Temperature requirements of Atlantic salmon *Salmo salar*, brown trout *Salmo trutta* and Arctic charr *Salvelinus alpinus*: predicting the effects of climate change

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Atlantic salmon *Salmo salar*, brown trout *Salmo trutta* (including the anadromous form, sea trout) and Arctic charr *Salvelinus alpinus* (including anadromous fish) provide important commercial and sports fisheries in Western Europe. As water temperature increases as a result of climate change, quantitative information on the thermal requirements of these three species is essential so that potential problems can be anticipated by those responsible for the conservation and sustainable management of the fisheries and the maintenance of biodiversity in freshwater ecosystems. Part I compares the temperature limits for survival, feeding and growth. *Salmo salar* has the highest temperature tolerance, followed by *S. trutta* and finally *S. alpinus*. For all three species, the temperature tolerance for alevins is slightly lower than that for parr and smolts, and the eggs have the lowest tolerance; this being the most vulnerable life stage to any temperature increase, especially for eggs of *S. alpinus* in shallow water. There was little evidence to support local thermal adaptation, except in very cold rivers (mean annual temperature <6·5° C). Part II illustrates the importance of developing predictive models, using data from a long-term study (1967–2000) of a juvenile anadromous *S. trutta* population. Individual-based models predicted the emergence period for the fry. Mean values over 34 years revealed a large variation in the timing of emergence with *c*. 2 months between extreme values. The emergence time correlated significantly with the North Atlantic Oscillation Index, indicating that interannual variations in emergence were linked to more general changes in climate. Mean stream temperatures increased significantly in winter and spring at a rate of 0·37° C per decade, but not in summer and autumn, and led to an increase in the mean mass of pre-smolts. A growth model for *S. trutta* was validated by growth data from the long-term study and predicted growth under possible future conditions. Small increases (<2·5° C) in winter and spring would be beneficial for growth with 1 year-old smolts being more common. Water temperatures would have to increase by *c*. 4° C in winter and spring, and 3° C in summer and autumn before they had a marked negative effect on trout growth.   © 2010 The Authors

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Key words: Arctic charr; Atlantic salmon; brown trout; climate change; growth models.

INTRODUCTION

Atlantic salmon *Salmo salar* L., brown trout (including the anadromous form, sea trout) *Salmo trutta* L. and Arctic charr *Salvelinus alpinus* (L.) provide important

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commercial and sports fisheries in western Europe. They are also the only species in the subfamily Salmoninae (family Salmonidae) that are native to Britain and Ireland. Klemetsen *et al.* (2003*a*) have produced a very comprehensive review of some aspects of their life histories and noted that several studies have raised concern as to how climate change, particularly global warming, will ultimately influence and affect salmonid populations in various ways (Power & Power, 1994; Minns *et al.*, 1995; Dempson *et al.*, 2001). Graham & Harrod (2009) recently reviewed the implications of climate change for the fishes of Britain and Ireland and concluded that changes in climate, especially water temperature, have and will continue to have an effect on fishes at all levels of biological organization. They add that the fish responses will vary according to their tolerances and life stage and are complex and difficult to predict. They present overviews for several marine and freshwater species, including *S. salar* and *S. alpinus* but, surprisingly, not *S. trutta*. Another recent review examined the effects of water temperature and flow on anadromous salmonids with emphasis on *S. salar* and *S. trutta* (Jonsson & Jonsson, 2009). It summarizes thermal and flow effects on activity, migrations and spawning, embryonic development, hatching, emergence, growth and life-history traits. There is inevitably some overlap between these two large reviews and also Part I of the present overview. The latter, however, stresses comparative aspects of the thermal requirements of *S. salar*, *S. trutta* and *S. alpinus*.

Temperature is often regarded simply as a factor affecting the physiology and behaviour of a fish, but it is also a characteristic of its habitat, being one axis of its multidimensional niche (Magnuson *et al.*, 1979). There is some evidence that river temperatures have already increased in several countries (Caissie, 2006). As water temperature increases due to climate change, it is important to obtain quantitative information on the thermal requirements of *S. salar*, *S. trutta* and *S. alpinus* so that potential problems can be anticipated by those responsible for the conservation and sustainable management of the fisheries, and the maintenance of biodiversity in freshwater ecosystems.

Fishes are obligate poikilotherms (ectotherms) and can often perceive temperature changes of $<0.5°$ C (Murray, 1971). Their gills are an effective heat exchanger, but most heat transfer (70–90%) is by conduction directly through the body wall (Elliott, 1981). When the water temperature changes, thermal equilibrium must occur in the fish, but there is a time lag. For example, in experiments with *S. trutta*, this time lag increased with fish mass so that the body temperature of larger fish was independent of small and rapid fluctuations in temperature (Elliott, 1981). It is therefore evident that small *S. trutta* are much more susceptible to fluctuations in water temperature than larger *S. trutta*; being large is a useful buffer against sudden changes in water temperature. Therefore, a large lake *S. trutta* could ascend rapidly from cooler, deeper water to take a prey item in the warmer, surface water and then descend again rapidly to cooler water without a major change in body temperature.

In spite of this buffering effect, there are clear temperature limits for different life stages and functions of fishes, and these can vary markedly among species. Therefore, this overview starts in Part I by comparing the temperature limits for survival, feeding and growth of *S. salar*, *S. trutta* and *S. alpinus*, using data from Europe and North America. In Part II, it demonstrates the importance of obtaining long-term data on water temperature and different life stages and emphasizes the importance of developing predictive models, using data from a long-term study (1967–2000)

of a juvenile anadromous *S. trutta* population. Finally, a validated growth model is used to predict growth under different temperature regimes that may arise as a result of climate change. Although these predictions are based on a growth model for a British population, they are probably applicable to populations of *S. trutta* in other countries.

PART I: TEMPERATURE LIMITS FOR SURVIVAL, FEEDING AND GROWTH

SURVIVAL

Although fishes occur in habitats from $-2 \cdot 5°$ C (polar species) to $44°$ C (desert species), no species can survive over this range and each species has a characteristic thermal niche with upper and lower lethal limits. Freshwater teleosts in temperate regimes are usually found within the range $0–30°$ C. Minimum temperatures may fall to $0°$ C in upland and northern streams in winter and maximum values may exceed $30°$ C in shallow ponds in summer or in waters that receive a thermal discharge. The thermal requirements of freshwater fishes may be species specific, and therefore genetically fixed among populations of the same species. The basic parameter is the critical thermal maximum for survival because it often correlates with other critical temperatures such as the optimum temperature for growth and the upper limits for feeding and growth (Jobling, 1981).

Two categories of methods have been used to investigate the critical thermal limits (Kilgour & McCauley, 1986; Elliott, 1994, 1995). In the first group, the rapid-transfer method, fishes are transferred abruptly from an acclimation temperature to a higher, or lower, constant temperature until a critical value for survival is found, usually for 50% of the fishes. Thus, they are subjected to handling stress as well as thermal shock. In the second group, the slow-heating method, the critical value is determined by changing the temperature at a constant rate from the acclimation value until the fish first shows signs of stress, usually equilibrium loss, or death occurs. Such methods overcome the disadvantages of those in the first group but have a new problem that the rate of temperature change can affect the final critical value. Arguments continue over the equivalence of values determined by the two groups of methods, but Kilgour & McCauley (1986) provided a reconciling view that was supported strongly by the detailed experiments of Elliott & Elliott (1995). To add further complexity, two values for critical thermal limits occur in the literature (Kilgour & McCauley, 1986; Elliott, 1994, 1995). The incipient lethal temperature (ILT) is that which fishes (usually 50% of the sample) can tolerate for a long period (7 days is usual standard), but beyond which they cannot survive indefinitely. The ultimate lethal temperature (ULT) is that which fishes cannot tolerate for even short time periods (10 min is the usual standard time). The latter value is sometimes called the critical thermal maximum or minimum.

Critical temperatures for the survival of the different life stages of *S. salar*, *S. trutta* and *S. alpinus* are compared in Table I. Most values increase with the acclimation temperature (Elliott, 1981, 1994), and the wide ranges for some values are due to this and the different methodologies mentioned above. *Salmo salar* have the highest temperature tolerance, followed by *S. trutta* and finally *S. alpinus* with the lowest

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TABLE I. Critical temperatures ($^\circ$ C) for survival of different life stages of *Salmo salar*, *Salmo trutta* and *Salvelinus alpinus*

	Salmo salar		*Salmo trutta*		*Salvelinus alpinus*	
	Lower	Upper	Lower	Upper	Lower	Upper
Eggs	0	16	0	13	0	8
Alevins						
Incipient	0–2	23–24	0–1	20–22	0–0·3	19–21
Ultimate	0–1	24–25	0	22–24	0–0·2	23–27
Parr + smolt						
Incipient	0–2	22–28	0–0·7	22–25	0–1	22–23
Ultimate	−0·8	30–33	−0·8	26–30	−1·0	26–27
Feeding	0–7	22–28	0·4–4	19–26	0·2	21–22

Alevins, hatched fish with yolk sac, feeding entirely on yolk, living in gravel nest; parr, after the yolk sac has been fully absorbed and until smoltification begins; smolt, when seaward migration occurs.
Values collated from references given in Elliott & Baroudy (1995) for all three species. Additional references: Grande & Andersen (1991), Cunjak *et al*. (1993), Bremset (2000), Jonsson *et al*. (2001), Lund *et al*. (2002) and Finstad *et al*. (2004) for *S. salar*; Grande & Andersen (1991), Bremset (2000) and Ojanguren *et al*. (2001) for *S. trutta* (including sea trout); Brännäs & Wiklund (1992), Lyytikäinen *et al*. (1997), Thyrel *et al*. (1999), Elliott & Klemetsen (2002) and Klemetsen *et al*. (2003*b*) for *S. alpinus*.

tolerance to high temperatures. *Salmo salar*, however, has the poorest tolerance to low temperatures compared with the other two species. The ultimate lower lethal temperature is for the anadromous form of each species in sea water; *S. alpinus* can tolerate temperatures as low as $-0\cdot99^\circ$ C compared with higher values of $-0\cdot81^\circ$ C for *S. trutta* and $-0\cdot75^\circ$ C for *S. salar*. Sea temperatures below the latter value caused high mortality in sea-caged *S. salar* on the north-east coast of North America. This problem was remedied by the introduction of an anti-freeze gene to produce genetically engineered freeze-resistant *S. salar* (Fletcher *et al*., 1988, 1992; Du *et al*., 1992). For all three species, the temperature tolerance for alevins is slightly lower than that for parr and smolts, and the eggs have the lowest tolerance. The egg stage would be clearly the most vulnerable life stage to any increase in temperature as a result of climate change.

In spite of the varied methodology and different acclimation temperatures used by different workers, values are remarkably similar over a wide geographical range. For example, *S. alpinus* is the species most adapted to cold water, and it has been suggested that southern populations of this species may have been selected to tolerate warmer conditions than more northern populations (Swift, 1964). There is no evidence, however, to support this hypothesis. Recent work indicates negligible geographical variation in the thermal limits for alevins and parr, with similar values for *S. alpinus* from four races (strictly gamodemes) from Windermere, U.K. at 54° N (Baroudy & Elliott, 1994*a*), from four lakes in Sweden between 63 and 68° N (Thyrel *et al*., 1999), from Lake Inari at $69–70^\circ$ N in Finland (Lyytikäinen *et al*., 1997) and from the oligotrophic Fjellfrøsvatn at 69° N in Norway (Elliott & Klemetsen, 2002).

FEEDING AND GROWTH

The upper limits for feeding are also highest for *S. salar* and lowest for *S. alpinus*, while the lower limits are close to zero for all three species (Table I). The upper limits, however, vary markedly among different studies with some workers reporting fishes continuing to feed at temperatures close to or even within the incipient and lethal temperature ranges. There have been several detailed experimental studies on the growth of the three species, and these provided estimates of the lower and upper temperature limits for growth as well as the optimum temperature for growth (Table II). They sometimes provided the temperature at which the conversion of energy intake into growth was most efficient. All these values for *S. salar* are generally higher than those for the other two species. The optimum temperatures are for fishes feeding on maximum rations. It is important to realize, however, that the optimum temperature is not fixed but decreases with decreasing energy intake (Elliott, 1994; Elliott & Hurley, 2000*b*). Therefore, the ration level should always be given when defining an optimum temperature for growth.

The optimum temperature for growth in *S. trutta* also changes with diet, being *c*. 3° C higher for piscivorous fish and fish feeding on pelleted food than for fish feeding on invertebrates (Table II). Although the maximum conversion efficiency is higher at 42% for piscivorous *S. trutta* than that of 32% for *S. trutta* feeding on invertebrates, the temperatures at which these values occur are remarkably similar at close to 9° C (Table II). Furthermore, it is notable that the preferred temperature for 0+ and 1+ year parr of *S. trutta* in a temperature gradient (5−25° C) in the laboratory was 9−10° C, close to the temperature for maximum conversion efficiency

TABLE II. Temperature limits for growth, optimum temperature for growth on maximum rations and temperature for maximum growth efficiency, for *Salmo salar*, *Salmo trutta* and *Salvelinus alpinus* (° C). Maximum conversion efficiencies for growth energy as a percentage of energy intake are also given in parenthesis for *S. salar* (Norway), and for piscivorous *S. trutta* and *S. trutta* feeding on invertebrates

	Lower	Upper	Optimum	Growth efficiency
Salmo salar				
U.K.	6·0	22·5	15·9	*c*. 13
Norway	1·0−7·7	23·3−26·7	16·3−20·0	12−18 (42−58%)
Salmo trutta				
Invertebrate food	2·9−3·6	18·2−19·5	13·1−14·1	8·9 (32%)
Fish food	*c*. 2·0	*c*. 19·5	16·6−17·4	9·3 (42%)
Pelleted food	1·2−6·1	19·4−26·8	11·6−19·1	
Salvelinus alpinus				
U.K.	1·4	21·5	15·2	
Norway	4·7−5·3	21·2−21·5	14·4−15·0	
Sweden	0−3·3	20·8−23·2	15·2−17·2	<10 (45−55%)

References: Elliott & Hurley (1997), Forseth *et al.* (2001), Jonsson *et al.* (2001) and Finstad *et al.* (2004) for *S. salar*; Elliott *et al.* (1995), Forseth & Jonsson (1994), Elliott & Hurley (1999, 2000*a*, *b*), Ojanguren *et al.* (2001) and Forseth *et al.* (2009) for *S. trutta* (including sea trout); Larsson & Berglund (1998, 2005) and Larsson *et al.* (2005) for *S. alpinus*.

(J. M. Elliott, unpubl. data). Similarly, the preferred temperature for *S. alpinus* was *c*. 12° C, a value lower than the optimum temperature (Larsson, 2005).

THERMAL ADAPTATION

There are two hypotheses for thermal adaptation in ectotherms: (1) adaptation to local optima and (2) the countergradient variation hypothesis. The first hypothesis (Levinton, 1983) implies that natural selection can shift the optimum temperature for growth to match the prevailing temperature in a new or changed thermal regime. There is little support for this hypothesis from studies of salmonids (Elliott, 1991, 1994; Forseth *et al.*, 2001, 2009; Larsson *et al.*, 2005; Jonsson & Jonsson, 2009). The second hypothesis (Levins, 1969; Conover & Schultz, 1995) suggests that populations from hostile environments (low temperatures, short season for growth and strong competition) perform better at all temperatures than conspecifics from benign environments. This hypothesis was supported by Norwegian and Spanish populations of *S. trutta* from very cold rivers with a mean annual water temperature <6·5° C (Jensen *et al.*, 2000; Nicola & Almodóvar, 2004) and also by studies of growth bimodality and digestive performance of juvenile *S. salar* from geographically disjunct populations (Nicieza *et al.*, 1994*a*, *b*). The statistical power of the latter studies, however, is low because only two populations were used. It is also notable that heritability for tolerance to high water temperatures was detected in an experimental study with Chinook salmon *Oncorhynchus tshawytscha* (Walbaum) from a northern cold-water stream but not from a southern warm-water stream (Beacham & Withler, 1991). In contrast, experimental growth data provided no indication of thermal adaptation or of support for the countergradient hypothesis for *S. alpinus* from 11 European water bodies between 54 and 70° N (Larsson *et al.*, 2005) and for anadromous, stream-resident and lake-resident *S. trutta* from Norway and Sweden (Forseth *et al.*, 2009). Similarly, Jonsson *et al.* (2001) investigated possible thermal adaptation of *S. salar* parr from five Norwegian rivers and found no correlations between either latitude or the thermal conditions in the river of origin and the temperature limits for growth, thermal growth optima or maximum growth. They did find, however, that growth rate varied significantly among populations. Since growth was not generally higher in these Norwegian populations than in the British populations studied by Elliott & Hurley (1997), there was no support for either hypothesis for thermal adaptation. Finstad *et al.* (2004), however, found that *S. salar* from three very cold rivers in north Norway (mean annual temperatures: 4, 6 and 9° C, respectively) fed and grew at temperatures in the range 1–6° C, whereas the models developed from the experiments of Jonsson *et al.* (2001) predicted a cessation of feeding and growth at temperatures <5° C. In the absence of further studies, the general conclusion is that salmonids show little intraspecific variation to support either of the two hypotheses for thermal adaptation, except in very cold rivers. The adaptive variation in growth potential appears to be related to life-history characteristics influencing reproductive success rather than their thermal conditions (Jonsson & Jonsson, 2009).

It is easy to conclude erroneously that thermal adaptation has occurred. For example, juvenile coho salmon *Oncorhynchus kisutch* (Walbaum) from three populations were heated in a tank alongside the stream to determine their critical thermal maximum (CTM) (Konecki *et al.*, 1995). Tolerances varied among the populations with the fish from the coolest stream having a lower CTM (28·2° C) than fish from

the two warmer streams (29·1 and 29·2° C). After the fish had been kept in the laboratory for 3 months at the same constant temperature (11° C, range ±1° C), however, the CTMs were no longer different, indicating that the population-specific differences resulted from different acclimation regimes rather than from genetic thermal adaptation.

A geothermal river in Yellowstone National Park is the one place where high thermal tolerance would be expected to occur, and *S. trutta*, rainbow trout *Oncorhynchus mykiss* (Walbaum) and brook trout *Salvelinus fontinalis* (Mitchill) have inhabited the river since 1889 (Kaya, 1977). The fishes were apparently unaffected by daily maximum water temperatures of 29–30° C in summer and were thus living at temperatures normally regarded as lethal. It was shown experimentally, however, that they were no more resistant to higher temperatures than those from two hatcheries, both groups of fishes having a ULT in the range 23·2–26·2° C with the ULT increasing with acclimation temperature (Kaya, 1978). Closer observation in the river revealed that the fishes simply avoided the high summer temperatures by migrating into a cold-water tributary as a refuge (Kaya *et al.*, 1977). If only the first paper had been published, it would have been cited erroneously as an example of genetically different, and more thermal tolerant, populations.

PREDICTING THE EFFECTS OF CLIMATE CHANGE

There is no evidence for thermal adaptation at the upper temperature limits for survival, feeding and growth in *S. salar*, *S. trutta* and *S. alpinus*. There is some evidence that *S. trutta* and *S. salar* living in very cold rivers (mean annual temperature <6·5° C) have become adapted to feed and grow at low temperatures approaching 0° C. As the name implies, *S. alpinus* can always cope with such low temperatures. Under ice in both lakes and streams, *S. alpinus* can feed and grow at temperatures <1° C and as low as 0·2° C (Klemetsen *et al.*, 2003b; Siikavuopio *et al.*, 2009). Thermal stress for parr and smolts will occur when water temperatures are in the range 22–28° C (*S. salar*), 22–25° C (*S. trutta*) and 22–23° C (*S. alpinus*), with slightly lower values for their alevins (Table I).

These limits may occur in streams and rivers during summer droughts. In a long-term study of a juvenile anadromous *S. trutta* population, summer drought led to increased mortality, especially for 1+ year fish; the four worst droughts being in order of severity: 1995 (most severe), 1976, 1983 and 1984 (Elliott *et al.*, 1997). The 1976 drought also caused high mortalities of adult *S. salar* in the River Wye, U.K. (Brooker *et al.*, 1977) and juvenile *S. salar* in a small tributary of the River Severn, U.K. (Cowx *et al.*, 1984). As pools in streams serve as refugia during droughts, *S. trutta* responses to thermal and oxygen stress in pools were studied in a population of resident *S. trutta* living above an impassable waterfall (Elliott, 2000). In non-drought years, measurements at the deepest point in five pools in July were 12–18° C and 7·8–9·8 mg O_2 l^{-1}, and all ages of *S. trutta* were present. In drought years (1976 and 1983), temperature increased to 24–29° C and oxygen concentration decreased to 1·2–2·5 mg l^{-1} in the smaller pools and *S. trutta* was absent, but values in two larger pools were 20–25° C and 3·6–4·8 mg l^{-1} at water depths where *S. trutta* was present. When *S. trutta* was absent, temperatures were close to, or above, the incipient lethal level of 25° C (Table I). *Salmo trutta* in the two larger pools was faced with a choice of higher temperature with higher oxygen concentration near the
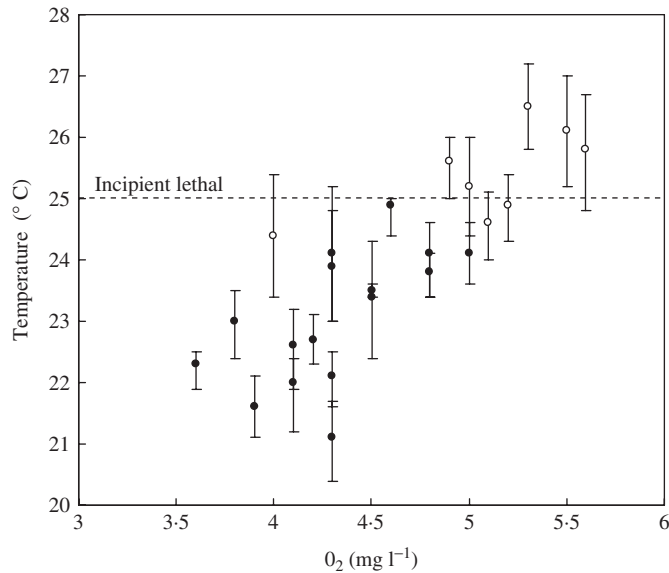
FIG. 1. Mean ± range temperature and mean oxygen concentration at different depths in two pools with (●) and without (○) *Salmo trutta* present in one or more of three depth layers (surface to 0·5, 0·5 to 1·0 m and 1·0 m to maximum depth) at midday and midnight during the droughts of 1976 and 1983 ($n = 24$); ---, incipient lethal temperature of 25° C (95% CL ± 0·5° C) (adapted from Elliott, 2000 with permission from The Fisheries Society of the British Isles).

surface, or lower temperature with lower oxygen concentration near the bottom, and showed a preference for the latter combination (Fig. 1). Similar results were obtained for *O. mykiss* in two stream pools in California, U.S.A. (Matthews & Berg, 1997). Most *O. mykiss* were found near the bottom at $17·5-21·0°$ C and $1-5$ mg O_2 l^{-1}, and they avoided the warmer surface waters with higher oxygen concentrations of $4-10$ mg l^{-1}. In both streams, the fish showed a similar behavioural response to thermal and oxygen stress and always chose lower temperatures in preference to higher oxygen concentrations. Such behavioural responses are clearly important factors for fish survival during severe droughts. As summer droughts will probably become more frequent as a result of climate change, the provision of suitable deep pools should be an essential part of a strategy for successfully managing populations of *S. trutta*, including anadromous forms, and juvenile *S. salar* in streams and rivers.

Salmo trutta are often found in ponds and small lakes, and rising water temperatures as a result of climate change will also lead to high mortality unless deep-water refugia are present or the fish can migrate to cooler inflow streams. Therefore, those responsible for their management should ensure that there are such refugia and no obstacles to prevent the fish entering the inflow streams. Climate change may also affect adversely *S. alpinus* inhabiting shallow, low altitude lakes because the fish may be unable to avoid harmful temperatures by moving to cool hypolimnetic water (Lehtonen, 1998).

The effects of rising temperature in large lakes are more complex than those in running water and small lakes because of the wide variation in temperature with depth. Of the three species, *S. salar* may pass through a lake as smolts or adults

returning to spawn in inflow streams. It was once thought that *S. salar* were only transient inhabitants of lakes, but it is now apparent that juvenile *S. salar* often use lacustrine habitat for rearing purposes in some river–lake systems (Klemetsen *et al*., 2003*a*). As *S. salar* has higher thermal requirements than *S. trutta* or *S. alpinus*, it could benefit from an increase in water temperature and smolt at a younger age, as in the southern part of their range. It is unlikely that lake temperatures will increase to values harmful to *S. salar*, *S. trutta* or *S. alpinus*, but the last species must move to cooler water when the surface waters attain values of 22–23° C (Tables I and II).

Rising temperature in lakes may affect feeding and growth because of the relationship between the optimum temperature for growth and the daily energy intake. For example, a *S. trutta* with a mass of 50 g cannot grow on a daily energy intake of 4·18 kJ (1000 cal) at 14·5° C, but growth is *c*. 1·46 kJ day^{-1} (350 cal day^{-1}) for the same energy intake at 8° C (Elliott, 1981). Similarly, to ensure the most efficient use of its maximum energy intake, *S. trutta* should move into water at 9·0° C, *i.e.* maximum 32 or 42% energy conversion for diets of invertebrates or fishes, respectively (Table II). Such a response may explain some of the movements of *S. trutta* from shallow to deeper water after feeding in lakes (Elliott, 1994). As long as this cooler water can be found in a lake and oxygen concentration remains suitable for *S. trutta*, they should not be subjected to thermal stress as a result of climate change. Other salmonid species often show vertical migrations in lakes (Elliott, 1994), and Brett (1971) was probably the first to propose that such movements may be related to various temperature optima for different physiological functions.

Salvelinus alpinus in lakes often shows vertical movements. For example, in Windermere, U.K., it is more numerous near the bottom during the day but moves upwards in the water column at night (Elliott & Baroudy, 1995). Fortunately, parr of *S. alpinus* are among the most tolerant of salmonid parr to low oxygen levels and can tolerate values as low as 2·2–2·4 mg l^{-1} (22–25% saturation) at 15–20° C and only 1·8–2·0 mg l^{-1} (15–17% saturation) at 5–10° C (Baroudy & Elliott, 1994*b*). If oxygen concentration decreased markedly in the pelagic zone, then parr of *S. alpinus* could probably cope better than those of *S. salar* or *S. trutta*. If oxygen levels near the lake bed fell below the values given above and surface temperatures increased above the incipient lethal level, then the volume of lake available to *S. alpinus* could be reduced. This happened in Windermere in the 1980s and led to a recovery programme to improve water quality and protect *S. alpinus* (Elliott *et al*., 1996). After some initial improvement, water quality deteriorated and catches of *S. alpinus* in the south basin of the lake are now at record low levels (Winfield *et al*., 2008). Hydroacoustic data showed that most *S. alpinus* avoid the upper 10 m of the water column, irrespective of temperature, and also avoid oxygen concentrations <2·3–3·1 mg l^{-1} in deep water (Jones *et al*., 2008). This range is similar to the tolerance limits for parr in the laboratory (Baroudy & Elliott, 1994*b*). The depth of the lower limits of the vertical distribution of *S. alpinus* in Windermere is highly correlated with deep-water oxygen concentration throughout the year prior to the autumn overturn, and this relationship leads to a marked reduction in the volume of habitat available to *S. alpinus* (Jones *et al*., 2008). The avoidance of the upper water column may also reduce the risk of being eaten by predatory fishes and birds. There are also ontogenetic changes in the habitat and sources of food for *S. alpinus*, especially when they occur with *S. trutta* in the same lake (Klemetsen *et al*., 2003*a*).

Finally, possible problems with egg development have to be addressed because this is the life stage with the lowest thermal tolerance for all three species (Table I). All three species usually spawn in late autumn and winter in Britain and Ireland, and water temperatures will not exceed the upper limits for egg survival unless there is a thermal discharge. Very few eggs, however, hatch at the upper limit, and the optimum range over which the highest percentage of eggs hatch is much lower at 4–7° C for *S. salar*, 1–8° C for *S. trutta* and 1–5° C for *S. alpinus* (Peterson *et al*., 1977; Humpesch, 1985). Stream temperatures in southern Britain have increased over 26 years (1980–2006) by 2·1–2·9° C in winter to values close to or exceeding 8° C (Durance & Ormerod, 2009). Such a high value is at the upper limit for eggs of *S. salar* and *S. trutta*. Autumn-spawning *S. alpinus* in Britain and Ireland often lay their eggs in shallow (water depth: 1–3 m) well-oxygenated water on the lake shore from late September to December, and their eggs and alevins require at least 9 mg O_2 l^{-1} (=70% saturation) at 5° C, a much higher value than that for parr (Elliott & Baroudy, 1995). If climate change leads to water temperatures >5° C and reduced oxygen levels in the spawning habitat, then the result could be catastrophic for the survival of *S. alpinus*. This is the most vulnerable of the three species to climate change, especially the egg and alevin stages. A recent survey of five Scottish populations, five English populations and one Welsh population in the U.K. has shown a decline in abundance, except for the most northerly Scottish population that showed a significant increase (Winfield *et al*., 2010). It would be tragic to lose populations of *S. alpinus*, a species recognized to hold significant biodiversity conservation value in Britain and Ireland (Maitland *et al*., 2007).

PART II: LONG-TERM DATA AND PREDICTIVE MODELS

THE IMPORTANCE OF LONG-TERM STUDIES AND A MODELLING APPROACH

Most ecologists agree that long-term studies are important but few conduct them. There are many reasons why they are rare. They are often more difficult to plan and execute than short-term studies and rarely yield immediate publications. They also require secure, long-term funding and such funding is rare. As ecology has moved from being a qualitative descriptive science to becoming a quantitative predictive science, awareness of the importance of long-term studies has increased. Elliott (1994) summarized some examples of how they have provided critical data on a number of practical issues that are of concern to society. Long-term studies are essential to provide estimates of baseline variation (it is naïve to assume a constant baseline), to detect long-term trends in the mean level of the baseline, to detect and evaluate the effects of rare events (*e.g.* droughts and spates) and to provide information for meaningful, testable hypotheses.

There is a strong link between long-term studies and mathematical modelling. The development of ecological theory is necessary for the advancement of the science and long-term studies are required for the testing of the theory. Both provide essential knowledge for the conservation and management of biodiversity in the natural environment. It must be remembered that all mathematical models are simplifications of reality. Complex models require many parameters and it is easy to become lost

in this complexity. The basic role of a model is to predict a baseline from which changes can be assessed. Modelling in population ecology is an iterative process in which a useful model is constantly tested and refined, then re-tested. Hence, the need for long-term data. Two case studies illustrate the importance of long-term studies and the development of predictive models, using data from a long-term study (1967–2000) of a juvenile anadromous *S. trutta* population in Black Brows Beck, a small stream in Cumbria, U.K. (Elliott, 1994). The first predicts the emergence period of fry and the second predicts the growth of juvenile *S. trutta* during the freshwater phase of their life cycle. Finally, the latter growth model is used to predict the possible effects of climate change on the growth of *S. trutta*.

CASE STUDY I: EMERGENCE OF FRY

Individual-based models were developed to predict the emergence period for *S. trutta* fry and their size at emergence (Elliott & Hurley, 1998*a*, *b*). The fry stage was defined as the short transition stage when the juveniles emerge from the safety of the gravel nest (or redd) and start to feed and disperse. Each model was developed from laboratory experiments and validated by field data for 8 years (1967–1971, 1974, 1975 and 1980). The first model was used to predict in each year the median date for fry emergence (50% emerged) and the dates on which 5 and 95% of the fry emerged [Fig. 2(a)]. Predicted values over 34 years (1967 to 2000) revealed a large variation in the timing of emergence with a difference of nearly 2 months between the extreme values for median emergence time (*i.e.* 22 March 1989 and 18 May 1979). Most of the variation in median emergence date was due to variations in water temperature with spawning date as a minor secondary factor; the latter, however, had a greater effect on the length of the emergence period (Elliott & Hurley, 1998*a*).

It was shown later that the emergence period correlated significantly ($r = 0.66$, $P < 0.001$) with the North Atlantic Oscillation Index (NAOI) [Fig. 2(a), (b)], and stream temperature during winter also correlated significantly ($r = 0.67$, $P < 0.001$) with the NAOI [Fig. 2(c)], providing a probable causal link (Elliott *et al.*, 2000). Therefore, the interannual variations in emergence may not be unique to this one stream, but may be typical of other *S. trutta* streams with similar climatic conditions. If fry emergence becomes consistently earlier as a result of warmer winters, then the length of the growth period in the first year of the life cycle could be extended. This could affect subsequent life stages, especially the timing of smoltification.

The North Atlantic Oscillation is a well-known climate pattern associated with changes in the strength of the surface westerly winds across the North Atlantic onto Europe. It has been observed for centuries through its effect on winter temperatures and affects a wide range of biota (Ottersen *et al.*, 2001). The NAOI is primarily a winter phenomenon, so its connection with wind, temperature and precipitation is strongest during winter. Therefore, attempts to link biological events to the NAOI in other seasons may not be successful. The NAOI used here is the winter index (December to March) based on the difference of normalized sea-level pressures between Lisbon, Portugal and Stykkisholmur, Reykjavik, Iceland (Hurrell, 1995). Positive indices are associated with stronger than average westerly winds over Europe, resulting in mild, wet winters. Conversely, negative values are associated with weaker westerly winds over the North Atlantic and correspondingly colder than
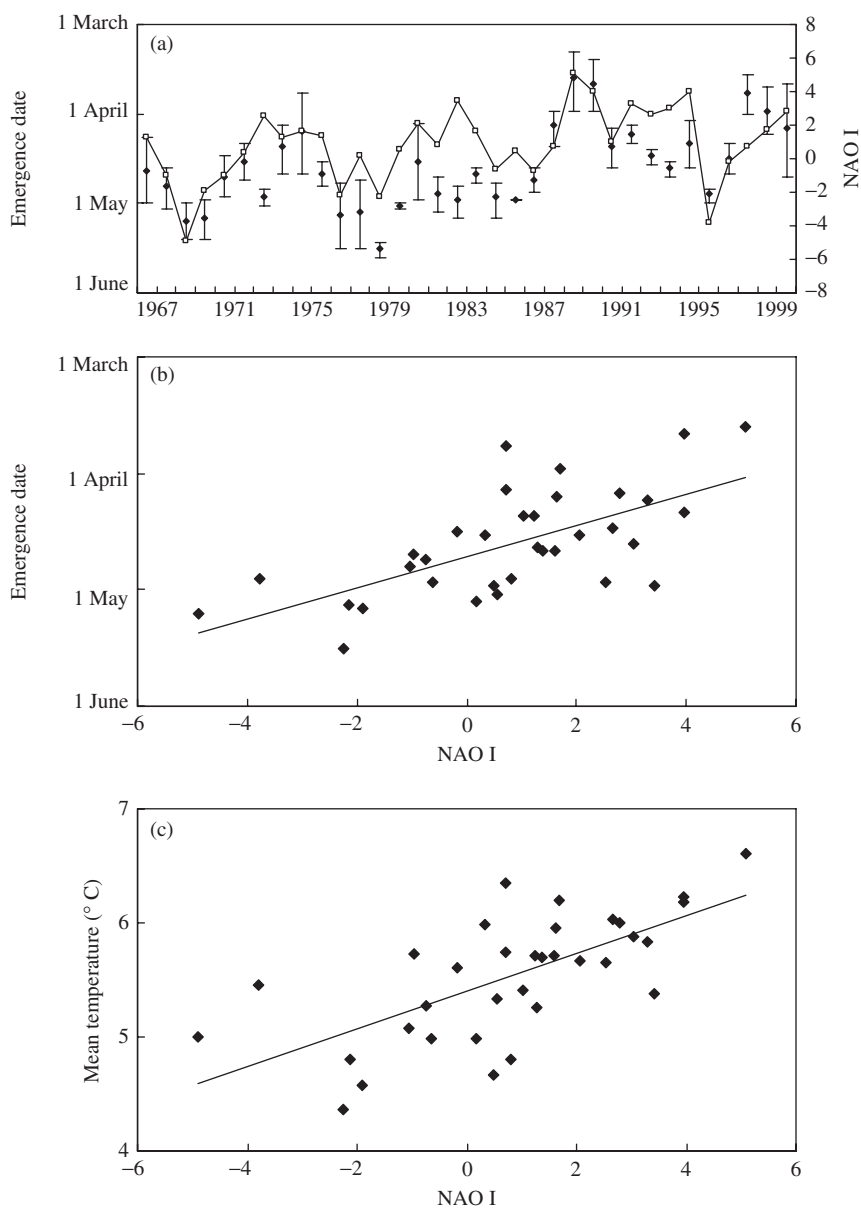
FIG. 2. (a) Variations in the North Atlantic Oscillation Index (NAOI) (-□-) and emergence times for fry ($\perp$) in each year from 1967 to 2000; marked dates are for 50% (●); limits of vertical lines are the dates on which 5 and 95% of the fry emerged, using the model in Elliott & Hurley (1998a). (b) Relationship between the NAOI and the day on which 50% of the fry emerged ($y = 38 \cdot 73 + 4 \cdot 02x$, y = days from 1 February; $r^2 = 0 \cdot 43$, $P < 0 \cdot 001$). (c) Relationship between the NAOI and mean water temperature in each year for the winter months of December, January and February ($y = 5 \cdot 40 + 0 \cdot 17x$; $r^2 = 0 \cdot 45$, $P < 0 \cdot 001$).

normal winters (Hurrell, 1996; Osborn, 2006). It is obvious from Fig. 2 that more values have been positive than negative in most years.

In their review of the earlier literature, Jonsson, B. & Jonsson (2004) cited several studies that identified the NAOI in winter as an important factor affecting the marine production of *S. salar*. Post-smolt growth in four stocks of *S. salar* in England and Wales, U.K. was also positively related to the index (Davidson & Hazlewood, 2005). The proportion of *S. salar* returning as grilse to a Norwegian river was positively related to the NAOI for the winter after their smoltification (*i.e.* warmer marine conditions during positive NAOI), as was also the total number of returning fish (Jonsson, N. & Jonsson, 2004). The mass increment of these grilse also correlated positively with the NAOI during spring and early summer (May to July) when the smolts first entered the sea. The positive NAOI, and hence warmer conditions for the smolts promoted rapid growth with better survival and feeding and facilitated the development of energy reserves for gonadal development after just one winter at sea. Hence, there was an increase in the number of *S. salar* returning as grilse. Parr growth and the proportion of 1 year-old smolts also correlated positively with the NAOI in the same population (Jonsson *et al*., 2005). These relationships with the NAOI clearly demonstrate the widespread effects of climate change on the life cycle of *S. trutta* and *S. salar*. They also show that the NAOI can be used as a useful indicator of climate change in the future. It is not the only factor operating. For example, the coefficient of determination (r^2) in Fig. 2(b) indicates that variation in the NAOI could explain 43% of the variation in emergence times, 57% was due to other factors.

CASE STUDY II: A GROWTH MODEL FOR *S. TRUTTA*

Unlike most vertebrates, many fish species exhibit indeterminate growth so that the mass of fish of similar age in the same species can vary considerably among populations. For example, the mass of 3 year-old mature female *S. trutta* can vary from only 75–100 g for resident stream fish to 5 kg or more for anadromous fish returning to spawn in fresh water (Elliott, 1994). As it shows such a wide variation in size, *S. trutta* is an ideal subject for studying the complexity of factors affecting its growth. In his comprehensive review of growth in fishes, Ricker (1979) emphasized the importance of developing mathematical models for growth. He showed that the early growth models were empirical equations fitting a course of growth in relation to time or age, usually at annual intervals, *e.g.* von Bertalanffy, Gompertz, Johnson and Richards growth curves. More than one model will often be found to describe satisfactorily the same set of observations, especially when applied to annual growth. These models also assume that growth is asymptotic, *i.e.* the size of a fish will tend towards some fixed limit no matter how long a fish lives. This assumption is clearly invalid for salmonids. Ricker (1979) concluded that more realistic models are required to describe growth over short periods of time and thus to determine if fishes are growing at their maximum potential.

It is 35 years since a predictive model was developed for the growth of *S. trutta* (Elliott, 1975). This model has now been used to investigate growth in at least 40 populations of *S. trutta*. In most populations, the fish were growing at or below their maximum potential with only a few populations in which they grew faster than the maximum rates predicted by the model (Elliott, 1994). The model underestimated growth of *S. trutta* at sea, however, and was thus not suitable for predicting sea

growth of anadromous *S. trutta* (L'Abée-Lund *et al*., 1989). Although the model has been widely used, it was developed from experimental data for a small sample of *S. trutta* and required a large number of parameters, only one of which, the mass exponent, had any biological significance. Therefore, more experiments were performed to increase the database to values for 185 fish feeding on maximum rations of invertebrate food at different temperatures in the range $3·8–21·7°$ C, and a new model was developed (Elliott *et al*., 1995). This model is continuous over the temperature range $3·8–21·7°$ C and has five parameters, all of which can be interpreted in biological terms: the optimum temperature for growth, the lower and upper temperatures at which growth is zero, the mass exponent for transformation of mass that produces linear growth with time and the growth rate of a 1 g fish at the optimum temperature. The model was validated by comparing values estimated from it with observed values for both mean mass and growth rate in 34 year classes (1967–2000) of juvenile anadromous *S. trutta* in Black Brows Beck (Elliott, 2009). These values were for the 2 years of the life cycle spent in fresh water. The date and mean mass at the start of the growth period were defined as the median date for fry emergence and their mean mass at emergence, both being estimated from the individual-based models mentioned earlier (Elliott & Hurley, 1998*a*, *b*).

There was good agreement in most year classes between model-estimated values and observed mean mass. Exceptions were the mean masses and growth rates for 0+ year fish after four summer droughts (1976, 1983, 1984 and 1995) that were lower than expected, but compensatory growth followed so that observed and expected masses were similar for 1+ year fish. Examples of growth curves for the earliest (22 March 1989) and latest (18 May 1979) median emergence times for fry showed that the difference in emergence times of nearly 2 months had little effect on the final mass of pre-smolts on the 30 April after 2 years of growth in fresh water. The final mean values were 49·3 g live mass for the 1989 year class and 45·3 g for the 1979 year class (Fig. 3). The latter value would equal the first only after another 15 days of growth.

Pre-smolt mean mass on the 30 April measured total growth achieved in the freshwater phase of the life cycle. This was significantly related to mean mass at the end of the first and second summer of the life cycle, but not to the emergence date or the mean mass of the newly emerged fry (Elliott, 2009). The overall mean ± 95% C.L. value was $47·1 \pm 2·5$ g for all year classes, but a polynomial curve indicated that mean mass increased with time [Fig. 4(a)]. The curve crossed the overall mean value at the 1986 year class, so that mean values were higher in more recent year classes (mean ± 95% C.L. mass = $53·2 \pm 1·5$ g for 1987–1998) than in previous ones (mean ± 95% C.L. mass = $43·2 \pm 2·1$ g for 1967–1986). Regression equations indicated that mean water temperature had increased significantly in winter (December to February) and spring (March to May) at a rate of $0·037°$ C $year^{-1}$ or by $1·22°$ C from 1966 to 2000 in both seasons [Fig. 4(b)]. There were no similar increases in mean temperature in summer and autumn [Fig. 4(c)]. This study showed the importance of developing realistic growth models in order to detect departures from maximum potential growth, and the more subtle effects of temperature change in winter and spring, probably due to the effects of climate change. The growth model will be used in the next section to explore the possible effects of climate change on *S. trutta* growth in the future.
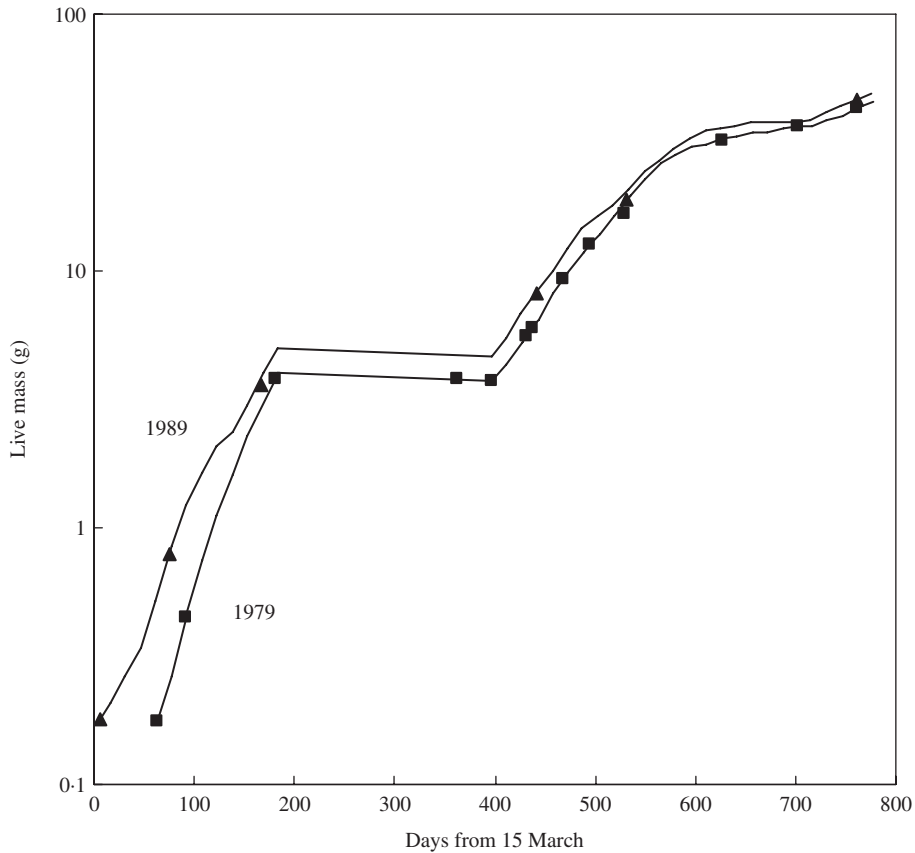
FIG. 3. Comparisons between temporal changes in *Salmo trutta* mean live mass estimated from the growth model (──) and observed mean live mass for the 1979 (■) and 1989 (▲) year classes. Time is given as days from the 15 March. Mass is on $\log_{10}$ scale. The straight lines indicate a period of negligible growth in the first winter of the life cycle.

Lobón-Cerviá & Rincón (1998) claimed that their study of *S. trutta* was the first to assess the model of Elliott *et al*. (1995). These data for Spanish *S. trutta* were re-analysed in a very comprehensive study that included data from 15 British, four Danish and 22 Norwegian populations of *S. trutta* (Jensen *et al*., 2000). Increases in mass were calculated over 10 day periods, using the growth model of Elliott *et al*. (1995). From a total of 365 comparisons, 261 of the observed growth rates were either similar to or below values predicted by the model and 104 were higher than predicted. The latter discrepancies were often for older (3+ years) fish with their observed growth rates up to 148% of the predicted values. Of the 42 populations, the ratio between observed and predicted annual growth rates was not significantly different from one in the single Spanish, four British, two Danish and eight Norwegian populations; was less than one in 11 British, two Danish and six Norwegian populations and exceeded one in eight Norwegian populations. Therefore, growth rates were as predicted in 15 populations and lower than predicted in 19 populations, *i.e.* the fish were growing below their maximum potential. Growth rates were higher
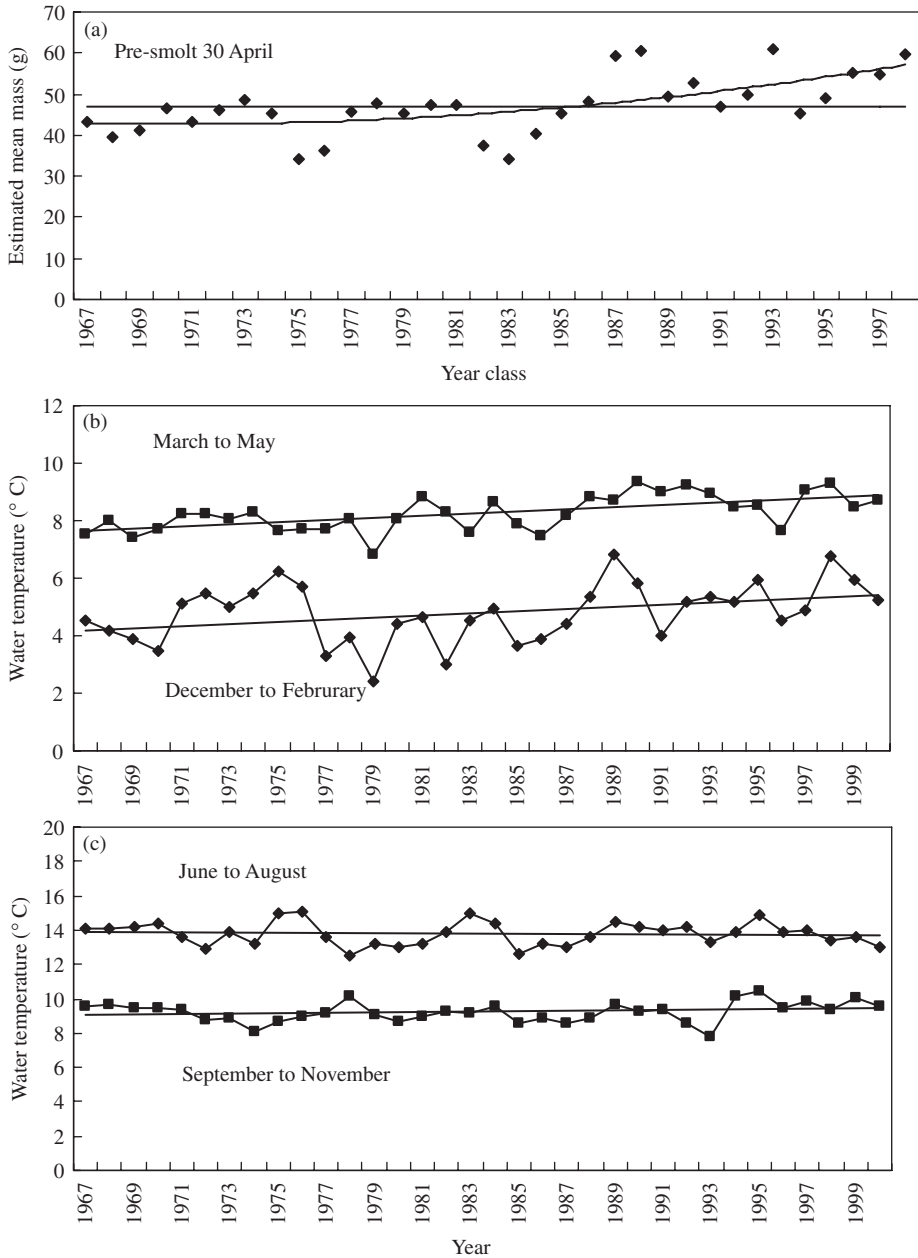
FIG. 4. (a) Estimated mean mass of *Salmo trutta* pre-smolts on the 30 April for all year classes (1967 to 1998); horizontal line indicates the arithmetic mean ±95% C.L. of 47·1 ± 2·5 g for all year classes (——). The increase in mean mass (W, g) with time (x, years) was well described by the polynomial curve given by: $W = 0.02x^2 - 0.17x + 43.07$ ($r^2 = 0.40$, $P < 0.001$). (b) Mean water temperature for winter (December to February) and spring (March to May) in each year. The increase in temperature (T, °C) with time (x, years) was well described by the regression: $T = 0.04x + 4.15$ ($r^2 = 0.13$, $P < 0.05$) for winter and $T = 0.04x + 7.60$ ($r^2 = 0.37$, $P < 0.001$) for spring. (c) Mean water temperature for summer (June to August) and autumn (September to November) in each year. Neither regression was significantly different from a horizontal line ($r^2 = 0.01$ for summer, $r^2 = 0.04$ for autumn, both $P > 0.05$).

than predicted in only eight populations and these lived in the coldest rivers with a mean annual water temperature $<5 \cdot 10°$ C. Six of these rivers were located north of $65°$ N and a seventh received its drainage from a glacier. In a study of *S. trutta* in seven Spanish rivers, the observed growth rate in the first year of the life cycle was $60-104\%$ of the predicted values, with the model underestimating growth in the coldest rivers with a mean annual temperature $<6 \cdot 5°$ C (Nicola & Almodóvar, 2004). As noted earlier, these studies in very cold rivers provide the only clear evidence for local thermal adaptation.

What was remarkable in the comprehensive study of Jensen *et al.* (2000) is how often the growth model of Elliott *et al.* (1995) was validated. The coefficient of determination (r^2) showed that values predicted from the model could explain $74 \cdot 9\%$ of the total variation in the observed annual growth rate for the 42 populations. The addition of four more variables (annual mean temperature, duration of twilight, latitude and amplitude of monthly mean temperature) increased this value by only $6 \cdot 4\%$ to $81 \cdot 3\%$. The underestimate of predicted growth in the coldest rivers was probably due to an unrealistic value of $3 \cdot 56°$ C for the lower limit for growth in the model and an adjustment of this value downwards may have improved the fit of the model. Other salmonid species can feed and grow at temperatures close to $0°$ C (Tables I and II). An optimum temperature for growth of $13 \cdot 11°$ C in the model may also have been unrealistic for the older $3+$ year *S. trutta*, because this value can change with type of diet and the size of the daily energy intake (Table II). It can also decrease with increasing fish size and when anadromous species move from fresh to salt water (Jonsson & Jonsson, 2009). These discrepancies show that the growth model is not a comprehensive model, such a model would require more parameters, but it does provide a useful baseline from which changes in growth can be assessed.

PREDICTING THE EFFECTS OF CLIMATE CHANGE ON *SALMO TRUTTA* GROWTH

Mean water temperatures in Black Brows Beck have increased in winter and spring at a rate of $0 \cdot 37°$ C per decade [Fig. 4(b)], but there have been no similar increases in summer and autumn over the period 1966–2000 [Fig. 4(c)]. Water temperature in winter and spring also increased over a similar period (1968–1997) in the Girnock Burn, Grampian, U.K., with no increases in summer and autumn, and no detectable change in mean annual temperature with time (Langan *et al.*, 2001). Increasing stream temperatures of $1-3°$ C have been recorded in other European countries: *e.g.* $1 \cdot 4$ and $1 \cdot 7°$ C in forest and moorland streams, respectively, in Wales (Durance & Ormerod, 2007), $1 \cdot 4-1 \cdot 7°$ C in three Austrian rivers with summer increases of $1 \cdot 5-2 \cdot 1°$ C (Webb & Nobilis, 2007), $2 \cdot 1-2 \cdot 9°$ C in winter and $1 \cdot 2-1 \cdot 9°$ C in *S. trutta* streams in southern Britain (Durance & Ormerod, 2009), *c.* $1 \cdot 5°$ C in the Upper Rhône River, France (Daufresne *et al.*, 2003), and $0 \cdot 1-1 \cdot 1°$ C in alpine streams in Switzerland (Hari *et al.*, 2006). The last study is notable because it showed regionally coherent warming in alpine rivers and streams at all altitudes with much of this warming occurring abruptly in 1987–1988, years similar to those in Black Brows Beck for the marked increase in pre-smolt mean mass [Fig. 4(a)]. For *S. trutta* in these alpine streams, there was an upward shift in thermal habitat with net losses and gains for *S. trutta* in streams below and above 600 m above

mean sea level, respectively. Extensive catch data for *S. trutta* indicated that these climate-related population changes have already occurred in Switzerland.

These different values for increasing water temperature were taken into account when using the growth model of Elliott *et al*. (1995) to predict possible future changes in *S. trutta* growth. In validating the model with data from Black Brows Beck, it soon became obvious that growth was negligible during the first, but not the second, winter of the life cycle. The estimated mass on the 15 September before the first winter was close to the observed mean mass on the 15 April after the winter in each year class with the latter value being consistently 93% of the value on the previous 15 September. Therefore, the estimated mean mass was adjusted to 93% of the value on the 15 September and thus agreed with the observed value. This was the only adjustment required in the growth model, and there was good agreement in all subsequent observed and estimated values in most year classes except those affected by summer droughts (Elliott, 2009). The earliest date for fry emergence was 22 March 1989 [Fig. 2(a)] after the warmest winter on record (1967–2000) with a mean water temperature of 6·85° C [Fig. 4(b)]. Therefore, this year class was used as a baseline for all subsequent model predictions. If winter and spring mean water temperatures continue to increase as shown by the regressions [Fig. 4(b)], then they would both have increased by 2·3° C from 1989 to 2050. Average water temperatures would be 7·2° C in winter and 10·7° C in spring 2050, both higher than the maximum values attained from 1967 to 2000: 6·85° C in winter of 1989, 9·3° C in spring of 1990.

For the first growth scenario, therefore, mean water temperature was increased by 2·3° C in each month from December to May but was not increased in summer and autumn, following the pattern shown in Black Brows Beck. These changes enhanced *S. trutta* growth so that the final pre-smolt mean mass on the 30 April was 76·2 g [S1 in Fig. 5(a)] compared with 49·3 g in the 1989 year class. It was assumed that growth ceased in the first winter of the life cycle but if this did not occur, then the pre-smolt mean mass would be 170·6 g as in the second scenario [S2 in Fig. 5(a)], perhaps an unrealistically high value. On the 30 April at the end of the first year of the life cycle (411 days after 15 March), however, the estimated mean mass was 33·6 g, a value close to the lowest value of 34·2 g in the 1983 year class [Fig. 4(a)]. Therefore, one possible result of this scenario would be that the young anadromous *S. trutta* smolted after the first year instead of the second year of their life cycle. One-year smolts occur for *S. salar* in the warmer streams at the southern limits of its range (Klemetsen *et al*., 2003*a*). Therefore, a similar change in the life cycle of anadromous *S. trutta* could occur as a result of climate change, provided they could feed on maximum rations throughout the first winter of their life cycle.

For the third scenario, the highest recorded rises in water temperature for *S. trutta* streams in southern Britain were used, namely an increase of 2·9° C for each month from December to May and 1·9° C from June to November. These changes retarded growth for most of the life cycle and values exceeded those for the 1989 year class only in the last few months (from day 671 from the 15 March) with warmer winter temperatures [S3 in Fig. 5(b)]. The final pre-smolt mean mass was 61·9 g, compared with 49·3 g in the 1989 year class, and markedly lower than that in the first and second scenarios.

The fourth and fifth scenarios assumed that mean temperature in each month increased by 3 and 4° C, respectively, not only in winter and spring but also in summer and autumn. There was a marked retardation in growth for both scenarios
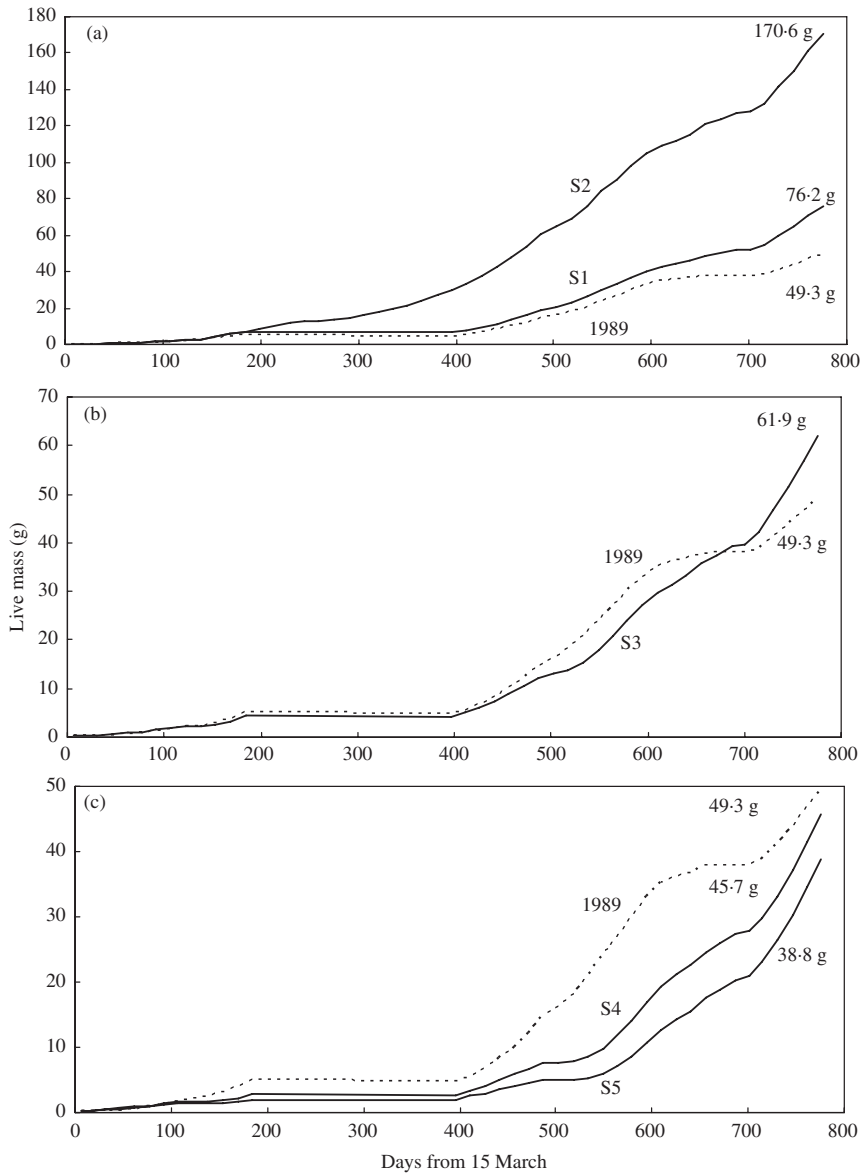
FIG. 5. Comparisons of temporal changes in mean live mass over the freshwater phase of the life cycle of juvenile anadromous *Salmo trutta*, using the 1989 year class as a baseline in each comparison (---) and with temperature changes under the following scenarios: (a) S1, mean water temperature increased by 2·3° C in each month from December to May, but not increased in summer and autumn, and with no growth in the first winter of the life cycle and S2, mean water temperature increased by 2·3° C in each month from December to May, but not increased in summer and autumn, and with growth in the first winter of the life cycle; (b) S3, mean water temperature increased by 2·9° C in each month from December to May and by 1·9° C from June to November, with no growth in the first winter of the life cycle; (c) S4, mean water temperature increased by 3° C in each month with no growth in the first winter of the life cycle and S5, mean water temperature increased by 4° C in each month with no growth in the first winter of the life cycle. (The mean mass of the pre-smolts on 30 April is given for each growth curve.)

with final values for pre-smolt mean mass of 45·7 g [S4 in Fig. 5(c)] and 38·8 g (S5), both below the value of 49·3 g in the 1989 year class.

These comparisons have shown that a small increase in water temperature in winter and spring (<2·5° C) could have a positive effect on the growth of *S. trutta*. They also showed that water temperatures would have to increase by *c*. 4° C in winter and spring, and 3° C in summer and autumn before they had a marked negative effect on growth.

GENERAL CONCLUSIONS

The following key conclusions are relevant to those responsible for the conservation and management of valuable stocks of *S. salar*, *S. trutta* and *S. alpinus*, including anadromous stocks of the three species: (1) water temperatures in rivers, streams, lakes and ponds have increased in recent years and will probably continue to increase as a result of climate change. Although there is some evidence for thermal adaptation to very low temperatures in cold rivers (mean annual temperature <6·5° C), there is no corresponding adaptation to increasing temperature, even in a hot geothermal river. (2) When water temperatures exceed 22–28° C for *S. salar*, 22–25° C for *S. trutta* and 22–23° C for *S. alpinus*, the fishes will soon die unless they can move to cooler water. Deep pools with cooler water near the bottom serve as refugia in streams and rivers and should be maintained or even created when scarce. Cooler inflow streams are also refugia in hot weather and access to them should be ensured. Oxygen concentrations in the deep-water refugia of lakes should be monitored and, if *S. alpinus* is present, management should ensure that they remain >2–3 mg l^{-1}. (3) There is limited evidence to suggest that the preferred temperature for the fish is lower than the optimum temperature, but close to the temperature for maximum conversion efficiency. This hypothesis has to be tested further. (4) The egg stage is the life stage with the lowest thermal tolerance and few eggs will survive if temperatures exceed *c*. 7–8° C for *S. salar* and *S. trutta*, and 5° C for *S. alpinus*. If winter stream temperatures in southern Britain and Ireland continue to increase at their present rate, then they will soon exceed the lethal limit for egg development in *S. salar* and *S. trutta*. Eggs and alevins of *S. alpinus* are probably the most vulnerable to increasing temperature and efforts must be made to maintain this species that holds significant biodiversity conservation value. (5) Long-term studies and the development of predictive models are essential for the sustainable management of all three species. A validated growth model for *S. trutta* was used to predict growth under possible future temperature conditions. These showed that small increases (<2·5° C) in winter and spring could be beneficial for growth, provided there is an adequate supply of food. They also showed that water temperatures would have to increase by *c*. 4° C in winter and spring, and 3° C in summer and autumn before they had a marked negative effect on growth.

References

Baroudy, E. & Elliott, J. M. (1994*a*). The critical thermal limits for juvenile Arctic charr *Salvelinus alpinus*. *Journal of Fish Biology* **45,** 1041–1053.

Baroudy, E. & Elliott, J. M. (1994*b*). Tolerance of parr of Arctic charr, *Salvelinus alpinus*, to reduced dissolved oxygen concentrations. *Journal of Fish Biology* **44,** 736–738.

Beacham, T. D. & Withler, R. E. (1991). Genetic variation in mortality of chinook salmon, *Oncorhynchus tshawytscha* (Walbaum), challenged with high water temperatures. *Aquaculture and Fisheries Management* **22,** 125–133.

Brännäs, E. & Wiklund, B. S. (1992). Low temperature growth potential of Arctic charr and rainbow trout. *Nordic Journal of Freshwater Research* **67,** 77–81.

Bremset, G. (2000). Seasonal and diel changes in behaviour, microhabitat use and preferences by young pool-dwelling Atlantic salmon, *Salmo salar*, and brown trout, *Salmo trutta*. *Environmental Biology of Fishes* **59,** 163–179.

Brett, J. R. (1971). Energetic responses of salmon to temperature: a study of some thermal relations in the physiology and freshwater ecology of sockeye salmon (*Oncorhynchus nerka*). *American Zoologist* **11,** 99–113.

Brooker, M. P., Morris, D. L. & Hemsworth, R. J. (1977). Mass mortalities of adult salmon, *Salmo salar*, in the R. Wye 1976. *Journal of Applied Ecology* **14,** 409–417.

Caissie, D. (2006). The thermal regime of rivers. *Freshwater Biology* **51,** 1389–1406.

Conover, D. O. & Schultz, E. T. (1995). Phenotypic similarity and the evolutionary significance of countergradient variation. *Trends in Ecology & Evolution* **10,** 248–252.

Cowx, I. G., Young, W. O. & Hellawell, J. M. (1984). The influence of drought on the fish and invertebrate populations of an upland stream in Wales. *Freshwater Biology* **14,** 165–177.

Cunjak, R. A., Caissie, D., El-Jabi, N., Hardie, P., Conlon, J. H., Pollock, T. L., Gibson, D. J. & Komadina-Douthwright, S. (1993). The Catamaran Brook (New Brunswick) habitat research project: biological, physical and chemical conditions (1990 –1992). *Canadian Technical Report of Fisheries and Aquatic Sciences* **1914.**

Daufresne, M., Roger, M. C., Capra, H. & Lamouroux, N. (2003). Long-term changes within the invertebrate and fish communities of the Upper Rhône River: effects of climatic factors. *Global Change Biology* **10,** 124–140.

Davidson, I. C. & Hazlewood, M. S. (2005). Effect of climate change on salmon fisheries. *Science Report W2-047/SR.* Bristol: Environment Agency.

Dempson, J. B., O'Connell, M. F. & Cochrane, N. M. (2001). Potential impact of climate warming on recreational fishing opportunities for Atlantic salmon, *Salmo salar* L. in Newfoundland, Canada. *Fisheries Management and Ecology* **8,** 69–82.

Du, S. J., Gong, Z., Fletcher, G. L., Shears, M. A. & Hew, C. L. (1992). Growth hormone gene transfer in Atlantic salmon: use of fish antifreeze/growth hormone chimeric gene construct. In *Transgenic Fish* (Hew, C. L. & Fletcher, G. L., eds), pp. 176–189. Singapore: World Scientific Publishing Co.

Durance, I. & Ormerod, S. J. (2007). Climate change effects on upland stream macroinvertebrates over a 25-year period. *Global Change Biology* **13,** 942–957.

Durance, I. & Ormerod, S. J. (2009). Trends in water quality and discharge confound long-term warming effects on river macroinvertebrates. *Freshwater Biology* **54,** 388–405.

Elliott, J. A. (1995). A comparison of thermal polygons for British freshwater teleosts. *Freshwater Forum* **5,** 178–184.

Elliott, J. M. (1975). The growth rate of brown trout (*Salmo trutta* L.) fed on maximum rations. *Journal of Animal Ecology* **44,** 805–821.

Elliott, J. M. (1981). Some aspects of thermal stress on freshwater teleosts. In *Stress and Fish* (Pickering, A. D., ed.), pp. 209–245. London: Academic Press.

Elliott, J. M. (1991). Tolerance and resistance to thermal stress in juvenile Atlantic salmon, *Salmo salar*. *Freshwater Biology* **25,** 61–70.

Elliott, J. M. (1994). *Quantitative Ecology and the Brown Trout.* Oxford: Oxford University Press.

Elliott, J. M. (2000). Pools as refugia for brown trout during two summer droughts: trout responses to thermal and oxygen stress. *Journal of Fish Biology* **56,** 938–948.

Elliott, J. M. (2009). Validation and implications of a growth model for brown trout, *Salmo trutta*, using long-term data from a small stream in Northwest England. *Freshwater Biology* **54,** 2263–2275.

Elliott, J. M. & Baroudy, E. (1995). The ecology of Arctic charr, *Salvelinus alpinus*, and brown trout, *Salmo trutta*, in Windermere (northwest England). *Nordic Journal of Freshwater Research* **71,** 33–48.

Elliott, J. M. & Elliott, J. A. (1995). The effect of the rate of temperature increase on the critical thermal maximum for parr of Atlantic salmon and brown trout. *Journal of Fish Biology* **47,** 917–919.

Elliott, J. M. & Hurley, M. A. (1997). A functional model for maximum growth of Atlantic salmon parr, *Salmo salar*, from two populations in Northwest England. *Functional Ecology* **11,** 592–603.

Elliott, J. M. & Hurley, M. A. (1998*a*). An individual-based model for predicting the emergence period of sea-trout fry in a Lake District stream. *Journal of Fish Biology* **53,** 414–433.

Elliott, J. M. & Hurley, M. A. (1998*b*). Predicting fluctuations in the size of newly-emerged sea-trout fry in a Lake District stream. *Journal of Fish Biology* **53,** 1120–1133.

Elliott, J. M. & Hurley, M. A. (1999). A new energetics model for brown trout, *Salmo trutta*. *Freshwater Biology* **42,** 235–246.

Elliott, J. M. & Hurley, M. A. (2000*a*). Daily energy intake and growth of piscivorous brown trout, *Salmo trutta*. *Freshwater Biology* **44,** 237–245.

Elliott, J. M. & Hurley, M. A. (2000*b*). Optimum energy intake and gross efficiency of energy conversion for brown trout, *Salmo trutta*, feeding on invertebrates or fish. *Freshwater Biology* **44,** 605–615.

Elliott, J. M. & Klemetsen, A. (2002). The upper critical thermal limits for alevins of Arctic charr from a Norwegian lake north of the Arctic circle. *Journal of Fish Biology* **60,** 1338–1341.

Elliott, J. M., Hurley, M. A. & Fryer, R. J. (1995). A new, improved growth model for brown trout, *Salmo trutta*. *Functional Ecology* **9,** 290–298.

Elliott, J. M., Fletcher, J. M., Elliott, J. A. Cubby, P. R. & Baroudy, E. (1996). Changes in the population density of pelagic salmonids in relation to changes in lake enrichment in Windermere (northwest England). *Ecology of Freshwater Fish* **5,** 153–162.

Elliott, J. M., Hurley, M. A. & Elliott, J. A. (1997). Variable effects of droughts on the density of a sea-trout *Salmo trutta* population over 30 years. *Journal of Applied Ecology* **34,** 1229–1238.

Elliott, J. M., Hurley, M. A. & Maberly, S. C. (2000). The emergence period of sea trout fry in a Lake District stream correlates with the North Atlantic Oscillation. *Journal of Fish Biology* **56,** 208–210.

Finstad, A. G., Naesje, T. F. & Forseth, T. (2004). Seasonal variation in the thermal performance of juvenile Atlantic salmon (*Salmo salar*). *Freshwater Biology* **49,** 1459–1467.

Fletcher, G. L., Shears, M. A., King, M. J., Davies, P. L. & Hew, C. L. (1988). Evidence for antifreeze protein gene transfer in Atlantic salmon (*Salmo salar*). *Canadian Journal of Fisheries and Aquatic Sciences* **45,** 352–357.

Fletcher, G. L., Davies, P. L. & Hew, C. L. (1992). Genetic engineering of freeze-resistant Atlantic salmon. In *Transgenic Fish* (Hew, C. L. & Fletcher, G. L., eds), pp. 190–208. Singapore: World Scientific Publishing Co.

Forseth, T. & Jonsson, B. (1994). The growth and food ration of piscivorous brown trout (*Salmo trutta*). *Functional Ecology* **8,** 171–177.

Forseth, T., Hurley, M. A., Jensen, A. J. & Elliott, J. M. (2001). Functional models for growth and food consumption of Atlantic salmon parr, *Salmo salar*, from a Norwegian river. *Freshwater Biology* **46,** 173–186.

Forseth, T., Larsson, S., Jensen, A. J., Jonsson, B., Näslund, I. & Berglund, I. (2009). Thermal growth performance of juvenile brown trout *Salmo trutta*: no support for thermal adaptation hypotheses. *Journal of Fish Biology* **74,** 133–149.

Graham, C. T. & Harrod, C. (2009). Implications of climate change for the fishes of the British Isles. *Journal of Fish Biology* **74,** 1143–1205.

Grande, M. & Andersen, S. (1991). Critical thermal maxima for young salmonids. *Journal of Freshwater Ecology* **5,** 275–279.

Hari, R. E., Livingstone, D. M., Siber, R., Burkhardt-Holm, P. & Güttinger, H. (2006). Consequences of climatic change for water temperature and brown trout populations in Alpine rivers and streams. *Global Change Biology* **12,** 10–26.

Humpesch, U. H. (1985). Inter- and intra-specific variation in hatching success and embryonic development of five species of salmonids and *Thymallus thymallus*. *Archiv für Hydrobiologie* **104,** 129–144.

Hurrell, J. W. (1995). Decadal trends in the North Atlantic Oscillation: regional temperatures and precipitation. *Science* **269,** 676–679.

Hurrell, J. W. (1996). Influence of variations in extratropical wintertime teleconnections on Northern Hemisphere temperatures. *Geophysical Research Letters* **23,** 665–668.

Jensen, A. J., Forseth, T. & Johnsen, B. O. (2000). Latitudinal variation in growth of young brown trout *Salmo trutta*. *Journal of Animal Ecology* **69,** 1010–1020.

Jobling, M. (1981). Temperature tolerance and the final preferendum – rapid methods for the assessment of optimum growth temperatures. *Journal of Fish Biology* **19,** 439–455.

Jones, I. D., Winfield, I. J. & Carse, F. (2008). Assessment of long-term changes in habitat availability for Arctic charr (*Salvelinus alpinus*) in a temperate lake using oxygen profiles and hydroacoustic surveys. *Freshwater Biology* **53,** 393–402.

Jonsson, B. & Jonsson, N. (2004). Factors affecting marine production of Atlantic salmon (*Salmo salar*). *Canadian Journal of Fisheries and Aquatic Sciences* **61,** 2369–2383.

Jonsson, B. & Jonsson, N. (2009). A review of the likely effects of climate change on anadromous Atlantic salmon *Salmo salar* and brown trout *Salmo trutta*, with particular reference to water temperature and flow. *Journal of Fish Biology* **75,** 2381–2447.

Jonsson, B., Forseth, T., Jensen, A. J. & Naesje, T. F. (2001). Thermal performance in juvenile Atlantic salmon, *Salmo salar* L. *Functional Ecology* **15,** 701–711.

Jonsson, N. & Jonsson, B. (2004). Size and age of maturity of Atlantic salmon correlate with the North Atlantic Oscillation. *Journal of Fish Biology* **64,** 241–247.

Jonsson, N., Jonsson, B. & Hansen, L. P. (2005). Does climate during embryonic development influence parr growth and age of seaward migration in Atlantic salmon (*Salmo salar*)? *Canadian Journal of Fisheries and Aquatic Sciences* **62,** 2502–2508.

Kaya, C. M. (1977). Reproductive biology of rainbow and brown trout in a geothermally heated stream: the Firehole River of Yellowstone National Park. *Transactions of the American Fisheries Society* **106,** 354–361.

Kaya, C. M. (1978). Thermal resistance of rainbow trout from a permanently heated stream, and of two hatchery strains. *Progressive Fish-Culturist* **40,** 138–142.

Kaya, C. M., Kaeding, L. R. & Burkhalter, D. E. (1977). Use of a cold-water refuge by rainbow and brown trout in a geothermally heated stream. *Progressive Fish-Culturist* **39,** 37–39.

Kilgour, D. M. & McCauley, R. W. (1986). Reconciling the two methods of measuring upper lethal temperatures in fishes. *Environmental Biology of Fishes* **17,** 281–290.

Klemetsen, A., Amundsen, P.-A., Dempson, J. B., Jonsson, B., Jonsson, N., O'Connell, M. F. & Mortensen, E. (2003*a*). Atlantic salmon *Salmo salar* L., brown trout *Salmo trutta* L. and Arctic charr *Salvelinus alpinus* (L.): a review of aspects of their life histories. *Ecology of Freshwater Fish* **12,** 1–59.

Klemetsen, A., Knudsen, R., Staldvik, F. J. & Amundsen, P.-A. (2003*b*). Habitat, diet and food assimilation of Arctic charr under the winter ice in two subarctic lakes. *Journal of Fish Biology* **62,** 1082–1098.

Konecki, J. T., Woody, C. A. & Quinn, T. P. (1995). Critical thermal maxima of coho salmon (*Oncorhynchus kisutch*) fry under field and laboratory acclimation regimes. *Canadian Journal of Zoology* **73,** 993–996.

L'Abée-Lund, J. H., Jonsson, B., Jensen, A. J., Saettem, L. M., Heggberget, T. G., Johnsen, B. O. & Naesje, T. F. (1989). Latitudinal variation in life-history characteristics of sea-run migrant brown trout *Salmo trutta*. *Journal of Animal Ecology* **58,** 525–542.

Langan, S. J., Johnston, L., Donaghy, M. J., Youngson, A. F., Hay, D. W. & Soulsby, C. (2001). Variation in river water temperatures in an upland stream over a 30-year period. *The Science of the Total Environment* **265,** 195–207.

Larsson, S. (2005). Thermal preference of Arctic charr, *Salvelinus alpinus*, and brown trout, *Salmo trutta* – implications for their niche segregation. *Environmental Biology of Fishes* **73,** 89–96.

Larsson, S. & Berglund, I. (1998). Growth and food consumption of 0+ Arctic charr fed pelleted or natural food at six different temperatures. *Journal of Fish Biology* **52,** 230–242.

Larsson, S. & Berglund, I. (2005). The effect of temperature on the energetic growth efficiency of Arctic charr (*Salvelinus alpinus* (L.)) from four Swedish populations. *Journal of Thermal Biology* **30,** 29–36.

Larsson, S., Forseth, T., Berglund, I., Jensen, A. J., Näslund, I., Elliott, J. M. & Jonsson, B. (2005). Thermal adaptation of Arctic charr: experimental studies of growth in eleven charr populations from Sweden, Norway and Britain. *Freshwater Biology* **50,** 353–368.

Lehtonen, H. (1998). Does global warming threat the existence of Arctic charr, *Salvelinus alpinus* (Salmonidae), in northern Finland. *Italian Journal of Zoology* **65** (Suppl.), 471–474.

Levins, R. (1969). Thermal acclimation and heat resistance in *Drosophila* species. *American Naturalist* **103,** 483–499.

Levinton, J. S. (1983). The latitudinal compensation hypothesis: growth data and a model of latitudinal growth differentiation based upon energy budgets. I. Interspecific comparison of *Ophryotrocha* (Polychaeta: Dorvilleidea). *Biological Bulletin* **165,** 686–698.

Lobón-Cerviá, J. & Rincón, P. A. (1998). Field assessment of the influence of temperature on growth rate in a brown trout population. *Transactions of the American Fisheries Society* **127,** 718–728.

Lund, S. G., Caissie, D., Cunjak, R. A., Vijayan, M. M. & Tufts, B. L. (2002). The effects of environmental heat stress on heat-shock mRNA and protein expression in Miramichi Atlantic salmon (*Salmo salar*) parr. *Canadian Journal of Fisheries and Aquatic Sciences* **59,** 1553–1562.

Lyytikäinen, T., Koskela, J. & Rissanen, I. (1997). Thermal resistance and upper lethal temperatures of underyearling Lake Inari Arctic charr. *Journal of Fish Biology* **51,** 515–525.

Magnuson, J. J., Crowder, L. B. & Medvick, P. A. (1979). Temperature as an ecological resource. *American Zoologist* **19,** 331–343.

Maitland, P. S., Winfield, I. J., McCarthy, I. D. & Igoe, F. (2007). The status of Arctic charr *Salvelinus alpinus* in Britain and Ireland. *Ecology of Freshwater Fish* **16,** 6–19.

Matthews, K. R. & Berg, N. H. (1997). Rainbow trout responses to water temperature and dissolved oxygen stress in two southern California stream pools. *Journal of Fish Biology* **50,** 50–67.

Minns, C. K., Randall, R. G., Chadwick, E. M. P., Moore, J. E. & Green, R. (1995). Potential impact of climate change on the habitat and population dynamics of juvenile Atlantic salmon, *Salmo salar* L., in eastern Canada. In *Climate Change and Northern Fish Populations* (Beamish, R. J., ed.), pp. 699–708. *Canadian Special Publication of Fisheries and Aquatic Sciences* **121**.

Murray, R.W. (1971). Temperature receptors. In *Fish Physiology*, Vol. 5 (Hoar, W. S. & Randall, D. J., eds), pp. 121–133. London: Academic Press.

Nicieza, A. G., Reiriz, L. & Braña, F. (1994*a*). Variation in digestive performance between geographically disjunct populations of Atlantic salmon: countergradient in passage time and digestion rate. *Oecologia* **99,** 243–251.

Nicieza, A. G., Reyes-Gavilan, F. G. & Braña, F. (1994*b*). Differentiation in juvenile growth and bimodality patterns between northern and southern populations of Atlantic salmon (*Salmo salar* L.). *Canadian Journal of Zoology* **72,** 1603–1610.

Nicola, G. G. & Almodóvar, A. (2004). Growth pattern of stream-dwelling brown trout under contrasting thermal conditions. *Transactions of the American Fisheries Society* **133,** 66–78.

Ojanguren, A. F., Reyes-Gavilán, F. G. & Braña, F. (2001). Thermal sensitivity of growth, food intake and activity of juvenile brown trout. *Journal of Thermal Biology* **26,** 165–170.

Osborn, T. J. (2006). Recent variations in the winter North Atlantic Oscillation. *Weather* **61,** 353–355.

Ottersen, G., Planque, B., Belgrano, A., Post, E., Reid, P. C. & Stenseth, N. C. (2001). Ecological effects of the North Atlantic Oscillation. *Oecologia* **128,** 1–14.

Peterson, R. H., Spinney, H. C. E. & Sreedharan, A. (1977). Development of Atlantic salmon (*Salmo salar*) eggs and alevins under varied temperature regimes. *Journal of the Fisheries Research Board of Canada* **34,** 31–43.

Power, M. & Power, G. (1994). Modelling the dynamics of smolt production in Atlantic salmon. *Transactions of the American Fisheries Society* **123,** 535–548.

Ricker, W. E. (1979). Growth rates and models. In *Fish Physiology*, Vol. 8 (Hoar, W. S., Randall, D. J. & Brett, J. R., eds), pp. 677–743. New York, NY: Academic Press.

Siikavuopio, S. I., Knudsen, R., Winger, A. C. & Kristoffersen, R. (2009). Is the winter period a severe bottleneck of anadromous riverine Arctic charr parr? *Ecology of Freshwater Fish* **18,** 126–131.

Swift, D. R. (1964). The effect of temperature and oxygen on the growth rate of the Windermere char (*Salvelinus alpinus willughbii*). *Comparative Biochemistry and Physiology* **12,** 179–183.

Thyrel, M., Berglund, I., Larsson, S. & Näslund, I. (1999). Upper thermal limits for feeding and growth of 0+ Arctic charr. *Journal of Fish Biology* **55,** 199–210.

Webb, B. W. & Nobilis, F. (2007). Long-term changes in river temperature and the influence of climatic and hydrological factors. *Hydrological Sciences* **52,** 74–85.

Winfield, I. J., Fletcher, J. M. & James, J. B. (2008). The Arctic charr (*Salvelinus alpinus*) populations of Windermere, UK: population trends associated with eutrophication, climate change and increased abundance of roach (*Rutilus rutilus*). *Environmental Biology of Fishes* **83,** 25–35.

Winfield, I. J., Hateley, J., Fletcher, J. M. & James, J. B., Bean, C. W. & Clabburn, P. (2010). Population trends of Arctic charr (*Salvelinus alpinus*) in the UK: assessing the evidence for a widespread decline in response to climate change. *Hydrobiologia* **650,** 55–65. doi: 10.1007/s10750-009-0078-1