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Thermal Performance of Arctic Charr: Intraspecific Variation and Competitive Ability

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Abstract

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Under experimental conditions, I have studied and compared the thermal performance of several geographically separated wild Arctic charr populations. In addition, I have studied the preferred temperatures of charr and brown trout. Fish were reared both singly and in groups. The data were analysed and fitted to baseline models in order to estimate the growth efficiency as well as the lower, the upper and the optimum temperatures for growth and feeding of charr. Overall, the optimum temperature for feeding and growth of charr was found in the range 14-17°C and only slight differences was found between populations. The lower and upper limit for feeding and growth were estimated at about 2-3°C and 21-22°C, respectively. The upper limits and the optimum temperatures for growth and feeding are clearly higher than suggested in previous studies. The unexpected high lower limit may result from fish being acclimatised to summer conditions and the rather short (14 days) experimental periods. Charr had remarkably high growth efficiency that varied between 40-60%. The growth efficiency was only moderately affected by temperature. The preferred temperature of charr was found to be 11.4°C, which is about 3.5°C lower than the temperature for maximum growth. This was significantly lower than for trout, which selected a temperature of 16.0°C. Thus, charr thermoregulation strongly contradicts the general rule of coincidence of preferred temperature and optimum temperature for growth of fish, while brown trout obeys it. This finding might partly explain why charr and trout are niche segregated, when they exists in sympatry. The summer temperature in the littoral of lakes containing sympatric charr and trout generally exceeds the preferred temperature of charr, which then will move to cooler and deeper areas. Today, the Arctic charr in Scandinavia appears to be on the southern edge of its distribution. Perturbations of the thermal environment of charr (e.g. hydroelectric power plants, nuclear power plants or forestry actions and global climate change) might escalate the erosion of charr habitats. The findings of this study can be used as a tool in order to identify and manage threatened habitats and populations. Furthermore, this basic knowledge of the thermal performance of charr could be used to improve the management of charr under farming conditions.

Key words: thermal adaptation, *Salvelinus alpinus, Salmo trutta*, growth model, diet, food conversion, thermal limits.

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Till Pappa

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Appendix

Papers I-V

The present thesis is based on the following papers, which will be referred to by their Roman numerals:

I. 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 50, 230–242.

II. 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.

III. Larsson, S. & Berglund, I. Effects of temperature on energy intake, growth and growth efficiency of four Arctic charr populations. Manuscript.

IV. Berglund, I., Forseth, T., Larsson, S., Jensen, A.J., Näslund, I., Elliott, J.M. & Jonsson, B. Thermal adaptation of Arctic charr – experimental studies of growth in eleven charr populations from Sweden, Norway and Britain. Manuscript.

V. Larsson, S. Niche segregation of Arctic charr and brown trout – a result of different thermo-regulatory behaviour? Manuscript.

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Introduction

Fish are, with few exceptions, obligate ectotherms (Wootton, 1990). In contrast to endotherms, ectothermic animals rely on external sources of heat (Eckert, Randall & Augustine, 1988). Metabolic heat produced is rapidly lost through the gills and the epidermis (Brett, 1971) and as a consequence, the body temperature of a fish fluctuates in close correspondence to the ambient water temperature (Jobling, 1996). Since the enzymatic rate in animals is strongly temperature dependent (Eckert, Randall & Augustine, 1988), the ambient water temperature influences all physiological processes in fish. For example, Brett (1971) studied different physiological responses of sockeye salmon (*Oncorhynchus nerka*) to increased acclimation temperature. For all eight general functions studied (tolerance, preference, metabolism, performance, growth, appetite, digestion and circulation) temperature had a marked non-linear effect with an optimum. Interestingly, it was found that all general functions but appetite were optimised at the same temperature.

Including the extensive work by Brett (1971), the thermal performance of numerous fish species has been thoroughly examined and temperature is generally regarded as one of the most pervasive abiotic factor affecting the physiological processes of fish (Brett, 1979; Magnuson, Crowder & Medvick, 1979; Coutant, 1987; Hutchison & Maness, 1979). Furthermore, several studies have also shown the pronounced direct effect of temperature on fish ecology. For example, Magnuson, Crowder & Medvick (1979) argued that the thermal niche of a fish could be treated equally to a food resource. Thus, when evaluating the competitive outcome of different fish species, temperature must be considered equally important as other consumable resources. In line with this, Persson (1986) suggested that foraging models will be improved by an incorporation of temperature as a factor and that temperature may mediate coexistence of species in environments in which temperature varies spatially and temporally.

Temperature – feeding, growth and growth efficiency

The food intake, growth and growth efficiency (the ratio between ingested food or energy and the weight or energy increase of the fish) of a fish increases with increasing temperature to a maximum. Thereafter, at higher temperatures, intake, growth and growth efficiency decreases (Elliott, 1994; Jobling, 1995). The temperatures at which these traits are maximised are often defined as the ‘optimum temperature’, for the respective trait. Notably, the definition for optimum temperature for growth is only valid under the assumption that the food is not limited (Jobling, 1981). Generally, the food intake is maximised at a higher temperature than at which the growth rate is maximised, which in turn is maximised at a higher temperature than at which the maximum growth efficiency is achieved (Jobling, 1995, 1997). Obviously, the growth and growth efficiency is affected not only by temperature but also by the amount of food ingested by the fish. The temperature at which maximum growth rate is achieved decreases with a decrease in food availability (Brett, 1976). In contradiction to growth, maximum growth efficiency is not achieved at maximum food intake. Instead, it has been shown that the growth efficiency is maximised at an intermediate food intake (Brett, 1971; Elliot, 1976).

Thermal limits

The range of temperatures, inhabited by a fish species is defined as the species thermal niche (Magnuson, Crowder & Medvick, 1979). The extension and the placement on the temperature scale of the thermal niche vary between species. For instance, the goldfish can tolerate a temperature range from 0 to 40°C (Fry, 1971). This is in strong contrast to some Antarctic fish species that will die at temperatures above 5°C (MacDonald, Montgomery & Wells, 1987). Furthermore, species as for example carp (*Cyprinus carpio*) are stressed at temperatures below 15°C (Elliott, 1981), which in turn is close to the optimum temperature for growth of many salmonids (for species list see Jobling, 1981). This has led researchers to classify fish species into cold-water and warm-water species.

The thermal limits of fish have been categorised according to their effects on fish. Outside the lower (LILT) and upper (UILT) incipient lethal temperature, an individual fish eventually die (Wootton, 1990). Feeding takes place in a more narrow temperature range, within the LILT and UILT. Furthermore, to experience growth, the fish is restricted to an even more narrow temperature range than for which feeding is possible (Wottoon, 1990; Elliott, 1994). The LILT and UILT sets definite limits for the geographical distribution of specific fish species.

Behavioural thermoregulation

Ectothermic animals presented to thermal gradients spend most of their time in a narrow range of temperatures, defined as their preferred temperatures (Fry, 1947, Johnson & Kelsch, 1998). This active behaviour of fish has been termed "behavioural thermoregulation" (Reynolds & Casterlin, 1979). Preferred temperatures have been suggested to be correlated to physiological optimums of various functions (Brett, 1971, Crawshaw & O'-Connor, 1997) and good correlation between preferred temperatures and optimum temperatures for growth of fish has been demonstrated (McCauley & Casselman, 1980, Jobling, 1981). Hence, by an active selection of the optimum temperature for growth, fish will be able to maximise their growth rate. Accordingly, Jobling (1981) suggested that the preferred temperature could be used as a predictor of the optimal temperature of growth.

Thermal adaptation

Local adaptation, in various traits, among fish populations has been shown for numerous fish species. Regarding thermal performance, two hypotheses have been put forward: (i) adaptation to local thermal optima; (ii) the countergradient variation hypothesis. In the hypothesis of adaptation to local thermal optima (i), Levinton (1983) suggests that natural selection can shift optimal temperatures to match the prevailing temperatures in a new or changed thermal niche. Hence, fish are suggested to evolve locally to maximise growth rate and if the thermal regime differ between populations, different thermal optima arise due to natural selection.

However, to the best of my knowledge, there is no support for this hypothesis from studies on vertebrates. The countergradient variation hypothesis (ii) (CgV; defined by Levins, 1969; reviewed by Conover & Scultz, 1995) suggests that populations in hostile environments (low temperature, short season for growth, strong competition) perform better at all temperatures than conspecifics from benign environments. This hypothesis has been supported by a few studies on vertebrates such as those on growth of green frogs (*Rana* spp.) (Berven, Gill & Gill-Smith, 1979), Atlantic silverside (*Menidia menidia*) (Conover & Present, 1990), and on growth and digestive performance of Atlantic salmon (*Salmo salar*) (Nicieza, Reiriz & Braña, 1994; Nicieza, Reyes-Gavilán & Braña, 1994).

Temperature and the Arctic charr

The Arctic charr (*Salvelinus alpinus* L.) is a holarctic salmonid fish species with both landlocked and anadromous populations (Maitland, 1995). In Scandinavia it is mainly found in the mountain area (Nilsson, 1963), but it also appears in deep and large lake further south. It is the northernmost freshwater fish (Hammar, 1998) and thus, the charr is generally regarded as the most cold-adapted freshwater fish. In the past, due to the exceptional variability in several morphological characters, the Arctic charr has been categorised in to different species. According to Savvaitova (1995), Europe inhabits 29 charr species but the prevailing view is that the species reported by Savvaitova (1995) all belong to a single polymorphic species (Jonsson & Jonsson, 2001). The Arctic charr appears in up to four different morphs: two epibenthic zoobenthos feeders and two pelagic forms of which one is a planktivore and the other piscivorous. The different morphs of charr have often been studied in context of speciation (for review see Jonsson & Jonsson, 2001). Prior to the studies of this thesis, the knowledge of thermal performance of Arctic charr was rather scattered. The feeding and growth of charr at low temperatures have been fairly well examined (Johnson, 1980; Brännäs & Wiklund, 1992; Jobling *et al.*, 1993). However, the thermal performance of charr at higher temperatures was to a large extent not known. Furthermore, there are no studies examining the possible effect of local thermal adaptation in charr. Good knowledge of the thermal performance of geographically separated stocks is vital since the general baseline models are only valid if there is no intraspecific variation in the studied baseline traits (Ugedal, Forseth & Jonsson, 1997). Finally, the only published study of temperature preference suggests that charr prefer a temperature around 9°C (Peterson, Sutterlin & Metcalfe, 1979). This strongly contradicts the prediction of good agreement between optimum temperature for growth and preferred temperature in fish.

Objectives and aims

Laboratory defined baseline models of the thermal performance of fish are useful tools in studies of the ecology and management of natural populations, in predictions of the effects of global climate change and in fish farming. Any observed deviations from the baseline may indicate resource competition, lack of the optimum temperatures for food intake or growth, competition for habitats containing optimum temperatures, or other circumstances that limits the species under consideration (Elliott, Hurley & Fryer, 1995; Forseth *et al.*, 2001). Thus, the objective of this thesis was to study the thermal performance of several Arctic charr populations in order to create baseline models of feeding and growth. Furthermore, in has been the purpose of this thesis to discuss the results in terms of interspecific competition. Therefore, the brown trout (*Salmo trutta*) was included in a study of temperature preference, since it is a major competitor to charr. The aims of this thesis was to:

1. fill the gaps of knowledge concerning the thermal performance of charr and thus, generate complete baseline feeding and growth models for charr.
2. examine if geographically separated charr populations are locally adapted in thermal traits such as optimum temperature for growth and growth capacity.
3. study the thermoregulatory behaviour of both charr and trout and use the result in interpretation of the interspecific competition between the two.

Materials and methods

Fish and rearing

In total, 11 charr populations and one trout population were studied (Tab. 1). All charr used in this thesis were the progeny of wild caught parents, except for Råstojaure charr, which were the progeny of first generation hatchery reared charr. The trout used were wild fish caught by electro-fishing. Prior to the experiments, fish were reared in standard hatchery trays, with through flowing water at about 10°C, and fed commercial pelleted fish food. Overall, in the feeding and growth experiments (Papers I, II, III and IV), fish were reared at temperatures ranging from 3.7 to 23°C. In the growth experiments (Papers I, II, III and IV), both singly and group reared fish were studied (Tab. 1). Slow adjustments to the experimental temperatures, from the holding temperatures, were done in order to allow fish to acclimatise to the new temperature before the experiments started. During the experiments, fish were fed commercial fish food in excess, except in paper I and II where fish also were fed natural prey (shrimps).

Experimental procedures

All weight measurements were taken after 24 h of starvation in order to minimise weighing errors due to variations in gut content of the fish. The initial and final weights of the fish were used to calculate the individual growth rate of the fish. Two different growth models (Paper I, III and IV) were fitted to the calculated growth rate of fish reared singly or in groups, at different temperatures. Both models included biologically interpretable parameters such as the lower (T_L) and upper (T_U) thermal limit for growth, the optimum temperature for growth (T_M) and the growth rate of a 1 g fish at the optimum temperature (c).

In the food intake experiments (Papers I, II and III), uneaten pellets or shrimps were removed and counted. Thereby, the food intake of each fish could be calculated by subtracting the uneaten food from the known amount of fed pellets or shrimps. In paper III, the calculated food intake of the fish was fitted to a consumption model with the same interpretable parameters as in the growth models. However, in this case the food intake was estimated, instead of the growth. The growth efficiency was calculated as the ratio between the amount of consumed food (or energy intake) and the gained weight (or energy) of the fish.

In the temperature preference experiment (Paper V), individual charr and trout were forced to choose between two unequally tempered chambers (~1°C difference). Food was provided in excess at both chambers. During the experiment, the temperature was increased or decreased simultaneous in both chambers and thus, fish had to choose between a warm or cold chamber throughout a realistic temperature range of the fish. The time spent by fish in each chamber was recorded by using PIT tags and antennas (Passive Integrated Transponder) or by video filming. The temperature at which the fish switched to spend more time in one chamber to the other was regarded as the preferred temperature.

Table 1. *Overview of the different charr stocks and the trout stock used in the thesis and the main studied traits, in the respective papers. Note, the studied trout stock is shown in italic font.*

Population	Location	Country	Paper	Rearing		Studied trait						
				Singly (N)	Group (N)	Feed.	Growth	Growth eff.	Diet	Limits	Adapt.	Pref.
Blåsjön	64°N, 14°E	Sweden	2, 4	x (137)		x	x			x	x	
Dunsjön	62°N, 12°E	“	3, 4, 5	x (128)		x	x	x			x	x
Hornavan	66°N, 17°E	“	2, 4	x (101)	x (400)	x	x			x	x	
Näckten	63°N, 15°E	“	4		x (399)		x				x	
Råstojaure	68°N, 20°E	“	2, 3, 4	x (118)		x	x	x		x	x	
Sommen	58°N, 15°E	“	4		x (400)		x				x	
Torrön	63°N, 13°E	“	2, 3, 4, 5	x (110)	x (393)	x	x	x		x	x	x
Vättern	58°N, 15°E	“	1, 3, 4	x (172)	x (304)	x	x	x	x		x	
Hals	70°N, 23°E	Norway	4		x (836)		x				x	
Liavatn	59°N, 06°E	“	4		x (828)		x				x	
Windermere	54°N, 03°W	England	4	x (50)			x				x	
Lycktorp	*63N, 15°E*	*Sweden*	*5*	*x (11)*								*x*

Results

Paper I. This study aimed to compare the effect of temperature and food type on growth and food consumption of Arctic charr. There was no effect of food type on the temperature-growth relationship. The growth rate of fish fed the shrimp Neomysis integer or pellets increased with increasing temperature to an optimum at 15.1°C. Thereafter, the growth rate decreased. The food intake of charr showed a similar pattern to that of the growth rate, with a peak at 16°C. However, the food consumption was generally higher for fish fed Neomysis than for fish fed pellets. The growth efficiency decreased linearly with increasing temperature from 9 to 20°C and the decrease was more rapid for fish fed Neomysis. The estimates of growth efficiency at 5°C were poor but tended to result in lower values than at 9°C.

Paper II. The purpose of this study was to determine the upper temperature limits for feeding and growth of charr reared under laboratory conditions. In all stocks studied, the proportion of feeding fish decreased markedly in the interval 20-22°C. The critical temperatures at which 50% of the fish stopped feeding differed slightly among experiments. Overall, however, the upper thermal limits for feeding and growth for Arctic charr were established in the interval 21–22°C. In experiment 1, both food intake and growth rate declined with increasing temperature, to zero at 22°C and 21.6°C, respectively. A similar pattern was found in the second experiment, with a decreasing proportion of feeding fish as temperature increased. At 22°C, all fish ceased feeding. However, after the temperature was decreased to 18°C, 75% of the fish had resumed feeding within a week.

Paper III. In this study, the observed energy intake and growth rates of individual charr from four different populations reared at different temperatures were fitted to statistical models. Thereby, the lower and upper thermal limits and the optimum temperature for energy intake and growth rate could be estimated. Moreover, since energy intake and growth of charr was known, the energetic growth efficiency could be calculated, at each temperature. Only slight differences in the response of feeding and growth to temperature was found between the populations. For each population, the optimum temperatures for energy intake and growth more or less coincided in the range 14-16°C. The lower and upper limits for energy intake and growth were found at about 3°C and at 21-23°C, respectively. The overall growth efficiency was high, about 40-60% depending on temperature and population. The effect of temperature was moderate and therefore, no optimum temperature for growth efficiency was found but the growth efficiency tended to be maximised at lower temperatures than the temperatures at which the energy intake and growth were maximised.

Paper IV. The main objective of this study was to examine if charr populations from different geographic regions differ in their thermal performance. The result of this study was evaluated in the context of two published hypotheses: adaptation to local thermal optima and the countergradient variation in growth hypotheses. The parameter estimates (T_L, T_U, T_M and c) were very similar for all populations, although the Swedish populations tended to have higher estimates of T_M than the Norwegian and British populations. Overall, no support for either of the two tested hypotheses was found. However, some degree of local adaptations was suggested for Swedish charr; Dunsjön charr had the lowest estimate of T_L and Vättern charr the highest estimate of T_U.

Paper V. In this experiment, two tanks of different temperatures were accessible for individual charr and trout. The temperature was increased or decreased stepwise in both chambers and the temperature at which the fish choose one of the chambers to the other was regarded as the preferred temperature of the fish. The mean preferred temperature of charr was found to be 11.4°C. This was significantly lower than the mean preferred temperature of trout, which was shown to be 16.0°C. Thus, in contradiction to trout, charr did not thermoregulate according to the general view of coincidence of the preferred temperature and the optimum temperature for growth of fish.

Discussion

In this thesis, two different models were used to describe the effect of temperature on the growth of Arctic charr. In paper I, a model originally designed for brown trout was applied (Elliott, Hurley & Fryer, 1995). Four biologically interpretable parameters were included in this model: the lower (T_L) and upper (T_U) thermal limits for growth, the optimum temperature for growth (T_M) and the growth rate of a 1 g fish at the optimum temperature (c). It was concluded that this model slightly underestimated the optimum temperature for growth and severely overestimated the upper thermal limit for growth. The growth of charr showed a parabolic pattern with a plateau at temperatures around the optimum temperature for growth. In studies by Elliott (1975, 1976) and Elliott, Hurley & Fryer (1995), the growth of trout showed a much more distinct peak at the optimum temperature for growth, which fitted the triangular shaped model well. An attempt to fit a model (Fryer, 1989) to the charr data that included a parameter that controlled the degree of curvature failed, mainly because of to few observations at high temperatures. However, it was believed that such a model would have rendered a more realistic estimate of the upper thermal limit for growth. In paper III and IV, instead of using the model by Elliott, Hurley & Fryer (1995), a re-parameterised version of a model described by Ratkowsky *et al.* (1983) was applied. This model included the same biologically interpretable parameters as the model by Elliott, Hurley & Fryer (1995), but was more appropriate where the growth showed at plateau in the region of the optimum temperature for growth. The same model was used to describe the energy intake of charr in paper III. In both models, a power law relationship (power to $-b$) between specific growth rate and fish mass was included. This parameter varied somewhat between stocks. However, in the experiments that covered a sufficient range of fish sizes, the estimated b was close to 0.3 (Paper IV). This is close to the estimate of b at 0.31 for salmon and brown trout, established by Elliott and Hurley (1997), but lower than the value for b at 0.35 suggested by Jobling *et al.* (1993).

The pervasive effect of temperature on the physiological processes and behaviour of fish has been shown for a large number of fish species (Beitinger & Magnuson, 1979; Crowder & Magnuson, 1982; Persson, 1979; Weetman, Atkinson & Chubb, 1998) Temperature limits and optimum temperatures for various traits are suggested to be species specific (Johnson & Kelsch, 1998). Hence, the magnitude of the effect and the range of effective temperatures differ between species (Iwama, 1996; Wootton, 1990). However, the general response is similar for different species; the energy intake and the growth rate increases with increasing temperature to an optimum temperature and thereafter, at even higher temperatures both these traits decreases (Paper I, III and IV). The effect of temperature on different traits a fish is, however, not rigid. The previous thermal history, for example, has been shown to affect the limits of temperature tolerance and the preferred temperature of fish (McCauley, Elliott & Read, 1977; Stauffer, Melisky & Hocutt, 1984; Kelsch & Neill, 1990; Baroudy & Elliott, 1994). Therefore, in all studies of feeding and growth in this thesis, fish were acclimatised for at least three days to the experimental temperature. In studies of thermal preference, Reynolds & Casterlin (1979) suggested that 24 hr is enough to allow fish to gravitate to the finally preferred temperature. Thus, it was believed that fish in this thesis were given sufficient time to acclimatise to the experimental temperatures in that sense that the previous storing temperatures did not affect the results.

The Arctic charr is the northernmost freshwater fish (Hammar, 1998) and it is generally regarded as the most pronounced cold adapted species among the salmonids. For instance, it has been shown that the Arctic charr can feed and grow at temperatures close to zero (Johnson, 1980; Brännäs & Wiklund, 1992). Regarding the optimum temperature for growth, Jobling *et al.* (1993) suggested that charr should grow at the highest rate at 14°C and Jensen (1985) suggested that charr from Nesjöen (Norway) had an optimum temperature of 11·8°C. Swift (1964) found that charr from Windermere, England, were growing best in the range 12–16°C. In that respect, the high optimum temperature for growth of charr (Paper I, III, IV) found in this thesis was unexpected. The overall mean temperature for growth, of 11 populations tested in 19 separate experiments, was estimated to be 15.8°C. The only study in consistence with the present study was conducted by Lyytikäinen (1997), in which charr showed highest growth rate at 15.1°C. In two recent corresponding studies of brown trout, the optimum temperature for growth was found at 16 and 17°C (Forseth, 1994; Ojanguren, 2001). In earlier studies, it has been found that trout fed invertebrates or pelleted food had an optimum temperature for growth of 13-14°C (Elliott 1975; Elliott, Hurley & Fryer, 1995; Elliott & Hurley 1999). For piscivorous trout, Elliott & Hurley (2000) suggested that the optimum temperature for growth is 17°C. Thus, in comparison, the optimum temperature for growth of charr is almost as high as for trout.

The definition of the optimum temperature for growth is only valid under the assumption that there are no food limitations (Jobling, 1981). Several studies have shown that the temperature at which the growth rate is maximised is progressively shifted to lower temperatures as the amount of available food is decreased (Brett, 1971; Lessmark, 1983; Russell, Fish & Wootton, 1996). Charr in natural waters is generally food limited and will consequently, achieve maximum growth at temperatures lower than the optimum temperature for growth. Furthermore, the typical charr lake is found at high latitudes and altitudes and is therefore cold. The water temperature may perhaps only occasionally exceed the optimum temperature for charr and even more seldom would conditions of optimum temperature for growth coincide with unlimited access to food. In this context, the optimum temperature for growth of charr of 16°C appears to be inappropriate.

In general, the temperature at which the energy intake is maximised does not correspond with the optimum temperature for growth of fish. This pattern has been shown for a number of species: brown trout (Elliott, 1976), perch (*Perca fluviatilis*) and roach (*Rutilus rutilus*) (Lessmark, 1983), Atlantic salmon (Koskela, Pirhonen & Jobling, 1997), sockeye salmon (Brett, 1971). In contradiction, the temperature for maximum energy intake of charr in this thesis more or less coincided with the optimum temperature for growth. The largest differences between these two temperatures found for a single stock (Torrön charr) was 0.4°C (Paper III). At large, the growth of charr in relation to temperature appears to be a direct function of the food intake; i.e. the decrease in growth at higher temperatures is solely a result of decreased appetite. A similar relationship has been demonstrated for Atlantic salmon. Jonsson *et al.* (2001) showed that the energy intake and growth curves in relation to temperature were functionally similar and that the temperature for maximum energy intake and growth nearly coincided.

Elliott & Baroudy (1995) found that the difference between the upper limit for feeding and the UILT for charr was about 3°C. All charr stocks in this thesis showed high growth rates at 20°C and in paper II, the upper thermal limits for energy intake and growth of charr were found in the interval 21-22°C. In contradiction to the study by Elliott & Baroudy (1995), this suggests that the difference between the temperature limit for positive growth and the upper incipient limit of charr is only about 1°C. This finding is supported by a study by Grande & Andersen (1991) who found that parr of four different salmonids were feeding close to their UILT. Presumably, fish that stopped feeding at 21-22°C would eventually have died. However, in paper II it was shown that if the temperature was lowered, fish were able to resume feeding within a week. This suggests that charr can endure short periods of high temperatures, for example during a warm summer scenario, and recover quickly. Interestingly, we observed that intensively feeding small charr (*c.* 1 g) suddenly died during acclimatisation at temperatures between 21-22°C, while some fish that did not feed or fed at low rates survived the acclimatisation period (unpublished observation). Probably, fish that did not stop feeding at high temperatures suffered from hypoxia. Thus, continued high rates of feeding at temperatures close to the UILT might be fatal. In paper I and IV, the estimated lower limit for growth for the different stocks varied from -1.7 to 5.3°C and the mean value for all experiments was 2.6°C. Experimental and field studies suggest that charr are able to feed and grow at temperatures close to zero (Brännäs & Wiklund, 1992; Johnson, 1980). Charr in this thesis where all well fed and reared at comparatively high temperatures prior to the experiments. It is therefore likely that the found lower limits for growth are only valid for fish acclimatised to summer conditions. Thus, if fish had been adapted to winter conditions, it is reasonable to assume that the estimate of lower limit for growth would have been in accordance with the studies by Brännäs & Wiklund (1992) and Johnson (1980).

The growth efficiency of fish increases with increasing temperature to an optimum and, thereafter, the growth efficiency decreases and the growth efficiency is generally maximised at a lower temperature than that at which the growth is maximised (Jobling, 1996). Consequently, in line with the bioenergetic hypothesis of salmonids proposed by Brett (1971), Wootton (1990) and Elliott & Hurley (2000) suggested that the discrepancy between the temperatures generating maximum growth and growth efficiency leads to a trade of for the fish between high growth rate and high growth efficiency. The mean growth efficiency over all temperatures of charr in this thesis was remarkably high and varied between 44-55% and the maximum values at a single temperature varied between 48.3-59.9%, for the four examined populations (Paper I, III). In a study on piscivorous brown trout, it was stated that the found maximum growth efficiency of 42% exceeded most of the earlier values for salmonids (Elliott & Hurley, 2000). In the same study, the maximum growth efficiency of trout fed invertebrates was 32% and Elliott stated that this value was similar to values obtained by other workers for salmonids feeding on invertebrates or pelleted food. The growth efficiency of charr fed shrimps in Paper I showed a maximum growth efficiency at 9°C of 59.4% (recalculated value according to the method in Paper III). Hence, the maximum growth efficiency of charr feeding on invertebrates appears to be about twice as high compared to other salmonids. This result must be considered as remarkable.

The effect of temperature on the growth efficiency of charr was moderate. For the pooled data, the mean growth efficiency was highest at 9°C (51%) but at 20°C the mean growth efficiency was only 6% lower (45%). Accordingly, Brett, Clarke & Shelbourn (1982) and Jonsson *et al.* (2001) found that temperature exhibited only minor effect on the growth efficiency of Chinook salmon (Oncorhynchus tshawytscha) and Atlantic salmon, at intermediate temperatures. Moreover, the response of growth efficiency to temperature differed among the stocks and it was not possible to estimate a temperature at which the growth efficiency was maximised. Although, no distinct peak in growth efficiency seems to exist in charr, the growth efficiency tended to be maximised at a temperature lower than 9°C, which is significantly lower than the temperature at which the energy intake and growth rate is maximised. This is in accordance with the suggestion that the optimum temperature for food conversion is generally lower than the temperature for optimum growth (Jobling, 1996). As stated, the effect of temperature on the growth efficiency of charr seems to be small and thus, the supposed trade off between growth and growth efficiency in fish (Wootton, 1990; Elliott & Hurley, 2000) appears to be inappropriate for charr. However, it is reasonable to assume that charr often is food limited in nature and as shown by Brett (1971) and Elliott (1976), the growth efficiency of fish seems to be optimised at an intermediate energy intake. In this context, knowledge of the response of growth efficiency to temperature of charr, reared at reduced ration, might be vital in the evaluation of a possible trade of in charr. Unfortunately, there are no studies of charr growth efficiency under conditions of food limitations published.

Fish populations within species have in several studies been shown to be adapted to their local environment. The majority of these studies are based on differences in life-history traits (e.g. L’Abée-Lund *et al.*, 1989; Gotelli & Pyron, 1991; review in Roff, 1992; Elliott, 1994). Only a few studies focus on physiological adaptations, such as population specific differences in growth. Prior to this thesis, knowledge about local thermal adaptation of charr was lacking. In paper IV, only minor differences in thermal performance among the different stocks of charr were observed and these differences gave no support for the two contrasting hypothesis of thermal adaptation (see introduction). Instead, the differences between the Swedish stocks seemed to be more related to life history than to climatic conditions. For example, the stocks that mature at a large size in the wild (Vättern, Dunsjön, Hornavan and Sommen) seemed to reach higher growth rates at T_M, than stocks which usually mature at a few hundred grams (Blåsjön, Näckten and Torrön).

As shown in paper I, III and IV, the optimum temperature for growth of charr is found at about 16°C, which is similar to the optimum temperature for growth of trout. Consequently, according to McCauley & Casselman (1980) and Jobling (1981), both charr and trout presented to thermal gradient are predicted to prefer a temperature close to 16°C. In contradiction, charr was shown to prefer the significantly lower temperature of 11.4°C (Paper V). Trout preferred a temperature of 16.0°C, which is close to its optimum temperature for growth and thus, in accordance with the general predictions of good correlation between the optimum temperature for growth and preferred temperatures (McCauley & Casselman, 1980; Jobling, 1981). Consequently, the result of this thesis suggests that trout thermoregulate in accordance with the prediction and that charr prefer a significantly lower temperature than that which produces maximum growth rate. Under the assumption that high growth rate is positively connected to fitness, it appears like charr has a maladapted thermoregulatory behaviour. However, the typical waters inhabited by charr are of low productivity (Hammar, 1998) and fish in these lakes are most likely subjected to food limitations. Under such conditions it might be that individuals that optimise their growth efficiency (i.e. indirectly their growth), instead of their growth rate (directly) are favoured. Consequently, since the growth efficiency of charr seems to be maximised at a lower temperature than the optimum temperature for growth (Paper I and III), a low preferred temperature might be advantageous.

Thermal performance has in many studies been shown to affect the outcome of competitive interactions between different fish species. In Scandinavia, charr and brown trout coexist in many lakes (sympatry) and in these lakes the two species has been observed to niche segregate (Langeland *et al.* 1991). During summer, trout occupy the more profitable littoral zone, whilst charr is suggested to be forced to stay in pelagic or deeper off shore areas. A similar pattern has been shown for the corresponding North American species pair Dolly Varden (*Salvelinus malma*) and cutthroat trout (*Salmo clarki*) (Andrusak & Northcote, 1971; Hindar *et al.*, 1988). However, in full-scale studies of niche segregating species, a main dilemma is to control for the effect of lakes. In the studies of the Scandinavian sympatric charr and trout, lakes inhabiting allopatric charr have often been used as control and in those lakes charr has been found to utilise the littoral zone. In this context, differences in thermal performance has been put forward as one explanatory factor. However, as suggested in this thesis, lakes with allopatric charr are in general situated at higher altitudes than lakes with sympatric charr and trout and thus, the temperature in the control lakes is presumably lower than in the sympatric lakes. Hence, as shown in Paper IV, the preferred temperature of charr is significantly lower than previously predicted and therefore, it can not be excluded that the observed niche segregation between charr and trout is merely due to the thermoregulatory behaviour of charr rather than competitive interactions with trout.

Conclusions

Earlier studies of the thermal performance of Arctic charr mainly focused on temperature at the lower and intermediate end of the relevant temperature range. The first aim of this thesis was therefore to evaluate the performance of charr at higher temperature and thus, to produce complete baseline models for feeding and growth of charr. Two models, originally designed for brown trout (Elliott, Hurley & Fryer, 1995) and bacterial growth (Ratkowsky *et al.*1983), were applied to charr growth. The latter fitted the parabolic data pattern of charr better and thus, it was concluded that the Ratkowsky model is the appropriate choice for describing charr feeding and growth. In this thesis, charr showed maximum feeding and growth rate at 16.0°C (±0.24 SE) and feeding and growth ceased at 21.6°C (±0.26 SE). The lower thermal limit for growth of charr has earlier been found close to zero degrees Celsius. As a result, the whole thermal performance window of charr is now described. The second aim of this thesis was to examine if geographically separated charr populations were locally adapted in thermal traits. Overall, the effect of temperature on the growth of 11 populations was approximately similar, but some differences among populations were found. These differences appeared to be more connected to life history, such as age at maturity, than to the local temperature regime. It has been suggested that fish in general prefer its optimum temperature for growth. The third aim was therefore to study the preferred temperature of charr and trout. This thesis demonstrates that charr and trout differ in thermoregulatory behaviour in that sense that trout prefer its optimum temperature for growth but charr chooses a significantly lower temperature than that which produces maximum growth. Thus, in interpretation of the observed niche segregation of charr and trout in the field, the thermal behaviour of the two species rather than their optimum temperatures for growth should be used as a predictor of preferred niches.

Today, there are only a few, if any, aquatic environments unaffected by man. Thermal disturbances of the environment of aquatic organisms is known to be of both local (e.g. hydroelectric power plants, nuclear power plants or forestry actions) and global (i.e. climate change) kind. Most Arctic charr populations in Scandinavia are on the southern edge of their distribution. Most likely, the few remaining charr populations far south, such as at high altitudes in the Alps and the larger lakes of southern Sweden, is present only because of suitable thermal conditions in these lakes. Compared to the present distribution, the charr in past days was found further down along the river valleys of northern Sweden. The reason for the disappearance is not known. However, as shown in this thesis the charr prefer temperatures around 11°C and it seems reasonable to assume that thermal changes (i.e. global warming) could affect the present distribution of charr. The situation is however, more complicated in that many of the Scandinavian lakes in which charr and trout coexist are not merely a result of their natural, overlapping distribution. For centuries, man has moved fish between lakes in different parts of

Sweden. In the northern part, charr, trout and whitefish have frequently been transplanted in to water systems, which they did not invade naturally. This has in many cases put even more pressure on native charr populations. In order to preserve still "unaffected" charr populations, or in management of populations used for their recreationally value (i.e. sportsfishing), a good knowledge of their thermal performance is a important. Furthermore, in the Northern countries, the farming of Arctic charr is a growing business. Being a quite new branch in aquaculture, rearing techniques must be improved. In this context, solid basic knowledge of the thermal performance of the farmed fish is essential. Thus, I believe that this thesis contributes to a better management of charr in their natural environment, as well as under farming conditions.

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