea trout in the River Leven (Lake District).



**Figure 4.2. Relationship between temperature and predicted growth (in per cent of body-weight per day) of brown trout of various sizes (weight in g) fed maximum rations.**

Several studies have used these laboratory-derived models to examine growth rates in the wild. Edwards *et al* (1979) used the earlier model from Elliott (1975) to demonstrate that most variation in trout growth in the wild, including their rapid growth in chalk streams, could be explained by temperature alone. A similar exercise looked at the growth of migratory trout parr in twelve rivers in Norway (Jensen 1990). While some stocks conformed closely to the Elliott model, some grew slower than predicted for maximum rations – perhaps indicating that ration was limiting in these rivers. However, in other rivers the trout grew significantly faster than the Elliott model predicted. Jensen suggested two possible explanations: a genetic difference between the stocks used in the two studies; and a complication to the relationship due to diurnal fluctuations in temperature rather than a steady level.

Forseth and Jonsson (1994) observed that the fastest growth rate in a population of piscivorous trout occurred at a temperature of 2-4°C above that predicted by the Elliott model. Lobón-Cervia and Rincón (1998) also observed faster growth rates than those predicted by the Elliott model at higher temperatures, and they suggested that this may represent adaptation to the local thermal regime; the observations were made in Northern Spain where higher temperatures are likely to prevail. Allen (1985) noted that the population of trout in the Horokiwi Stream in New Zealand, which had been introduced from Britain via Tasmania in the late 1860s, performed better in terms of feeding and growth at higher temperatures than the Elliott model suggests. The mean stream temperature of 13.5°C, and the maximum monthly mean of 19.5°C, is generally higher than temperatures in British waters. The fieldwork on which Allen's observations were based was conducted in the 1940s, and he suggests a strain of fish had developed over half a century or more that was adapted to higher temperatures.

Elliott (1994) reviewed the evidence for genetic variation in the relationship between water temperature and growth and concluded that evidence was lacking. He pointed out that other potentially complicating factors need to be ruled out before a conclusion can be drawn regarding genetic adaptation. Such factors include:

- greater daylength during the growing season - which might also explain the faster growth in parr of migratory trout in Norway (Jensen 1990, above);
- marked diurnal variation in water temperature;
- more energetically efficient diets - which might explain the faster growth in piscivorous trout (Forseth and Jonsson 1994, above).

This is clearly an important issue with respect to climate change, as evidence of local adaptation to higher temperatures would give hope that populations in marginal temperature regimes may be able to adapt. Further investigation is required.

## 4.4 Preferred and avoided temperatures

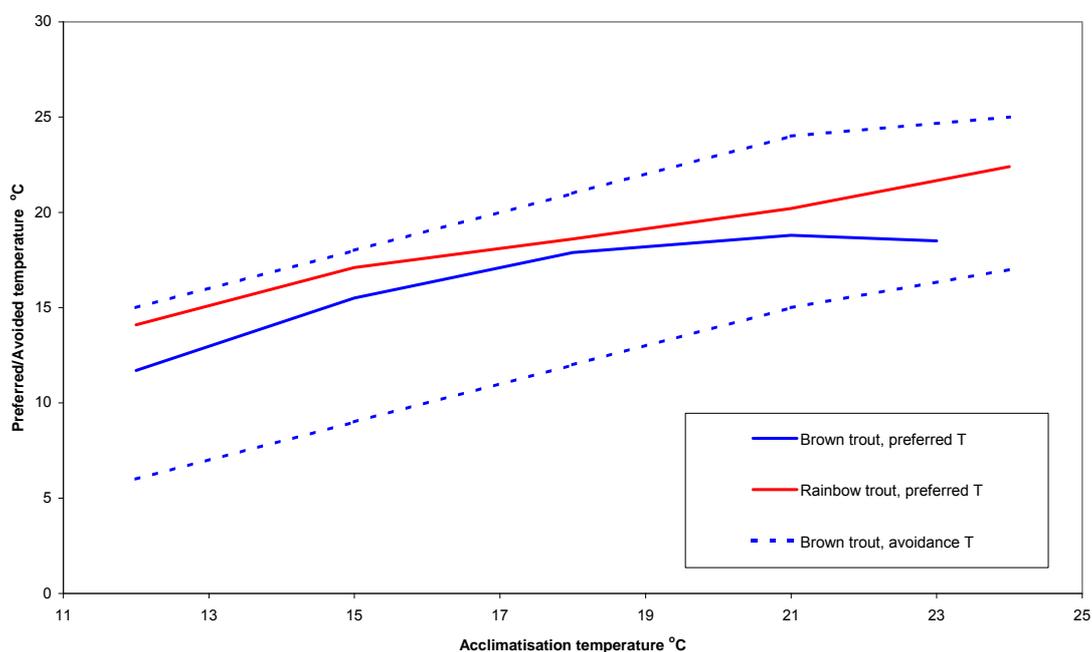
Coutant (1977) summarised early work on preferred temperatures in a wide range of species, including brown trout. The range produced from different studies was rather wide (12 to 17.6°C), presumably reflecting the different conditions under which the studies were conducted. Cherry *et al* (1977) conducted a detailed study on several species including brown trout. Their results for preferred and avoided temperatures for a range of acclimation temperatures are shown in Figure 4.3; these fish were obtained from a commercial hatchery in North America.

Alabaster and Downing (1966) observed the behaviour of brown trout in an experimental channel with a temperature gradient which changed throughout the day. The fish moved to avoid areas where the water temperature exceeded 20°C. These fish were of hatchery stock.

Elliott (1981) introduced the concept of upper and lower critical ranges of temperature. These are the areas that lie between the feeding polygon and the ultimate lethal temperature polygon (Figure 4.1). Elliott gives these limits as about 19-30°C and 0-4°C for brown trout, varying somewhat with acclimation temperature. Within these critical ranges may occur "significant disturbance in the normal behaviour of the fish, i.e. there may be obvious signs of thermal stress".

Within the upper critical range Elliott describes three progressive stages of stress response as temperature rises. First, there is a reluctance to feed, sudden bursts of activity and rapid ventilation movements. In the second phase the fish become

quiescent with short bursts of weak swimming; they may float on their side or back, and ventilation movements increase. In the third phase, movements are restricted to the opercula, pectoral fins and eyes. Elliot noted that fish transferred to cooler well-oxygenated water from the first two phases usually recovered, but did not do so from phase three.



**Figure 4.3. Preferred and avoidance temperatures for brown trout, and preferred temperature for rainbow trout.**

It will be noted that the lower limit of the upper critical range for brown trout is close to the avoidance temperature reported by Alabaster and Downing (above).

## 4.5 Other factors

Increasing water temperatures may affect a range of other environmental conditions which have the potential to cause harm and have an impact on fish at temperatures that fall well short of the lethal levels defined in Section 4.2.

The toxicity of many pollutants is greater at higher temperatures (Alabaster and Lloyd 1982). Moreover, dissolved oxygen may become a major issue in warm water because:

- the solubility of oxygen in water falls as temperatures rise, so air saturation levels are lower;
- oxygen-consuming processes, such as decay of vegetation, are accelerated at higher temperatures; and
- the ability of most species to withstand depleted levels of oxygen is reduced at elevated temperatures.

The susceptibility of salmonids to pathogens and parasites may also be influenced by temperature. Some diseases such as UDN are most virulent in cool conditions, but most thrive at increased temperatures. Hari *et al* (2006) attribute at least part of the decline in brown trout populations in warming streams in Switzerland to a temperature-dependent increase in the incidence of Proliferative Kidney Disease (PKD).

# 5 Atlantic salmon parr

## 5.1 Lethal temperatures

Elliott (1991) examined the tolerance of Atlantic salmon to high temperatures in a similar manner to the investigation on brown trout described in Section 4.2 (Elliott 1981). The 1000 minute upper lethal temperature (with acclimation) for the stocks used in the experiment was 29.5 °C, and the seven day level 27.8°C; these values are both approximately 3°C higher than the equivalent values for brown trout. The fish were reared from eggs and milt taken from wild stocks in the Rivers Lune and Leven.

## 5.2 Feeding and growth

Elliott and Hurley (1997) undertook growth experiments with salmon parr from the Rivers Leven and Lune in north west England to develop a growth model similar to that for trout discussed in Section 4.3:

$$G_w = cW_t^{-b} (T - T_{lim}) / (T_M - T)$$

Where:

G is the specific growth rate in weight (per cent per day)

W is the weight of the fish

T is the temperature (°C)

c is a constant with a value of 3.53, equivalent to the growth rate of 1 g fish at the optimal temperature of 15.94°C

b is a constant with a value of 0.31

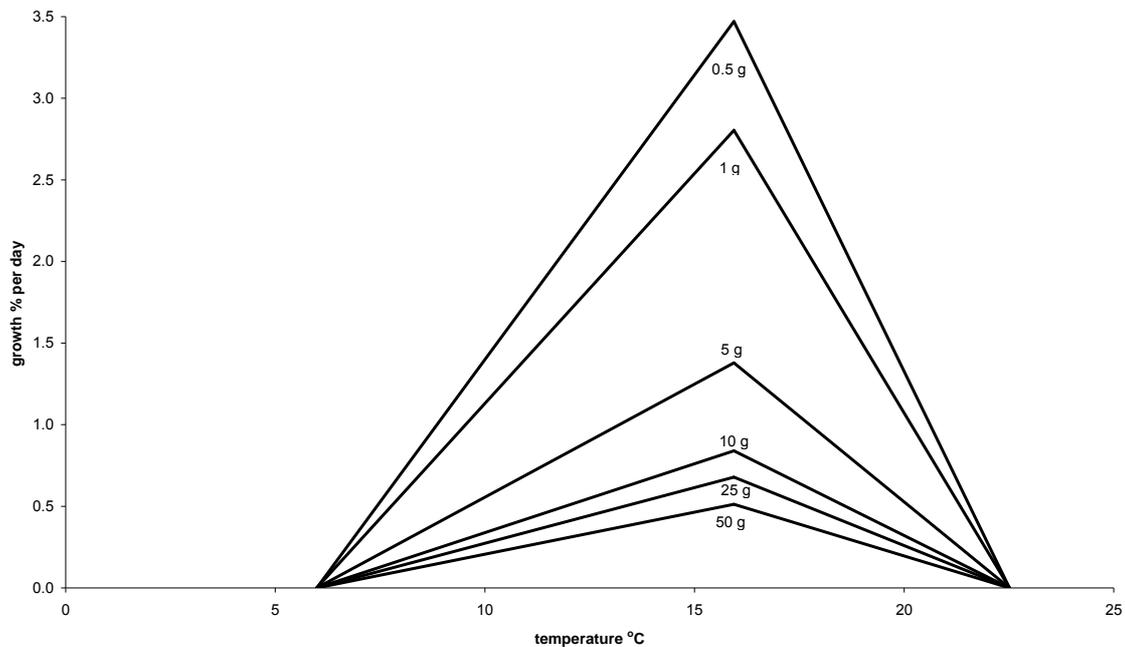
T<sub>M</sub> is the optimal growth temperature with a value of 15.94°C

T<sub>lim</sub> is the limiting temperature, i.e. the temperature at which growth is zero (where T is less than T<sub>M</sub> use T<sub>L</sub>; where T is more than T<sub>M</sub> use T<sub>U</sub>)

T<sub>L</sub> is 5.99°C

T<sub>U</sub> is 22.51°C.

The growth predicted for a range of fish sizes and temperatures are shown in Figure 5.1.



**Figure 5.1. Relationship between temperature and predicted growth (in per cent of body-weight per day) of Atlantic salmon of various sizes (weight in g) fed maximum rations.**

The optimum temperature was 15.9°C (compared with 13.11°C for brown trout) and the growth range 6.0°C-22.5°C (3.56-19.48°C for brown trout). Again, these temperatures are about 2-3°C higher than the equivalent values for brown trout.

Dwyer and Piper (1987) observed the growth rate of Atlantic salmon parr fed maximum rations at a range of temperatures between 4 and 19°C. Overall size after 112 days increased with increasing temperature between 4 and 16°C, but was a little lower at 19°C. These figures are in close agreement with the findings of Elliott and Hurley described above, although it must be noted that the growth of the fish held at 19°C was higher than that of the 16°C fish after 84 days, but fell away somewhat after this period. The origin of the fish was not stated.

Davidson and Hazlewood (2005) used the model of Elliott and Hurley (above) to explain the decline in mean smolt age (MSA) on a number of rivers in England and Wales. The age at which the fish become smolts is growth-dependent (see Section 6.1). River temperature records from the main stems of the rivers were used. While significant increases in temperature and falls in MSA were coincident, the model predicted only a minor and non-significant increase in growth. The authors suggested that some factor other than increased temperature may be the main cause of faster growth. Alternatively, it may be that the use of main-stem temperatures as a surrogate for the situation in the nursery areas masked a direct relationship. This suggested limitation is important to note; in any study assessing the effects of temperature on fish it is important to know what temperature the fish were actually experiencing.

### 5.3 Preferred and avoided temperatures

There is rather less information regarding preferred and avoided temperatures for Atlantic salmon than for brown trout. The range from the literature quoted by Coutant (1977) was wide and probably meaningless, reflecting a wide range of experimental and observation approaches to establish preferred temperatures.

Fisher and Elson (1950) observed a preferred temperature (in a temperature gradient experiment) of 14°C for Atlantic salmon fry acclimatised to 4°C. The origin of the fish was not stated.

# 6 The parr to smolt transformation, and smolt migration

## 6.1 Smolt age

The time at which Atlantic salmon and migratory brown trout become smolts is dependent much more on size than on age. Smolts tend to be much younger in the southern part of the latitudinal range of both species, reflecting the increased growth opportunity.

Jonsson and L'Abée-Lund (1993) examined the characteristics of the smolts of migratory trout between 54 and 70°N mainly in Scandinavia, Scotland and Ireland. They observed an increase in mean smolt age (MSA) of about 0.15 years per additional degree northwards.

Solomon (1995) however found that this relationship did not appear to hold for stocks in England and Wales at latitudes between 50 and 55°N, as MSA remained steady or even increased slightly in the south. A likely explanation for this observation is that the latitude of 50°N is approaching the southern limit of occurrence for lowland sea trout; the stocks in this area that find a migratory habit advantageous are those where the growth opportunity is limited by some factor other than latitude, for example. moorland nursery areas (with relatively low temperatures) or a small nursery stream that suffers from low summer flows. However, Solomon (1995) did note that in every case where samples of scales were available from English and Welsh stocks over a period of many years, there had been an increase in the frequency of one-year-old smolts. This situation is likely to have been due to increasing temperatures.

A similar latitudinal trend has been noted for Atlantic salmon by Metcalfe and Thorpe (1990). However, these authors noted a different relationship on each side of the Atlantic. The rate of change was 0.097 years per degree of latitude in Western Europe, and 0.255 years per degree of latitude in Canada. Their best model was one of growth opportunity based on the extent to which water temperature exceeded 5.5°C on a month by month basis, and day length. Temperature is likely to rise moving south, and the duration of daylight decrease, at least during the growing season. Day length has an invariable relationship with latitude so the difference on each side of the Atlantic is most likely due to temperature.

Saltveit (2006) reported that both Atlantic salmon and brown trout smolted a year later in the lowermost reaches of the River Surna in Norway, which was cooled by hypolimnetic releases from a reservoir, compared to upstream of the reservoir release point.

Davidson and Hazlewood (2005) reported a significant increase in the growth rate of parr and a decline of MSA in Atlantic salmon in the Severn, Wye and Dee during the 1980s and 1990s. The fall in MSA and increase in growth rate were associated with an increase in temperature but the authors were unable to explain most of the increased growth rate using the model developed by Elliott and Hurley (1997, see Section 5.2).

## 6.2 Development of smolt characteristics

Photoperiod (day length) appears to be the main stimulus for the development of smolt characteristics in Atlantic salmon but water temperature can play a part (McCormick *et al* 1998). Temperatures below about 3°C restrict smolt development, whilst increasing the mean daily rearing temperature from 2°C to 10°C can advance smolting by up to a month (McCormick *et al* 1996). Staurnes and Sigholt (1994) succeeded in causing development of smolting by manipulation of temperature alone in a regime of constant light.

It has also been observed that increased temperature hastened the rate of loss of physiological smolt characteristics; a study calculated an 80 per cent loss in the activity of enzymes associated with smolting, effectively returning the smolt to parr status, 400 degree days after the peak. (McCormick *et al* 1996, 1999).

## 6.3 Smolt migration

Although large-scale migration of smolts of Atlantic salmon is often associated with elevated river flow, temperature also has a major influence. McCormick *et al* (1998) reviewed numerous field studies of smolt migration, many of which had shown that that warming water in the spring is strongly correlated with the initiation of the smolt run; most of the studies concluded that a temperature of around 10°C appears to be a trigger for migration.

Jonsson and Ruud-Hansen (1985) examined many environmental factors with respect to salmon smolt migration on the River Imsa in Norway; they concluded that only water temperature had a major influence, accounting for 89-95 per cent of the variance in the date of 25, 50 and 75 percentiles of the smolt run. The influence of river flow and lunar cycle were insignificant.

In a study on a small chalk stream in southern England, where spate conditions are the exception, Solomon (1982, 1984) found that water temperature was the main environmental factor influencing smolt migration, with 10°C acting as a trigger. However, there was some evidence that the exact trigger temperature varied between years, perhaps affected by the temperature over the preceding weeks; warmer conditions generally increased the trigger temperature. There is evidence that the timing of smolt migration may have an influence over marine survival, with early migration being associated with reduced survival (see Section 7.3).

There is also evidence that aspects of smolt migratory behaviour are under genetic control. Stewart *et al* (2006) observed the onset of smolt migration from an upland and a lowland tributary of the river Tay, and noted that the migration started earlier in the upland tributary. This stock-specific trait was maintained even when fish were transferred between the two locations or were stocked into a third, common location.

With regard to smolts of sea trout, Solomon (1978, 1982) noted that their migratory behaviour appeared less influenced by water temperature. These fish migrated somewhat earlier and at a wider range of temperatures, predominantly in the hours of darkness. However, it may be that the critical temperatures are lower for this species, occur more frequently and may be associated with meteorological events such as rainfall.

Whelan *et al* (1994) reported on the emigration of sea trout smolts from the Burishoole system in Ireland. Migration commenced at temperatures as low as 3°C, but the main migration took place above 7°C. Once this threshold was reached pulses of migration occurred, generally associated with rainfall. Migration was severely curtailed by temperatures above 13°C, and if the water warmed to this level before the peak of migration had occurred recruitment was adversely affected.

# 7 Salmon in the sea

“Ocean climate impacts on survivorship and growth of Atlantic salmon are complex....”

Todd *et al* (2008)

## 7.1 Introduction

It is only with the advent of data storage tags that we can directly observe the temperatures actually experienced by salmon at sea. But oceanographic studies have been providing information on this aspect of the marine environment for many years. There is evidence that variation in sea surface temperature (SST) throughout the areas frequented by feeding and growing salmon affects their growth, condition, sea age and survival.

## 7.2 Sea age at return

Martin and Mitchell (1985) explored the relationship between the sea age of returning Atlantic salmon in and around the Aberdeen Dee, and SST. They used commercial catch records from 1877 to 1972, along with concurrent SST records from Grimsey, North Iceland, to indicate the conditions in the sub-arctic range of the fish. They found a good correlation between temperature and the proportion of fish returning as grilse (a lower temperature was associated with a preponderance of grilse).

This observation is perhaps counter-intuitive given that earlier authors (e.g. Saunders *et al* 1983) had found that low winter temperatures were associated with a decreased tendency to mature as grilse among fish reared in cages. However, as Martin and Mitchell pointed out, in this latter case the fish were forced to remain within the area of cold water, whereas in the wild they are free to move away to avoid the coldest conditions. This explanation suggests that the relationship between maturation and SST is more complex than at first sight.

## 7.3 Marine survival

Reviewing a wide range of SST data, Friedland and Reddin (1993) developed a concept of a “thermal habitat area” that could be associated with stock abundance in the north east Atlantic. They noted that abundance was directly correlated with the area of ocean having an SST of between 7°C and 13°C between 0°W and 20°W in spring. Increases in temperature reduced this area by warming from the south; catches were consequently reduced.

Following the publication of this study, its authors realised that this model involved a high level of spatial and temporal averaging. Moreover, more information was becoming available on the distribution of post-smolts in the sea, which was discontinuous and generally associated with fronts, boundary currents and gyres (Dickson and Turrell 1999). Friedland (1998) refined the original analysis by considering the abundance of two specific stocks (fish from North Esk in Scotland and Figgjo in Southern Norway). Friedland found that abundance was negatively correlated with the extent and location of the area with a sea surface temperature of 5-7°C, and

positively correlated with the extent of 8-10°C SST in May – about the time that the smolts enter the sea. Friedland observed faster spring increases in SST during the years of higher survival than during the recent period of lower survival. The first few weeks that smolts spent in the sea are generally considered to account for much of the overall marine mortality, and the variation therein (Eriksson 1994). Cairns (2003) suggested that the increased mortality at lower temperatures could be due to slower growth and greater susceptibility to predation in the first weeks in the sea. It is of interest to note that the spatial and temporal refinement of the earlier analysis by Friedland (1998) identified a local cooling effect as the likely cause of the lower survival rate, rather than the apparent warming of a much greater area. This finding highlights the difficulty associated in identifying cause and effect in the marine environment.

The timing of smolt emigration is influenced by temperature (Section 6.3), and it is also considered to critically influence their arrival during the optimal “window” of conditions in the marine environment (McCormick *et al* 1998). Using the long-term data set from the River Bush in Northern Ireland, Crozier and Kennedy (2003) postulated that increasing freshwater temperature could play a part in the observed decline in marine survival. A similar observation has been made on the Girnock Burn, within the Aberdeen Dee catchment (Alan Youngson, personal communication). Here the median date of the smolt run is correlated with the catchment spring rod catch two years later (most of the spring fish catch being 2 SW fish); an early smolt season is associated with a lower catch. In warm years the freshwater environment is likely to warm more rapidly than the marine environment. Indeed, the observations of Friedland (1998, above) suggest that in warm years, inshore SST may actually drop, perhaps causing the smolts to enter the sea under sub-optimal conditions.

## 7.4 Growth and condition

The recent decline in marine survival of Atlantic salmon has been associated with a reduction in their physical condition, culminating in the widespread occurrence of “thin grilse” in 2006.

Todd *et al* (2008) examined this phenomenon and found that linked statistically to an increase in winter SST. They examined two 14-year data sets, one from a single river stock (North Esk) and the other a mixed stock (Strathy Point bag nets), and noted virtually identical inter-annual variations in condition (weight of a standard length of fish) for grilse. They observed an overall decline in condition of 11 per cent at Strathy Point and 13 per cent on the North Esk over the 14 year period, associated with an increase in SST in January of the order of 1°C.

Of even greater concern is the observation that the fish in the poorest condition (i.e. around 30 per cent underweight) showed an 80 per cent reduction in stored lipid content. Adult salmon do not feed after returning to coastal waters and subcutaneous adipose deposits and lipids in the musculature represent the main energy store for metabolism and egg production. Todd *et al* (2008) suggest that the observed decline in condition has major implications for effective fecundity as well as for the survival of individuals.

# 8 Returning adults in estuaries and rivers

## 8.1 Introduction

Salmon and migratory trout have to pass through, and may spend considerable time within, coastal waters, estuaries and the lower reaches of rivers in order to reach their spawning grounds. These water bodies may be very different in temperature terms to both the feeding areas in the open sea and the middle and upper reaches of rivers where the fish spawn.

## 8.2 Estuaries

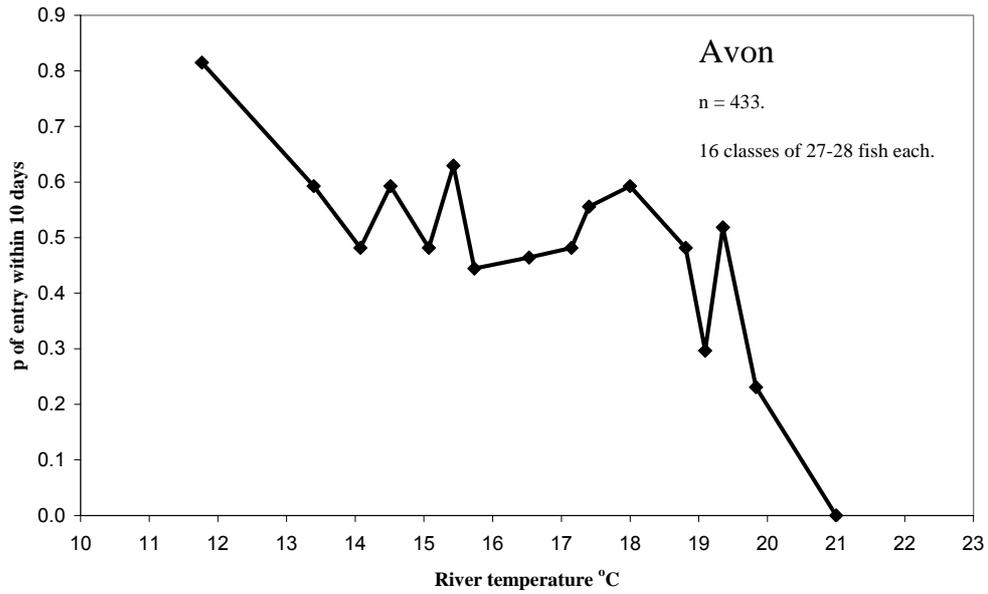
An analysis of the critical conditions in estuaries is complicated by the inter-relationships between water temperature, river flow and dissolved oxygen. High temperature and lower dissolved oxygen (DO) act synergistically to create limiting conditions for adult salmon in estuaries. Alabaster *et al* (1991) quote laboratory results indicating the value for a lethal level of DO at a little over 3 mg/l at 15°C, and around 7 mg/l at 25°C. They observed a water temperature of 24.2°C associated with a complete inhibition of trap catch at the tidal limit on the River Thames, and a 50 percentile of 21.5°C associated with a zero monthly return.

Solomon and Sambrook (2004) examined the relationships between water temperature, river flow and salmon migration through estuaries in south west England, based upon a series of radio tracking studies. It was clear that hot, dry summers delayed the fish passing through the estuary; many of the fish that remained in the estuaries for more than a few days were lost, though definitive identification of the factors responsible for the delays and losses was not possible. On the Hampshire Avon there was a strong relationship between the proportion of fish passing through the estuary promptly and both river flow and water temperature (Figure 8.1). In this study, more than 400 salmon were tagged as they entered the estuary from the sea over a five-year period.

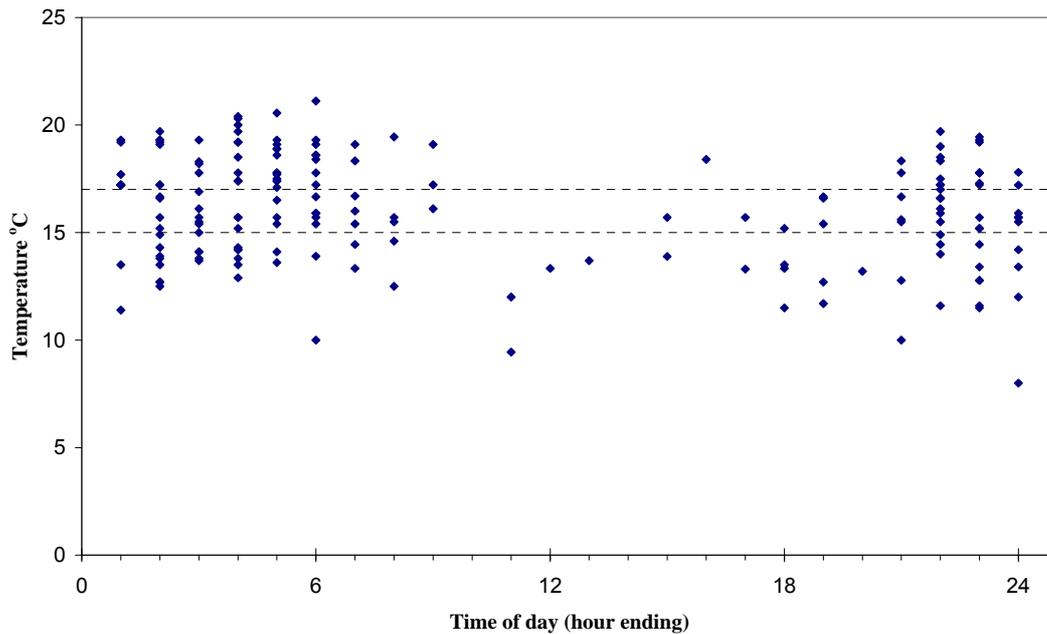
The authors suggested that high temperature was more likely to be responsible for the difficult migration than low flow because:

- it was more likely to be exerting a direct physiological effect;
- it was more readily discernible by the fish;
- “low flows” on the Avon were in reality relatively high for the size of the river, being groundwater-fed.

It was noted that half or more of the run could be lost in a hot dry summer. Of the 37 fish which were tagged on days when the 09:00 hours river water temperature was more than 19.8°C, none passed the tidal limit within 10 days. Six fish that had been tagged on days when the 09:00 temperature was a little below 19.8°C subsequently passed the tidal limit on days when the 09:00 temperature was in excess of 19.8°C. However, of these six fish, at least five passed the tidal limit between 03:00 hours and 06:00 hours, when the river water temperature was likely to be at its lowest (Figure 8.2); the hour of passage of the sixth fish is not known.



**Figure 8.1. Relationship between river water temperature at 09:00 hours on the day of tagging of salmon at the entrance to the estuary of the Hampshire Avon, and the probability of passing the tidal limit within 10 days of tagging.**



**Figure 8.2. Relationship between the time that radio-tagged salmon passed the tidal limit on the Hampshire Avon, and the 09:00 river water temperature on the day of passage. On warmer days the fish avoid passage at the warmer times of day.**

### 8.3 Migration within the river

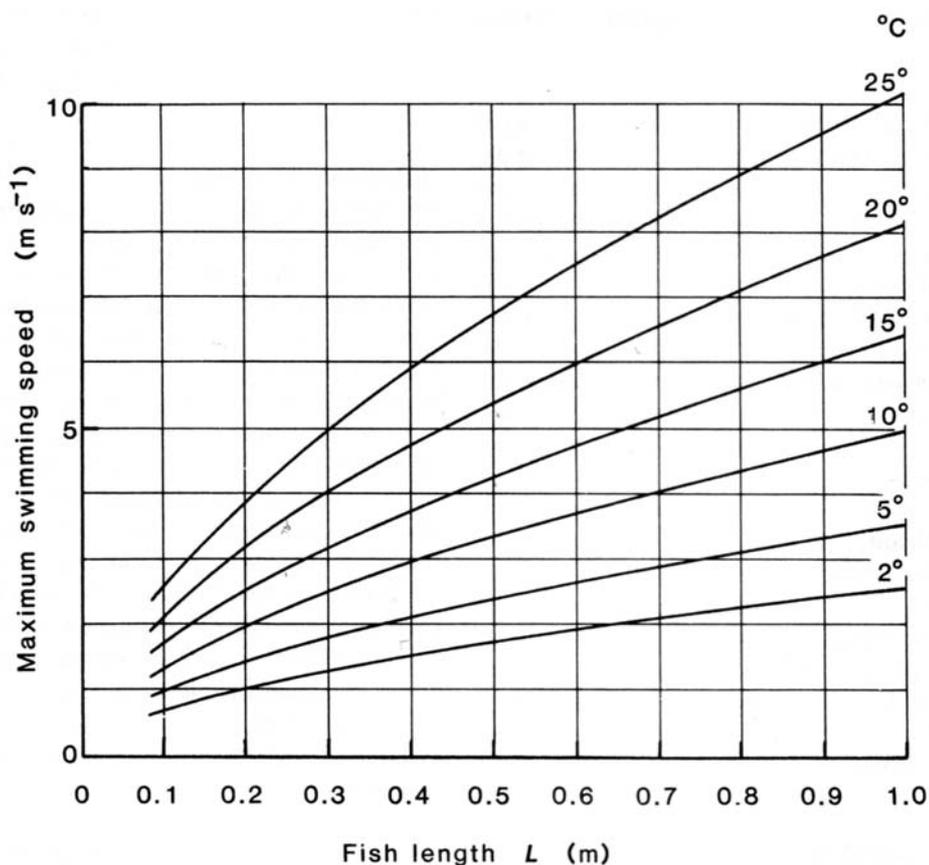
Brayshaw (1966) analysed migrating salmon trapped a few hundred metres upstream of the tidal limit on the Hampshire Avon. He noted that when the water temperature

exceeded about 16°C and dropped below about 8°C the numbers of fish migrating declined, regardless of river discharge.

Radio-tagged salmon in the Penobscot River in Maine often entered the river at times of high freshwater temperatures, but few progressed upstream at temperatures in excess of 23°C (Shephard 1995). At higher temperatures many fish would gather at the mouths of small tributary streams, the most “popular” of which was routinely several degrees cooler than the main river. However, fish also gathered at the mouths of side streams which did not represent a thermal refuge – possibly they offered some other comfort such as higher dissolved oxygen. Shephard commented that the present Penobscot stock was introduced from further north. The original (extirpated) stock was noted for spring running, numbers peaking at least a month earlier than the present situation; such fish would have had the opportunity to pass through the lower river to cooler streams before the summer peak.

In light of these findings, it is of interest to note that Juanes *et al* (2004) have noted a gradual shift to earlier running in several re-introduced New England salmon stocks including the Penobscot, which showed the run peak (50 per cent of total annual return) shift 12 days earlier in the 24 years between 1978 and 2001. The date by which 95 per cent of the annual run has been observed had shifted to an even greater extent, being 67 days earlier. Whether these shifts are real adaptations by the stock or the result of increased mortality of the later-running fraction of the stock is uncertain.

Pero (1994) also reported adult Atlantic salmon using thermal refuges. He noted that many thousands of salmon gathered in three large junction pools where cool tributaries entered the Southwest Miramichi in Canada, when the main river temperature exceeded 19°C.



**Figure 8.3. Theoretical maximum swimming (burst) speeds for salmonids at different temperatures. From Beach (1984).**

Although Atlantic salmon migration stops at high temperatures, clearly the fish must be able to withstand the highest temperature that the river can reach, unless they are able to seek thermal refuges. Brooker *et al* (1977) record a large-scale mortality of salmon in the River Wye during the night of 28-29 June 1976. The daily mean river temperature increased from 21.4°C on June 23 to 26.3°C on June 28. The highest temperature recorded on June 28, the day before the large fish-kill, was 27.6°C recorded at 16:00 BST. Coinciding with the rising water temperature, a die-off of dense macrophyte growth in the river caused dissolved oxygen levels to drop markedly, falling to less than 2 mg/l on June 28 and less than 1 mg/l on June 29.

Low temperatures also affect salmon migration. Swimming ability (burst speed) is limited by low temperatures (Beach 1984; Figure 8.3). Pyefinch (1955) noted that salmon were unable or unwilling to ascend the fish pass at Pitlochry at water temperatures below 5-5.5°C, and Mills and Graesser (1981) describe a series of falls and rapids of increasing severity on the lower Cassley that fish cannot ascend at temperatures below 7.2, 8.9 and 11.1°C, respectively.

## 8.4 Angling

Water temperature affects angling success. Danie *et al* (1984) state that angling is rarely successful at water temperatures in excess of 20°C. It is also widely believed that angling is likely to be more successful when the air temperature exceeds that of the water.

Exercising salmon to exhaustion, such as capture by rod and line, can cause mortality at high temperatures. Wilkie *et al* (1996) trapped upstream migrating grilse and held them in cages. A group of ten fish were then hooked in the upper jaw, placed in the river, and played to exhaustion (fish no longer able to maintain equilibrium in the water) when the water temperature was 22°C. The fish were then returned to the cages; four died within 12 hours. No control fish, which had been trapped and held in cages throughout, died. This finding contrasts with an earlier study where no mortality was associated with fish angled at 6°C. Physiological analysis suggested that the replacement of depleted glycogen and removal of increased levels of lactate in the white muscles was compromised at 20°C compared to 6°C, although a subsequent study (Wilkie *et al* 1997) gave conflicting results in this respect.

# 9 Gamete development and spawning

## 9.1 Development of gametes

The temperatures experienced by female salmon in the months before spawning can have a major effect upon egg quality and survival. Working on a stock transferred to the southern hemisphere, King *et al* (2003) maintained developing broodstock in water of 14, 18 and 22°C for three months from mid summer (January to March, equivalent to July to September in the natural range of the species); the temperature was maintained at 8°C thereafter for all three groups. Eggs derived from fish experiencing the 22°C regime were smaller, exhibited reduced fertility (i.e. percentage of eggs fertilised by a standard technique) and experienced reduced survival to the eyed stage compared to those from the fish held at lower temperatures (Table 9.1).

**Table 9.1. Effects of holding female broodstock of Atlantic salmon at different temperatures on egg quality.**

Attribute	14°C	18°C	22°C
Mean egg diameter	5.760	5.668	5.396
Mean egg fertility	93.4%	86.5%	69.4%
Mean egg survival	85.6%	84.5%	41.9%

Later work by the same group in Tasmania (King *et al* 2007) narrowed down the temperature-sensitive period as mid February to mid March (equivalent to mid August to mid September in the northern hemisphere); a four-week period of elevated temperature (22°C from a base of 14°C) centred on March 1 appeared to be as damaging as a three-month period at the higher temperature, whereas similar periods centred on February 1 and April 1 showed a much reduced impact. The authors suggest that high-temperature “spikes” may be as damaging as prolonged exposure, depending upon the timing. Watts *et al* (2004) suggest a physiological pathway for this effect through impaired synthesis or activity of cytochrome P540 aromatase. Low activity of this enzyme reduces levels of plasma 17β-estradiol and vitellogenin which play an important role in egg development.

Taranger and Hansen (1993) studied the effect of temperature manipulation on ovulation in Atlantic salmon. Three groups of fish were held at ambient temperature until the end of October, after which they were subjected to three different regimes: ambient (gradually falling from about 10°C); warm (ambient plus about 4°C) and cool (ambient minus about 3°C). Following the manipulation temperature regime, from November 1 ovulation progressed similarly in all groups for about a week, but faltered thereafter in the warm-water group. At the end of the experiment on December 19, only 10 of the 32 females in the warm-water group had ovulated, whereas a total of three failed to do so from the other two groups. Survival of eggs from fertilisation to the eyed stage was also reduced in the warm-water group at 76. per cent, compared to 84.5 and 92.1 per cent in the control (ambient) and cool-water groups respectively. These fish were derived from a hatchery strain developed from fish from several Norwegian rivers.

## 9.2 Spawning

Shields *et al* (2004) discuss the possibility that the timing of spawning by different salmonid stocks might be genetically determined by the winter temperature regime of their environment so that the fry start to feed at the optimum time in the spring. Native brown trout in chalk streams, which are groundwater fed and are generally warmer than surface-water fed streams in winter, generally spawn in January. Shields *et al* noted a bimodal timing of spawning in the upper Hampshire Avon and its tributaries, with the wild fish spawning in January and February, and introduced hatchery fish spawning in November.

Webb and McLay (1996) examined the timing of spawning of Atlantic salmon throughout the catchment of the Dee in Aberdeenshire. Spawning occurred earlier in the upper catchment where winter temperatures were lowest, but hatching occurred first in the lower catchment. Again, it was concluded that the variation in spawning time was a genetic adaptation to allow hatching at the most opportune time in the spring. The temperature at spawning in the upper catchment ranged from 0.8 to 8°C, and was on average 2.5°C higher for the lower catchment. The authors suggested that the dichotomy of spawning time was an adaptation for optimising the emergence timing and not driven by the occurrence of a specific temperature for spawning.

Work at INRA by Edward Beall is described on the INRA website ([www.international.inra.fr](http://www.international.inra.fr)). It suggests that an upper threshold for spawning of Atlantic salmon in France is 11.5°C, and that temperatures above this level cause “inhibiting discomfort or physiological stress”. Females must be able to expel their eggs within eight to 10 days of ovulation, otherwise their fecundity or the survival of the eggs is considerably impaired. Beall has noted that over the past 20 years the water temperature has increasingly exceeded 11.5°C, increasing from 4 per cent to 11 per cent of the spawning period; such temperatures now occur at some point on 60 per cent of days. During such periods the fish cannot reproduce, but the eggs continue to mature. Thus the spawning window is narrowing and may lead to winters without effective reproduction.

# 10 Integrating for population-level effects

**“Effects at the population and community levels are probably the least understood aspects of thermal stress and are probably the most important in relation to the impact of man’s activities on the freshwater ecosystem.”**

**Elliott (1981)**

The presence and well-being of populations of salmonids depends on more subtle factors than a simple absence of directly lethal conditions. According to Brett (1956) “it is interesting to note that speckled trout are not usually found at temperatures exceeding 19°C, which is the upper limit of their preferred range, although considerably below the upper lethal level.” Similarly, Huet (1962) concluded that he would expect to find that running water in which salmonids were the dominant fish would have maximum temperatures not exceeding 20°C, and when the fauna was mixed salmonid and cyprinid, 22°C. Alabaster and Lloyd (1982) suggest that “for salmonids of the genus *Salmo*, 20-21°C should be accepted as the upper permissible temperature during the warmest season of the year.” Again, these levels fall far short of directly lethal conditions.

While it is clear that populations do sometimes experience conditions close to, or even in excess of, directly lethal levels, such circumstances are unlikely to determine the presence or dominance of salmonid populations. The situation is summed-up well in the words of Hari *et al* (2006), who noted a reduction in the range and abundance of brown trout in streams in Switzerland associated with an increase in river water temperature:

*“Although the observed annual increase in RWT (River Water Temperature) lies well within the range of natural fluctuation to which the fish are adapted, it does result in a systematic shift in habitat conditions, thus exerting a selective pressure towards more tolerant individuals (or even species) and disturbing established balances in the ecosystem affected. Additionally, temporal effects, such as the acceleration of egg, alevin and fry development may result in mismatching problems that are more dramatic than the RWT increase itself.”*

The above quotation does, however, raise the possibility that natural selection could allow populations to adapt to changing conditions. It is likely that genetics are involved in many aspects of the thermal biology of salmonids, such as the timing of spawning and smolt development, and their migratory behaviour. There is evidence of a shift in some of these characteristics in response to recent climate changes, for example the timing of river entry of Atlantic salmon at the southern edge of their range in North America (Section 8). The extent to which other such adaptive changes will take place will depend upon a number of factors including the extent, variability and rate of change of the temperature regime, and the genetic variation available to the populations affected.

There is also the possibility of introducing fish from elsewhere, perhaps where historically conditions have naturally approximated to the changed regime, to replace stocks that are extirpated or compromised by climate changes.

Webb and Walsh (2004) modelled the effect of increased river temperatures, based upon predicted climate change scenarios, on fish populations in 27 rivers in the UK. For salmon and brown trout they used a “physiological thermal tolerance zone” based on the results of Elliott (1981, 1991).

For salmon, their modelling suggested adverse effects on spawning and embryo survival in the River Barle (Exe) and the Test by 2050. Under the scenario of high global warming, they predicted that 12 of the 27 rivers would be uninhabitable by Atlantic salmon by 2080, mainly those in the south and east.

For brown trout, the model suggests that seven of the 27 rivers are currently uninhabitable, and that this will increase to 9 by 2050 and 12 by 2080 under the low global warming scenario. Under the high global warming scenario, the number of uninhabitable rivers would increase to 14 in 2020, 15 in 2050 and 18 in 2080. Rivers in south west England that currently support brown trout would no longer provide a suitable habitat.

At the northern end of the distribution range of Atlantic salmon, Power (1969) examined the situation in Canada, Greenland, Iceland and Europe and concluded that the limit of distribution was represented by the number of days per year with an average air temperature of 6°C or more falling below 100.

From the experimental studies considered in this report, critical temperatures for Atlantic salmon appear to be about 2°C higher than the equivalent for brown trout, suggesting that salmon should be less susceptible to any adverse impacts of climate change involving warming.

Care is needed in interpreting this finding at face value because it is possible that the specific stocks used experimentally may not represent the full range of characteristics of the species. For example, many studies involved brown trout originating from hatcheries. Ferguson (2006) noted that most hatchery stocks in the UK were of remarkably similar genetic composition, which is markedly different to natural stocks. Some trout studies discussed in Section 6 noted that they observed somewhat higher temperatures for certain threshold levels compared to those observed by Elliott (1981) who used fish of hatchery origin. It is possible that some of the apparent differences between threshold temperatures for trout and salmon are due, at least in part, to inter-stock rather than inter-specific differences.

However, the growth models developed by Elliott and Hurley (1997) for brown trout and Elliott *et al* (1995) for Atlantic salmon both used wild stocks from the Rivers Lune and Leven and thus should be directly comparable. These two models showed threshold values for salmon for the lower, upper and optimal temperatures for growth being of the order of 2°C higher for salmon. It may be that salmon, and perhaps sea trout too, are particularly susceptible to warm conditions in the sea, estuary and lower river that non-migratory trout simply do not experience. Certainly it is salmon, at least in the southern parts of the natural range, that appear to have declined to a greater extent than brown or sea trout in recent years.

Overall, it would appear that any change in the environment which increases the time when the fish are subjected to the upper or lower critical temperature ranges (Section 4.4) is likely to have an impact on the well-being of the population. In addition, we can identify critical temperature ranges for specific life-history stages such as egg maturation, spawning and estuary passage.

# 11 Summary and conclusions

1. This document reviews the thermal biology of brown trout and Atlantic salmon with particular reference to aspects that may be affected by climate change (Section 1).
2. The incubation period (fertilization to hatching) is dependent upon water temperature. The incubation period for both species is 100 days at 5°C, and 50 days at 10°C (Section 2.1).
3. The range of temperatures in which eggs survive is around 0-13°C for brown trout and 0-16°C for Atlantic salmon. However, mortality and deformity rates increase markedly in salmon eggs above 12°C (Section 2.2).
4. The period between hatching and first feeding, when the fish subsist on their yolk sacs, is similarly influenced by water temperature; it is around 38 days at 7.5°C (Section 3.1).
5. Alevins can survive in a wider range of temperatures than can eggs; Atlantic salmon alevins can develop normally up to 22°C (Section 3.2).
6. Temperature polygons are presented for trout and salmon showing the effect of acclimation temperature on lethal temperatures and the range of temperatures at which feeding occurs (Section 4.1).
7. Upper lethal temperatures are dependent upon acclimation and the length of time that the fish are subjected to them. With acclimation to warm water the 1000 minute upper lethal temperature is 26.7°C for brown trout and 29.5°C for Atlantic salmon parr. The seven-day upper lethal temperature is 24.7°C for trout and 27.8°C for salmon parr (Sections 4.2 and 5.2).
8. Brown trout (and presumably salmon) may survive short-term high stream temperatures by seeking cooler thermal refuges in pools and deeper water (Section 4.2).
9. For brown trout, growth can occur between 3.5 and 19.5°C, with maximum growth (given feeding to satiation) at 13.1°C (Section 4.2).
10. For Atlantic salmon, growth can occur between 6.0 and 22.5°C, with maximum growth at 15.9°C (Section 5.2).
11. Where a choice is available, salmonids appear to avoid areas with temperatures outside their growth range (see previous). The zone between the growth range and lethal temperatures has been called the critical range, over which increasing stress and disturbance to normal behaviour is apparent (Sections 4.4 and 5.3).
12. Increasing temperature increases the effect of many pollutants and increases the susceptibility of fish to many pathogens (Section 4.5).
13. Smolt age is dependent on growth, which is in turn dependent upon a number of factors including the temperature regime. A decrease in mean smolt age has been recorded in many populations of sea trout and salmon (Section 6.1).

14. The development of smolt characteristics is temperature dependent, as is the rate of loss of smolt characteristics (including the ability to make the transition to salt water) if migration is delayed or prevented (Section 6.2).
15. The timing of smolt migration is influenced by a number of factors including temperature. Early migration of salmon smolts in warm seasons may have consequences for marine survival – see below (Section 6.3).
16. Conditions in the sea, including sea surface temperature (SST), clearly have a major effect on the survival, condition and growth of salmon, but the situation is complex. Major shifts in the balance of sea-age at return appear to be linked to SST (Section 7.2).
17. The marine survival of Atlantic salmon from two European stocks has been negatively correlated with the extent and location of sea surface temperatures between 5 and 7°C, and positively correlated with the extent and location of SST of 8-10°C in May during the year of smolt migration (Section 7.3).
18. There is evidence from the River Bush (Ireland) and the Girnock Burn (Scotland) that a lower survival is associated with early salmon smolt migration in warm years (Section 7.3).
19. There has been a decline in marine survival and the condition of salmon in recent years (culminating in the widespread occurrence of “thin grilse” in 2006) which is correlated with an increase in winter SST (Section 7.4).
20. Survival in, and passage through, the estuary by returning adult salmon is influenced by temperature, especially where other water quality parameters are critical. The lethal level of dissolved oxygen is around 3 mg/l at 15°C, and 7 mg/l at 25°C (Section 8.2).
21. Temperatures exceeding about 16°C may be associated with reduced migration in estuaries and rivers, with very little migration above about 20-23°C, but varying between rivers (Sections 8.2 and 8.3).
22. Atlantic salmon delayed in estuaries in hot, dry summers may suffer significant mortality (Section 8.2).
23. Swimming ability (burst speed) is limited by low temperatures, resulting in reduced migration under cold conditions (Section 8.3).
24. The temperature experienced by adult female salmon in the months before spawning can affect gamete quality. Eggs produced by females kept at 22°C were smaller, less fertile and less viable than those produced by fish held at 18°C or below (Section 9.1).
25. Ovulation falters or fails in fish maintained at an elevated temperature, for example 4°C above ambient temperatures in one experiment (Section 9.1).
26. Spawning appears to be timed so that the resulting fry start to feed at the optimum time in the spring. As the rate of egg development is temperature dependent there is a wide variation in spawning time, presumably under genetic control (Section 9.2).

27. Spawning only occurs within a limited temperature range, e.g. below 11.5°C for Atlantic salmon in France. Recent climatic warming has reduced the time available for successful spawning in this case (Section 9.2).
28. The presence of viable populations of brown trout and salmon appears to be limited by temperatures well below those considered to be directly lethal (Section 10).
29. Critical temperatures for Atlantic salmon appear to be about 2°C higher than equivalent figures for brown trout, suggesting that trout would probably suffer sooner from environmental warming. However, it is the salmon that appear to have declined to the greater extent, especially in the southern part of their range (Section 10).
30. Overall, it appears that occurrence of temperatures within the upper critical temperature range (i.e. above 19.5°C for brown trout and 22.5°C for Atlantic salmon) represents a stress that may affect the long-term well-being of the population. In addition, there may be effects on specific aspects of life-history at temperatures below this level (Section 10).

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