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Temperature preference of juvenile Arctic charr originating from different thermal environments

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Abstract Temperature preference of juvenile (age 1+) Arctic charr (*Salvelinus alpinus* L.) originating from four arctic and sub-arctic populations (Svalbard and mainland northern Norway), representing a range of habitats with different temperature conditions, was studied by use of a shuttle-box system which allowed individual fish to control their environmental temperature. Based on the assumption that adaptations to long-lasting differences in thermal environments would affect temperature preference, we expected that Arctic charr from the high arctic Svalbard would prefer a lower temperature than the charr from two well-studied sub-arctic mainland lakes (i.e. one anadromous charr population from Storvatn, Hammerfest and two sympatric resident charr morphs from Fjellfrøsvatn, Målselv). There were, however, no significant differences in temperature preference among the four populations after 24 h exposure to the shuttle-box system, although the charr from the omnivore upper-water sympatric morph of Fjellfrøsvatn used significantly longer time to reach a stable thermal preferendum than the fish of the other populations. The average temperature preference at the end of the trials ranged between 10.9 and 11.6 °C among the populations. The lack of population differences suggests that temperature preference is not a polymorphic trait under strong selection in Arctic charr.

Keywords Fish · *Salvelinus alpinus* · Sub-arctic and arctic populations · Temperature preferences

Introduction

Polymorphism in several, e.g. physiological, ecological, genetic and life history, traits is common among some freshwater fish species that inhabit postglacial lakes (Skulason and Smith 1995). This has resulted in a wide variety of populations with specialised and contrasting lifestyles and the origin of sympatric sister morphs adapted to different trophic habitats (Skulason and Smith 1995; Klemetsen et al. 2003a). During the process of phenotypic diversification, physiological adaptations to different environments should be important and fixation of phenotypic traits could occur (e.g. Skulason et al. 1999; Ohlberger et al. 2008b). In fish species with high phenotypic plasticity such as early invaders after the ice retreat in postglacial lakes, adaptations to different environmental conditions (e.g. temperature regimes) could be important for survival in these harsh and unpredictable glacial water systems.

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Here, we explore whether the highly polymorphic Arctic charr (*Salvelinus alpinus*), a species that has adapted to contrasting thermal environments (high arctic conditions, deep-water cold habitats, anadromous populations and landlocked stocks), show different temperature preferences depending on the thermal environment to which they have adapted.

Fish are poikilothermic animals, which, with few exceptions, have a body temperature only slightly different from that of their surrounding water. Fish are not only temperature sensitive; with variability in temperature conditions, the fish can control their body temperature by actively seeking their preferred temperature regime (Lagler et al. 1977). The selected temperature (after 24 h) is considered to be species specific and unaffected by previous acclimation (Reynolds et al. 1976) and is called the final thermal preferendum (Fry 1947). The final thermal preferendum seems to be influenced by size or age, as juveniles tend to select higher temperatures than adults (Coutant 1977; McCauley and Huggins 1979; Jobling 1994). Usually, there is a correlation between the temperature the fish experience in their natural habitat and its thermal preferendum. Thus, fish species from Polar regions have lower thermal preferenda compared with fish from temperate regions (Schurmann and Christiansen 1994). Differences have also been found among different populations of the same species originating from habitats with different water temperatures (Konecki et al. 1995). In many fish species, the preferred temperature correlates with the optimum temperature for growth and physiological performance (Brett 1971; Beitinger and Fitzpatrick 1979; Jobling 1981; McCauley and Casselman 1981; Kellogg and Gift 1983). Measurement of final thermal preferendum has therefore been suggested as a rapid method for determining optimum temperature for growth (Jobling 1981). Thus, the study of temperature preference may contribute both to the understanding of the ecology of the species and provides valuable knowledge for the management of the species.

The Arctic charr has the northernmost distribution among freshwater fishes, and it is considered to be the most cold-adapted salmonid (Johnson 1980; Klemetsen et al. 2003a; Siikavuopio et al. 2009, 2010). But at the same time, it is probably also the salmonid with the lowest tolerance to increased water temperatures (Elliott and Elliott 2010). It is therefore a concern that Arctic charr populations may be increasingly affected by global warming and become extinct in some areas at the edge of its southern distribution (Elliott and Elliott 2010; Winfield et al. 2010; Finstad et al. 2011). This view is supported by a recent review of field data from a number of European lakes, which suggests that Arctic charr was the species most affected by climate warming (Jeppesen et al. 2012).

Larsson (2005) reported preferred temperatures between 10.8 and 11.8 °C in Swedish charr. Peterson et al. (1979) found that the acute thermal preferendum of Arctic charr fry, acclimated to about 12 °C, was 9.2 °C. In the high Arctic, charr populations may have other thermal adaptations as water temperature rarely exceed 6–8 °C during the entire season (Svenning et al. 2007). Furthermore, reproductively isolated deep-water morphs of Arctic charr live in stable, low thermal habitats as found in Lake Fjellfrøsvatn, subarctic Norway (Klemetsen et al. 1997; Knudsen et al. 2006). This deep-water morph has heritable adaptations in several traits such as trophic behaviour and morphology (Klemetsen et al. 2002, 2006). Hence, thermal preference of cold-water adapted populations or morphs of Arctic charr originating from different temperature environments remains to be investigated. The present study was, therefore, undertaken in order to investigate temperature preference of Arctic charr from different populations living under longstanding stable, but contrasting temperature environments, such as high arctic lakes on Svalbard to deep-water adapted landlocked morphs and anadromous populations. We hypothesize that the Svalbard stock and the deep-water morph from Fjellfrøsvatn show lower temperature preference as compared to the upper-water omnivore morph from Fjellfrøsvatn and the anadromous population from Storvatn, Hammerfest.

Materials and methods

Fish and rearing

The Arctic charr used in this experiment originated from Lake Fjellfrøsvatn (69°N, 19°E) in the Målselv River System and Lake Storvatn in Hammerfest (HF) (70°N, 23°E), Northern Norway, and Lake Vårfluesjøen from Svalbard (SV) (80°N, 16°E). From Fjellfrøsvatn, we used two genetically different and reproductively isolated lake resident morphs; the profundal spawning benthivore morph (PB) and the littoral spawning omnivore morph (LO) (Klemetsen et al. 1997; Westgaard et al. 2004; Knudsen et al. 2006).

The experiment lasted from May to June 2013 at the Kårvika Research Station near Tromsø. Fish were held under a simulated natural light regime (Tromsø, 69°N), with light (fluorescent lamp) intensity measured to 150 lux at the water surface during the light part of the day, and at natural ambient temperatures 4.4 °C (±2.6 SD). During the experimental period, the fish were fed to excess using a commercially formulated feed (Skretting salmon feed), containing 50 % protein and 23 % crude oil. Individual fish ($n = 6$) from each population were exposed to the shuttle-box system (see further down) for 24 h. Individual length (cm) of all the experimental fish was recorded at the beginning of the shuttle-box experiment. The age of the juvenile charr in the experiment was 1+. The average length of the PB-morph and the LO-morph from Fjellfrøsvatn was 10.3 cm (±0.6 SEM) and 10.1 cm (±0.9 SEM), respectively. The average length of Hammerfest and Svalbard strains was 10.5 cm (±0.5 SEM) and 10.8 cm (±0.2 SEM), respectively.

Shuttle-box system

To determine the preferred temperature, individual fish was allowed to thermoregulate in an electronic shuttle-box device (Loligo; minimum 4 °C, maximum 16 °C). The shuttle box consisted of a warm and a cold-water chamber connected by a passage (system from Loligo, see Stol et al. 2013). The fish was able to move freely between these chambers. The temperature difference between the chambers was kept constant at 1 °C by the use of two buffer tanks (warm and cold), a hot-water reservoir, a cold-water reservoir, two temperature probes, a DAQ-M instrument (Loligo Inc.) connected to a computer and six pumps (Eheim 1046). The position of the fish was determined by a CCD camera (uEye USB camera) connected to the computer software (ShuttleSoft, Loligo Inc.). Background subtraction is used to separate the object from static components in the image. After this subtraction, the centre of mass of the object is calculated and the respective coordinates are determined. The software determined the position of the fish (x- and y-coordinate) by means of subtracting its darker-than-the-background appearance from a static image of the tanks (without a fish inside). When the ShuttleSoft software detected the fish inside the cold chamber, the temperature of both chambers was lowered at a rate of 1 °C h^{-1}, and if the fish were in the hot chamber, the temperature of both chambers was increased at a rate of 1 °C h^{-1}. Hence, the fish could use their natural behaviour to seek optimal temperatures, by moving between chambers, and thereby controlling their body temperature towards their preferred temperature.

Statistical analyses

Statistical analyses were performed using SYSTAT (Systat Software, Inc., USA). Possible differences in the development of temperature preferences between populations were analysed using a general linear model with a log-transformed time variable and populations grouped as dummy variables. The GLM was performed using a stepwise backward iterative method, removing grouping variables not contributing significantly ($P < 0.05$). Possible differences in final preferred temperature (with the endpoint set to 23 h due to missing data on 24 h) were analysed using ANOVA, with distribution of studentised residuals found not to differ from normal distribution (Kolmogorov–Smirnov Lilliefors; $n = 26$, $P = 0.841$) (Zar 1996). The temperature preference data are presented as mean ± standard deviation (SD) (Fig. 1).

Results

The general linear model described 95 % (R^2) of the variation and revealed that the temporal pattern of the temperature preference curve differed significantly ($F_{2,93} = 803.8$; $P < 0.001$) between populations, with one population (LO-morph from Fjellfrøsvatn) using significantly longer time to stabilise (lower slope) as compared to the other populations. However, by 23 h, there were no significant differences in preferred temperature between the populations ($F_{3,22} = 0.423$; $P = 0.738$). The average final temperature preference ranged between 10.9 and 11.6 °C among the four tested populations (Fig. 1).

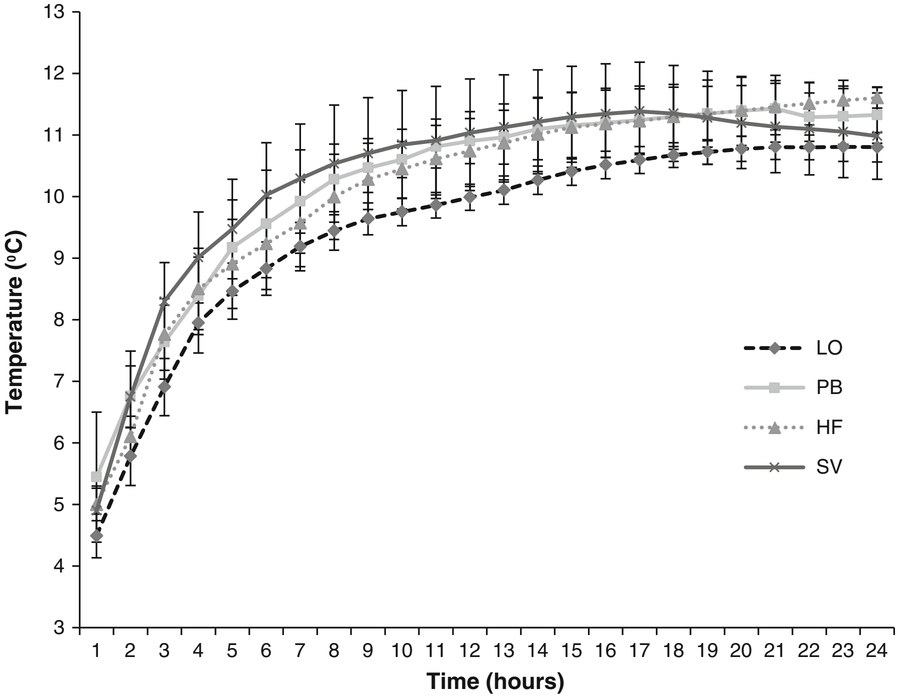

Fig. 1 Temperature preference (°C) of juvenile Arctic charr from four different populations; i.e. Svalbard (SV), Hammerfest (HF) and profundal spawning benthivore (PB) and littoral spawning omnivore (LO) morphs from Fjellfrøsvatn. Values are presented as mean ± SD

Discussion

Temperature is one of the most important environmental factors for fish fitness and affects mortality, feeding, growth and maturation (Jobling 1994). The thermal niche and the ability to tolerate thermal stress vary between fish species (e.g. Jobling 1994; Elliott and Elliott 2010; Siikavuopio et al. 2010), and fish adapted to low temperature may be expected to develop lower thermal preferenda than fish adapted to higher temperatures (Schurmann and Christiansen 1994), even within the same species (Konecki et al. 1995). Genetic differences between populations can be responsible for differences in the thermal preferences (Schurmann and Steffensen 1992: Bjørnsson et al. 2001). According to Petersen and Steffensen (2003), different final thermal preferenda across Atlantic cod populations seem to be associated with differences in haemoglobin genotypes. However, the present study on Arctic charr populations originating from completely different thermal environments did not reveal such differences in temperature preference. The result was surprising as one might expect that the temperature preference should reflect their latitudinal distribution, with arctic populations showing preference for lower temperatures as compared to conspecifics exposed to higher temperatures in lakes further south (Fangue et al. 2009). Also, the charr used in this study displayed temperature preferences within the range found for charr populations from more southern latitudes (Larsson 2005; Larsson et al. 2005; Amundsen and Knudsen 2009, 2007). This contradicts the idea of a latitudinal gradient with respect to temperature preference in Arctic charr and suggests that cold-water adaptation is not a trait under strong selection in this species. Still it remains to be verified if the small differences in temperature preference reflect the growth response of the different populations, as temperature-driven effects on growth may be present in Arctic charr populations (Power et al. 2000; Kristensen et al. 2006). In addition to other factors such as ontogenetic stages, feeding regimes and seasonality may affect the temperature selection of fish (Larsson 2005; Amundsen and Knudsen 2009, 2007; Elliott and Allonby 2013), and these combined factors should be considered in future studies of thermal preferenda of northern/arctic populations of Arctic charr.

The absence of a longitudinal gradient in temperature preference in the present study suggests that temperature preference is not a polymorphic trait under strong selection in Arctic charr. Our data partly contradict earlier empirical and theoretical work of postglacial coregonid salmonid species (Ohlberger et al. 2008a, b, 2013), suggesting that temperature-related trait is polymorphic and potentially under selection. This can be related to the broad temperature range that these coregonid species exhibit by their wide geographical distribution. This in turn could lead to an advantage in divergence along environmental gradients like the thermal niche axes. If a species exploits a broad niche, a subdivision of the resource spectrum into two diverged and narrower niches is likely to happen. However, if the species have a narrow thermal niche (e.g. cold stenotherm), the environmental gradient will probably not be wide or large enough for such a divergence. In addition to the niche space, the time for natural selection to operate could be another constraining factor related to the colonisation history of the Arctic charr to explain the lack of thermal diversification. Arctic charr was the earliest freshwater fish invading these novel areas several thousand years ago, and they are still the only freshwater fish species at Svalbard (Klemetsen et al. 2003a; Sandlund and Hesthagen 2011). The coastal areas in sub-arctic Norway and Svalbard were probably invaded during the same time period shortly after the ice retreat. Thus, the number of generations for selection to operate should probably be higher in lakes from the mainland Norway than in the arctic Svalbard lakes. There should therefore be enough time to express differences between high Arctic population and more southern populations (Larsson et al. 2005), if this was a favourable trait (i.e. thermal preference) under selection, especially when comparing with other salmonids, such as coregonids that seem to be able to diverge in their thermal niche, but invaded the sub-arctic areas much later (Sandlund and Hesthagen 2011).

High arctic lakes should form highly stable environments for trait (i.e. thermal preference) selection over a time period of several thousand years. By comparison, the two sympatric morphs from mainland Norway should also have stable environments for trait selection (e.g. deep-water adaptations) as the two morphs have temporal stable diverged trophic niches in, e.g. habitat choice across years (Knudsen et al. 2006, 2010) and throughout all seasons also during the winter period (Klemetsen et al. 2003b; Amundsen et al. 2008; Amundsen and Knudsen 2009). Furthermore, the two morphs are found to have heritable differences in specific deep-water adaptations, e.g. morphological traits and trophic behaviour (Klemetsen et al. 2002, 2006). One explanation for lack of different thermal preference for the LO- and PB-morphs is a theoretical possibility of double invasion of Arctic charr to the lake. If the deep-water PB-morph entered the lake relatively recently, the time for natural selection to operate could be too short. Double invasion seems less likely as this is a landlocked lake and the potential period for invasion of Arctic charr was short (Klemetsen et al. 1997). The ecological and genetic studies of the charr morphs in the lake suggest a local split of the morph-pair (Westgaard et al. 2004; Knudsen et al. 2006). Thus, no final conclusive study regarding their origin has been completed, as no advanced genetic analyses are performed of this morph-pair (Westgaard et al. 2004). Altogether, the time necessary for a thermal divergence both between the two morphs in Fjellfrøsvatn (local scale) and between the Svalbard population and the more southern populations (regional scale) should have been long enough.

One explanation for the apparent similarity in temperature preference across populations could be related to the fact that Arctic charr is a typical early invader in these novel northern areas and therefore, it is beneficial to keep a generalist strategy related to environmental factors. Most Arctic charr populations experience large fluctuations in temperature regimes seasonally with winter temperatures down to almost 0 °C (Klemetsen et al. 2003b; Svenning et al. 2007). Additionally, landlocked population of Arctic charr seems to avoid summer temperatures above 12 °C (Larsson 2005) and anadromous fish seems to actively select low temperatures after entering the freshwater habitats (Rikardsen et al. 2007; Spares et al. 2013; Jensen et al. 2014). Accordingly, as high arctic populations and deep-water morphs experience temperatures of 8–10°C during the summer season, their upper limit temperature is not very different from most Arctic charr populations. Consequently, strong adaptations to a narrow temperature regime seem not to be a selective advantage for long-term survival of the population. Hence, when the adaptable ancestral invader (anadromous populations) diversify into more specialised descendant, reproductively isolated populations (the profundal spawning population) or invades high arctic lakes, they will have relatively uniform temperature preferences. Thus, as temperature preference is closely linked to several fitness components via growth performance, the Arctic charr populations that live in cold environments may have an advantage by utilising the food resources more cost-effective (e.g. higher conversion efficiency) and thereby may be adapted to grow better at lower temperatures (Klemetsen et al. 2002). Such traits could be valuable for survival in colder areas. This, however, remains to be tested across Arctic charr populations.

The lack of population-specific cold-water adaptations indicates that Arctic charr populations inhabiting high arctic lakes or deep mainland lakes could be less affected by a moderate global warming, as they achieve some protection in their habitats by actively avoiding the warm upper-water layers. By contrast, Arctic charr populations confined to shallow lakes, rivers or living at the southern edge of their distributions (e.g. Malmquist et al. 2009; Winfield et al. 2010; Murdoc and Power 2012; Jeppesen et al. 2012) may be more affected by global warming as the buffer of cold water becomes limited. Additionally, by being exposed to a potentially warmer climate in the future, Arctic charr in sub-arctic areas will most likely experience higher resource competition from southern invaders or coexisting species such as brown trout and European whitefish (e.g. Finstad et al. 2011; Eloranta et al. 2011, 2013; Hayden et al. 2013) as these species seem more warm water adapted (e.g. Amundsen and Knudsen 2009, 2010; Elliott and Elliott 2010). Altered resource competition due to climate change could also have indirect effects on polymorphic Arctic charr populations. There are recent examples that interspecific resource competition has caused breakdown of reproductive isolation between sympatric morph-pairs of fishes due to invasion or introduction of southern non-native species in postglacial lakes (Taylor et al. 2006; Sandlund et al. 2013; Bhat et al. 2014). Both European whitefish and brown trout co-occur with Arctic charr in many lakes and show higher optimum temperature for growth and preferences (Siikavuopio et al. 2012; Elliott and Allonby 2013). The Arctic charr may therefore be affected both directly and indirectly by global warming.

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References

Amundsen P-A, Knudsen R (2009) Winter ecology of Arctic charr (*Salvelinus alpinus*) and brown trout (*Salmo trutta*) in a Subarctic lake. Aquat Ecol 43:765–775

Amundsen P-A, Knudsen R, Klemetsen A (2008) Seasonal and ontogenetic variations in resource use by two sympatric Arctic charr morphs. Env Biol Fish 83:45–55

Beitinger TL, Fitzpatrick LC (1979) Physiological and ecological correlates of preferred temperature in fish. Am Zool 19:319–329

Bhat S, Amundsen P-A, Knudsen R, Gjelland KO, Fevolden S-E, Bernatchez L, Præbel K (2014) Speciation reversal in European whitefish (*Coregonus lavaretus* (L.)) caused by competitor invasion. PLoS One 9:e91208

Bjørnsson B, Steinarsson A, Oddgeirsson M (2001) Optimal temperature for growth and feed conversion of immature cod (*Gadus morhua* L.). J Mar Sci 58:29–38

Brett JR (1971) Energetic responses of salmon to temperature. A study of some thermal relations in the physiology and Freshwater ecology of sockeye salmon (*O. nerka*). Amer Zool 11:99–113

Coutant CC (1977) Compilation of temperature preference data. J Fish Res Board Can 34:739–745

Elliott JM, Allonby JD (2013) An experimental study of ontogenetic and seasonal changes in the temperature preferences of Unfed and fed brown trout, *Salmo trutta*. Freshw Biol 58:1840–1848

Elliott JM, Elliott JA (2010) Temperature requirements of Atlantic salmon *Salmo salar*, brown trout *Salmo trutta* and Arctic charr *Salvelinus alpinus*: predicting the effects of climate change. J Fish Biol 77:1793–1817

Eloranta A, Siwertsson A, Knudsen R, Amundsen P-A (2011) Dietary plasticity of Arctic charr (*Salvelinus alpinus*) facilitates coexistence with competitively superior European whitefish (*Coregonus lavaretus*). Ecol Freshw Fish 20:558–568

Eloranta A, Knudsen R, Amundsen P-A (2013) De-coupling of food webs associated with interspecific and intraspecific Niche segregation of Arctic charr (*Salvelinus alpinus*) coexisting with brown trout (*Salmo trutta*) in subarctic lakes. Freshw Biol 58:207–221

Fangue NA, Podrabsky JE, Crawshaw LI, Schulte PM (2009) Countergradient variation in temperature preference in populations of killifish Fundulus heteroclitus. Physiol Biochem Zool 82:776–786

Finstad FB, Anders G, Forseth T, Jonsson B, Bellier E, Hesthagen T, Jensen AJ, Hessen DO, Foldvik A (2011) Competitive exclusion along climate gradients: energy efficiency influences the distribution of two salmonid fishes. Glob Chang Biol 17:1703–1711

Fry FEJ (1947) Effects of the environment on animal activity. Univ. Toronto Stud. Biol. Ser. 55 Publs Ontario Fish Res Lab 68:1–62

Hayden B, Holopainen T, Amundsen P-A, Eloranta AP, Knudsen R, Præbel K, Kahilainen KK (2013) Ecological interactions between invading benthivores and native whitefish in Subarctic lakes. Freshw Biol 58:1234–1250

Jensen JLA, Rikardsen AH, Thorstad EB, Suhr AH, Davidsen JG, Primicerio R (2014) Water temperatures influence the marine area use of Arctic charr *Salvelinus alpinus* and brown trout *Salmo trutta*. J Fish Biol. doi:10.1111/jfb.12366

Jeppesen E, Mehner T, Winfield IJ, Kangur K, Sarvala J, Gerdeaux D, Rask M, Malmquist HJ, Holmgren K, Volta P, Romo S, Eckmann R, Sandstrom A, Blanco S, Kangur A, Stabo HR, Tarvainen M, Ventela AM, Sondergaard M, Lauridsen TL, Meerhoff M (2012) Impacts of climate warming on the long-term dynamics of key fish species in 24 European lakes. Hydrobiologia 694:1–39

Jobling M (1981) Temperature tolerance and the final preferendum—rapid methods for the assessment of optimum growth temperatures. J Fish Biol 19:439–455

Jobling M (1994) Fish bioenergetics. Chapman and Hall, London

Johnson L (1980). The Arctic charr, *Salvelinus alpinus*. In: Balon EK (ed) Charrs, salmonid fishes of the genus *Salvelinus*. The Hague, Netherlands, pp 15–92

Kellogg RL, Gift J (1983) Relationship between optimum temperatures for growth and preferred temperatures for the young of four fish species. Tran Am Fish Soc 112:424–430

Klemetsen A, Amundsen P-A, Knudsen R, Hermansen B (1997) A profundal, winter-spawning morph of Arctic charr *Salvelinus alpinus* (L.) in lake Fjellfrøsvatn, northern Norway. Nordic J Freshw Res 73:13–23

Klemetsen A, Elliott JM, Knudsen R, Sørensen P (2002) Evidence for genetic differences in the offspring of two sympatric morphs of Arctic charr. J Fish Biol 60:933–950

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

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

Klemetsen A, Knudsen R, Primicerio R, Amundsen PA (2006) Divergent, genetically based feeding behaviour of two sympatric Arctic charr, *Salvelinus alpinus* (L.), morphs. Ecol Freshw Fish 15:350–355

Knudsen R, Klemetsen A, Amundsen P-A, Hermansen B (2006) Incipient speciation through niche expansion an example from the Arctic charr in a subarctic lake. Proc Roy Soc B 273:2291–2298

Knudsen R, Primicerio R, Amundsen P-A, Klemetsen A (2010) Temporal stability of individual feeding specialization may promote speciation. J Anim Ecol 79:161–168

Konecki JT, Woody CA, Quinn TP (1995) Temperature preference in two populations of juvenile coho salmon, *Oncorhynchus kisutch*. Env Biol Fish 44:417–421

Kristensen DM, Jørgensen TR, Larsen RK, Forchhammer MC, Christoffersen KS (2006) Inter-annual growth of Arctic charr (*Salvelinus alpinus*, L.) in relation to climate variation. BMC Ecol 6:10–18

Lagler KF, Bardach JE, Miller RR, Passino DRM (1977) Ichthyology, 2nd edn. Wiley, New York

Larsson S (2005) Thermal preference of Arctic charr, *Salvelinus alpinus*, and brown trout, *Salmo trutta*—implications for their niche segregation. Env Biol Fish 73:89–96

Larsson S, Forseth T, Berglund I, Jensen AJ, Näslund I, Elliott JM, Jonsson B (2005) Thermal adaptation of Arctic charr: experimental studies of growth in eleven charr populations from Sweden, Norway and Britain. Freshw Biol 50:353–368

Malmquist HJ, Antonsson T, Ingvason HR, Ingimarsson F, Arnason F (2009) Salmonid fish and warming of shallow Lake Elliðavatn in Southwest Iceland. Verh Interne Verein Limnol 30:1127–1132

McCauley RW, Casselman JM (1981) The final preferendum as an index of the temperature for optimum growth in fish. In: Tiews K (ed) Proceedings of the world symposium, aquaculture in heated effluents and recirculation systems, vol 2. Heenemann, Berlin, pp 81–92

McCauley RW, Huggins NW (1979) Ontogenetic and nonthermal seasonal effects on thermal preferenda of fish. Am Zool 19:267–271

Motensen A, Ugedal O, Lund F (2007) Seasonal variation in temperature preference of Arctic charr (*Salvelinus alpinus* L.). J Therm Biol 32:314–320

Murdoc A, Power M (2012) The effect of lake morphometry on thermal habitat use and growth in Arctic charr populations: implications for understanding climate-change impacts. Ecol Freshw Fish 22:453–466

Ohlberger J, Mehner T, Staaks G, Hoelker F (2008a) Temperature-related physiological adaptations promote ecological divergence in a sympatric species pair of temperate freshwater fish, *Coregonus* spp. Func Ecol 22:501–508

Ohlberger J, Staaks G, Petzoldt T, Mehner T, Hoelker F (2008b) Physiological specialization by thermal adaptation drives ecological divergence in a sympatric fish species pair. Evol Eco Res 10:1173–1185

Ohlberger J, Brännström A, Dieckmann U (2013) Adaptive phenotypic diversification along a temperature-depth gradient. Am Nat 182:359–373

Petersen MF, Steffensen JF (2003) Preferred temperature of juvenile Atlantic cod *Gadus morhua* with different haemoglobin genotypes at normoxia and moderate hypoxia. J Exp Biol 206:359–364

Peterson RH, Sutterlin AM, Metcalfe JL (1979) Temperature preference of several species of *Salmo* and *Salvelinus* and some of their hybrids. J Fish Res Board Can 36:1137–1140

Power M, Dempson JB, Power G, Reist JD (2000) Environmental influences on an exploited anadromous Arctic charr stock in Labrador. J Fish Biol 57:82–98

Reynolds WW, Casterlin ME, Covert JB (1976) Behavioural fever in teleost fishes. Nature 259:41–42

Rikardsen AH, Diserud O, Elliott JM, Dempson JB, Sturlaugsson J, Jensen A (2007) The marine temperature and depth preferences of Arctic charr and sea trout, as recorded by data storage tags. Fish Ocean 16:436–447

Sandlund OT, Hesthagen T (2011) Fish diversity in Norwegian lakes: conserving species poor systems. In: Jankun M, Furgala-Selezniow WM, Wisniewska A (eds) Water biodiversity assessment and protection. Faculty of Environmental Protection and Fisheries, University of Warma and Mazury, Olsztyn, Poland, pp 7–20

Sandlund OT, Gjelland KØ, Bøhn T, Knudsen R, Amundsen P-A (2013) Contrasting population and life history responses of a young morph-pair of European whitefish to the invasion of a specialised coregonid competitor, vendace. PLoS One 8:e68156

Schurmann H, Christiansen JS (1994) Behavioral thermoregulation and swimming activity of two Arctic teleosts (subfamily *Gadinae*)—the polar cod (*Boreogadus saida*) and the navaga (*Eleginus navaga*). J Thermal Biol 19:207–212

Schurmann H, Steffensen JF (1992) Lethal oxygen levels at different temperatures and the preferred temperature during hypoxia of the Atlantic cod, *Gadus morhua* L. J Fish Biol 41:927–934

Siikavuopio SI, Knudsen R, Winger AC, Kristoffersen R (2009) Is the winter period a severe bottleneck of anadromous riverine Arctic charr parr? Ecol Freshw Fish 18:126–131

Siikavuopio SI, Knudsen R, Amundsen P-A (2010) Growth and mortality of Arctic charr and European whitefish reared at low temperatures. Hydrobiologia 650:255–263

Siikavuopio SI, Knudsen R, Amundsen P-A, Sæther B-S (2012) Effects of high temperature on the growth of European whitefish (*Coregonus lavaretus* L.). Aquac Res 44:8–12

Skulason S, Smith TB (1995) Resource polymorphism in vertebrates. Trends Ecol Evol 10:366–370

Skulason S, Snorrason SS, Jonsson B (1999) Sympatric morphs, populations and speciation in freshwater fish with emphasis on Arctic charr. In: Magurran AE, May RM (eds) Evolution of biological diversity. Oxford University Press, Oxford, pp 70–92

Spares AD, Stokesbury MJW, O’Dor RK, Dick TA (2013) Temperature, salinity and prey availability shape the marine migration of Arctic char, *Salvelinus alpinus*, in a macrotidal estuary. Mar Biol 159:1633–1646

Stol JA, Svendsen JC, Enders EC (2013) Determining the thermal preferences of Carmine Shiner (*Notropis percobromus*) and Lake Sturgeon (*Acipenser fulvescens*) using an automated shuttlebox. Can Tech Rep Fish Aquat Sci 3038

Svenning MA, Klemetsen A, Olsen T (2007) Habitat and food choice of Arctic charr in Linnevatn on Spitsbergen, Svalbard: the first year-round investigation in high Arctic lake. Ecol Freshw Fish 16:70–77

Taylor EB, Boughman JW, Groenenboom M, Sniatynski M, Schluter D, Gow JL (2006) Speciation in reverse: morphological and genetic evidence of the collapse of a three-spined stickleback (*Gasterosteus aculeatus*) species pair. Mol Ecol 15:343–355

Westgaard JI, Klemetsen A, Knudsen R (2004) Genetic differences between two sympatric morphs of Arctic charr *Salvelinus alpinus* (L.) confirmed by microsatellite DNA. J Fish Biol 65:1185–1191

Winfield IJ, Hateley J, Fletcher JM (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

Zar JH (1996) Biostatistical analysis, 3rd edn. Prentice-Hall, Englewood Cliffs