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Knowledge of fish physiology used to set water temperature thresholds for in-season closures of Atlantic salmon (*Salmo salar*) recreational fisheries

Connaissances de la physiologie des poisons servant à définir des seuils de températures de l'eau pour déclencher des fermetures durant la saison de pêches récréatives du saumon atlantique (*Salmo salar*)

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TABLE OF CONTENTS

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ABSTRACT

In a number of rivers in Eastern Canada, water temperatures may exceed 25°C during the summer, and often in combination with low water levels. During these high temperature events, salmonids which cannot escape the high temperatures must cope in order to survive. Temperature tolerance is species and life-stage specific with adult salmon being less tolerant than juveniles. As temperatures increase from optimal temperature (T_{opt}) to critical temperature (T_{crit}) values, thermal tolerance of fish decreases. During stress, metabolic byproducts accumulate in the white muscle of the fish. Concentrations of these byproducts must return to lower and specific levels for metabolic recovery. This document presents information on fish physiology to develop temperature thresholds that could be used to trigger in-season closures of the Atlantic salmon recreational fisheries. Catch and release angling imposes additional stress on the fish and the goal is to determine a temperature threshold above which this additional stress should be managed. Information with which to define T_{opt} and T_{crit} for adult Atlantic salmon is lacking. As a result, information from juvenile Atlantic salmon and other salmonid species were used to define these temperature thresholds for adult salmon. The probability of full metabolic recovery is reduced when the minimum nighttime water temperature remains above 20°C.

RÉSUMÉ

Dans nombre rivières de l’est du Canada, des températures d’eau élevées, dépassant 25ºC durant l’été, sont souvent accompagnées par des faibles niveaux d’écoulement. Durant ces périodes de températures élevées, les salmonidés qui ne peuvent échapper à ces conditions doivent les tolérer dans l’espoir de survivre. La tolérance aux températures dépend de l’espèce et aux stades de vies, les saumons atlantiques adultes étant moins tolérants que les juvéniles de saumon. À mesure que la température augmente de Topt à Tcrit, la capacité à tolérer ces températures élevées diminue. Durant ces périodes de stresses, les produits métaboliques s’accumulent dans les cellules musculaires blanches. Seul le retour de la concentration de ces produits à des niveaux plus bas et très spécifiques permet le rétablissement métabolique. Ce document présente les informations sur la phyisologie des poissons afin d’établir des seuils de températures qui pourraient servir comme déclencheurs de fermetures de pêches récréatives au saumon durant la saison de pêche. La capture avec remise à l’eau induit un stresse additionnel sur le poisson capturé. Le but des seuils déclencheurs est de permettre une meilleur gestion du stresse additionnel attributable à l’activité de pêche durant des périodes de températures élevées. Il n’existe pas d’information directe qui pourrait servir à établir les niveaux correspondants à Topt et Tcrit pour les adultes de saumon atlantique. En conséquence, les résultats d’études entreprises sur les juvéniles de saumon atlantique et d’autres espèces de salmonidés ont servi à définir ces seuils de températures. La probabilité d’un rétablissement métabolique complet est réduite lorsque la température de nuit minimale de l’eau est supérieure à 20ºC.

INTRODUCTION

Environmental temperature dictates large-scale ecosystem processes, geographical distributions of species, and migrations of animals (Magnuson et al. 1979). In most fish species and in ectotherms in general, environmental temperature governs metabolic processes, including respiration and cardiac functions (Farrell 2002). Ectotherms can perceive a temperature difference of 0.5°C in their surroundings (Murray 1971) and these organisms will behaviourally thermoregulate by selecting environmental temperatures for optimal physiological performances (Pörtner and Knust 2007). Studies have shown that the preferred and selected temperatures by ectotherms correspond to the temperature for optimal physiological performances. Hence, the preferred temperature is a good indicator of physiological temperature optima (Brett 1971). Most fishes are ectotherms and their tolerance to extreme temperatures is directed by the effects of environmental temperature acting on the energy allocation at the organism level such that the energy is re-directed to meet metabolic demands at high temperatures (Pörtner 2002).

A number of rivers in Eastern Canada reach water temperatures in excess of 20°C during summer months, in combination with low water conditions. Adult salmon return to rivers during the spring through fall for the fall spawning in headwaters of rivers. In large rivers, such as the Margaree, Miramichi and Restigouche rivers, in-river movements of adult salmon typically occur from May until late fall (Breau et al. 2009; Cameron et al. 2009; Chaput et al. 2010). In smaller rivers with early-run salmon, water levels influence time of entry into the rivers. In years with low water levels, fish remain in estuaries and migrate to headwaters in the fall. In years with higher water levels, early-run fish hold in pools during the summer until migrating to headwaters to spawn in the fall. High temperature events are especially critical for early-migrating adult Atlantic salmon that spend the summer in rivers. During the past several years, an increased proportion of adult salmon have been returning to the Miramichi River during the summer (Douglas et al. 2013), which exposes more fish to these high river temperatures. Adult and juvenile Atlantic salmon aggregate at cool water sites (e.g. entrance to tributaries) to escape or cope with the high temperatures (Breau et al. 2007). Mortalities of adult salmon have been observed in the Miramichi River during temperature events although most salmon that die likely sink to the river bottom and are never seen.

Angling is considered a severe form of exhaustive exercise (Booth al. 1995) when fish can experience large physiological disturbances (Wood 1991). The exact cause of the delayed mortality is not fully understood but believed to be related to the magnitude of the physiological disturbance (Wood et al. 1983). The International Council for the Exploration at Sea (ICES) compiled studies estimating the levels of pre-spawning mortality of salmon caught and released by anglers and the potential implications for stock assessments (ICES 2009). Water temperature was cited as the most important factor affecting survival of salmon during catch and release (ICES 2009). Salmon mortalities were low when angling occurred at water temperature below 17 to 18°C (ICES 2009). They reported a lack of studies on survival of salmon at higher temperatures and survival post-released and prior to spawning.

In-season management measures in rivers of the Gulf Region have been implemented in the past to reduce mortality of Atlantic salmon (*Salmo salar*) in catch and release recreational fisheries. In-season closures were *ad hoc* with no specific temperature thresholds guiding closures. The purpose of this document is to develop temperature thresholds for in-season closures of the recreational fisheries based on fish physiology. In a companion paper, the temperature threshold elaborated in this document are used on data from past years to quantify the implications of using the intervention trigger for in-season closures (Breau and Caissie 2013).

FISH BIOENERGETICS

Fish bioenergetics is modeled using the following energy budget equation in which energy intake is partitioned into various physiological components:

$$C = P + R + F + U$$

In this equation, C is the energy consumed, P is the energy invested in somatic and gonadal growth, R is the energy involved in heat production during metabolism, F is the energy lost in the faeces, and U is the energy lost in the excretory products such as ammonium and urea (Wootton 1990).

The respiration component (R) can be further divided into the following three metabolic components:

$$R = BMR + R_A + SDA$$

Where BMR is the basal metabolic rate, R_A is the metabolism related to activity such as foraging and SDA is the specific dynamic action, the metabolism related to digestion.

Basal metabolic rate (BMR) is the minimum energy level required to sustain vital life supporting functions such as breathing and blood circulation (Brett 1971). BMR is an aerobic process, driven by temperature, which increases with increasing temperature. Organisms can only consume a maximum amount of oxygen per period of time and this maximum is termed the active metabolic rate (AMR). AMR increases with water temperature until a given point where AMR remains constant (Fig. 1). The difference between AMR and BMR is termed the aerobic scope which is the energy available to perform activities such as swimming, feeding and escaping predators (Fry 1947).

THERMAL WINDOW

Changes in body temperature of ectotherms require physiological and biochemical adjustment to maintain a certain level of biological activities (Taylor et al. 1997). Organisms can live only in a limited range of external temperatures because structural, molecular and cellular processes have evolved to be optimized within a limited range of temperatures (Pörtner and Farrell 2008). This limited range of temperature is termed the thermal window and it is species and population-specific. The thermal window of aquatic animals depicts the aerobic performance in relation to water temperature (see Pörtner and Farrell 2008). Changes in temperature are not problematic unless the temperature experienced by the animal is near the upper lethal limit (Taylor et al. 1997).

The optimal temperature (T_{opt}) is the temperature at which the aerobic scope (difference between AMR and BMR) is greatest and corresponds to the highest level of energy available for routine metabolism (e.g. used for swimming). The aerobic capacity is species- and life-stage specific. Aerobic capacity and thermal tolerance are lower in adult fish than in juveniles (Pörtner and Farrell 2008; Fowler et al. 2009). Brett (1971) demonstrated that the optimal temperature for maximum aerobic scope in juvenile sockeye salmon corresponded to the optima for cardiac output and critical swimming speed. At a given temperature, called “Pejus” temperature, aerobic limitations begin to set in, with the aerobic scope decreasing and approaching zero as temperature increases. Pejus temperature corresponds to the onset of loss of individual performance and abundance of individuals (Pörtner and Farrell 2008). Aerobic scope for activity is minimal at T_{crit} and anaerobiosis sets in to supply energy to meet the high metabolic demands. At water temperatures varying between T_{opt} and T_{crit}, aerobic scope decreases with increasing temperature and anaerobic metabolism contributes increasingly to energetic demands (Breau et al. 2011). The aerobic scope is maximized at optimal temperature (T_{opt}) and minimal at critical temperature (T_{crit}). Beyond T_{crit}, survival is time-limited and fish live in a passive state with limited behavioural responses (Pörtner and Farrell 2008). The cardiac performance in fishes is maximal at the optimal temperature and the upper limit for heart rate is at the lethal temperature limit (Farrell et al. 1991; Farrell 1997).

Anaerobic metabolism is typically used in white muscle to supply energetic demands relating to short-term burst-type exercise such as predator escape (Taylor et al. 1997). A fish held at T_{opt} (maximum aerobic scope) will use anaerobic metabolism for short-term, strenuous exercise and physiological recovery will occur relatively rapidly. At high temperature, metabolism increases. As metabolism exceeds the maximum aerobic rate, anaerobic metabolism is increasingly used to meet basic demands such as respiration and blood circulation (Brett 1971). The use of anaerobic metabolism is short-term and will lead to mortality by hypoxemia if conditions persist (Pörtner and Knust 2007). Hypoxemia occurs when the cardio-circulatory systems can no longer meet the oxygen demands of the tissues (Pörtner and Knust 2007). The insufficient supply of oxygen to the tissue can occur under normoxic condition because of the inability of the cardio-circulatory system to deliver the oxygen to the tissues quickly. Anaerobic metabolism is energetically costly, creates an oxygen “debt”, and leads to the production of metabolic by-products such as lactic acid. Lactic acid concentrations are hypothesized to be the proximate mechanism triggering the movement of ectotherms to cooler sites during warm temperature conditions (Pörtner et al. 1994).

Farrell et al. (2008) showed that the temperature difference between T_{opt} and T_{crit} varied only by 6 to 7°C for three Pacific salmon populations in the Fraser River and that these values varied by salmon stock (e.g. Weaver Creek sockeye salmon: T_{opt}=15°C and T_{crit} =21°C). The maximum temperature at which fish can still perform daily activities without compromise and limitations has been defined by Farrell et al. (2008) as the functional $T_{crit.}$ The functional T_{crit} has not been measured in salmonids but is nevertheless highlighted as a key factor for understanding salmon fishery collapses during high river temperatures on the Canadian West Coast. The functional T_{crit}, a temperature that allows a level of activity while coping with the temperature, is lower than T_{crit} and depends on the level of activity required by the fish. The fish need a certain (unknown) percentage of the maximum aerobic scope to support some level of activity. Farrell et al. (2008) assumed that possibly 25% of the maximum aerobic scope is needed.

ACCLIMATIZATION

Acclimatization is the process whereby an organism physiologically adjusts to an environmental condition such as temperature (Schmidt-Nielsen 1990). The physiological adjustment to a condition under controlled conditions by an experimenter is termed acclimation (Fry 1971). For both processes, the surroundings that the animal is exposed to changes but the physiological mechanisms are the same for both processes. Animals in the wild have evolved to tolerate temperature variations through acclimatization and temperature sets the lethal limits of life (Brett 1956). The tolerance limits of an animal can be extended by acclimatization up to a certain point (Brett 1956). In conditions of low oxygen concentrations, acclimation to high temperatures is inhibited (Brett 1944) presumably due to the inability of the tissues to adjust to the new temperature. Fish exposed to temperatures in the resistance zone will succumb within 10 min to 7 days. At higher temperatures, 100% mortality of the sample would occur under controlled conditions. Fry (1947) defined the resistance time as the period of tolerance prior to death. In the wild, fluctuating water temperatures will prolong the resistance time but literature on the topic is lacking.

SALMONIDS

In temperate regions, fish experience water temperatures of 0 to 30°C (Elliott and Elliott 2010) and fishes are categorized as warm water, cool water or cold water species. The family Salmonidae has the lowest thermal tolerance found to date with maximum upper lethal temperatures barely exceeding 25°C (range for salmonids: 20 to 26°C) (Brett 1956). Thermal sensitivity is size-specific whereby adult salmonids prefer lower temperatures than juveniles (McCauley and Huggins, 1975) and are less tolerant of high temperatures (Fowler et al. 2009). Of the salmonids, the Atlantic salmon has the highest temperature tolerance (Elliott and Elliott 2010).

There is limited scientific literature on thermal tolerance of adult salmonids in the wild with available data focusing on trout and Pacific salmon species. Studies show blockage in salmonid migration at water temperatures of 20 to 23°C (e.g. Chinook salmon: Bumgarner et al. 1997). Alabaster et al. (1991) observed that returns of small Atlantic salmon (known as 1SW or grilse) to the Thames River negatively correlated with water temperature with no catch of salmon at the trapnet when water temperature reached 24.2°C. There was no similar finding for adult Atlantic salmon on the Northwest Miramichi River (Elson 1969), but the study was not designed for that purpose. In the River Dee, Scotland, Atlantic salmon remained at sea when water temperature exceeded 20°C (Hawkins 1989). In the River Wye, Brooker et al. (1977) observed salmon mortality on a large scale after a day when the mean daily water temperature was 27.6°C and the mean during the day with mortalities was 26.3°C. There was a mass die-off of macrophytes in the river during the day of the fish mortalities. Moore et al. (2011) monitored body temperature of adult Atlantic salmon using telemetry. They found that on days with ambient water temperature between 18 and 24°C, fish found cool water sites and were able to decrease their body temperature by 5.4°C compared to the water temperature found in the salmon holding pools. In the Moose River (Nova Scotia), Huntsman (1942) observed size-related mortality with large salmon (known as multiseawinter salmon) mortality occurring first, followed by small salmon (also known as grilse or 1SW) and no parr mortalities. In their study, 2+ parr mortality occurred at 32 to 33°C, a value higher than found under laboratory conditions (Elliott 1991; Breau et al. 2011). Heterogeneous thermal conditions in rivers and possibly the calming effects of aggregative behaviour could explain the higher temperature tolerance in the wild. Elliott (1994) showed that the upper critical water temperature range for juvenile Atlantic salmon was between 22 and 33°C with 27.8°C corresponding to the lethal temperature for parr. One should keep in mind that aerobic capacity can be further constrained if oxygen availability is limited (Brett 1952).

Adult Atlantic salmon prefer water temperatures in the range of 14 to 20°C (Elson 1969) and this life stage is sensitive to water temperatures above 20ºC. Alabaster and Lloyd (1982) suggested that 20 to 21°C should be the upper permissible temperature for salmonids of the genus *Salmo* during the warmest season of the year. Again, these levels fall far short of directly lethal conditions. T_{opt} and T_{crit} for adult Atlantic salmon are not known however, the fish likely have reduced aerobic scope at temperatures near and exceeding 20°C. Metabolic rate of adult Atlantic salmon was quantified in 19 published articles (see Enders and Scruton (2005) for a compilation). In these experiments, the minimum energy required to sustain life, known as standard metabolic rate, was measured for adult salmon at low temperatures (4-10°C) and mostly in seawater conditions. No literature on active metabolic rate or maximum aerobic scope has been found for adult Atlantic salmon.

Fish have metabolic and physiological limitations at water temperature exceeding T_{opt} leading to behavioural and survival challenges. Oxygen consumption of adult sockeye salmon peaked at 19°C and fish ceased swimming at 24°C (Steinhausen et al. 2008) demonstrating that aerobic scope was compromised at temperatures exceeding 19°C. The study showed that fish experienced a cardiac limitation at temperatures above 19°C because the cardiac output did not increase with the increasing temperature. Weaver Creek sockeye salmon held at 4°C above T_{opt} for 24 days experienced a lower survival rate (32% vs. 62%) than fish held 4°C below T_{opt} (Crossin et al. 2008). These fish were released for their spawning migration, but only 35% of the fish held at 18°C survived compared to 68% for fish held at 10°C and 62% for the control group. Hence, few fish entering the river at water temperature exceeding T_{crit} would survive and spawn. Farrell et al. (2008) clearly showed that migration success of tagged sockeye salmon was negatively related to the river temperature during the migration. The same limitations occur for the Atlantic salmon and therefore studies designed to measure T_{opt} and T_{crit} are needed.

Until data specific to adult Atlantic salmon is available, information from juvenile Atlantic salmon will be used as an indicator to establish thresholds temperatures for management interventions during warm water conditions. Trudel at al. (2004) cautioned against “species borrowing” and “life stage borrowing” when referring to metabolism of ectotherms. Even within the same genus, metabolic rate of ectotherms varies and should not be substituted. There is also evidence that aerobic fitness is greater in wild rainbow trout compared to hatchery individuals (Gamperl et al. 2002). Therefore, the threshold temperature defined in this document should be evaluated in an experiment and adjusted accordingly.

ATLANTIC SALMON

During 2003 to 2005, the behaviour, movements and physiology of juvenile Atlantic salmon in response to high temperature events were studied (Breau 2011). Aggregations of juvenile Atlantic salmon at cool water sites in the Little Southwest Miramichi River were monitored to understand the trigger involved in fish movement. There were three known sources of cool water in the area of Catamaran Brook, a tributary of the Little Southwest Miramichi River.

The maximum daily water temperature exceeded 23°C on 15, 31 and 46 days in 2003, 2004 and 2005, respectively (Fig. 2). However, fish movement to cool water sites only occurred on three days in 2003, nine days in 2004 and 13 days in 2005. There were days when water temperatures exceeded 25°C but no aggregations of fish at cool water sites were observed. Aggregations occurred on days when the average daily temperature exceeded 23°C indicating that the minimum water temperature in the morning played a role in fish movement (Fig. 3). The sustained aggregation of juvenile salmon over consecutive days occurred when the average daily temperature exceeded 23°C and the minimum water temperature remained above 18°C (Fig. 4) (Breau 2011).

BMR of 2-yr old Atlantic salmon reached AMR at 24°C (Breau et al. 2011) meaning that T_{crit} for 2+ Atlantic salmon is 24°C. Movement of 1-yr and 2-yr old salmon to sources of cooler water in the Little Southwest Miramichi River occurred on days when minimum water temperature remained above 18 to 20°C and daytime temperatures were well above 20°C (Breau et al. 2007). In the laboratory study, 2+ salmon juveniles were behaviourally stressed at ≥24°C leading to a depletion of glycogen levels and the production of lactic acid in the white muscle of the fish. No by product from anaerobic metabolism was measured in 0-yr old salmon juveniles held at temperatures varying between 16°C to 28°C in a laboratory experiment. Interestingly, the 0+ fish did not move to cool water in the wild in the study of Breau et al. (2007). Presumably, movements of 0-yr old salmon would occur at higher temperatures based on the temperature-dependent oxygen-limitations function.

In the Little Southwest Miramichi River, juvenile and adult Atlantic salmon moved to cool water sites during periods when the minimum temperatures (usually corresponding to an early morning temperature) remained above 18 to 20°C. Several years of field observations of tagged juvenile Atlantic salmon in the Little Southwest Miramichi River showed that fish move to cool water sites when T_{min} (minimum temperature) remained above 20°C for two nights (Breau, 2011; Corey et al. unpublished data). These findings suggest that setting T_{min} at 20°C for management interventions would cover the days when behavioural changes and physiological challenges occur.

ESTABLISHING T_{OPT} AND T_{CRIT} FOR ADULT ATLANTIC SALMON

T_{opt} for three stocks of Pacific salmon has been shown to be similar to the temperature experienced by the fish during upstream river migration (Lee et al. 2003), suggesting that physiology was optimized at the temperature experienced in the river (Steinhausen et al. 2010). Using a time series of many decades, T_{opt} for Pacific salmon was shown to correspond to the water temperatures experienced in the river during the river migration (see Farrell et al. 2008). Assuming the same relationship holds for Atlantic salmon, water temperature in the Miramichi River during the river migration of salmon (June 1st to September 30) was analyzed. The mean water temperature in the Miramichi River over a nine year period was 18.5°C (Fig. 5), a value that is in the optimal range reported in the literature for Atlantic salmon (Elliott 1991; Jonsson and Jonsson 2009). The temperature window between T_{opt} and T_{crit} for three populations of salmonids was shown to be 6 to 7°C (Farrell et al. 2008). Assuming that the same temperature window occurs in all salmonids, T_{crit} for Atlantic salmon is expected to be near 25°C. Hence, the complete collapse of the aerobic scope due to temperature alone would occur at ≥25°C. Under this scenario, fish mortalities would occur at 25°C if no cool water sites are available to decrease their metabolic rate. The aerobic scope for Atlantic salmon would decrease from 18°C to nil at 25°C. Adult Atlantic salmon acclimated to three water temperatures (12°C, 18°C and 23°C) did not die after being held at the acclimation temperatures for three days (Wilkie et al. 1997). However, adult Atlantic salmon will survive only for short periods at temperatures of 24 to 27°C (Huntsman 1946).

CATCH AND RELEASE AT HIGH WATER TEMPERATURE

The effects of catch and release on fish survival at different water temperatures was summarized in a literature review (Gale et al. 2013). The review showed that fish mortality occurred even within the temperature preference range with mortality being the greatest at high temperatures. Mortality rates are usually between 2 to 8% at water temperatures below 18°C (Whoriskey et al. 2000; Dempson et al. 2002; Thorstad et al. 2003). At water temperatures above 20°C, mortality rates are predicted to exceed 20% (Fig 6; Dempson et al. 2002; Thorstad et al. 2003). Atlantic salmon can be caught during high water temperatures. On the Restigouche River, Mowbray and Locke (1999) reported angling catches of Atlantic salmon on days when water temperature ≥20°C at 10h00 in the morning. Even though catch per unit effort was lower on those days, many adult Atlantic salmon were caught.

The Crown Reserve data on the Miramichi River (see Dubee et al. 2011 for details) was used to determine the number of fish caught and catch per unit effort in this river. To avoid the issue of temperature measurement sites being at a distant location or downstream of fishing reaches, only the Bridge Pool site was used because it was upstream of the fishing sites on the Northwest Miramichi River. So, the Bridge Pool temperature data and the angling data for the Crawford, Depot, Sullivan, Stony Brook and Elbow were used for the analysis (these sites are located immediately below the temperature logger and are similar or warmer in temperature). Fewer warm water conditions were experienced at these stretches than elsewhere in the river because of the monitored sites, Bridge Pool has the coolest water temperatures (see Caissie et al. 2013). Hence, the fishing stretches were not ideal to determine high temperature effects on angling opportunities. At the Bridge Pool site, warm water conditions (T_{min} ≥18°C) occurred in 2004, 2005, 2006 and 2010. Within each year, catch of salmon per rod days was slightly lower on days with T_{min} exceeding 18°C but comparable to the 15-17°C category and fish were caught (Fig. 7). The angling effort on days with T_{min} exceeding 18°C was over 70 rod-days (except for 2004: 26 rod-days; Fig. 8). Figure 9 shows the angling effort and salmon catches at four other fishing stretches (Adams, Charlie's Rock, Groundhog Landing and Squirrels Falls) for the same days as analyzed above (T_{min} at Bridge Pool ≥18°C so warmer at those sites). Even if salmon do not become hooked during the warm water conditions, stress is imposed by wading in the vicinity of fish or fish being disturbed by the fly.

Many studies have shown physiological impairment (Gale et al. 2011) and fish mortality at higher water temperatures (Fig. 4; see Dempson et al. 2002). Dempson et al. (2002) showed that 12% (3 of 25) of the 1SW salmon angled in water temperature ≥17.9°C did not survive. Fish were held in cages to monitor survival. Mortality of brown trout angled during days when daily maximum water temperatures exceeded 20°C was 4% (Boyd et al. 2010). Air exposure time was another important factor affecting fish condition and survival (Gingerich et al. 2007). In the Escoumins River (Québec), 40 adult salmon were angled and released at water temperatures varying between 10.5 and 19.1°C (Richard et al. 2012). Thirty-six of these fish migrated up the fish ladder whereas many factors including the catch and release could have caused the other fish not to cross the fish ladder. Air exposure time was cited as an important factor for re-sighting fish. Even though there are a number of studies on catch and release of Atlantic salmon, there are few studies addressing survival and sub-lethal effects of catch and release practices on fish during high temperatures.

Wilkie et al. (1997) showed that physiological stress in adult Atlantic salmon occurred at 23°C without any fish mortality under controlled conditions. However, with exercise, mortalities occurred. Fish mortalities were observed in groups of fish acclimated to 18°C and 23°C and exercised. A total of 44% of the fish exercised at 18°C (3 of 10) and 23°C (4 of 6) resulted in post-angling mortality that occurred within a 4h period.

In the wild, fish mortalities related to high temperatures can not be controlled however, mortalities related to human activities can be reduced. In the heterogeneous environment found in rivers, fish are skillful at seeking sources of cool water or finding ways to cope with the high temperatures. However, the fish are at the limit of survival and any additional stress will lead to mortality. At near lethal temperatures, the metabolic rate and the physiological processes of angled fish are maximized (or approaching maximum rates); therefore any additional stress will lead to fish not being able to cope. Minimizing disturbance during high temperatures will increase the chances that fish will survive such events.

PHYSIOLOGICAL RECOVERY POTENTIAL

Physiological recovery of fish from high temperatures involves the recovery of both the metabolic and cardiac systems (Steinhausen et al. 2008). Factors that influence the recovery process are: acclimatization temperature, exposure time and the magnitude of the stress. The temperature at which stress begins to occur is largely dependent on a fish's prior exposure history or acclimation. One aspect that is little known is the physiological recovery period during stress accumulation. Physiological recovery is prolonged by any limitations on the aerobic scope such as reduced oxygen availability or prolonged periods of high temperatures. The recovery process in a fluctuating temperature environment is complex and dependent on many factors.

During periods of high temperatures, it is important to account for stress recovery during the hours with lower temperatures. Daily fluctuating temperatures will subject the fish to chronically high temperature for short durations with the build-up of an oxygen debt. The best recovery temperature is the temperature experienced by the fish prior to the high temperature event that is within the tolerance zone for the fish. Rainbow trout having depleted glycogen stores and metabolic by-product accumulations demonstrated complete recovery after four hours (Milligan 1996). However other studies show that the recovery of acid-base (e.g. protons) and metabolites (e.g. muscle lactate) required up to eight hours (see Kieffer et al. 1994). Glycogen resynthesis in the muscle occurs when muscle pH levels have returned to a level compatible with glyconeogenesis (Milligan and Wood 1986; Walsh and Milligan 1989). However, recovery in a fluctuating environment is likely more complex.

Wilkie et al. (1997) showed metabolic recovery in adult Atlantic salmon acclimated (habituated to controlled conditions) and exposed to 18°C and 23°C under controlled settings. However, mortalities occurred with added activity. Adult Atlantic salmon were angled in the Main Southwest Miramichi River when the mean water temperature was 20°C and during the fall at water temperatures of 6°C (Wilkie et al. 1996). The glycogen levels in adult Atlantic salmon acclimatized (habituated to conditions in the wild) to 20°C were significantly lower compared to fish held at 6°C which suggests that anaerobic metabolism was being used to meet some level of activity at 20°C. At 20 to 22°C, Wilkie et al. (1996) did not find evidence that oxygen supply limited the glycogen re-synthesis. However, this could be an issue at higher temperatures. Milligan and Wood (1986) showed that the re-synthesis of glycogen in the white muscle of exhausted rainbow trout took 24h at optimal water temperature. Adult Atlantic salmon acclimatized to 23°C recovered within a 4h time period. However, there was a 40% post-angling mortality associated with angling the fish. Based on the PCr and NAD/NADH values, there was no limitation in the O_2 delivery to the tissues. The physiological recovery of returning Atlantic salmon exposed to angling was unchanged after four hours of recovery time (Wilkie et al. 1996).

A maximum water temperature of 23°C has often been cited as the threshold temperature at which human activities around salmon pools should be avoided. However, based on the behaviour of fish in the wild and the physiological responses of the fish, the daily minimum water temperature is likely more important than maximum temperature because of the metabolic recovery potential during hours with lower temperatures. Bonneville cutthroat trout exposed to a temperature cycle of 16-26°C survived the experiment, but fish exposed to a 18-28°C cycle died quickly (Johnstone and Rahel 2003). It is unclear whether the mortality was due to the high temperature of 28°C, or to the minimum not being low enough to allow for metabolic recovery. During a warm water event, a T_{min} temperature closer to the optimal range would allow fish to physiologically recover from the high temperatures. Juvenile Atlantic salmon in the Little Southwest Miramichi formed aggregations at cool water sites when T_{min} exceeded 20°C but fish left aggregations and were feeding later in the evenings. These findings indicate that T_{min} plays an important role during these warm water events.

SUB-LETHAL EFFECTS OF ELEVATED TEMPERATURES

Fish mortality is the most obvious indicator of thermal stress. At intermediate high temperatures, the temperature per se may not lead to death but other factors such as bacterial infection in combination with the temperature could lead to mortality (Brett 1956). Studies have shown that reduced growth rate or weight loss is a more sensitive indicator of stress (Beamish et al. 1997). Sublethal effects of high temperature include a reduction in gamete production and weight loss. Elevated temperatures can also lead to disease, depletion of energy fuels, and gamete damage.

UNCERTAINTIES

The biggest unknowns pertain to aspects of physiological recovery and cumulative stress response during warm water events. We do not know the time period of cool temperatures required for a complete physiological recovery. The cumulative effects of many high temperature days are also not known but this is important in assessing tolerance to temperature. Ideally, functional T_{crit}, the temperature that allows fish to maintain some level of activity without compromising survival, should also be known.

Based on fish physiology, cool nights should allow salmon to tolerate and recover from hook and release related physiological stress. The potential to tolerate and recover from hook and release during warmer days should be tested in the field to ensure that fish mortality is reduced.

There are ample anecdotal reports that mortality of salmon occurs during high temperature events. However, no detailed tracking of information describing the days and locations of these mortalities or the number of fish mortalities was kept. It should also be kept in mind that some salmon that die during these high temperature events sink to the bottom and may go unnoticed. Therefore, there are likely more fish mortalities during high temperature events than are actually reported. It is unknown whether mortalities of fish during these events are related to human activities or solely due to the temperature conditions or both.

Another source of uncertainty is the borrowing of data from juvenile Atlantic salmon and relying on other fish species to anticipate the physiological responses of Atlantic salmon. The information in this document included many studies on other salmonids and juvenile Atlantic salmon. Studies specific to adult Atlantic salmon should be conducted to refine the temperature threshold value developed in this document.

CONCLUSION AND RECOMMENDATIONS

The information available for salmonids indicates that T_{crit} for adult Atlantic salmon is likely 25°C. Field observations on the Little Southwest Miramichi River indicate that juvenile Atlantic salmon use cool water sites when T_{min} exceeds 20°C for two consecutive days. Fish mortalities are also observed on days with warm minimum temperatures (even though most mortality is probably not detected). On days with high daytime temperatures but cool nights, no changes in fish behaviour are observed. On days with nighttime temperatures ≥ 20°C, juvenile Atlantic salmon seek cool water sites in the Little Southwest Miramichi River.

In the wild, fish will escape or cope with warm water conditions until more favourable conditions arise. The heterogeneous thermal environment in rivers allows them to seek more suitable conditions to increase the probability of survival. Thermally-induced mortality could occur without any human disturbances, however, additional stress will exacerbate the physiological conditions and reduce the probability of survival. Many studies have shown that adult Atlantic salmon are susceptible to angling capture at high water temperatures (Locker et al. 1993, Gale et al. 2013). Survival rate of salmon angled at various water temperatures show a sharp decrease in survival at water temperatures ≥20°C. A fish caught on a fishing line will fight (if it has energy left) in an attempt to escape. It requires lots of energy that the fish needs to survive the warm water conditions. The metabolic energy invested in the exhaustive exercise could have been used to cope with warm water.

Based on knowledge of fish physiology, T_{min} is recommended as the threshold temperature for management intervention during warm water events. In such days, changes in behaviour are observed and the aerobic scope for activity decreased with the ambient temperatures experienced by the fish. On days with $T_{min} \geq 20°C$, physiological recovery are likely reduced and fish presumably have to cope with cumulative temperature stress if high temperatures persist. Once T_{min} decreases below 20°C, the day and night conditions will improve and fish will be less at risk of thermally-induced mortality.

REFERENCES

Alabaster, J. S., and Lloyd, R. 1982. *Water Quality Criteria, for Freshwarer Fish,* 2nd ed. London: Butterworths for FAO.

Alabaster, J.S., Gough, P.J. and Brooker, W.J. 1991. The environmental requirements of Atlantic salmon, *Salmo salar* L., during their passage through the Thames estuary, 1982-1989. J. Fish Biol. 38: 741-762.

Beamish R.J., Neville, C.E.M., and Cass, A.J. 1997. Production of Fraser River sockeye salmon (*Oncorhynchus nerka*) in relation to decadal-scale changes in the climate and the ocean. Can. J. Fish. Aquat. Sci. 54: 543–554.

Breau, C. 2011. The ecophysiology, behaviour and movement patterns of juvenile Atlantic salmon (*Salmo salar*) during elevated water temperatures and the importance of cool water sites. (Doctoral dissertation). Retrieved from ProQuest Dissertations and Theses.

Breau, C., and Caissie, D. 2013. Adaptive management strategies to protect salmon (*Salmo salar*) under environmentally stressful conditions. DFO Can. Sci. Adv. Secr. Res. Doc. 2012/164. iv+14 p.

Breau, C., Cunjak, R.A., and Bremset, G.G. 2007. Age-specific aggregation of wild juvenile Atlantic salmon (*Salmo salar*) at cool water sources during high temperature events. J. Fish Biol. 71: 1-13.

Breau, C., Cunjak, R.A., and Peake, S.J. 2011. Behaviour during elevated water temperatures: can physiology explain movement of juvenile Atlantic salmon to cool water? J. Anim. Ecol. 80: 844-853.

Breau, C., Chaput, G., LeBlanc, P.H., and Mallet, P. 2009. Information on Atlantic salmon (*Salmo salar*) from Salmon Fishing Area 18 (Gulf Nova Scotia) of relevance to the development of the COSEWIC status report. DFO Can. Sci. Adv. Secr. Res. Doc. 2009/076. iv + 53p.

Brooker, M.P., Morris, D.L. and Hemsworth, R.J. 1977. Mass mortalities of adult salmon, *Salmo salar*, in the R. Wye, 1976. J. Appl. Ecol. 14: 409-417.

Booth, R.K., Kieffer, J.D., Davidson, K., Bielak, A.T., and Tufts, B.L. 1995. Effects of late-season catch and release angling on anaerobic metabolism, acid-base status, survival, and gamete viability in wild Atlantic salmon (*Salmo salar*). Can. J. Fish. Aquat. Sci. 52: 283-290.

Boyd, J.W., Guy, C.S., Horton, T.B., and Leathe, S.A. 2010. Effects of catch-and-release angling on salmonids at elevated water temperatures. N. Amer. J. Fish. Manag. 30: 898-907.

Brett, J.R. 1944. Some lethal temperature relations of Algonquin Park Fishes. Univ. Toronto Stud. Biol. Ser. 52; 63: 1-49.

Brett, J.R. 1952. Temperature tolerance in young Pacific salmon genus *Oncorhynchus.* J. Fish. Res. Board Can. 9: 265-323.

Brett, J.R. 1956. Some principles in the thermal requirements of fishes. The Quarterly Review of Biology 31: 75-87.

Brett, J.R. 1971. Energetic responses of salmon to temperature: a study of some thermal relations in the physiology and freshwater ecology of sockeye salmon (*Oncorhynchus nerka*). Amer. Zool. 11: 99-113.

Bumgarner, J., Mendel, G., Milks, D., Ross, L., Varney, M., and Dedloff, J. 1997. Tucannon River spring chinook hatchery evaluation. 1996 Annual report. Washington Department of Fish and Wildlife Hatcheries Program Assessment and Development Division. Report #H97-07. Produced for US Fish and Wildlife Service, Cooperative Agreement 14-48-0001-96539.

Caissie, D., Breau, C., Hayward, J., and Cameron, P. 2013. Water temperature characteristics within the Miramichi and Restigouche rivers. DFO Can. Sci. Advis. Sec. Res. Doc. 2012/165. vii + 31 p.

Cameron, P., Chaput, G., and Mallet, P. 2009. Information on Atlantic salmon (*Salmo salar*) from Salmon Fishing Area 15 (Gulf New Brunswick) of relevance to the development of the COSEWIC status report. DFO Can. Sci. Adv. Secr. Res. Doc. 2009/078. iv + 40 p.

Chaput, G., Moore, D., Hardie, P., and P. Mallet. 2010. Information on Atlantic salmon (*Salmo salar*) from Salmon Fishing Area 16 (Gulf New Brunswick) of relevance to the development of a COSEWIC status report. DFO Can. Sci. Advis. Sec. Res. Doc.2010/064. iv + 50 p.

Crossin, G.T., Hinch, S.G., Cooke, S.J., Welch, D.W., Patterson, D.A., Jones, S.R.M., Lotto, A.G., Leggatt, R.A., Mathes, M.T., Shrimpton, J.M., Van Der Kraak, G., and Farrell, A.P. 2008. Exposure to high temperature influences the behaviour, physiology, and survival of sockeye salmon during spawning migration. Can. J. Zool. 86: 127-140.

Dempson, J.B., Furey, G., and Bloom, M. 2002. Effects of catch and release angling on Atlantic salmon, *Salmo salar* L., of the Conne River, Newfoundland. Fish. Manag. Ecol. 9: 139-147.

Douglas, S.G., Chaput, G., Hayward, J., and Sheasgreen J. 2013. Assessment of Atlantic salmon (*Salmo salar*) in Salmon Fishing Area 16 of the southern Gulf of St. Lawrence. DFO Can. Sci. Advis. Sec. Res. Doc. 2012/104. vi + 64 p.

Dubee, R.L., MacEachern, R., and Legere, J. 2011. Salmon catch and effort on regular crown reserve waters of the Miramichi River system New Brunswick 2011. N.B. Department of Natural Resources Miramichi, New Brunswick. 9 p.

Elliott, J.M. 1991. Tolerance and resistance to thermal stress in juvenile Atlantic salmon, *Salmo salar*. Freshwater Biol. 25: 61-70.

Elliott, J.M. 1994. Quantitative Ecology and the Brown Trout. Oxford: Oxford University Press.

Elliott, J.M., and Elliott, J.A. 2010. Temperature requirements of Atlantic salmon Salmo salar, brown trout *Salmo trutta*, and artic charr *Salvelinus alpinus*: predicting the effects of climate change. J. Fish Biol. 77: 1793-1817.

Elson, P.F. 1969. High temperature and river ascent by Atlantic salmon. ICES Andromous and Catadromous Fish Commission. 12 p.

Enders, E.C., and Scruton, D.A. 2005. Compilation of existing literature data on the standard and routine metabolic rate of Atlantic salmon *(Salmo salar*). Can. Data Rep. Fish. Aquat. Sci. 1176: v + 43 p.

Farrell, A.P., 1997. Effects of temperature on cardiovascular performance. pp. 135–158. In: Wood, C.M., McDonald, D.G. (Eds.). Global Warming Implications for Freshwater and Marine Fish. Cambridge University Press, Cambridge.

Farrell, A.P. 2002. Cardiorespiratory performance in salmonids during exercise at high temperature: insights into cardiovascular design limitations in fishes. Comp. Biochemistry and Physiology A. 132: 797-810.

Farrell, A.P., Johansen, J.A., and Suarez, R.K. 1991. Effects of exercise-training on cardiac performance and muscles enzymes in rainbow trout, *Oncorhynchus mykiss*. Fish Physiology and Biochemistry 9: 303-312.

Farrell, A.P., Hinch, S.G., Cooke, S.J., Patterson, D.A., Crossin, G.T., Lapointe, M., and Mathes, M.T. 2008. Pacific salmon in hot water: Applying aerobic scope models and biotelemetry to predict the success of spawning migrations. Physiological and Biochemical Zoology 81: 697-709.

Fowler, S.L., Hamilton, D., and Currie, S. 2009. A comparison of the heat shock response in juvenile and adult rainbow trout (*Oncorhynchus mykiss*) – implications for increased thermal sensitivity with age. Can. J. Fish. Aquat. Sci. 66: 91-100.

Fry, F.E.J. 1947. Effects of the environment on animal activities. Univ. Toronto Studies Biological Series 55:1-62.

Fry, F.E.J. 1971. The effect of environmental factors on the physiology of fish. Pp. 1–98. In W.S. Hoar and D.J. Randall (eds.). Fish Physiology. Academic Press, New York.

Gale, M.K., Hinch, S.G., Eliason, E.J., Cooke, S.J., and Patterson, D.A. 2011. Physiological impairment of adult sockeye salmon in fresh water after simulated capture-and-release across a range of temperatures. Fish. Res. 112: 85-95.

Gale, M.K., Hinch, S.G., and Donaldson, M.R. 2013. The role of temperature in the capture and release of fish. Fish and Fisheries 14: 1-33.

Gamperl, A.K., Rodnick, K.J., Faust, H.A., Venn, E.C., Bennett, M.T., Crawshaw, L.I., Keeley, E.R., Powell, M.S., and Li, H.W. 2002. Metabolism, swimming performance, and tissue biochemistry of high desert Redband Trout (*Oncorhynchus mykiss* ssp.): evidence for phenotypic differences in physiological function. Physiological and Biochemical Zoology 75: 413–431.

Gingerich, A.J., Cooke, S.J., Hanson, K.C., Donaldson, M.R., Hasler, C.T., Suski, C.D. and Arlinghaus, R. 2007. Evaluation of the interactive effects of air exposure duration and water temperature on the condition and survival of angled and released. Fish. Res. 86: 169-178.

Hawkins, A.D. 1989. Factors affecting the timing of entry and upstream movement of Atlantic salmon in the Aberdeenshire Dee. pp. 100–105. In *Salmon and Trout Migratory Behaviour and Dispersal Symposium* (Brannon, E. and Jonsson, B., eds), Seattle, WA: School of Fisheries, University of Washington.

Huntsman, A.G. 1942. Death of salmon and trout with high temperature. J. Fish. Res. Board Can. 5: 485-501.

Huntsman, A.G. 1946. Heat stoke in Canadian Maritime stream fishes. J. Fish. Res. Board Can. 6: 476-482.

ICES. 2009. Report of the Working Group on North Atlantic Salmon (WGNAS), 30 March – 8 April 2009 Copenhagen, Denmark. ICES CM 2009/ACOM: 06.291p.

Johnstone, H.C., and Rahel, F.J. 2003. Assessing temperature tolerance of Bonneville Cutthroat Trout based on constant and cycling thermal regimes. Trans. Amer. Fish. Soc. 132: 92-99.

Jonsson, B., and Jonsson, N. 2009. A review of the likely effects of climate change on anadromous Atlantic salmon *Salmo salar* and brown trout *Salmo trutta*, with particular reference to water temperature and flow. J. Fish Biol. 75: 2381-2447.

Kieffer, J.D., Currie, S., and Tufts, B.L. 1994. Effects of environmental temperature on the metabolic and acid-base responses of rainbow trout to exhaustive exercise. J. Exp. Biol. 194: 299-317.

Kieffer, J.D., Alsop, D., and Wood, C.M. 1998. A respirometric analysis of fuel use during aerobic swimming at different temperatures in rainbow trout (*Oncorhynchus mykiss*). J. Exp. Biol. 201: 3123-3133.

Lee, C.G., Farrell, A.P., Lotto, A., MacNutt, M.J., Hinch, S.G., and Healey, M.C. 2003. The effect of temperature on swimming performance and oxygen consumption in adult sockeye (*Oncorhynchus nerka*) and coho (*O. kisutch*) salmon stocks. J. Exp. Biol. 206: 3239-3251.

Magnuson, J.J., Crowder, L.B., and Medvick, P.A. 1979. Temperature as an ecological resource. Amer. Zool. 19: 331-343.

McCauley, R., and Huggins, N. 1975. Behavioral thermal regulation by rainbow trout in a temperature gradient. Thermal Ecology II, Proceedings of a Symposium held at Augusta, Georgia, April 2-5, 1975. pp. 171-175.

Milligan, C.L. 1996. Metabolic recovery from exhaustive exercise in rainbow trout. Comp. Biochem. Physiol. 113A: 51-60.

Milligan, C.L., and Wood, C.M. 1986. Tissue intracellular acid-base status and the fate of lactate after exhaustive exercise in the rainbow trout. J. Exp. Biol. 123: 123-144.

Moore, A., Bendall, B., and Barry, J. 2011. River temperature and adult anadromous Atlantic salmon, *Salmo salar*, and brown trout, *Salmo trutta*. Fish. Manag. Ecol. 19: 518-526.

Mowbray, F., and Locke, A. 1999. The effect of water temperature on angling catch of Atlantic salmon in the Upsalquitch River. DFO Can. Stock Assess. Sec. Res. Doc. 99/56. 17p.

Murray, R.W. 1971. Temperature receptors. p. 121-133. In Fish Physiology, Vol. V (W. S. Hoar, and D. J. Randall, eds), London and New York: Academic Press.

Pörtner, H.O. 2002. Climatic variations and the physiological basis of temperature dependent biogeography: systemic to molecular hierarchy of thermal tolerance in animals. Comparative Biochemistry and Physiology Part A 132: 739-761.

Pörtner, H.O., and Knust, R. 2007. Climate change affects marine fishes through the oxygen limitation of thermal tolerance. Science 315: 95-97.

Pörtner, H.O., and Farrell, A.P. 2008. Physiology and climate change. Science 322: 690-692.

Pörtner, H.O., Branco, L.G.S., Malvin, G.M., and Wood, S.C. 1994. A new function for lactate in the toad *Bufo marinus*. J. Appl. Physiol. 76: 2405-2410.

Richard, A., Dionne, M., Wang, J., and Bernatchez, L. 2012. Does catch and release affect the mating system and individual reproductive success of wild Atlantic salmon (*Salmo salar* L.). Mol. Ecol. 22: 187-200.

Schmidt-Nielsen, K. 1990. Animal Physiology: Adaptation and environment, 5th ed. pp.217-238. Cambridge University Press. New York.

Steinhausen, M.F., Sandblom, E., Eliason, E.J., Verhille, C., and Farrell, A.P. 2008. The effect of acute temperature increases on the cardiorespiratory performance of resting and swimming sockeye salmon (*Oncorhynchus nerka*). J. Exp. Biol. 211: 3915-3926.

Taylor, E.W., Egginton, S., Taylor, S.E., and Butler, P.J. 1997. Factors which may limit swimming performance at different temperatures. pp. 105–133. In: Wood, C.M., McDonald, D.G. (Eds.), Global Warming Implications for Freshwater and Marine Fish. Cambridge University Press, Cambridge.

Thorstad, E.B., Naesje, T.F., Fiske, P., and Finstad, B. 2003. Effects of hook and release on Atlantic salmon in the River Alta, northern Norway. Fish. Res. 60: 293-307.

Trudel, M., Geist, D.R., and Welch, D.W. 2004. Modeling the oxygen consumption rates in Pacific salmon and steelhead: an assessment of current models and practices. Trans. Amer. Fish. Soc. 133: 326-348.

Walsh, P.J., and Milligan, C.L. 1989. Coordination of metabolism and intracellular acid-base status: ionic regulation and metabolic consequences. Can. J. Zool. 67: 2994-3004.

Whoriskey, F.G., Pruso, S., and Crabbe, S. 2000. Evaluation of the effects of catch-and-release angling on the Atlantic salmon (*Salmo salar*) of the Ponoi River, Kola Peninsula, Russian Federation. Ecol. Freshw. Fish 9: 118-125.

Wilkie, M.P., Davidson, K., Brobbel, M.A., Kieffer, J.D., Booth, R.K., Bielak, A.T., and Tufts, B.L. 1996. Physiology and survival of wild Atlantic salmon following angling in warm summer waters. Trans. Amer. Fish. Soc. 125: 572-580.

Wilkie, M., Brobbel, M., Davidson, K., Forsyth, L., and Tufts, B.L. 1997. Influences of temperature upon the postexercise physiology of Atlantic salmon (*Salmo salar*). Can. J. Fish. Aquat.Sci. 54: 503-511.

Wood, C.M., Turner, J.D., and Graham, M.S. 1983. Why do fish die after severe exercise? J. Fish Biol. 22: 189-201.

Wood, S.C. 1991. Interactions between hypoxia and hypothermia. Annual Reviews in Physiology 53: 71-853.

Wootton, R.J. 1990. Ecology of teleost fishes. Chapman & Hall, London.

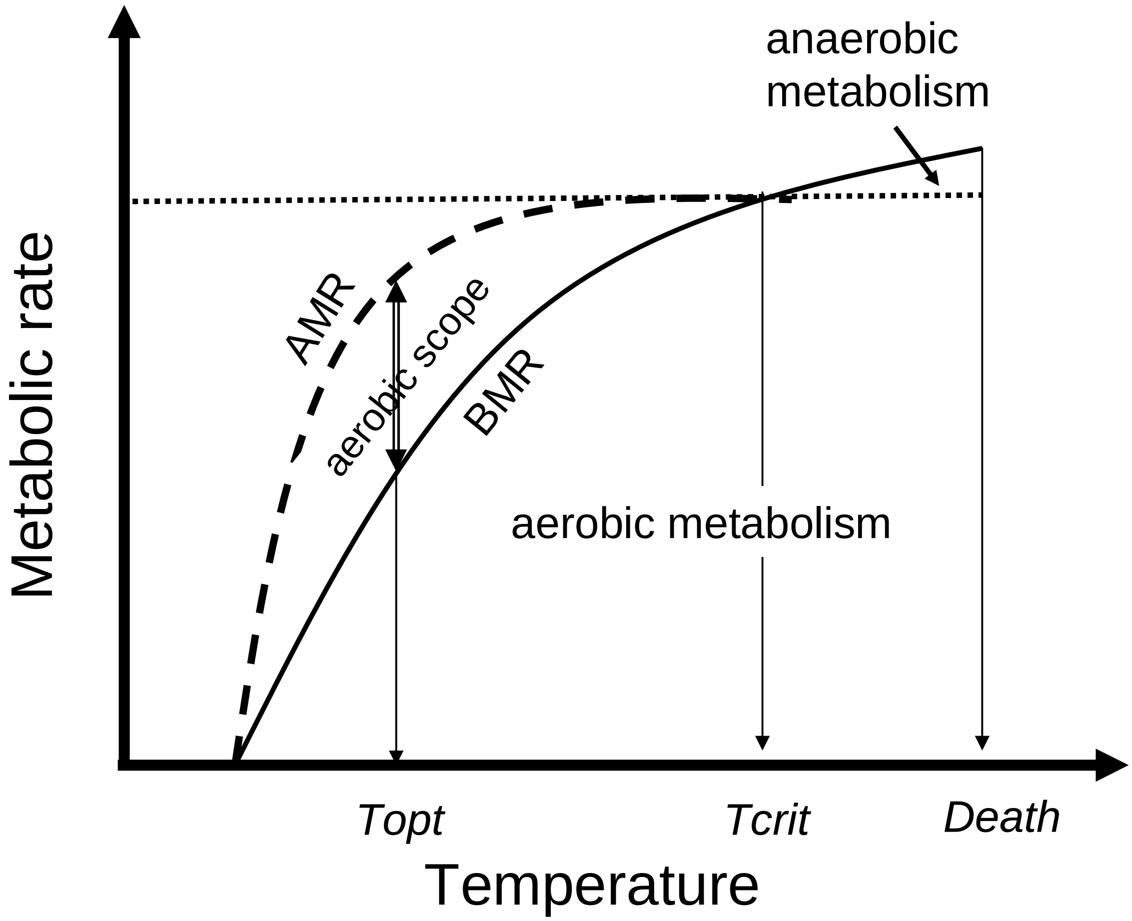

Figure 1. Basal metabolic rate (BMR) and active metabolic rate (AMR) of aquatic ectotherms in relation to water temperature. The difference between AMR and BMR represents the aerobic scope. The aerobic scope is maximized at optimal temperature (Topt) and nil at critical temperature (Tcrit). Both aerobic and anaerobic metabolism supply energetic demands at temperature exceeding Tcrit.

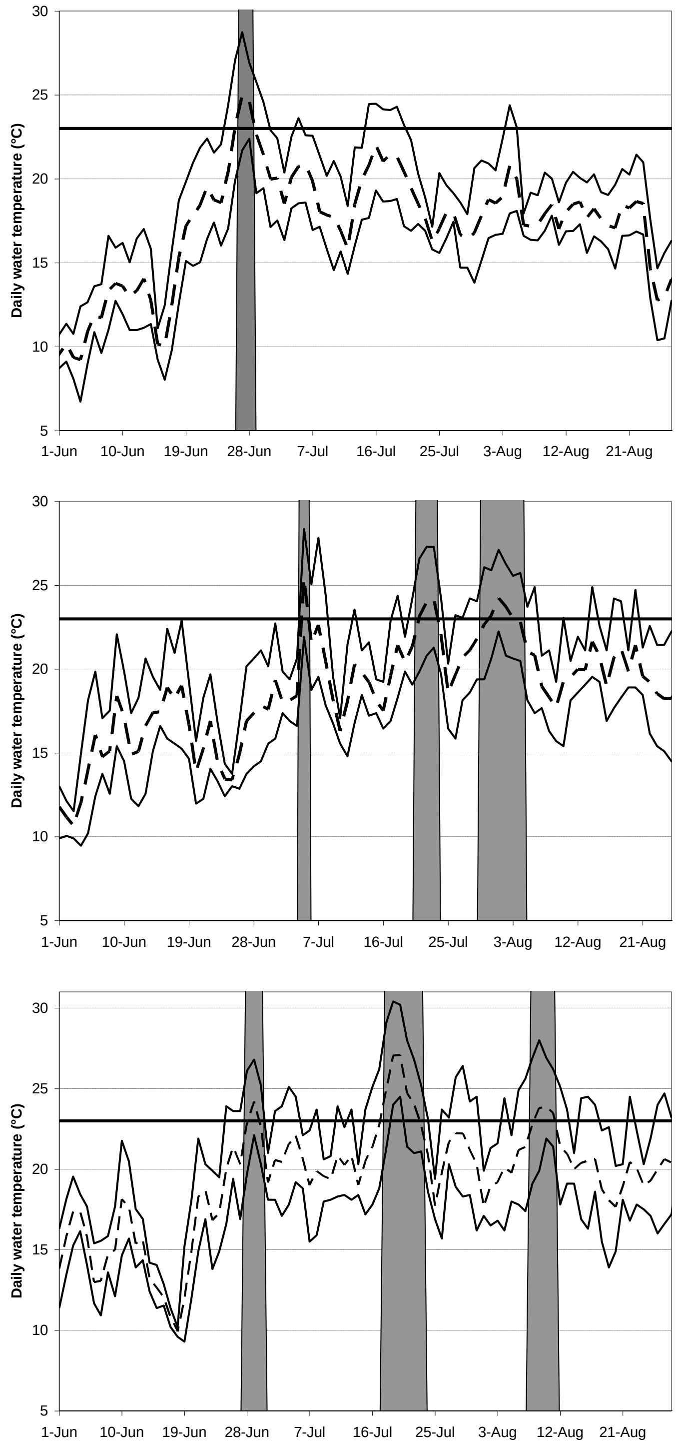

Figure 2. Dates (grey shading) when movements of marked 1+ and 2+ Atlantic salmon to cool water sites were noted in relation to the daily mean (dashed line) and the minimum and maximum (solid lines) water temperatures recorded in the Little Southwest Miramichi River during the summers of 2003 (upper panel), 2004 (middle panel), and 2005 (lower panel). The solid line represents 23°C. The 0+ salmon did not move to cool water (From Breau 2011).

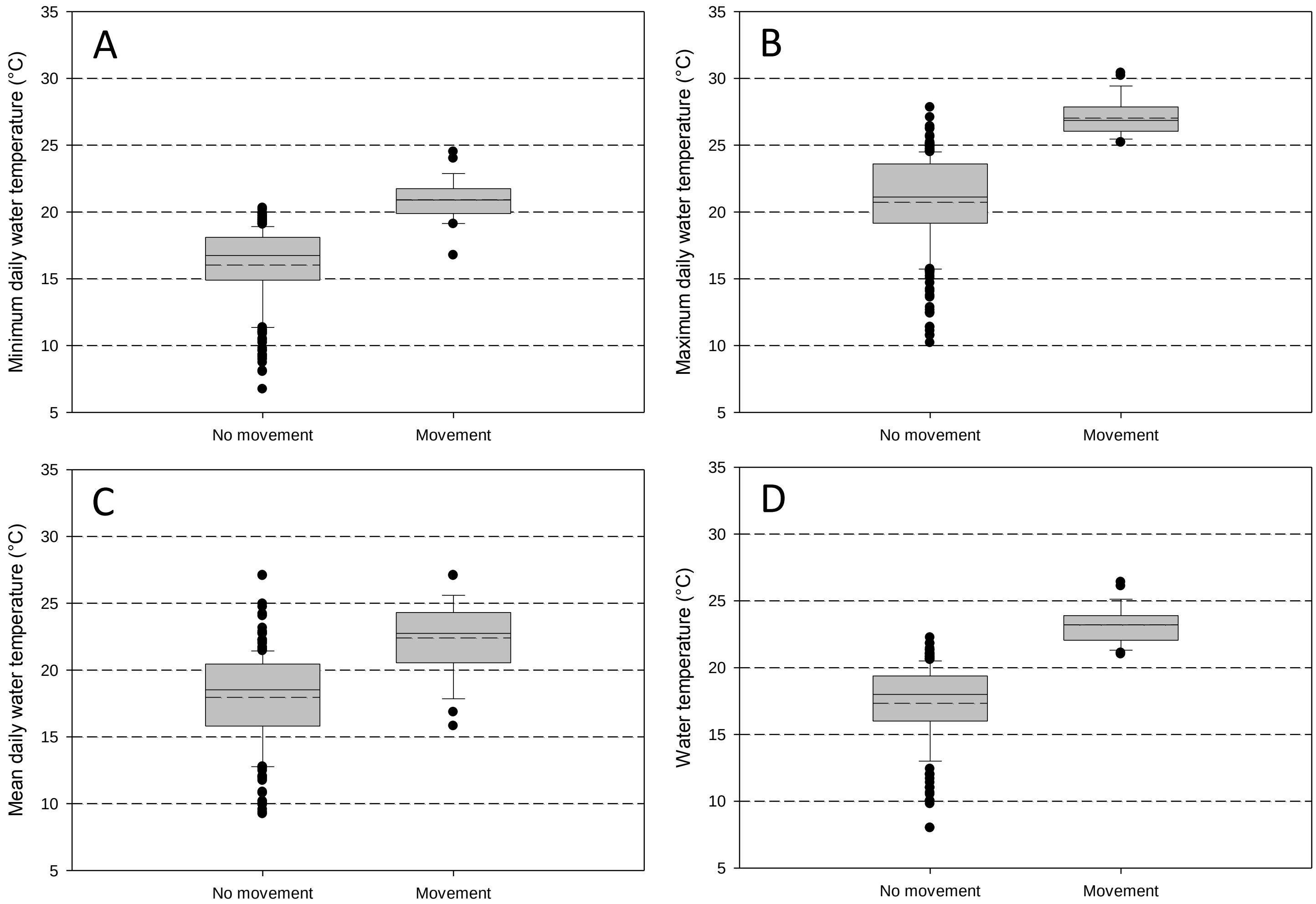

Figure 3. The a) minimum b) maximum, c) mean daily water temperature and d) the water temperature one hour prior to the movement of marked fish to cool water sites in the Little Southwest Miramichi River, NB during the summers of 2003 to 2005. The box plots are interpreted as follows: median (solid line), mean (dashed line), 90% range (vertical line), range (25% and 75% quartiles) and outliers (circles) (From Breau, 2011).

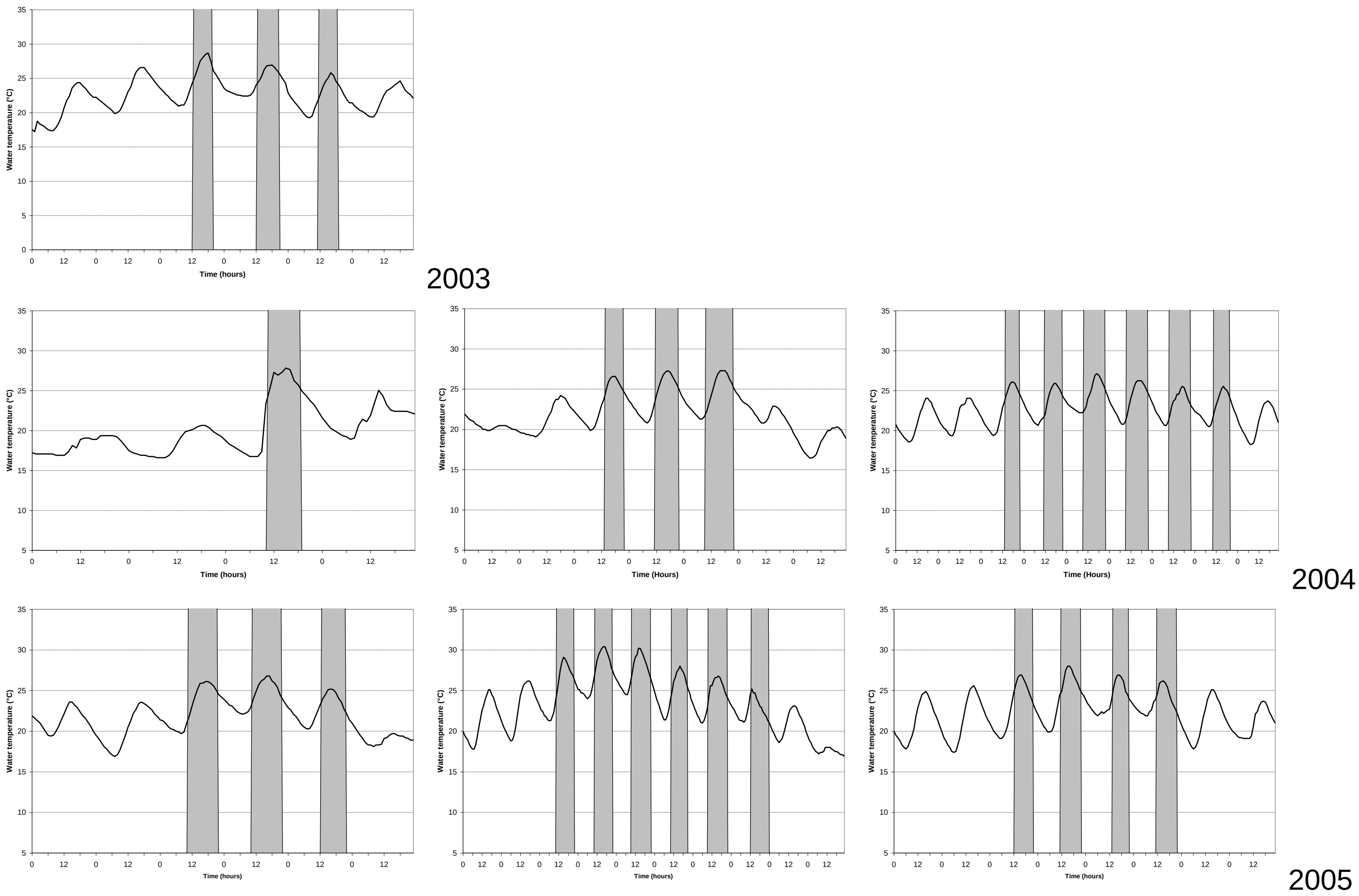

Figure 4. The hourly water temperature when marked juvenile Atlantic salmon moved to cool water sites in relation to elevated water temperatures of summers 2003 to 2005 in the Little Southwest Miramichi River, NB. Hourly water temperatures are shown for two days prior to an event and one day after an event. The shaded area represent the time of day when fish aggregation was observed in cool water sites.

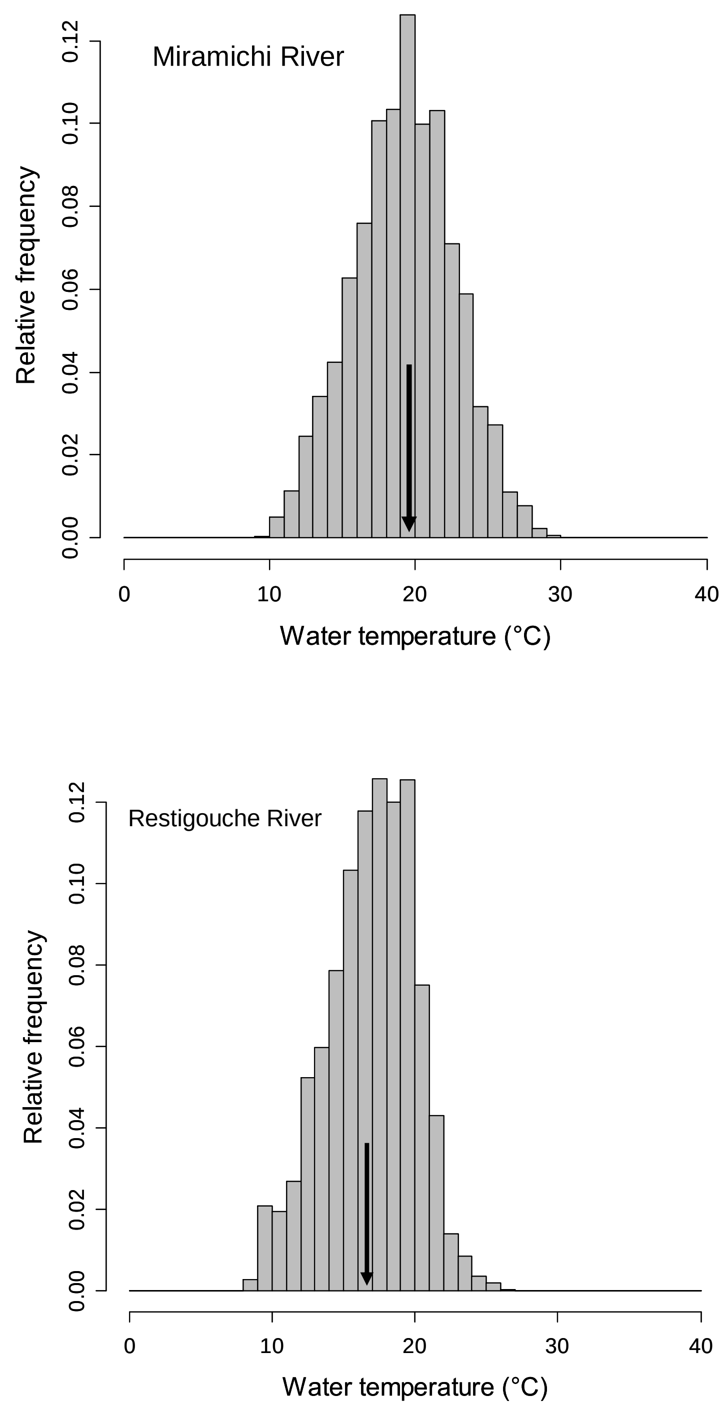

Figure 5. Frequency distributions of daily mean water temperatures in the Miramichi River (two sites: Nelson Hollow and Moose Landing) (upper panel) and the Restigouche River (two sites: Butter Island and Moose Landing) (lower panel) during the migration period of early-run Atlantic salmon (June 1 to July 31) for 2005 to 2010. Arrows indicate median temperatures of the time series.

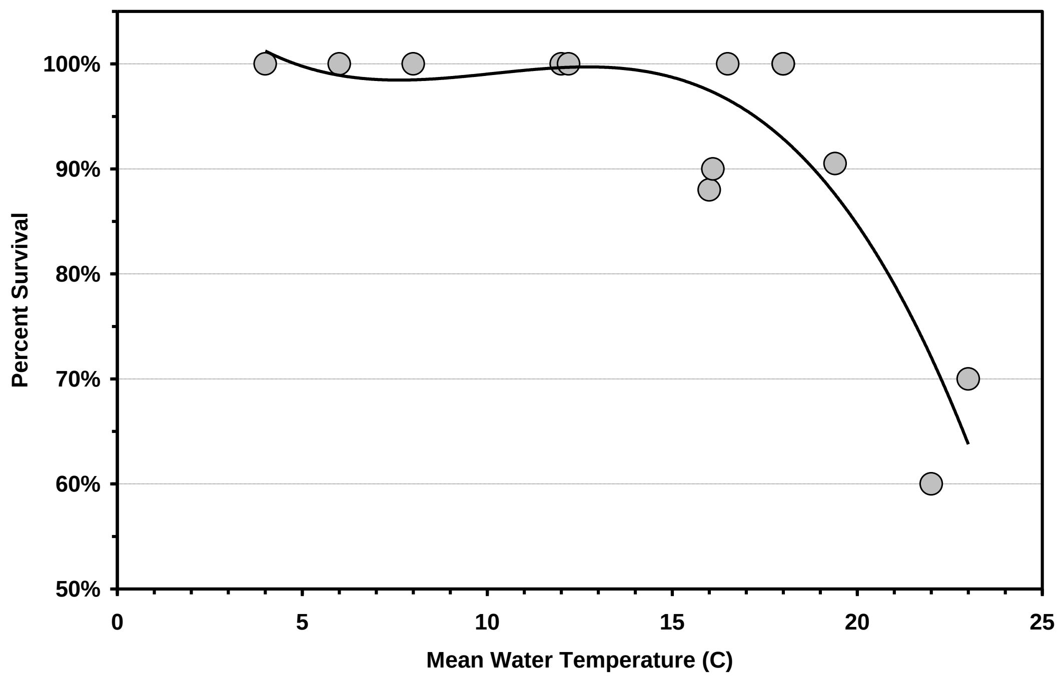

Figure 6. Survival of angled and released Atlantic salmon in relation to water temperature, based on studies summarized by Dempson et al. (2002). The fitted line is a third degree polynomial.

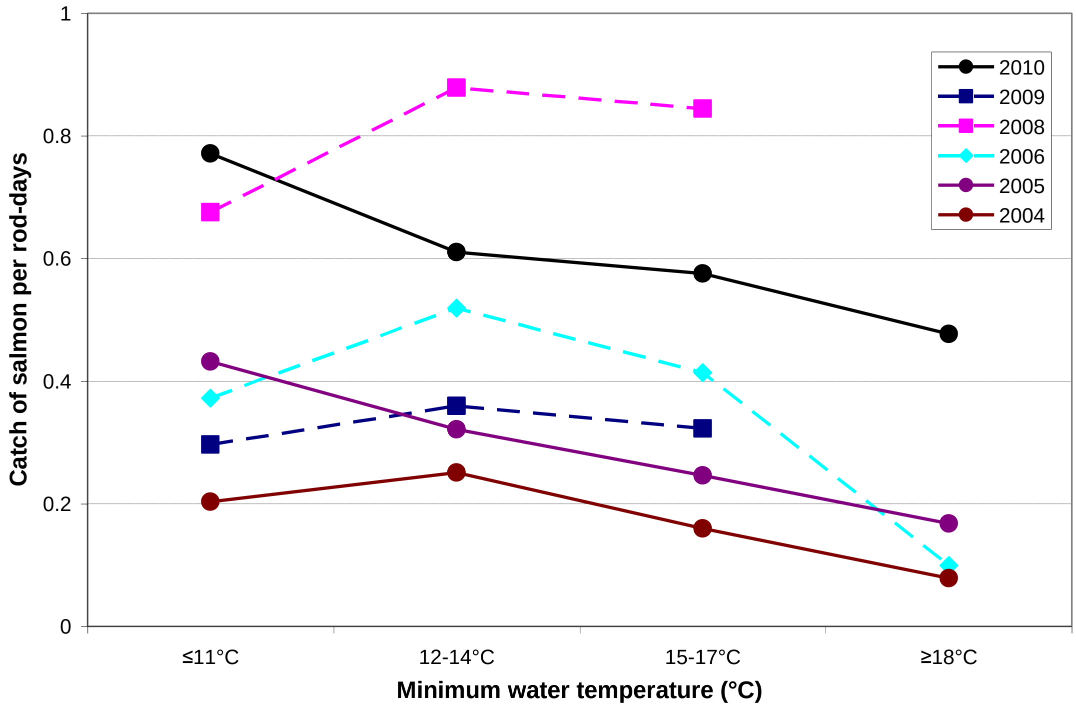

Figure 7. Catch of Atlantic salmon per rod-day in five Crown Reserve fishing stretches (Crawford, Depot, Sullivan, Stony Brook and Elbow) on the Northwest Miramichi River in relation to minimum water temperature categories as recorded at an upstream site (Bridge Pool) for 2004 to 2010.

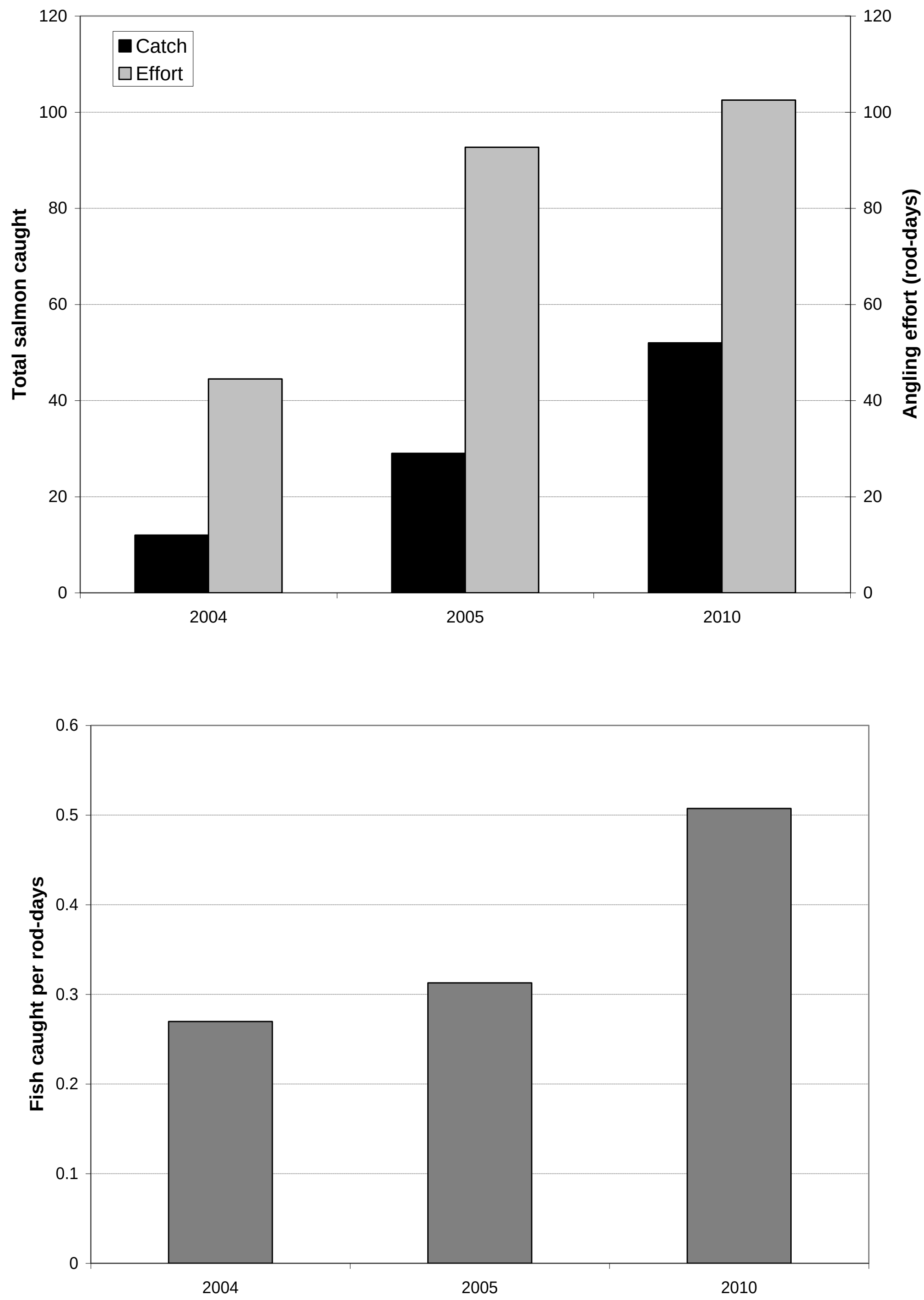

Figure 8. Angling catch and effort and the catch per unit effort of Atlantic salmon in Crown Reserve stretches during days when T_{min} at Bridge pool remained above 18°C (2004: 3 days, 2005: 5 days and 2010: 9 days). Note: Bridge Pool is the site with the coolest water temperature in the Miramichi watershed; other sites will be warmer.

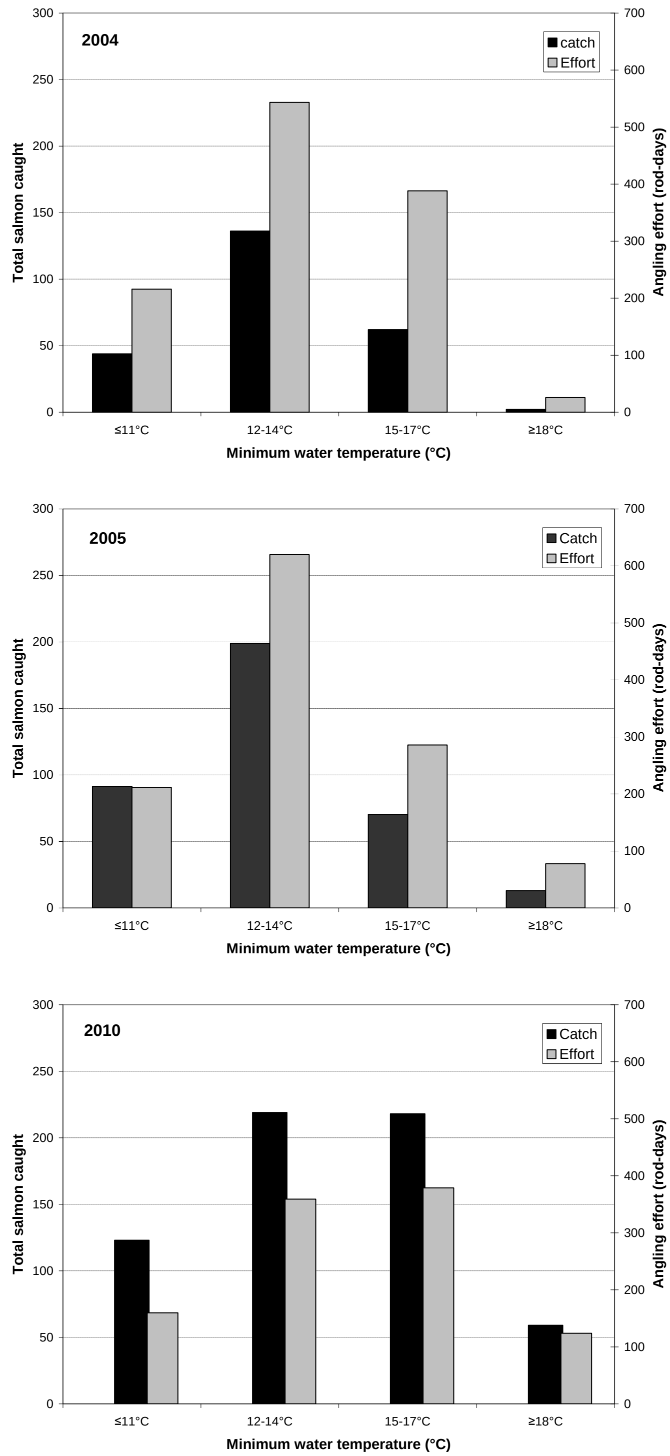

Figure 9. Angling catches of adult Atlantic salmon (1SW and MSW) and effort in the Crown Reserve stretches (Adams, Charlie's Rock, Groundhog Landing and Squirrels Falls) of the Northwest Miramichi River during three years with high temperatures. Water temperatures were recorded at Bridge Pool, a site upstream of the angling stretches.