THE ASSESSMENT OF THERMAL IMPACTS ON HABITAT SELECTION, GROWTH, REPRODUCTION, AND MORTALITY IN BROWN TROUT (*Salmo trutta* L): A REVIEW OF THE LITERATURE.

By:

John M. Bell, Ph.D. [1]

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Project Manager: Kim Alan Chapman, Ph.D.[2]

Applied Ecological Services, Inc.
21938 Mushtown Road
Prior Lake, Minnesota 55372
952.447.1919
www.appliedeco.com

[1] Applied Ecological Services, Inc., 17921 Smith Road, PO Box 256, Brodhead, Wisconsin 53520.
Tel: (608) 897-8641. Email: john.bell@appliedeco.com

[2] Applied Ecological Services, Inc., 21938 Mushtown Road, Prior Lake, Minnesota 55372.
Tel: (952) 447-1919. Email: kim@appliedeco.com

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1.0 Background

The Vermillion River Watershed Joint Powers Organization (VRWJPO) is undertaking initiatives to attenuate the impact of increased seasonal surface water flow and its thermal consequences on water quality and in-stream micro environmental conditions affecting the Vermillion River. The VRWJPO is concerned that increase in development in the region may reduce the amount of ground-water infiltration and increase warm-water surface runoff into the Vermillion River, ultimately impacting its cold-water fishery resources.

The Vermillion River watershed is the largest in the Twin Cities (Minneapolis/Saint Paul) region, flowing across the south metro area to the Mississippi River. Groundwater inputs cool the Vermillion River, making it an ideal cold-water trout stream. Increasing surface water runoff and seasonal variability in stream flow has the potential for both indirect and direct effects on fish populations (Schlosser 1990). Indirect effects include alteration in habitat suitability, nutrient cycling, production processes, and food availability. Direct effects include decreased survival of early life stages and potentially lethal temperature and oxygen stress on adult fish. Reduction in cool groundwater inputs and/or increases in warm-water runoff, especially during the mid-summer months, when water temperatures are at their peaks and flows are at their minimums, may have significant indirect and direct consequences on the fishery if the Vermillion River experiences a significant warm-water surface flow/thermal event from a summer rain storm.

The focal species of this review is the brown trout *Salmo trutta* L. The VRWJPO has identified the brown trout as an important indicator species of stream health. The VRWJPO is concerned that continuing development in the watershed may compromise the viability of the self sustaining brown trout fishery. The purpose of this literature review is to answer the following questions:

1. What are the temperature effects on mortality of juvenile and adult brown trout?

2. What are the temperature effects on growth of juvenile and adult brown trout?
3. How does temperature variability and rapid fluctuations in temperature affect mortality rates?
4. What effects do prolonged sub-lethal temperatures have on juvenile and adult brown trout?
5. How is the spatial and temporal pattern of brown trout distribution affected by temperature?

Findings from this review will be incorporated into the VRWJPO initiatives to advance the short- and long-term management strategies of the Vermillion River and address the issue of cumulative water quality impacts resulting from increasing development and runoff.

2.0 Methodology

A scientific literature review was conducted using *BIOSIS* as the primary search engine at both the University of Wisconsin and University of Wisconsin - Milwaukee libraries. The input of related and topical keywords generated multiple potential references (Figure 1). The literature is replete with references on brown trout (*Salmo trutta*). The titles and abstracts of the references generated by *BIOSIS* were reviewed to determine relevance to the subject of this paper. Relevant references were then sourced from the libraries holdings and reviewed in detail. Due to time constraints, references that were not in the libraries holdings or available on line were not sourced using the interlibrary loan departments. Additionally, this literature review was limited to papers that were either in English or German languages.

Keyword or words	Number of related Hits
Trout	11060
Brown Trout (*Salmo trutta*)	1103
Brown Trout and Temperature	320
Brown Trout and Temperature and Mortality	60

Figure 1. Keywords used to generate the initial list of potential references that were initially screened for relevance to the subject of this review.

The references that were essential to the preparation of this literature review were copied and bound separately as supporting documentation and are available for a copying fee from Applied Ecological Services, Inc., 21938 Mushtown Road, Prior Lake, MN 55372, (952) 447-1919.

3.0 Discussion

Numerous studies have examined the habitat requirements of stream fish to determine the optimal range of habitat variables and patterns of distribution for different fish species (Ferguson 1958; Coutant 1977; Horwitz 1978). However, these have often been "snapshot" studies attempting to reveal universal patterns of microhabitat selection with limited season sampling. The habitat requirements and behavior of stream-dwelling brown trout have been studied extensively; however, most studies have focused on the direct environmental linkage between seasonal movement and feeding behavior (Bachman 1984; Clapp and Clark 1990; Meyers et al. 1992; Mäki-Petäys et al. 1997; Burrell et al. 2000). Because fish are ectothermic, temperature mediates all physiological processes and strongly influences the geographic range that a species can inhabit (Baltz et al. 1987). Subsequently, the seasonal movement and feeding behavior of brown trout are also directly linked to the physiological affects of water temperature (Reynolds and Casterlin 1979*a*; Olson et al. 1988; Meyers et al. 1992; Keleher and Rahel 1996; Rahel and Nibblelink 1999).

Recently, several studies described the regional variation in environmental gradients to classify stream fish community patterns (Wehrly and Wiley 2003; Brazner et al. 2005). These studies provided insights into how abiotic factors such as temperature, current velocity, and substrate can determine the distribution and abundance of individual species. Unfortunately, the studies did not provide insight into how temperature influences behavior and habitat use at a species level. The paucity of this type of study is partly attributable to the historical focus on longitudinal micro-environmental patterns within an individual stream (e.g., availability of spawning habitat and cool water refuges) and to the general lack of systematic life history data across broad geographic regions (Schlosser 1990).

The ability of fish, in particular brown trout, to regulate its body temperature behaviorally and the effects of temperature on habitat selection, metabolism, movement, and reproduction will be discussed in the following sections. The intent is to understand the range and tolerance limits of temperature that are necessary to maintain a self-sustaining brown trout fishery.

3.1 Life History and Habitat Selection

Brown trout are a species native to Eurasia that arrived in North America in the early to mid-1800's. They are presumed to be more tolerant of high siltation and warmer waters than many native North American salmonid species. Brown trout spawn in the fall when water temperatures drop to the 5 -10°C range (e.g., McFadden et al. 1965; Garrett and Bennett 1995; Pender and Kwak 2002). Eggs are deposited in a stream in a gravel depression that the female prepares with swimming actions of her fins and body. Large females produce 4,000 to 12,000 eggs. Several males may accompany the female during spawning. The eggs hatch the following spring, with no parental attention. Brown trout mainly eat other fish, and also aquatic and terrestrial insects, crayfish and other crustaceans. Larger fish may eat salamanders, frogs, turtles and small mammals such as mice. Adult brown trout feed mainly at night, especially during the summer. Their life span in the wild can be 10 to 12 years.

Brown trout exhibit strong site fidelity, often spending the majority of their lives within a small, well defined home range, encompassing a single pool and the adjacent riffles (Bachman 1984; Burrell et al. 2000). In some cases, the same tagged brown trout were routinely found in the same location over multiple samplings periods (Bachman 1984; Burrell et al. 2000). Habitat selection may also vary with the size of the fish (Mäki-Petäys et al. 1997). Larger trout generally preferred deeper stream areas than smaller trout. Mäki-Petäys et al. observed that the optimal ranges for depth were 5-35cm, 40-60cm and 50-75cm for small, medium, and large juvenile trout, respectively.

The "bigger fish – deeper habitat" relationship seems to hold for stream fish in general. There are differing hypotheses that may explain this relationship. The first hypothesis is that larger streams typically have more "living space" and habitat complexity (Rahel and Hubert 1991) and are more likely to have deep pools that provide refuge during periods of thermal stress or reduced summer flows (Fausch and Bramblett 1991; Matthew et al. 1994). An alternative hypothesis is be that there exists a simple mechanistic function that may not be water temperature related; i.e., the need of larger fish to balance predation risks from wading or diving piscivorous predators (Alexander 1979; Schlosser 1987, 1990).

Recent experiments by Greenberg (1994) showed that juvenile brown trout (ca. 12cm average size) preferred fast-flowing riffles and runs to deeper, slow-flowing margins and pools. Juvenile brown trout typically used the deeper pools only when overall trout densities were high. Greenberg also found the presence of northern pike (*Esox lucius*), a fish predator, decreased the use of deeper pools by juvenile brown trout. Predator-free riffle margins with undercut banks that offer both suitable refuge sites and nearby feeding areas may represent the best combination of habitat conditions for juvenile brown trout.

Many behavioral traits including movement are size dependent. Some evidence suggests that the largest adults represent a unique stage in brown trout life history (Clapp and Clark 1990). In a mark-and-recapture study, Shetter (1968) found that brown trout longer than 365mm (14.4in) moved greater daily distances than smaller fish. Shetter (1968) hypothesized that large fish experience greater food resource limitations and require a large feeding range. This hypothesis was tested by Clapp et al. (1990). Clapp et al. observed that larger individuals demonstrated more nomadic movements than smaller fish, including long-range displacements (especially at night), and that they returned to the same home site the same or following day. However, these nomadic movements are hypothesized to be foraging related and not temperature related. Differing results were found by Jenkins (1969) where only a few large brown trout moved daily outside the observation area while foraging and the majority remained in dense cover. These contrasting results are mostly likely due to differences in stream characteristics between the two studies.

3.2 Temperature, Growth, and Mortality

Temperature is a limiting environmental factor affecting the distribution of many fish. Generally, temperature of the environment is assumed to be the most important physiological factor affecting the growth of fish (Allen 1985), especially in the temperate zone where there is great annual variation in air and water temperature (Brown 1946*b*). Temperature is also the controlling factor of the rate of metabolic processes because it influences the solubility of oxygen. Temperature and oxygen have an inverse relationship:

As temperature increases, the solubility of oxygen decreases. At higher temperatures less oxygen is available for fish respiration than at lower water temperatures. The maximum rate at which aerobic respiration can occur at a given temperature will be governed by the rate at which oxygen can be supplied (Fry 1971).

Seasonal changes in thermal tolerance and studies of the effect of temperature on metabolism indicate that there are biochemical and physiological systems which modulate the effect of temperature (Wootton 1998, Chapters 1 & 4). Fish can survive over a range of temperatures bounded by the upper and lower incipient lethal limits. The temperature responses of fish are divisible into three categories: resistance, preference and tolerance. The upper resistance temperature at which mortality occurs is the critical thermal maximum (CTMax). The preference range of temperatures for adult brown trout varies between 12.4 – 17.6°C and rarely exceeds water temperatures above 19°C (Ferguson 1958; Coutant 1977; Nettles et al. 1987; Garrett and Bennett 1995). A laboratory study by Coutant (1975) found that the tolerance range for brown trout was 18-20°C and the resistance range 20-22°C. This confirms Gardner and Leetham's (1914) observation that adult trout mortality is high above 20°C and complete above 25°C.

Early authors studying growth deduced that salmonids do not grow when water temperature is less than 7°C (Pentelow 1939; Wingfield 1940). Subsequent studies explored the range of temperatures that optimized growth. In studies by Brown (1946*a*, 1957), two-year old brown trout were maintained at a constant temperature, 11.5°C, and a constant photoperiod (12L:12D). Under these constant conditions the trout displayed a two-cycle growth phase that alternated between increase in weight followed by increase in length. Brown also noted that the growth rate gradually fell throughout the summer and that slower growth was associated with sexual maturity and the onset of the breeding season. Brown concluded that temperature is the primary factor influencing growth, but not the exclusive factor. Other factors working in combination with temperature (e.g., fish density and competition for food) also influence growth (Brown 1957).

Rising water temperature increases the respiratory metabolism and maintenance requirements of fish. In another experiment by Brown (1946*b*), it was determined that two-year brown trout experienced two temperature optima for growth, one at 7°C - 9°C and the other at 16°C - 19°C. These optima occurred whether fish were grown in varying temperatures or in different constant temperatures. This effect of temperature on growth rate can be explained by considering the appetites and maintenance requirements at different temperatures. Appetite is at a maximum at 10-19°C and maintenance requirements increase rapidly at 9-11°C (Brown 1957). In later laboratory studies, Brungs and Jones (1977) tested the upper limits of the optimal temperature range and confirmed that water temperatures above 19°C had adverse effects on brown trout feeding and growth rates. Interestingly, both of these studies are in contrast to Brynildson et al. (1977) who found that brown trout activity and growth were maximized at 18.3-23.9°C. One possible explanation for this contradiction may be the expression of genetic variation and co-adapted gene complexes (Watt 1983; Watt el al. 1983) which have evolved in response to the specific micro-environmental conditions in specific streams. Simply put, a naturalized[3] fish population's temperature tolerance is a function of its genetics which is not fixed but can change to match environmental conditions.

Fishery biologists have often suspected *a priori* that domesticated[4] stock has a lower tolerance to high water temperatures in the summer compared to wild[5] populations. A study by Carline and Machung (2001) demonstrated that the CTMax for wild strains was consistently higher than that for domesticated strains. They presumed that the observed difference was attributable to genetic differences and not the acclimation history of a population. In their study, both groups were equally acclimatized. However, the wild trout CTMax was higher than the domesticated trout. Therefore, acclimation to the higher temperatures did not determine high temperature tolerance. The most plausible factor for this was the difference in genetic make-up between the wild strains and domesticated trout. In another study on mosquitofish (*Gambusia holbrooki),* Meffe et al. (1995) showed that fish from different populations had different tolerances to high temperatures and that these differences were attributable to the degree of genetic heterozygosity in each population. These studies all strongly suggest that thermal tolerance is a genetically determined trait in

[3] Introduced fish stock that is adapted to local stream conditions.
[4] Stock typically hatchery-reared for multiple generations and not necessarily adapted to local stream conditions.
[5] Indigenous fish stock adapted to local stream conditions

fish and that selection pressures in the local environment determine the expression of the trait in terms of temperature tolerance. The application for fishery biologists is that domesticated, hatchery-reared stock often exhibits a higher degree of inbreeding depression (i.e. lower heterozygosity) and that stocking programs may reduce a naturalized population's high temperature tolerance.

3.3 Behavior and Movement

Behavioral traits affecting thermoregulation provide a mechanism by which fish can control the effect of temperature on metabolism. Fish movement and migration are adaptive behavioral traits in response to changing micro environmental conditions. These behavioral traits also have a direct effect on either the rate of food consumption or the rate of energy expenditure (Wootton 1998, Chapter 6). Earlier evidence suggests that fish do not move to water of a given temperature and then remain there, but tend to make exploratory movements into waters of both lower and higher temperature. Recent evidence suggests that these exploratory movements probably occur while fish are foraging and that fish stay within a preferred range of temperatures while foraging. Several authors demonstrated that higher water temperatures increase the metabolic demands of fish and that many species, including salmonids, may detect or seek out cooler waters when ambient stream temperature is high (Meyers et al. 1992; Nielsen et al. 1994; Matthew et al. 1994; Armour 1994). Other studies experimentally tested fish behavior and temperature to determine if fish consistently seek an optimal range of temperatures to inhabit (e.g., Jobling 1981). Reynolds and Casterlin (1979*a*, 1980) placed a variety of fish including trout in a shuttle-box temperature gradient system and found that within two hours or less, the fish began to spend most of their time within a relatively narrow temperature range. They defined the range as the "thermal preferendum" of the fish. They also determined that there may be a diurnal pattern to temperature preference but concluded that the 24-hour thermal preferendum mean across all water inhabited was 12.2°C. From a management perspective, it is more realistic to consider the thermal preferendum as a temperature range rather than a single average temperature (Jobling 1981). This is realistic because the thermal preferendum may vary in concert with other environmental parameters (Reynolds and Casterlin 1979*b*), and shift over time due to genetic changes in a trout population in response to selection pressures.

The high specific heat of water forces changes in temperature to be relatively slow such that fish can often detect developing unfavorable conditions and move into more favorable ones to avoid the lethal effect of temperature. However, escape may be blocked by low water and restricted water flow. Furthermore, escape may not be possible when there is a surge in heated surficial water from rainstorm events, resulting in a rapid increase in temperature across the entire thermal regime of the stream or river. This stochastic event can have secondary effects. Oxygen becomes less soluble as water temperature increases thereby influencing metabolic rate. In summary, the thermal impacts of key rainstorm events may have synergistic effects by potentially complicating the oxygen profile of a stream or river while also influencing the metabolic rate of fish (Wootton 1998, Chapter 4).

Many habitat characteristics influence the thermal regime of a stream and thus thermoregulation behavior in fish. Undercut banks and overhanging vegetation are important thermal components of brown trout habitat (Wesche et al. 1987). Reduction in these habitat features may affect the thermal regime of a stream. Zones of cool water in pools are apparently caused by at least two mechanisms: influx of cool seepage water and retention of cool water deeper in the water column (Ozaki 1988; Nielsen et al. 1994; Matthews et al. 1994). Cool seepage water originates from groundwater and tributary inflow which is physically isolated or prevented from rapidly mixing with warmer stream water (Ozaki 1988). Cool water retention in deeper pools is established by stratification of the dense cooler waters below the warmer surface waters (Ozaki 1988).

There are differing studies in the literature regarding brown trout avoidance of stochastic warm-water events. Several studies documented the formation of cold water in stream pools and suggested this may be important in creating a thermal refuge for fish during periods of thermal stress (Bilby 1984; Nielsen et al. 1994; Matthew et al. 1994). Burrell et al. (2000) observed high mortality of adult brown trout from summer water temperatures in the Chattooga River when water temperature exceeded 19°C for an extended period. During this period, brown trout did not seek available thermal refuge in cooler nearby tributaries. Instead, they stayed in the pool habitat where possible groundwater intrusions may have buffered water temperatures. The authors assumed that the prolonged period of high water temperatures may have warmed the waters in the pool habitat or affected the available food supply, accounting for the high mortality of fish. A possible explanation as to why fish did not relocate to more favorable water is that the energetic costs of movement or increased exposure to predators were too high. In other studies, brown trout were observed to seek thermal refuge during periods of extreme temperature (McMichael and Kaya 1991; Garrett and Bennett 1995). In an unpublished study, Wilfond and Moeckel found that the movement of large brown trout in the Vermillion River system over long distances was behavioral and related to the physical environment. Using radio transmitters over a two-year period, they found that brown trout exhibited strong site fidelity and that some fish did seek thermal refuge when temperatures at those sites exceeded 20°C. It may be that the behavioral differences among these studies are the result of variation in individual stream characteristics. Wilfond and Moeckel suggest that their results may result from the naturalization of brown trout in the Vermillion River over time, producing a population of fish which can seek cooler tributary waters as a thermal refuge. Obviously, the ambiguity of the literature merits further investigations into the relationship between seasonal movement patterns and warm-water temperature avoidance, perhaps on a stream-by-stream basis in order to better understand the mechanisms influencing brown trout behavior.

3.4 Reproduction

The genus *Salmo* is iteroparous (produces offspring in successive seasonal batches). This requires specific spawning, incubation, and rearing habitats to maintain wild populations. The onset of brown trout reproduction in the fall is triggered when water temperatures are in the 5-10°C range (e.g., McFadden et al. 1965; Garrett and Bennett 1995; Pender and Kwak 2002). The onset of egg development and fry emergence occurs in the spring and is temperature dependent (Crisp 1981; 1988). The uniformly low water temperature during the spring in temperate northern climates does not expose the young to deleterious threatening spikes in water temperature.

Brown trout are total spawners; i.e., breeding season fecundity and batch fecundity are the same (Wootton 1998, Chapter 7). The female condition at the time of spawning is critical to fecundity and egg viability. Warm water temperatures, available food base, and general water quality during the summer and early fall can impact the adult female condition and fecundity by affecting egg size (Bagenal 1969; Wootton 1998, Chapter 7; Pender and Kwak 2002). This relationship was demonstrated by Ojanguren et al. (1996) who determined that juvenile trout survival was positively related to egg size. In short, temperature before and at the time of spawning can significantly influence the female condition at the time of spawning and have significant fitness consequences for offspring when one considers egg size as a measure of future expected juvenile fitness (Einum and Fleming 2000).

4.0 Summary

The majority of authors suggest relatively few general habitat characteristics provide as significant an influence on the temporal and spatial distribution of brown trout in a stream as does temperature. This is a conclusion substantiated in a study by Barton et al. (1985) that examined multiple environmental parameters across 38 streams in southern Ontario. Barton et al. determined that the only variable which clearly distinguished between trout and non-trout streams was a weekly mean temperature of <22°C. Southern Ontario has a temperature and precipitation regime similar to southern Minnesota, although mean annual temperature and precipitation are slightly higher and the probability of extended severe drought is lower in southern Minnesota due to the effect of the Great Lakes

This literature review supports the idea that temperature is the most critical habitat factor affecting trout distribution in a stream, regardless of age class and fish density. Studies tend to agree that the stream distribution of healthy adult brown trout is largely bounded by the 19°C thermal physiological limit, with a maximum not to exceed 22°C for an extended period. In this thermal window of 19-22°C, brown trout may be physiologically stressed and living at the edge of their survival tolerance. Furthermore, temperatures of 19-22°C are near the upper metabolic limit of trout and may affect their ability to gain weight or maintain normal physiological functions. Brown trout do not grow in the 19-22°C range and are likely to experience high mortality rates from both the direct and indirect effects of inhabiting this temperature range. Reproductive efforts may also be limited by depressed juvenile fitness following a reduction in the female condition prior to spawning.

The key findings of this review are:

1. There are no environmental studies comparing the effect of temperature on mortality across all brown trout ages. This gap prevents a full understanding of temperature effects on an entire brown trout population.
2. The optimal range of water temperatures for brown trout is consistently reported as 12-18°C.

3. Brown trout regardless of age will not select water that exceeds 22°C when given a choice of suitable water with forage and ample oxygen at lower temperatures.
4. The metabolic rate of active brown trout (as well as other fish) increases at high temperature (>19°C), stimulating high energy demands that may not be sustainable for prolonged periods.
5. Brown trout can change their micro habitat preferences as environmental factors change. In studies where brown trout were able to select temperature as well as other environmental factors, temperature proved to be a better predictor of fish habitat choice.
6. Brown trout may have evolved a fine-scale genetic make-up that permits stream-specific micro environmental adaptation. The mechanism behind micro environmental adaptation may be co-adapted gene complexes. As a result, naturalized and wild trout populations have the capacity to change their thermal tolerance level over time.
7. Brown trout exhibit strong site fidelity but also have relatively long migratory ranges for spawning, and in response to flooding or increasing water temperatures. Foraging also appears to extend the range of trout beyond the home site.
8. Changes in the groundwater profile or volume of surface water runoff can disrupt thermal stream profiles, especially deep pool refuges. Deep pool refuges and areas of groundwater intrusion may be used by trout to escape increasing stream temperatures.
9. To contribute to the maintenance of a population, young brown trout must not only survive but mature. The upper physiological threshold for water temperature is the same for juvenile fish and adults. The only difference is that juvenile fish have a greater opportunity to seek refuge in deeper pools and stream undercuts during low-flow warm water periods.
10. From a management perspective, many environmental variables influence the quality of a trout stream, including water temperature, stream size and flow rate, stream origin and water source, seasonal events, sediment and turbidity, stream and pool geometry, and available food resources. The characteristics are stream-dependent and must be considered on a stream-by-stream basis, with the only consistent variable across all streams being temperature.

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