Topic: Salmonid Habitat Preference in Response to Temperature

Organization: The articles are organize by order of appearance in the topic summary. The first article is an overall review to get a basic understanding of the all aspects of the behaviour and the rest follow by describing the behavior and different mechanisms driving the behaviour.

**Review:**

McCullough, D. A., Bartholow, J. M., Jager, H. I., Beschta, R. L., Cheslak, E. F., Deas, M. L., Ebersole, J. L., Foott, J. S., Johnson, S. L., Marine, K. R., Mesa, M. G., Petersen, J. H., Souchon, Y., Tiffan, K. F., & Wurtsbaugh, W. A. (2009). Research in thermal biology: Burning questions for coldwater stream fishes. *Reviews in Fisheries Science*, *17*(1), 90–115. <https://doi.org/10.1080/10641260802590152>

**Summary:** Temperature is a key factor in fish biology, especially for cold water fishes. Climate change is expected to cause increased stream temperatures in the coming years. The authors aimed to examine the growing body of research to link information between different thermal biology disciplines to summarize an integrated understanding of what is known and areas with knowledge gaps. The umbrella of thermal biology was broken down into four biological scales of adaptation (molecular, organismal, population/species, community/ecosystem) and the implications were discussed in the context of management and policy. Research has shown that genetic variation plays a big role in thermal tolerance but, the specific molecular and physiological ability to adapt to thermal tolerance and the limitations of these mechanisms are unknown. Physiological studies have shown the combined effect of thermal stress and other water chemistry parameters on metabolic function, but it is often unclear how these lab-based studies translate to natural systems. The authors recommend identifying biomarkers in lab studies, to use in field studies to compare results. Biomarkers identify a molecular response to a stressor in an individual, but species-specific biomarkers are lacking, and existing biomarkers are not consistent across studies. Many studies focus on the lethal effects of elevated temperatures, but the authors point out theories discussing thermal minima as a refuge period that have yet to be explored in detail. If these theories are true, it would indicate there is a relationship between thermal minima and maxima that needs to be better described as thermal global thermal minima are projected to increase more than global thermal maxima. Additionally, the authors recommend more studies should focus on the sublethal effects of thermal stress and the associated reproductive and intergenerational effects. Their synthesis stresses the importance of integration between the disciplines to provide a clearer understanding for management purposes.

**Contribution:**This article reviews current literature to establish what is known, identify knowledge gaps, and generate new ideas for future research. This review provides a summary of what is known about the effects of thermal tolerance on gene expression, metabolism, and behaviour and the limitations of this knowledge. Specifically, table 2 concisely summarizes current knowledge. The authors compare past studies that show conflicting results in these areas to highlight what is yet to be understood and propose new questions. Understanding the limitations of current knowledge is helpful when interpreting results of other papers.

**Description and variation in behaviour:**

Ritter, T. D., Zale, A. V., Grisak, G., & Lance, M. J. (2020). Groundwater upwelling regulates thermal hydrodynamics and salmonid movements during high-temperature events at a montane tributary confluence. *Transactions of the American Fisheries Society*, *149*(5), 600–619. <https://doi.org/10.1002/tafs.10259>

 **Summary:** River temperatures are rising above cold-water salmonid temperature thresholds. As a result, their species distributions are moving upstream to colder, higher latitude waters. However, salmonids must still migrate through these warmer waters and so must adapt to these warming conditions. One avenue for adaptation is behavioural thermoregulation by aggregating in thermal refuges. Increased habitat fragmentation of these cold-water refuges decreases access to critical resources and so the importance of thermal refuges must be assessed. Here the authors explored hydrodynamics of a tributary outflow into a main stem river and the role it served as a thermal refuge for salmonid populations. They measured the temperature of the tributary and the mainstem river over the summer, tracked the movement of all salmonid species present in the river (n=610), and compared aggregation occurrence in the confluence of the two waterways to thermal critical thresholds for each species. They found the tributary to have lower temperatures than the main stem, but the confluence had the lowest temperatures, likely a result of hyporheic upwelling. This confluence only had a short range and complete thermal mixing was found shortly down stream. They also found the occurrence of fish during extended thermally stressful periods was significantly higher at the outflow of the tributary as compared to PIT antenna further away from the confluence. However, use of this refuge was mainly at night when chance of predation was lower indicating a trade-off between thermoregulation and predation. Few fish swam upstream into the tributary which suggests a benefit to accessing resources in warmer waters while saving energy by staying down stream in the confluence. Recreationally and reproductively valuable larger fish were seen using the refuge more often which suggests this thermal resource was physiologically important and therefore larger, territorial fish were blocking smaller fish from accessing these waters.

 **Contribution:** The authors describe the role thermal refuges for salmonid behavioural thermoregulation during high stress warming events. Overall, they found fish utilized the thermal refuge more often during stressful warming periods. They found increased usage at night conflicting with past studies which found increased usage in the late afternoon when temperatures were highest. This indicates the trade-off between behavioural thermoregulation and chance of predation as the confluence had little shelter. Additionally, they found larger fish were more likely to utilize the refuge agreeing with past studies which found increased fish body sizes have lower tolerance for high temperatures.

Armstrong, J. B., & Schindler, D. E. (2013). Going with the flow: Spatial distributions of juvenile coho salmon track an annually shifting mosaic of water temperature. *Ecosystems*, 16(8), 1429–1441. <https://doi.org/10.1007/s10021-013-9693-9>

**Summary:** Juvenile coho salmon (*Oncorhynchus kisutch*) habitat temperature spatial patterning can vary due to temporal variation as conditions change from year to year. As water levels change, habitat heterogeneity and connectivity can vary as different parts of the river experience different temperatures and affect access to food resources. Juvenile coho are known to have a diel horizontal migration (DHM) to lower temperatures to forage on sockeye salmon (*Oncorhynchus nerka*) eggs at night and then return to warmer temperatures during the day as a means of thermoregulation for increased digestion rates. The authors of this paper aimed to characterize how coho spatial distribution changes in response to the changing thermal distribution patterns due to variation in precipitation over five years during the sockeye salmon run. They did this by enumerating coho salmon and monitoring the sockeye spawning locations, precipitation, river flow rates, and temperature in various sections of the stream for five years. They found during dry years juvenile coho preferred upstream where the waters were warmer and in the wet years, they preferred the downstream regions and side channels which were warmer than the upstream region. All years saw the sockeye spawning in the cool waters downstream. They found eggs in the coho diet contents in both wet and dry years suggesting the coho migrated to feed and then track the changing temperature distribution over the years to find optimal temperatures for digesting. This study also revealed that juvenile coho will migrate further distances for warmer waters indicating a trade off between feeding and thermal resources.

**Contribution:** This article explores the effect of thermal habitat spatial heterogeneity on thermoregulatory behaviour of coho salmon (*Onchorhynchus kisutch*). This study identifies a spatial change of critical habitat use of juvenile coho in relation to a change in thermal habitat. While a few studies have observed how critical habitat varies seasonally, this study adds an inter annual component to the existing body of knowledge. This article is important for my literature review as it adds an ecosystem level of understanding on how coho interact with thermal resources in relations to other resources such as food.

Dugdale, S. J., Franssen, J., Corey, E., Bergeron, N. E., Lapointe, M., & Cunjak, R. A. (2016). Main stem movement of Atlantic salmon parr in response to high river temperature. *Ecology of Freshwater Fish*, *25*(3), 429–445. <https://doi.org/10.1111/eff.12224>

 **Summary:** JuvenileAtlantic salmon (*Salmo salar*) are known to behaviourally thermoregulate when exposed to high, stressful temperatures. They do this by seeking out cold patches of water (thermal refugia), sometimes going great distances, when temperatures get too high. This is an important trait for Atlantic salmon as their rivers frequently exceed critical thermal limits. However, it is unclear what cues are triggering this response and how far they are traveling to find these thermal refugia. The authors characterize the thermal and temporal cues prior to the onset of behavioural thermoregulation in juvenile Atlantic salmon. The authors tracked the movement of juvenile salmon (n=293) through a mainstem stream reach in relation to their normal territory and two thermal refuge tributaries during a heat wave using PIT telemetry. PCA analysis identified three patterns of aggregation seen: discharge (movement associated with high flow events), diel cycling (movement associated with nighttime feeding and daytime shelter), and high water temperature (movement associated with high water temperatures). These results suggest aggregations identified in the high water temperature group are salmon in search of thermal refuge triggered by extreme water temperatures. They also found main stem movement occurred several hours before the thermal refuge aggregates reached their peak size allowing time for fish to move up or downstream to the thermal refuges. Aggregations started around 25°C, but mainstem movements began around 29°C. These results imply that fish living close to the streams will opportunistically use thermal refuges, but fish living farther away will wait until temperatures raise above a threshold before expending energy to find refuge. They found that number of degree hours >28°C was a good indicator of mainstem movement but did not find that cumulative temperature stress predicted behavioural thermal regulation any better than maximum daily temperature potentially indicating adaptation to local conditions.

**Contribution:** This paper explores temperature cues driving behavioural thermoregulation in Atlantic salmon. The findings show number of degree hours >28°C accurately predict main stem movement and therefore describe the thermal conditions which induce behavioural thermoregulation. They also imply the difference in habitat use for fish near thermal refuges compared to fish further away (either upstream or downstream). Interestingly, the mainstem movements occur at higher temperatures than those described as lethal in lab studies so these results may reflect population adaptations to local conditions. This paper adds to the understanding of the role of temperature cues in the initiation of behavioural thermoregulation.

**Trade-offs affecting behaviour:**

Armstrong, J. B., Ward, E. J., Schindler, D. E., & Lisi, P. J. (2016). Adaptive capacity at the northern front: Sockeye salmon behaviourally thermoregulate during novel exposure to warm temperatures. *Conservation Physiology*, 4(1). <https://doi.org/10.1093/conphys/cow039>

**Summary:** Behavioural thermoregulation is thought to be a critical adaptation for cold water fish, such as sockeye salmon (*Oncorhynchus* *nerka*), to cope with climate change. Most studies observing thermoregulation focus on populations in the southern range of the fishes where temperature extremes occur more regularly and so they may have an opportunity to adapt to higher heat conditions. Few studies have examined behavioural thermoregulation of northern salmonid populations in response to extreme heat events. This study aimed to determine if northern populations exhibit a behavioural thermal regulation response to high heat events and the associated thermal limits both individually and at the population level and estimate the bioenergetic implications of the observed response. The authors observed the response of returning adult sockeye salmon (n=40) in the lake by attaching temperature loggers to the fish and recording what temperatures the fish move from and the temperature of the location they end up during a heatwave. The results showed sockeye salmon generally avoided temperatures above 15°C and preferred temperatures of 12°C. This result coincides with previous studies which found 12°C to be the most optimal temperature for physiological performance with a decline in physiological performance and fitness at temperatures higher than 15°C. Their energetic models suggested this behaviour saved about 4 days of energy, which is important for a migrating species which will not eat for the rest of its life. The authors noted that the salmon had access to cooler waters well below 12 degrees which, according to their models, would save them an extra 50% of expended energy. It is not yet understood what this trade-off is between higher energy expenditure in 12°C water. It is also speculated this behaviour may also reduce susceptibility to disease, but the effect has not yet been quantified.

**Contributions:** This study confirms patterns of cool-seeking behavioural thermoregulation found in populations in the southern range of sockeye salmon (*Oncorhynchus nerka*) are also seen in the populations in northern ranges. This suggests that northern populations also have the ability to behaviourally adapt to warming waters despite having less frequent exposure to higher suboptimal temperatures (>15°C). These results confirm previous physiological laboratory studies describing optimal and suboptimal temperatures and confirms these patterns are also found at northern latitudes. These results confirm fish respond to suboptimal temperatures on a physiological, organismal, and population level.

Corey, E., Linnansaari, T., Dugdale, S. J., Bergeron, N., Gendron, J., Lapointe, M., & Cunjak, R. A. (2020). Comparing the behavioural thermoregulation response to heat stress by Atlantic salmon parr (*Salmo salar*) in two rivers. *Ecology of Freshwater Fish*, *29*(1), 50–62. <https://doi.org/10.1111/eff.12487>

 **Summary**: The effects of climate change is predicted to cause elevated water temperatures in freshwater systems. This will push many species of fish, including salmonids, to their thermal limits. Juvenile salmonids will respond to temperatures near their thermal thresholds through behavioural thermoregulation by seeking out cool areas of the river, known as an aggregate response. However, previous studies have focused on one population or a uniform thermal history and so it is unclear if the aggregate response is triggered by a common cue across populations or if it is dependent on the thermal history of the river. The authors compared the thermal regime histories of two rivers, the Little Southwest Miramichi River (LSWM) the Ouelle River (OR), over three years in relation to the temperature which induced the aggregate response of juvenile Atlantic Salmon (*Salmo salar*) living in those streams (n=120 per stream). They found that the OR had a significantly higher mean temperature in the first year, but the two rivers had comparable means in the following years. The aggregation response occurred more frequently in the OR, but the temperature at onset of the aggregate response was significantly higher in the OR. Additionally, the temperature that induced the aggregate response was influenced by the temperatures leading up to the stressful thermal event. The differences in the thermal onset of the aggregation response between the two populations indicate behavioural thermoregulation is phenotypic plastic trait which can be influenced by the temperatures experienced in the lifetime of the fish. However, it is unknown how fast and to what extremes salmonids can adapt and the uncertainty of the effects of climate change on thermal regimes may have dramatic trait selection consequences leading to a reduction in genetic variation.

 **Contribution:** This article describes the changes of behavioural thermoregulation of juvenile Atlantic salmon in response to habitat level thermal histories. These results agree with past studies which have found fish from different populations exhibit the same thermal tolerance when they experience identical conditions in common garden experiments. As well, this study agrees with past studies which found salmonids have ability to adapt to warming temperatures. This paper provides insight to the specific factors (thermal regime history) which may affect the ability of salmonids to respond and adapt to warming rivers.

Matthews, K. R., & Berg, N. H. (1997). Rainbow trout responses to water temperature and dissolved oxygen stress in two southern California stream pools. *Journal of Fish Biology*, *50*(1), 50–67. <https://doi.org/10.1111/j.1095-8649.1997.tb01339.x>

**Summary:** Rainbow trout (*Oncorhynchus mykiss*) living in the southern edge of their range frequently experience lethal temperatures in the summer. Anecdotal evidence suggests trout may be aggregating in cool groundwater seeps to behaviourally thermoregulate. However, groundwater tends to have low dissolved oxygen (DO) levels and may be below rainbow trout thresholds. The authors examined the trade-off between thermal refuges and oxygen depleted waters by describing rainbow trout habitat use during thermally stressful periods in the summer compared to thermal regimes and oxygen levels of the river. The range of temperatures and DO levels available to rainbow trout over one summer were recorded. Cold river seeps, areas of thermal stratification, and two pools were characterized throughout the study reach. Trout were tracked by counting the number present and mapping their location. Both pools were found to have thermal stratification, but pool 1 was found to have higher temperatures and all fish left or died during the study. The deeper water of Pool 2 had colder temperatures and lower DO levels thought to be caused by a cold groundwater seep. This means movement between the thermally stratified layers was a trade off between temperature and DO availability. Significantly more fish were found in the coldest region of the pool during the day compared to the warmest regions and fish abundance decreased significantly with increasing temperature and DO. These results show trout will choose cooler temperatures when faced with a choice between lethal temperature or potentially lethal DO levels. However, the resulting stress was seen as the trout were not observed feeding when exposed to low DO. While the results show a tight link between trout distribution and temperature, the authors note other factors, such as food and shelter, were not accounted for in this study and warrant further consideration.

**Contribution:** The unique relationship of water temperature to DO found in this river allowed the study of the relevant influence of temperature vs DO on trout distribution. It also highlights the importance of cold ground water seeps despite the low levels of DO. The daily migrations seen are comparable to previous studies which found temperature to be an important predictor of trout aggregation in cool waters when temperatures were warmest. Other studies have found a similar trade-off between low DO and high food abundance. Overall, trout show a tolerance to hypoxic conditions allowing them to select in favor of other resources.

Breau, C., Cunjak, R. A., & Peake, S. J. (2011). Behaviour during elevated water temperatures: Can physiology explain movement of juvenile Atlantic salmon to cool water? *Journal of Animal Ecology*, *80*(4), 844–853. <https://doi.org/10.1111/j.1365-2656.2011.01828.x>

**Summary:** Fish behaviourally thermoregulate to find an optimal temperature for peak performance of physiological functions. The ability to distribute oxygen is likely a key factor in of thermal tolerance limits in fish. Suboptimal temperatures lead to a reduction in aerobic scope, meaning there is no difference between resting and maximum consumption rate of oxygen and fish will go into anerobic metabolism. Studies have shown larger fish are more sensitive to temperature than their conspecifics and as a result juvenile fish can handle a wider range of temperatures. Previous research has shown adult Atlantic salmon (*Salmo salar*) will cease territorial and foraging behaviours in search for cooler waters at higher temperatures while juvenile Atlantic salmon will stay in their territories and continue foraging. The authors of this paper explored the physiological effect of suboptimal water temperatures on adult (n=150) versus juvenile (n=150) salmon that would likely cause behavioural thermoregulation. To do this, they measured behavioural and physiological changes in adult and juvenile salmon across preferred to near lethal temperatures. They found a decrease in feeding and an increase in stress behaviours in both age classes but found a stronger response which started at lower temperatures in adult salmon. Additionally, adult salmon oxygen consumption rate plateaued at 24°C, while juvenile oxygen consumption rate did not plateau at the tested temperatures. This suggests adults entered an anerobic metabolic state, while the juveniles maintained a positive aerobic scope. Similarly, they found higher levels of lactate at higher temperatures indicating anerobic metabolic pathways were used in adults while juveniles showed no change. These results suggest changes in metabolic functions drive thermoregulation behaviour in salmon and juveniles have a higher tolerance to heat. Past studies have shown smaller body size show higher tolerance to higher temperatures, but why this occurs is still unknown.

**Contribution:** This paper explores the mechanism that drives thermoregulatory behaviour. Like previous studies, the authors found evidence showing physiological changes at higher temperatures suggesting a change from aerobic to anerobic metabolism. Furthermore, this change occurs at the same temperature that behavioural changes occur in adult salmon. This paper also shows these changes happen at higher temperatures in juvenile fish suggesting juvenile fish can withstand warmer temperatures. Understanding this physiological mechanism in a fish when it experiences higher temperatures helps explain why fish need to find cooler waters, and therefore partially explains why we see a change in behaviour.

**Molecular Mechanisms influencing behaviour**

Sauter, S. T., Crawshaw, L. I., & Maule, A. G. (2001). Behavioral thermoregulation by juvenile spring and fall chinook salmon, *Oncorhynchus tshawytscha*, during smoltification. *Environmental Biology of Fishes*, 61(3), 295–304. [https://doi.org/10.1023/A:1010849019677](https://doi.org/10.1023/A%3A1010849019677)

 **Summary:** Hyporheic upwellings are an important source of cold water creating spatial thermal diversity in salmonid habitat. These areas of upwellings are decreasing due to human mediated causes and so it is crucial to understand the impacts of this disappearing feature. This is a particularly important habitat feature for migrating salmon going through smoltification, the change juvenile salmon undergo as they transition from freshwater to saltwater. During this time, they go through significant physiological, behavioural, and morphological changes. This study examines the impact of thermal refuges during high temperature events on two races of chinook salmon (*Oncorhynchus tshawytscha*) with different life history patterns living in the same river. Spring chinook spawn in smaller tributaries and migrate as yearlings in the spring when water flow is high and river and ocean temperatures are similar. Fall chinook spawn in the main stem and larger tributaries migrating in their first summer as sub yearlings during the summer months when river flow is low and temperature is high. The authors aimed to describe the different temperature preferences, if any, of smolts from the different races. Researchers monitored spring (n=270) and fall (n=250) chinook salmon alevin temperature preference physiological as they went through smoltification. Spring chinook showed no change in temperature preference as they went through smoltification while fall chinook temperature significantly decreased. Given water temperature and flow change seasonally and are known cues for migration, it would seem temperature cues are stronger for fall chinook which experience larger temperature changes while migrating. Fall chinook may be avoiding high temperatures through behavioural thermoregulation to maintain optimal temperatures for gill ATPase and osmoregulatory activity as they tend to have longer migrations.

 **Contribution:** This research examines the role of thermal refuges during the migration of juvenile salmon to the ocean**.** They found fall chinook salmon behaviourally thermoregulate possibly to prepare for new environmental sea conditions. These results agree with past findings which show ATPase and osmoregulatory behaviour decrease when chinook are held at high temperatures for extended periods of time. Additionally, fall chinook in this experiment chose temperatures close to those of previous studies outlining optimal temperatures for metabolic and osmoregulatory functions. As well past field studies have found Pacific salmon preferred ocean temperatures matched those of fall chinook during late smoltification.

Tomalty, K. M. H., Meek, M. H., Stephens, M. R., Rincón, G., Fangue, N. A., May, B. P., & Baerwald, M. R. (2015). Transcriptional response to acute thermal exposure in juvenile chinook salmon determined by rnaseq. *G3 Genes|Genomes|Genetics*, 5(7), 1335–1349. <https://doi.org/10.1534/g3.115.017699>

**Summary:** Thermal stress is known to affect both physiology and behaviour of juvenile chinook salmon. Tomalty *et al* (2015) aimed to identify gene clusters responding to thermal stress. They placed fish in one of five temperatures (n=11 per temperature) ranging from ideal to potentially lethal (12- 25°C). After three hours of exposure, they sampled gill tissue. RNAseq and qPCR was used to determine gene expression levels for the different treatments. The contigs that were found to be significantly upregulated were then compared to various databases to annotate the genes and determine their functional roles. The authors identified genes that were upregulated around 18°C or higher that belonged to one of twelve functional gene groups: managing denatured proteins, cell death, oxidative stress, inflammation/immunity, ion transport, metabolic changes, transcription/translation, cell cycle and growth, cell signaling, cell trafficking, and structure/cytoskeletal. The exact roll of some of the responding genes is unknown, but overall, these findings suggest there is stress response at the transcriptional level in response to rising temperature.

**Contribution:** The research shows a complex multimodal cellular level response to thermal stress in juvenile chinook. It identifies many genes which have been associated with thermal stress as well as identifies new genes which need to be examined further to understand their role in the response to thermal stress. These results provide new understanding to the physiology driving the behavioural response to heat stress that have been observed in juvenile chinook.