fishes

Review

Thermal Effects on Ecological Traits of Salmonids

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Abstract: Here, I review thermal influences on metabolic rates and aerobic scope; growth; adult body size; and reproductive and behavioural traits, such as tendency and timing of the migration of salmonid fishes. A thermal window bounded by the upper and lower incipient lethal temperatures (UILT and LILT) determines where salmonids can survive. For most salmonids, LILT is close to 0 and UILT is between 20 and 30 °C. UILT and LILT are influenced by the acclimation temperature. Thermal tolerance is affected by fish size and ambient oxygen content, which decreases with increasing temperature. Standard metabolic rate (SMR), the energy required to maintain essential functions, increases with temperature, whereas maximum metabolic rate (MMR) increases with temperature until reaching a peak (pejus). Then, it decreases gradually to zero, i.e., the upper critical limit (T_{Crit}). Aerobic scope (AS = MMR-SMR) reaches its maximum at the pejus temperature. Metabolic rates and aerobic scope can be modified by temperatures that the fish experiences during embryogenesis and possibly also as larvae and young fry. At maximum feeding, maximum growth increases to a point at or below the pejus temperature. The optimum temperature for growth decreases with reduced food intake and increased body size. As for metabolic rate, the growth rate is influenced by the temperature during embryonic development. In a warmer climate, adult body size is expected to decrease chiefly because of a younger age at maturity. Parental fish retained at a higher temperature during maturation produce larger eggs, and this change in egg size may also be transferred to next-generation offspring. Furthermore, embryogenesis in warmer water leads to larger gonad and egg sizes at maturity. Water temperature influences locomotion, foraging and migratory activity. In a warmer climate, juveniles migrate to the sea earlier in spring. In addition, higher embryo temperature leads to delayed return of adult salmon from the ocean. Thus, temperature affects life history traits of salmonid fishes, partly as a direct effect on metabolic rates and food consumption and partly induced as a phenotypically plastic effect. The phenotypically plastic response may preadapt offspring to perform better in the expected future thermal environment.

Keywords: adaptive developmental programming; behaviour; climate; life history traits; metabolism; Salmonidae; temperature

Key Contribution: This paper summarizes the literature on how water temperature—via influences on metabolic rates and growth—affects life history traits of salmonid fishes. In addition, temperature during embryogenesis and early life of the organisms may have phenotypically plastic knock-on effects on these traits through epigenetic mechanisms such as DNA methylation.

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1. Introduction

The global climate is gradually becoming more variable and warmer. Mean surface temperature has increased by ca. 1 °C during the last 100 years and is expected to increase even faster towards 2100 [1,2]. Climate change is one of the reasons why animal populations decline, and local extinctions occur at the warmest part of their distribution areas [3]. Fish are vulnerable to temperature increases because their body temperature varies with that of the surrounding water, and the oxygen content in water is low and decreases when the water becomes warmer [4]. Higher temperatures also have sublethal effects, such as changes in biochemical reactions in the body and ecological traits such as growth, body size, age at maturity and behaviour [5]. Many of the ecological changes in species are linked to changes in life history and behavioural traits. Herein, I review how water temperature affects these traits of salmonid fishes.

Salmonidae, with subfamilies Coregoninae (freshwater whitefishes), Thymallinae (graylings), and Salmoninae (trout, salmon, charr, lenoks, and taimens), are globally distributed in fresh water and as anadromous fish migrating in sea water [6]. This is an important fish family not only economically but also culturally and ecologically [7]. These species provide food for millions of people, as well as recreation and sport, and they play key roles in ecosystem functioning and health [8,9]. However, many salmonid species are in decline because of a multitude of human-induced pressures including climate warming [10–13]. For instance, brown trout (*Salmo trutta* L., 1759) has been in strong decline in southern Europe because of climate warming and an increased prevalence of extremely warm events [14–16]. Many other salmonids also show strong climate-associated declines, such as chinook salmon (*Oncorhynchus tshawytscha* Walbaum, 1792) [17], bull trout (*Salvelinus confluentus* Suckley, 1859) [18], Arctic charr (*Salvelinus alpinus* L., 1759) [19] and Atlantic salmon (*Salmo salar* L., 1759) [20,21].

Climate warming concerns Salmonidae because they are cold water species with high oxygen demands. Oxygen has low solubility in water, and dissolved O_2 content in fully saturated water decreases by approximately 2% per 1°C increase in temperature within the thermal niche of salmonids [22]. The species become stressed when the temperature increases above their normal thermal niche and go extinct if temperatures increase too quickly or too much [23]. The optimal temperatures for growth of the juveniles of most species are around 15 °C, and thermal stress and death occur between 20 and 30 °C (Table 1).

Table 1. Thermal sensitivity of selected salmonids. Optimal temperature for growth, upper critical maximum temperature at which death is almost instantaneous and upper incipient critical temperature over which the juveniles do not feed and eventually die with sources of reference.

Species	Optimal Temperature for Growth (°C)	Upper Critical Maximum Temperature (°C)	Upper Incipient Critical Temperature (°C)	References
Atlantic salmon *Salmo salar*	16–20	28–33	27	[24,25]
Brown trout *Salmo trutta*	13–17	26–30	22–25	[25–28]
Rainbow trout *Oncorhynchus mykiss* (Walbaum, 1792)	15–19	30	24–27	[29–32]
Chinook salmon *Oncorhynchus tshawytscha*	15–19	29	25	[33]
Sockeye salmon *Oncorhynchus nerka* (Walbaum, 1759)	15		23–26	[34,35]
Cutthroat trout *Oncorhynchus clarkia* (Richardson, 1836)	13–14	28	19–25	[29,36,37]
Coho salmon *Oncorhynchus kisutch* (Walbaum, 1792)	12–15	29	25–26	[33,38]
Chum salmon *Oncorhynchus keta* (Walbaum, 1792)	12–14	32–34	22–24	[33,38,39]
Brook trout *Salvelinus fontinalis* (Mitchill, 1814)	12–16	28–31	25	[36,40–42]
Arctic charr *Salvelinus alpinus* (L.)	14–17	26–27	22–23	[25,43,44]
Whitespotted charr *Salvelinus leucomaenis* (Pallas, 1814)			26–28	[45]
Lake trout *Salvelinus namaycush* (Walbaum, 1792)	12	28–29	24	[46–49]

Table 1. *Cont.*

Species	Optimal Temperature for Growth (°C)	Upper Critical Maximum Temperature (°C)	Upper Incipient Critical Temperature (°C)	References
Bull trout *Salvelinus confluentus*	12–16	25–29	21	[41,42,44]
Dolly varden *Salvelinus malma* (Walbaum, 1792)			22–23	[45]
European grayling *Thymallus thymallus* (L., 1759)	17		21	[50]
Arctic grayling *Thymallus arcticus* (Pallas, 1776)		29	23–25	[51,52]

Individuals have a limited ability to face thermal stress and adjust to rapidly changing temperature. Consequently, populations may decline, extirpate, or even go extinct when the climate changes quickly [53–56]. Fish are ectotherms, and their metabolic and developmental rates, as well as behaviour, are strongly affected by their ambient temperature. However, owing to heritability and phenotypic plasticity, vulnerability varies among individuals and populations [57]. Variations in genetic structure, composition and function influence the capacity of individuals and populations to endure warmer conditions [55,58], and individual variations in thermal tolerance have important implications for the vulnerability to both short-term extreme heat waves and long-term, gradual warming [53]. In addition, thermal sensitivity varies ontogenetically. Young, highly oxygen-requiring stages are more sensitive to warming than older stages [59]. Furthermore, the rate of change in body temperature is inversely related to the mass of the fish, making small salmonids more susceptible to variations in water temperature than larger conspecifics [60]. Embryos are also more sensitive to thermal stress than advanced stages because of their rapid formation of tissues, structures, and organs [61].

Thermal limits increase with increasing acclimation temperature but only to a certain point. For instance, the upper incipient critical temperature (cf. Table 1) of brown trout increases from 20 to 25 °C as the acclimation temperature increases from 0 to 18 °C, but it does not increase any further at higher acclimation temperatures [60]. The incipient critical temperature defines a tolerance zone that is stressful, but the fish can stay alive for a considerable length of time in even warmer water. However, outside the tolerance zone, the thermal stress is lethal. The upper critical maximum temperature is the temperature at which death is almost instantaneous, i.e., the limit of the critical range.

Phenotypic plasticity can buffer against the immediate impacts of thermal stress and reduce the sensitivity of individuals [3]. Phenotypic plasticity may develop as a knock-on effect, which is the ability of a genotype to later express alternative phenotypes in response to environmental differences [46]. Knock-on effects consist of cues or imprints experienced in a sensitive phase, transferred as a parental effect, or induced early in life, which change developmental rates, activities, or resource use [62]. Salmonids appear to be sensitive to environmental knock-on effects during embryogenesis or at the alevin stage, with later effects on morphology, life history, physiology, and behaviour. This plasticity may be an epigenetic effect [62]. Epigenetic effects are transcriptional regulators of DNA. Methylations of CpG sites in DNA sequences are the most extensively studied mechanism of epigenetic effects in ecology [63]. Methylation of CpG sites in regulatory regions of DNA downregulates genetic expression, and demethylation upregulates genetic expressions [64]. Other epigenetic mechanisms include histone modifications and microRNA, which alter the transcriptional capacities of genomes [63]. However, little is known about how phenotypic plasticity is genetically or epigenetically regulated.

Herein, I review thermal influences on metabolic rates; aerobic scope; growth; adult body size; and reproductive and behavioural traits such as tendency and timing of migration of salmonid fishes. Many examples from studies of brown trout and Atlantic salmon are included. These fishes have been used for scientific studies for more than 100 years, but examples are also available from other genera and species. My view is that temperature acts as a controller of these traits by governing the metabolic rate. There are both maximum and minimum temperatures outside which the metabolic rate is no longer sufficient to maintain life of the fish. I provide examples of direct thermal effects and how the temperature during early life stages causes phenotypic changes later.

2. Metabolic Rates and Aerobic Scope

Metabolic rates, which are the sum of all energy-yielding processes, vary with temperature and reflect the energetic cost of living [65,66]. The standard metabolic rate (SMR) is a measure of the energy required to maintain essential functions, such as breathing and blood circulation. SMR increases approximately proportionally with water temperature [67] and decreases with increasing body mass. Mass-specific SMR declines as a negative power function of body mass as organisms grow to maturity [68]. SMR should be measured in unfed and not growing fish, as both digestion of food and growth use energy, which may influence metabolic measurements [69]. For shorter time intervals, such as weeks or a few months, the mass-specific SMR of a salmonid is stable and repeatable and may hold even under variable thermal conditions [66,70]. For instance, McCarthy [71] demonstrated the stability of SMR by correlating the mass-specific SMR of individual Atlantic salmon measured 5 and 22 weeks after first feeding (June and October, respectively). This stability makes SMR a useful measurement when considering physiological traits underlying organismal performance [66].

The maximum metabolic rate (MMR) is the maximum rate of oxygen consumption that fish can achieve and use to oxidize matter for ATP generation without accumulating oxygen debt. MMR increases with temperature until reaching a peak called the pejus temperature; then, it decreases gradually to zero, which is known as the upper critical limit (T_{Crit}) [60,72]. Pejus temperature corresponds to the point at which individuals start to lose individual performance capacity. At T_{Crit}, the survival of fish is time-limited, and they live in a passive state [3]. The difference between the maximum and standard metabolic rates is called the aerobic scope (AS = MMR-SMR) [72]. AS corresponds to the highest level of energy available for activity. Individuals with higher aerobic scope are better able to take advantages of high food abundance [66] and have improved locomotor ability [73], boldness and competitive dominance, as well as increased levels of territorial aggression [74]. The optimal temperature of a species or population is the temperature resulting in the highest AS and determines their capacity to carry out functions such as foraging, growth, competition, patrolling, immune reactions, and predator defence. As these activities are temperature-dependent and influence spatial distributions and phenology of populations, they are important in contexts of climate change [75,76].

Fish can only survive for long periods of time within temperature ranges where AS is positive. The upper thermal limit is set by the physiological limits of aerobic capacity. Thermal limit diversity among populations with different adaptive histories is likely a result of adaptations in aerobic capacity to different environmental temperature regimes. Thus, thermal tolerance may vary among populations within species as a response to past selection. The ability to cope with global warming is determined by the upper thermal tolerance limit, and populations exposed to high temperatures over their evolutionary history exhibit higher thermal tolerance than conspecific populations developed under colder thermal regimes [77]. For instance, Eliason et al. [78] reported that sockeye salmon (*Oncorhynchus nerka*) in the Fraser River that experienced more challenging migratory environments have greater AS than those with less arduous migrations and that variations in AS are consistent with the historic river temperature ranges for each local population. Thus, thermal adaptation appears to occur at a local scale, with population-specific thermal limits set by physiological limitations in aerobic performance.

Variable environmental conditions influence metabolic rates. Oligney-Hébert et al. [79] compared the metabolic rates of juvenile Atlantic salmon from two rivers with different thermal regimes and acclimated the fish to either 15 or 20 °C and constant (±0.5 °C) or diel fluctuating (±2.5 °C) water temperature. Fluctuating temperature at 15 ± 2.5 °C did not influence SMR relative to stable temperature (15 ± 0.5 °C). However, diel temperature fluctuation at 20 ± 2.5 °C increased the SMR of Atlantic salmon from the warmer river by 33.7% and in the colder river by 8 % compared with the same fish acclimated to a constant temperature of 20 ± 0.5 °C. Thus, the mean temperature to which the juveniles is exposed may affect their responses to diel temperature fluctuation, and this response may vary between populations originating from rivers with different natural thermal regimes.

On the other hand, intraspecific variations in AS need not be caused by genetic differences. Instead, this may be a phenotypically plastic response induced by previously experienced differences in thermal climate [80]. For instance, Cook et al. [81] reported that temperatures experienced by brook trout (*Salvelinus fontinalis*) embryos affected body mass and routine metabolic rates as free-swimming fry. Furthermore, prehatching temperature influenced the metabolic rate of brown trout. Durtsche et al. [82] found that the SMR, MMR and AS of young brown trout (parr) were reduced when incubated as embryos in 3°C warmer water. This result is consistent with the counter-gradient variation hypothesis (CGV), according to which phenotypic variation—in this case, variation in metabolic rates—is inversely related to thermal conditions experienced by the organisms in early life [83]. This hypothesis was originally proposed in relation to altitudinal or latitudinal gradients [84]. Thus, the temperature experienced when the fish develop within the eggshell may preadapt individuals to life in either colder or warmer temperatures. Trout experiencing cold environments as embryos prepare for life in a cold environment and have higher metabolic rates at the same temperature than those that developed in warmer water. Accordingly, those that develop in cold water compensate for negative effects of low temperatures. A warm early environment favours low metabolic rates later, enabling fishes to conserve energy in an otherwise costly environment. Thus, direct environmental influences counteract inherited differences among natural populations growing up under different thermal conditions through a process of thermal plasticity. There may also be sensitive periods later in life during which SMR is programmed. For instance, Álvarez et al. [85] found a negative correlation between the temperature experienced by brown trout fry during the first 2 months after yolk resorption and SMR later. Thus, exposure to low temperatures at an early stage in life increases the temperature-dependent SMR. Such an early influence on metabolic rate has consequences for later growth, feeding and locomotor activity.

3. Growth

The aerobic scope represents the capacity of organisms to concurrently supply oxygen and energy for swimming, food digestion, absorption, assimilation (specific dynamic action SDA) and growth. High energy intake leads to faster growth, although SDA also increases with higher SMR food consumption and assimilation [86,87]. Typically, increased growth is advantageous because it protects against gape-limited predators and increases competitive ability and reproductive capacity [88]. However, a cost of faster growth may be reduced life span. There is still little information about how individual fish share their resources between these functions and restrict meal sizes to maximize growth and minimize the probability of death.

Like AS, growth rate and food consumption increase with temperature to a maximum point (optimal temperature for growth (T_{Opt})) at which oxygen availability starts limiting a further increase and the growth rate starts to decline [24,68]. The optimal temperature depends on the oxygen content in the water. For individual fish, T_{Opt} is reduced if the water is not fully saturated and increased if the water is supersaturated [89]. Temperature-dependent reaction norms for growth and food consumption are maximized at approximately the same temperature [24], and the maximum point decreases with decreasing food consumption [90,91]. Therefore, maximum growth of brown trout is reached at 13 °C for invertebrate and pellet feeding and 16 °C for fish feeding on conspecifics [26,27].

There are small differences in T_{Opt} among salmonid species, and all have relatively low thermal tolerances associated with their high oxygen requirements (Table 1). Typically, the optimal temperature for growth is round 15 °C and is lowest in lake trout (12 °C) and highest in Atlantic salmon (16–20 °C). There are intraspecific variations in thermal performance among studies, which may be partly due to methodological variation across studies, such as variation in size of test fish, acclimation temperature, oxygen content in water and other stressful conditions [89]. In addition, there may be some genetic variation in thermal performance [92,93]; however, when experimental conditions are similar, intraspecific variation in thermal performance is small. Debes et al. [94] investigated population differences and within-population genetic variation and plasticity in thermal performance traits of Atlantic salmon reared under common-garden conditions and found heritability for growth, condition and CT_{Max}. However, with increasing acclimation temperature, differences in the heritability of CT_{Max} diminished. CT_{Max} and body size were negatively correlated at the genetic and phenotypic levels, and there was indirect evidence of a positive correlation between maximum growth and thermal performance breadth for growth. Thus, population differences in thermal performance and plasticity may represent a genetic resource, in addition to the within-population genetic variance, to facilitate thermal adaptation.

Optimal temperature for growth decreases with increasing fish size [73,95]. Therefore, in lakes and at sea, large individuals often tend to live deeper and in colder water than smaller conspecifics [95,96], and small individuals may show increased growth at the same temperature as larger conspecifics experience negative growth because of lower individual optimal temperature [97]. The effect of rearing temperature on the relationship between growth and the metabolic rate of brown trout was studied by Archer et al. [98]. For 15 months, they kept study groups in either cold water ranging between 5.9 °C and 16.4 °C or in 1.8 °C warmer water (7.9–18.2 °C). They found that SMR was positively related to growth in the cool water but negatively related to growth in the warmer water. The opposite patterns were found for MMR and growth associations (positive in warm and negative in the cool regime). Mean SMR but not MMR was lower in warm regimes within both populations. Thus, there appears to be a phenotypic plastic reaction in the relationship between growth and metabolic rate depending on the thermal regime of the fish. Furthermore, a study by Finstad and Jonsson [99] demonstrated that embryo temperature had a knock-on effect on the growth of young Atlantic salmon. Young juveniles (parr) grew faster at the optimal temperature when the eggs were incubated in 7.2 ± 0.6 SD instead of 2.6 °C ± 0.4 SD water. A higher temperature during egg incubation also increases smolt size at 1 year of age and size at maturity at 2 years of age in Atlantic salmon, but it showed no effect on mass specific growth at sea after smolting [100,101] (Appendix A). Higher egg incubation temperature appeared to stimulate the fish to feed more at 1 year of age and therefore grow faster as young juveniles; however, this growth effect in the salmon disappeared after smolting.

Although the optimal temperature for growth declines with increasing body size, embryos, and alevins, which are very small, have narrower thermal limits and are more vulnerable to high temperatures than larger fish. Early life stages are highly oxygen-demanding, and high temperatures may have a negative effect on cellular functions through thermally induced oxygen diffusion limitation [102]. In addition, cell proliferation, migration, differentiation, and apoptosis (programmed cell death) are adversely affected by elevated embryo temperature. In particular, the development of the central nervous system and the notochord is highly susceptible to high temperatures [103]. The development of the notochord is thermally sensitive because of effects on the sheath cells [104]. These cells accumulate misfolded protein at elevated temperatures, leading to structural failure of the notochord and other anatomic defects in the embryo, causing malformations and death. Thus, both oxygen limitations and malformations during foetal development are causes of the high temperature sensitivity of embryos and larvae.

There are inherited differences in reaction norms of temperature-dependent growth among conspecific populations of Atlantic salmon, brown trout and Arctic charr [24,27,43] that may also hold for other salmonid species. Juveniles from large-sized, late-maturing salmonids grow better at the same temperature than those from populations of small-sized, late-maturing conspecifics. Growth differences possibly reflect different personalities of the fish, as offspring of large, late-maturing fish also feed more at the same temperature than those from populations of earlier-maturing conspecifics [24]. The optimal temperature for growth is similar among Norwegian populations of Atlantic salmon, although the thermal regimes of the rivers vary. Thus, differences in maximum growth among conspecific populations appear to reflect habitat differences rather than differences in thermal regimes [43,105,106].

4. Adult Size

According to the temperature–size rule for ectotherms, individuals maintained at a lower temperature grow more slowly but become larger at sexual maturity than those maintained at a higher temperature [107]. This is at least partly because age at maturity is growth-dependent, and slower growth means delayed maturation [108–110]. However, this does not necessarily mean that those that live in warm water are smaller in mean size than those from colder environments. This depends on the difference in annual length increment at the two temperatures and the fraction of the population that mature younger in the warmer water. Experimentally, Jonsson et al. [109,110] showed that the probability of that Atlantic salmon attained maturity for the first time during their second year in sea water increased with increasing growth rate during the last winter before maturation. Increased summer temperature had no additional effect. Atlantic salmon reared at elevated temperature attained maturity at a larger body mass and exhibited higher mass–length ratios than those of similar age reared in colder water. Temperature functions similarly to the accelerator of a motor, and higher temperatures induce faster growth if the oxygen supply is sufficient, i.e., below the pejus temperature.

Faster growth requires increased energetic assimilation, and recent findings indicate poorer feeding opportunities of Atlantic salmon in the North Atlantic Ocean resulting in poorer survival, reduced production, and smaller size for their age. However, size at maturity may, on average, be larger in many rivers because the fish attain maturity at an older age because of poorer growth [111,112]. Pacific salmon along the west coast of North America, on the other hand, mature younger with decreased production because of ocean warming, as found in large-scale investigations in Alaska [113,114]. The same declining trends hold for chinook, chum, coho and sockeye salmon. Because of the smaller fish size and reduced production, the effect is reduced nutrient transport from the ocean to rivers and riparian and terrestrial ecosystems [115,116], reduced fisheries value and fewer meals for rural people [114].

Polymorphism with sympatric morphs of different sizes occurs in several salmonids, such as brown trout [117], Sevan trout (*Salmo ischchan* Kessler, 1877) [118], Arctic charr [119] and freshwater whitefish (*Coregonus* spp.) [120]. Sympatric phenotypes often occur in pairs, exhibiting a large and a small adult morphotype of the same species [121,122]; however, in some systems, there are more than two sympatric forms. Sevan trout in Lake Sevan, Armenia [118] and Arctic charr in Lake Thingvallavatn, Iceland, exhibit four sympatric morphotypes [118,123]. The morph variation is partly inherited [121], and in several cases, clear genetic foundations of morph differentiation have been demonstrated, along with divergent life histories [120,124]. However, differences in egg incubation temperature may also influence phenotypic differentiation.

Two forms of European whitefish (*Coregonus lavaretus*) segregate vertically in Traunsee, Austria. The forms exhibit different metabolic adaptations and behavioural preferences for different temperatures [125]. In the lake, the two forms diverge by incubating embryos at either 2 °C or 6 °C, i.e., the typical temperature during embryogenesis of the two. Offspring of the two forms were reared and subjected to similar thermal conditions after hatching. The offspring differentiated in muscle growth and body size depending on the egg temperature; offspring incubated as eggs in 2 °C water grew larger than those incubated at 6 °C, regardless of whether their parents were large or small whitefish. The experiment also revealed that muscle hypertrophy (increased fibre size) and hyperplasia (increased fibre number) were affected by the thermal histories. Immunolabeling showed that the cellular mechanisms leading to increased growth after cold incubation were increased proliferation and reduced differentiation rates of muscle precursor cells, most probably associated with epigenetic differences. Thermal plasticity possibly arises from changes in physiological and endocrinological pathways, in which epigenetic regulation is likely to play an essential role [126].

Many salmonids are anadromous in addition to having freshwater living forms. This is, for instance, observed in sockeye salmon, Arctic charr, brown trout and masu salmon (*Oncorhynchus masou* Brevoort, 1856). For masu salmon, Morita et al. [127] showed that these alternative tactics were associated with temperature gradients. The occurrence of mature resident males increased, and the proportion of immature migrant males decreased with increasing temperature in Japanese rivers. They suggested that the change in the ratio of anadromous to freshwater resident males resulted from improved growth opportunities in warmer water. According to Morán and Pérez-Figueroa [128], resident and anadromous male Atlantic salmon differ in DNA methylation, although they are genetically similar. Earlier maturation and freshwater residency may be mediated by epigenetic processes rather than by genetic differences between young fish. How these differences develop is still obscure.

5. Reproductive Traits

Reproductive processes of fish are affected by the environmental temperature. Moderate thermal variation affects endocrine functions and either advance or retard gametogenesis and maturation. Above-normal temperatures may have deleterious effects on reproductive functions, and low temperatures can arrest the maturation process. For instance, in Atlantic salmon females, exposure to elevated temperatures during gametogenesis may impair both gonadal steroid synthesis and hepatic vitellogenin production, alter hepatic oestrogen receptor dynamics and ultimately result in reduced maternal investment and gamete viability [129]. High temperatures during maturation also impair gonadal steroidogenesis and delay or inhibit the preovulatory shift from production of androgens to maturation-inducing steroids. Similar effects are observed in rainbow trout and Arctic charr [129]. In Atlantic salmon, higher temperature may increase maturation of male parr [130,131], although in another study, Baum et al. [132] observed no effect of high temperature on parr maturation. In male Arctic charr and rainbow trout, high temperatures can inhibit spermiation (maturation-inducing steroids [129]), and it is reasonable to assume that the same effect also holds for other salmonid species.

Furthermore, both egg size and fecundity tend to increase with female body size. Thus, in a warmer climate with smaller females, egg sizes decrease. On the other hand, egg size is larger for similarly sized conspecifics spawning in warmer streams [133–135]. The transformation from yolk to tissue is less effective under warmer conditions. Large eggs are also favourable under poorer oxygen conditions [136]. Thus, increased egg size may give offspring an adaptive benefit in a warmer climate and should be favoured by natural selection. This is probably the reason why the egg size of salmonids decreases with increasing latitude and altitude [133,135,137,138]. Egg size differences appear to diminish when fish from different populations are reared under common thermal conditions, showing that this trait is phenotypically plastic [133]. Furthermore, egg size is influenced by the temperature that females experience during their own embryogenesis. A higher incubation temperature stimulates females to produce larger eggs as a phenotypically plastic knock-on effect [139,140]. Total ovary mass but not fecundity increases with incubation temperature years earlier. Male gonad mass is also larger in fish incubated in warmer water.

Females retained in warmer water during maturation produce larger eggs. There is also a transgenerational effect of temperature on egg size. Experimentally, Jonsson and Jonsson [140] exhibited that the mass of eggs produced by next-generation females was larger when their mothers experienced warmer water during the last two months of egg maturation relative to similar fish that experienced unheated water. This is possibly caused by an epigenetic modification of the parental fish. In brook trout, using whole-genome bisulphite sequencing, Venney et al. [141] found 188 differentially methylated DNA regions due to parental maturation temperature. Stable intergenerational inheritance of DNA methylation may transfer the epigenetic states to offspring, priming them for a warming environment. This has implications regarding the role of intergenerational epigenetic inheritance in response to climate change.

6. Behavioural Traits

Temperature influences fish behaviour, such as swimming activity and foraging, exploratory behaviour, prey capture and predator avoidance [142,143].

The timing of smolt migration, i.e., when young anadromous salmonids migrate from fresh water to the sea, occurs coincidentally with environmental changes such as increasing temperature and day length in spring. The warmer the water is and faster the temperature increase, the earlier in the season the smolts migrate downstream and out to sea [144–146]. Earlier outmigration from a warmer river appears to decrease smolt size and increase the mortality of the fish, as found for brown trout and Atlantic salmon [147–149]. Thus, the body size at migration is influenced by river temperature, with smaller smolts in warmer rivers, as found for brown trout along the Norwegian coast [150]. However, river temperature may not be the only factor that influences smolt size. Smolts are selected to survive in sea water [151]. As the ionic stress in sea water increases with decreasing temperature, smolts entering colder seas should be relatively large, as observed in anadromous brown trout in Europe [152]. There is evidence that reduced survival is associated with earlier smolt migration, as found for brown trout and Atlantic salmon in Norway [147,148].

During the spawning migration, high temperatures may lead to anaerobic locomotion, energy losses and prespawning mortality [153–155]. River-dwelling salmonids may avoid high temperatures by entering cooler water (thermal refuging) to maintain a body temperature close to optimal levels and minimize energetic costs associated with high temperature [156–159]. Thermal refuges include cold water tributaries, groundwater seeps, deep pools, and cold alcoves [159–162]. This holds for both juveniles and adults of various species and at both low and high latitudes [163,164]. In addition, salmonids experiencing suboptimal temperature during migration may reduce energy use by burst-and-coast swimming [165]. Burst-and-coast swimming, whereby bursts of fast swimming are in cyclic alternation with phases of coasting and the body is kept straight and motionless, can be an energetically advantageous behaviour. It allows the fish to gain fast swimming speeds during short bursts while preventing the effects of fatigue by allowing metabolic recovery of muscle fibres during the coast phases [166].

Higher temperature may also affect salmonid spawning migrations. These fish feed little or not at all during the migration [167,168], as they rely on endogenous energy stores to fuel the migration back to their home river and spawning sites and the development of sexual characters and reproduction [165]. Adipose tissue reserves are the primary source of energy used for upriver migration and gonad production [169], and protein from muscular tissue fuels the development of secondary sexual characters and metabolism during spawning activities [170]. Migratory energy costs increase with temperature and reduce the capacity of the fish to recover from exhaustive exercises [171].

Temperature may also influence where in the ocean the salmon feed. During warmer summers, Atlantic salmon in the Baltic Sea fed closer to their home river in the Gulf of Bothnia, while in colder summers, they fed farther south in the Baltic Main Basin [172]. Furthermore, the temperature influences the timing of the return migration. Elevated water temperature may induce either earlier [173,174] or later arrival in the spawning area [175]. Salmon may migrate outside the peak summer temperatures [175] and respond to suboptimal water temperatures by delaying migration in cool thermal refuges [176–178]. In addition, temperatures during embryogenesis may influence phenological decisions such as when to return from the ocean and spawn in rivers. Jonsson and Jonsson [179] released groups of juvenile Atlantic salmon (smolts) produced from eggs incubated at either ambient (~4 °C) or 3 °C warmer water temperature. After hatching, both experimental groups were reared under similar thermal conditions until smolting and released. The fish migrated concurrently to the sea as juveniles, and after feeding in the ocean for one or two years, they returned to the experimental river for spawning. Atlantic salmon that were developed from eggs incubated in warmer water returned from the sea ca. 2 weeks later in the summer/autumn than adults of the same age developed from colder eggs. The later return was independent of the body size of the juveniles at outmigration and similar for offspring of three different tested populations. Hence, thermal conditions during early development appeared to prepare the offspring, when adult, to return for spawning later in the year. Later return to a warmer (or earlier return to a colder) river may be advantageous both because metabolic rates are higher in warmer water, reducing the reserve energy used during migration and spawning faster, but also because egg incubation time decreases with increasing temperature, so the fish may spawn later under warmer conditions. The mechanism driving this phenotypic plastic response has not been investigated but may be linked to the maturation process.

At high latitudes, climate change leads to higher winter temperatures when the eggs of autumn-spawned salmonids develop within their gravel beds [88]. Recent investigations have exhibited that temperature during embryogenesis affects the behaviour of young brown trout. Exposing the fertilized eggs to 1.5–2–5 °C warmer water reduced activity level of the young juveniles after hatching [180]. It is difficult to predict the overall consequences on fitness of this response to warmer egg incubation temperature, as the activity of their ectothermic predators and prey may also change [181]. Nevertheless, the results of this and previous studies [82,182] suggest that juvenile brown trout in a warmer climate have lower metabolic rates and aerobic scopes and are less active, with similar consequences across migratory and non-migratory phenotypes.

Temperature during egg incubation influences later river emigration. Jonsson and Greenberg [182] showed that the proportion of warm-incubated brown trout released in the River Imsa, Norway, moved downstream towards the sea to a greater extent than those incubated as embryos in colder water. Most of the emigrants moved downstream in the autumn. The cold-incubated offspring possibly had a higher metabolic rate and kept their position at low temperature in the fast-flowing river, while more of the warm-incubated fish moved downstream towards the sea. A similar difference was observed with respect to whether the parents were anadromous or lacustrine adfluvial phenotypes or crosses between the two. Thus, the difference in emigration regarding embryonic temperature was phenotypically plastic and may be associated with an epigenetic effect of the thermal conditions during early development. However, the outmigration ratios varied between offspring of geographically isolated populations, suggesting that there are genetic divergences in this trait among populations.

7. Discussion

Temperature has a pervasive and direct effect on biochemical and physiological functions of ectotherms and a strong influence on life history traits. Temperature regulates metabolism and aerobic scope, growth, body size, gonadal size, behavioural locomotion and phenological patterns. Variations in thermal responses are caused by inherited differences, such as that of metabolic rates. Auer et al. [66] measured SMR, MMR and AS of juvenile brown trout and observed that metabolic rates were repeatable over time periods of months, even under changing thermal conditions. The among-individual differences in metabolism appear to have fitness-related effects and be related to individual differences in growth, body mass, reproduction, survival, behaviour, and phenology. Thus, temperature plays an important role in determining evolutionary trajectories of species [183,184].

In addition to the direct phenotypic effect of temperature, recent research suggests that embryo and larval temperature or the temperature experienced by parents may affect life history traits. Although not extensively investigated, these latter findings indicate that past temperatures may prepare offspring for conditions that they may encounter later in life. Some of these effects, such as that on growth, appear to be strongest early in life [100], whereas others, such as that on migration, may also influence the phenology of adults [141]. These latter knock-on effects have been demonstrated for Atlantic salmon and brown trout, and effects on growth have also been demonstrated for other species, for instance, common carp (*Cyprinus carpio* L., 1759) [185], haddock (*Melanogrammus aeglefinus* L., 1759) [186] and Senegalese sole (*Solea senegalensis* Kaup, 1858) [187]. However, population-specific variations are expected, although scarcely investigated [188].

There are also transgenerational effects of temperature. For instance, the temperature during egg maturation prior to fertilization influences egg size, gonad size and the amount of energy available for the offspring after hatching. These thermal effects are transferred to the next-generation offspring of Atlantic salmon [140] and may positively affect early juvenile growth in a warmer climate [189,190]. Knock-on effects of previous temperature appear to parallel changes observed among conspecific populations living under different thermal regimes. These effects reduce phenotypic differences among individuals experiencing different climatic conditions, as explained in the subchapter “Metabolic rates and aerobic scope”. However, there is an urgent need for further research on transgenerational, thermal effects on the ecology of fishes and the mechanism by which they are transferred from parents to offspring.

Phenotypic plasticity in thermal response appears to be initiated by influences experienced during a sensitive period, although the consequences may be long-lasting after the sensitive period has ended [139,191]. Such processes initiated by early priming are referred to as adaptive developmental plasticity [192]. Typically, thermal conditions during early development or at a parental phase may have effects that change developmental trajectories, which may be helpful later in life [62]. The influences stimulate genotypes to express different phenotypes in response to thermal differences during early development [193,194]. For instance, knock-on effects that are initiated by cues or imprints experienced in individuals’ early life, transferred as a parental effect, or induced at embryo or larval stages may affect developmental trajectories, activities, and resource allocations within an organism’s life span [62]. The effects may be short-term or long-term and prepare individuals for conditions that they may encounter later, thereby buffering otherwise detrimental effects of environmental change [195–197]. Such parental or early thermal effects should be advantageous when parents or early environments provide a reliable forecast about the thermal climate that offspring may encounter later [198–200]. Like local adaptation [201], developmental knock-on effects should evolve through natural selection in responses to the environments to which offspring are repeatedly and consistently exposed over evolutionary time, whereas responses to novel or atypical environments may be maladaptive [202,203]. The latter is likely to occur in response to extreme temperatures and severe temperature variation. However, at present, there is no quantitative study demonstrating how beneficial such early programming of salmonids is.

The mechanisms involved in thermal plasticity have not been extensively investigated. However, DNA methylation is sensitive to thermal climate [204] and may be involved. Polar fishes show higher DNA methylation levels than temperate fishes, and Antarctic icefishes (Channichthyidae) have the highest DNA methylation level on record. There is an inverse relationship between DNA methylation and body temperature when maintained over evolutionary time. DNA methylation links thermal conditions to subsequent changes in genetic expressions [205], but the response differs among iso-genetic lines, as shown for rainbow trout.

There are also examples from other fish families suggesting effects of temperature on DNA methylation. For instance, Atlantic cod (*Gadus morhua* L., 1759) embryos exposed to a 4 °C increase in temperature exhibited changes in the expression of genes involved in one carbon pathway [206]. Furthermore, higher temperature affected the DNA methylome of a coral reef fish (*Acanthochromis polyacanthus*; Bleeker, 1855) and influenced phenotypic plasticity, which enabled some populations to maintain their performance under thermal stress [207]. Anistadiadi et al. [208] exposed European sea bass (*Dicentrarchus labrax* L., 1759) larvae to periods of moderate temperature increases. The authors found that a 2 °C increase in temperature changed global DNA methylation and the expression of ecologically relevant genes related to stress response, muscle development and organ formation. DNA methylation changes were more pronounced in larvae previously acclimated to a different temperature.

Both in early and later life, temperature change may lead to DNA methylation. Beemelmanns et al. [209] challenged Atlantic salmon post smolts with increasing temperatures from 12 to 20 °C. They reported that exposure to high temperature affected the methylation of CpG sites. There were distinct CpG methylation profiles for different treatment groups, indicating that each environmental condition may induce different epigenetic signatures.

8. Future Research

Little is known about how temperature influences distributions of salmonid species. Finstad et al. [210] hypothesized that differences in temperature-dependent growth efficiencies were a main reason for differences in distributional patterns of brown trout and Arctic charr. Their thermal optima are similar, but Arctic charr outcompete brown trout in cold and ultraoligotrophic lakes and rivers because they have twice as high growth efficiency in cold water. Little is known about the degree to which a similar effect may influence distributional patterns of other salmonids. They all have similar thermal niches, but differences in metabolic rates and growth efficiencies may still exist. Such knowledge is important in understanding geographical distributions, immigration, and local extinction of species.

Some studies indicate intraspecific variation in thermal growth performance. However, as many factors influence the results of growth experiments, such as light conditions, fish size, food rations, acclimatization temperature, early temperature, stressful environmental conditions and parental temperature during egg development, experimental results may be difficult to compare [29,90,99,100]. Because experimental results differ [60,78,93], there is a need to reveal how much of the variation in thermal performance is due to phenotypic plasticity and how much is because of additive genetic variation.

Research supports the hypothesis that thermal conditions early in life affect life histories of organisms. It is important to identify to what degree developmental plasticity is adaptive. Influences encountered by organisms long before experiments start can affect the results. If not considered, this may lead to incorrect interpretations of trait differences. One may believe that observed differences are genetically adapted, while they may be an early environmental effect. Such misinterpretation may lead to incorrect decisions when managing populations under climate change.

Epigenetics appear to be central in the understanding of how the early thermal environment affects the development of phenotypes. There are examples suggesting a role of epigenetics in developmental plasticity. However, the field of epigenetics is still young, and I expect that many new studies soon will be performed to better understand how environmental temperature influences the ecology of salmonid fishes. Studies using whole-genome approaches should be performed, as such studies may reveal new relationships between phenotypes and epigenetic determinants.

There is strong evidence supporting the hypothesis that thermal cues experienced at an early stage in life can affect the development of organisms, with consequences for life in environments encountered at a later stage. However, at present, there is little if any knowledge about energetic costs involved in thermal plasticity and whether thermal plasticity is adaptive and affects fitness. Such tests are needed, as populations' responses in changing environments are critical to their persistence. Their capacity to exhibit adaptive plasticity to a warmer climate may determine their future success.

9. Conclusions

Temperature has pervasive effects on growth, life history and behavioural traits of salmonid fishes. This is caused by a direct effect on metabolic rates and food consumption. Intraspecific genetic variability in these thermal effects needs further investigation. In addition, there is an indirect, phenotypically plastic effect induced by temperature during embryogenesis and early life, as well as possibly by temperatures experienced by mothers during maturation. This phenotypically plastic response may preadapt offspring to perform better in anticipated future thermal environments. An epigenetic mechanism such as DNA methylation may be responsible for the phenotypic effect. Future research should investigate this and other possible epigenetic mechanisms and how they may influence fitness and induce alternative phenotypes.

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Appendix A

Smolting

Smolting is a preparatory physiological adaptation process that occurs in spring prior to the seaward migration of anadromous salmonids. The young fish become slimmer, with a more streamlined body with darker back, more silvery flanks and a whiter belly. Physiologically, the Na^+,K^+-ATPase activity and salinity tolerance increase, as do the density of visual pigment porphyropsin in the retinae of the eyes. On the other hand, the fat density of the muscle tissue decreases, and the activities of metabolic enzymes change. These changes precede downstream migration and prepare the fish for marine life in pelagic waters.

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