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Using meta-analysis to derive a respiration model for Atlantic Salmon (*Salmo salar*) to assess bioenergetics requirements of juveniles in two Canadian rivers

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Lay summary

Standard metabolic rates (SMR) for Atlantic Salmon have been estimated for specific life stages and/or temperatures, but the absence of a comprehensive metabolic rate model for the species limits its transferability to different fish masses and river temperature conditions. In the face of increasing river temperatures resulting from climate change, we propose a comprehensive respiration model derived from SMR meta-data that may serve to predict the metabolic rates and energetic requirements for juvenile Atlantic Salmon inhabiting rivers of varying water temperatures. Results may inform conservation efforts for the species throughout its current range and predict the energetic requirements for juvenile life stages.

Keywords: respiration, water temperature, Atlantic Salmon, standard metabolic rate, conservation physiology, meta-analysis, Miramichi, bioenergetics
Abstract

Standard metabolic rates (SMR) for Atlantic Salmon have been calculated independently for different life stages and populations, but the absence of a comprehensive SMR model limits its application for modelling the energy use or life stage-specific growth. Atlantic Salmon respiration data were compiled from a meta-analysis of 26 publications and exponential or optimal relationships were fitted to the meta-data to estimate respiration equation parameters and generate confidence intervals dependent on temperature and body mass. While model parameters were significant for both models, mass corrected standard metabolic rates (g O₂·d⁻¹) increased as a function of water temperature (°C) and decreased beyond ~16 °C, following an optimal relationship (AIC_{optimal} = -9185.5 vs. AIC_{exponential} = -8948.95; ΔAIC = 236.55). Juvenile Atlantic Salmon growth (cohorts 1 and 2) from bioenergetics simulations did not vary between Little Southwest Miramichi and Northwest Miramichi rivers, however, variation between simulations using the different respiration models (i.e., exponential vs. optimal) led to differences in the way fish allocate energy throughout the year. Results from this analysis will inform conservation efforts for the species throughout its current range and predict the energetic requirements at juvenile life stages.

Introduction

A bioenergetics model is an energy balance equation in which the energy consumed by a fish is balanced by metabolism, waste losses, and growth (Kitchell et al. 1974; Deslauriers et al. 2017). Using species-specific estimates of consumption or growth, respiration, egestion, and excretion, the energy equation obtained for given environmental conditions may provide an alternative approach to the traditional methods of modelling abiotic habitat suitability (i.e., field
and laboratory studies; Trudel et al. 2004; Enders and Scruton 2006). Consequently, a measure of habitat quality may be derived from the energy gained or growth by individuals occupying specific habitats (Fausch 1984; Boisclair and Rasmussen 1996).

The metabolic rate of fishes is commonly measured in terms of oxygen consumption using intermittent-flow respirometry. The standard metabolic rate (SMR) is the minimal maintenance or resting metabolic rate (respiration) of unfed animals, below which physiological function is impaired (Beamish 1964; Cutts et al. 2002; Chabot et al. 2016). SMR is known to represent the greatest component of the energy budget of fishes (Niklitschek and Secor 2009), varies widely between species (Trudel et al. 2004), and is strongly affected by several biotic and abiotic factors, primarily body mass and water temperature (Kitchell et al. 1974; Millidine et al. 2009; Niklitschek and Secor 2009; Pörtner 2010). For instance, temperature is known to affect the physiology and behaviour of fishes, in addition to acting as a characteristic of fish habitats by driving species-specific niche occupancy (Magnuson et al. 1979). The role of temperature driving the growth and metabolic rates of salmonid fishes has been widely studied (Breau et al. 2011; Imholt et al. 2011; Beauregard et al. 2013; Oigny-Hebert et al. 2015), which is why species-specific SMR models include mass and temperature-dependent functions. Several temperature-dependent SMR models accounting for the allometric relationship between metabolic rate and body mass have been suggested, however, differences in the temperature function in model equations have resulted in SMR-temperature curves following exponential ($e^{cT}$) (Brett and Glass 1973; Pörtner 2010; Chabot et al. 2016), logistic/sigmoid (Beamish 1964; Thornton and Lessem 1978; Claireaux and Lagardère 1999; Paakkonen et al. 2003; Niklitschek and Secor 2009) or optimal relationships (Kitchell et al. 1974; Deslauriers et al. 2017). Since SMR is defined for temperatures where physiological function is unimpaired, SMR-temperature
relationships often focus on temperatures that reach but do not exceed optimal temperatures for respiration (RTO) for which fish are considered healthy.

Atlantic Salmon (Salmo salar) is a significant species for commercial, recreational, and Aboriginal fisheries in Canada, thus, the protection and management of rearing, spawning, and migration Atlantic Salmon habitat is thought to be one of the key factors for conservation (Armstrong et al. 2003). SMR for Atlantic Salmon have been estimated independently for different life stages and populations, but the absence of a comprehensive SMR model for the species, combining data from a wide range of body masses and environmental conditions, limits its application in management. Extrapolating SMR models to different size-classes, habitats or from closely related species has become common-place. This practice has, however, been shown to inappropriately depict true metabolic requirements (Trudel et al. 2004; Enders and Scruton 2006). Moreover, the assumptions underlying the different approaches for modelling SMR and skew for modelled- vs. empirically-derived data may further complicate and limit the scope of such extrapolations (Enders and Scruton 2006).

Water temperature is among the most important environmental variables determining the distribution, emergence time, and growth of salmonids in freshwater habitats (Elliott and Elliott 2010). As air temperatures are expected to increase by 2 – 6 °C within the next 100 years in the Maritime Provinces of eastern Canada, increases in corresponding water temperatures will have an impact on river habitats (Swansburg et al. 2002; Caissie 2013; Brodeur et al. 2015). Consequently, we expect that temperature-dependent SMR will also increase and ultimately reduce fish growth and/or increase mortality. The preferred temperature for Atlantic Salmon is between 14 – 18 °C and lethal temperature occurs from 28 – 33 °C (Elliott 1991; Elliott and Elliott 2010; Breau et al 2011), which means that a SMR optimum (i.e., optimal temperature for
physiological functioning) should occur around preferred temperatures (Fry 1947). We may also expect to see growth differences for select life stages, as specific energetic requirements associated with juvenile growth and/or smoltification may be affected by water temperatures. Atlantic Salmon in the Little Southwest Miramichi River (LSWM) are known to emerge from gravel during the first weeks of June and remain in their nursery stream between two to five years, eating drifting invertebrates, namely chironomid larvae (Keeley and Grant 1997; Breau et al. 2007b; Chaput et al. 2016). Smoltification generally occurs around mid-May to mid-June (Chaput et al. 2016), but variations in the timing of these events largely depend on the water temperatures in a given year (Randall and Paim 1982; Johnston 1997). A shift in spring and summer water temperatures resulting from climate change (i.e., rising water temperatures) in the Maritime provinces may alter the timing of Atlantic Salmon emergence and shorten the effective growing season (Randall and Paim 1982). Alternatively, an earlier spring freshet due to increasing air temperatures may contribute to early emergence of alevins and extend the length of the growth period in the first year (Elliott and Elliott 2010). As important life-history decisions are based on water temperature, differences in temperatures among rivers will likely affect juvenile Atlantic Salmon growth and consumption rates, with possible ramifications for subsequent life stages (e.g., smoltification).

This paper proposes a comprehensive SMR model (hereafter referred to as ‘Atlantic Salmon respiration model’) that may serve to predict SMR and energetic requirements for juvenile life stages of Atlantic Salmon in rivers of varying water temperatures. Our specific objectives were threefold: 1) contrast mass- and temperature-dependent Atlantic Salmon respiration models based on exponential and optimal temperature functions, measured from oxygen consumption rates or SMR collected on individuals across a large range of body masses,
life stages, and at varying water temperatures using a meta-analysis approach; 2) compare the
Atlantic Salmon respiration models with four published respiration models; and 3) simulate how
different water temperatures in two Canadian rivers may influence Atlantic Salmon growth and
inform the energetic requirements for two cohorts (0 – 1+ and 1+ – 2+) in these systems,
according to both respiration models. Results from this study may better inform management and
species recovery strategies by understanding how temperature-dependent respiration varies for
key life stages and populations of Atlantic salmon.

Material and methods

Data retrieval

A literature review was conducted to collect standard metabolic rate data for Atlantic
Salmon using the online publication search engine, Web of Science, and keywords search:
Atlantic Salmon, Bioenergetics, Metabolism, Oxygen Consumption, Respiration, Metabolic
Rate, Exercise, Swimming, and Activity. To be included in the meta-analysis, the publication
had to meet the following criteria: 1) publication in a peer-reviewed scientific journal or a special
publication that underwent a peer-reviewed vetting process; 2) methodology focused on
quantifying the standard metabolic rate of Atlantic Salmon, rather than routine or active
metabolic rates; and 3) comprehensive reporting of means or individual standard metabolic rate
in a results table or figure along with appropriate variables such as, fish mass and water
temperature tested (Table 1). While some studies performed respirometry trials under saline
environments (4 – 35 ppt), none of these studies looked at the effects of salinity on respiration
rates (i.e., salinity was not used as a treatment). Therefore, salinity was left out of models, with
the assumption that the main metabolic rate drivers were body mass and water temperature once
fish had been properly acclimated to their respective salinity concentrations. It is important to
note that only control treatments were selected in cases where SMR were measured under non-
normal conditions (e.g., water pollution, genetically-modified organisms). Standard metabolic
rates for Atlantic Salmon found in figures were quantified using digitizer software (PlotDigitizer,
http://plotdigitizer.sourceforge.net).

Atlantic Salmon respiration models

The Atlantic Salmon respiration models are based on mass- and temperature-dependent
respiration equations following:

\[ R = R_A \cdot W^{R_B} \cdot F(T) \cdot Act \]

where \( R \) is the specific rate of respiration in g \( O_2 \cdot g^{-1} \cdot d^{-1} \) and is dependent on the fish
body mass \( W \) in g, water temperature \( T \) in °C, and activity \( Act \). \( R_A \) and \( R_B \) are the intercept
and slope coefficients, respectively, of the allometric mass function of oxygen consumed by a 1
g fish at 0 °C. We considered respiration at the resting or inactive state, therefore, the activity
multiplier was set to 1 (Boisclair and Legget 1989; Boisclair and Sirois 1993). The SMR values
sourced from literature along with associated body mass and temperature provided the input data
for the Atlantic Salmon respiration model (equation 1).

Two different temperature functions were used to account for differences in SMR
models: an exponential (equation 2; Stewart et al. 1983) and an optimal relationship (equation 3;
Kitchell et al. 1977). The temperature dependent function \( F(T) \) for the exponential model is
derived from Stewart et al. (1983):

\[ F(T) = e^{(RQ \cdot T)} \]
where $RQ$ approximates the rate at which the function increases over relatively low water temperatures. The temperature dependent function $F(T)$ for the optimal model is derived from Kitchell et al. (1977):

\[
F(T) = V^X \cdot e^{X \cdot (1 - V)}
\]

where

\[
V = (RTM - T)(RTM - RTO)
\]

\[
X = \frac{Z^2 \cdot \left(1 + \left(1 + \frac{40}{Y}\right)^{0.5}\right)^2}{400}
\]

\[
Z = \ln(RQ) \cdot (RTM - RTO)
\]

\[
Y = \ln(RQ) \cdot (RTM - RTO + 2)
\]

where $RTO$ (°C) is the optimum temperature for respiration (where respiration is highest) and $RTM$ (°C) is the maximum or lethal water temperature set to 30 °C (an average lethal temperature for laboratory and wild conditions (Elliott 1991; Breau et al. 2011)).

Both nonlinear regression models were fitted to the respiration meta-data collected from the literature using the “nls2” package in R (Grothendieck 2013; R core Team 2017). The ranges used for starting parameter values were derived from models published for other fish species (Deslauriers et al. 2017); specifically, $RA$ ranged between 0.00535 – 0.01605, $RB$ ranged between -0.09 – -0.27, $RQ$ ranged between 0.02 – 2.25 or 0.9 – 2.7 for the exponential and optimal models, respectively, while $RTO$ ranged between 10 – 30 for the optimal respiration model. In each case, the regression model determines the nonlinear least-squares parameter.
estimates by generating a random set of starting values within the specified range and then
performs a least-squares optimization (Grothendieck 2013). Respiration models were evaluated
by comparing Akaike information criterion (AIC) and ∆AIC.

To visually compare Atlantic Salmon respiration models, mass corrected standard
metabolic rates ($SMR_{corr}$ in g $O_2 \cdot d^{-1}$, for 1 g of fish) were plotted as a function of water
temperature (°C). To represent both respiration models together with meta-data, we multiplied
SMR with body mass ($W$) and used 0.1272 as a power value that represents the average $RB$
(slope coefficient) from both models:

$\text{(4) } SMR_{corr} = SMR \cdot W^{0.1272}$

Atlantic Salmon respiration model evaluation using published SMR models

To evaluate the performance of the Atlantic Salmon respiration models explained in the
previous section (i.e., exponential vs. optimal relationships), we compared our predicted
respiration estimates with those of four previously published models, each model accounting for
differences in mass and temperature to predict respiration rates (Table 2). These models were
selected because they provided independent data separate from those used to construct the
Atlantic Salmon respiration model. To evaluate the performance of the Atlantic Salmon
respiration models with the four published models, we generated 1000 random values for body
mass and temperature within the range specified by each model and calculated respiration
outputs for each one of these mass and temperature combinations. These models collectively
represent respiration rates for Atlantic Salmon ranging from 60 to 3500 g and for experiments
conducted from 5 to 19 °C (Table 2). Published model predictions were compared against the
Atlantic Salmon respiration models using a Bonferroni-adjusted 97.5% intercept and slope joint
confidence intervals. In instances where the intercept or the slope between the observations and predictions were not equal to 0 or 1, respectively, the null hypothesis was rejected. Probability density plots were generated to visualize the performance of both respiration models against the independent dataset.

*Atlantic Salmon bioenergetics simulations for Little Southwest (LSWM) and Northwest Miramichi (NWM) rivers*

A bioenergetics approach was used to test how different river temperatures may impact the growth and consumption rates of Atlantic Salmon fry and parr life stages using daily water temperature records from two Atlantic Salmon rivers in the Miramichi River basin, New Brunswick (Figure 1). Specifically, we used mean daily river temperatures between June and October 2003 – 2015, for the LSWM and NWM rivers in New Brunswick, Canada to generate representative river temperature profiles that are unique to each river. Average daily temperature records from 18 gauging stations on the LSWM and a single station on the NWM were sourced from the RivTemp network (www.rivtemp.ca) for all years. Watershed area from hydrometric information for LSWM station (01BP001) and NSW station (01BQ001) were 1340 and 948 km², respectively (www.wateroffice.ec.gc.ca).

Mass values were quantified for fry (0+) and parr (1+, 2+) Atlantic Salmon collected in two locations of the LSWM (distance between sampling locations = 13.26 km) in summer and early fall in 2011 and 2012 (fish sampling sites (▲), Figure 1; Corey unpublished data). Using these growth data along with the temperature profiles for both rivers, two types of simulations were performed. First, we estimated total consumption for Atlantic Salmon ages 0+ and 1+ in 2011 – 2012 (first cohort) and ages 1+ and 2+ in 2011 – 2012 (second cohort) inhabiting LSWM.
Since empirical growth data was unavailable for NWM, we used the total consumption values estimated for fish in the LSWM to estimate growth of fish in the NWM. Likewise, we used the growth rates observed in the LSWM to simulate food consumption under NWM temperature conditions in the second simulation. Each simulation was run twice using the exponential and optimal respiration models, respectively.

Based on the empirical growth values provided for Atlantic Salmon in the LSWM ($G$), the Atlantic Salmon respiration model developed from the meta-analysis ($SMR$; converted to an energy unit using a oxy-calorific coefficient of $13,560 \text{ J} \cdot \text{g}^{-1} \text{ O}_2$ (Stewart et al. 1983)), the temperature profiles for LSWM and NWM rivers, and excretion ($Ex$), egestion ($Eg$), and specific dynamic action ($SDA$) costs borrowed from a model developed for juvenile Rainbow Trout ($Oncorhynchus mykiss$) (Tyler and Bolduc 2008), consumption estimates could then be calculated according to the equation:

$$C = G + SMR + Ex + Eg + SDA$$

Certain bioenergetics assumptions were made to further improve simulation outputs, including: 1) prey energy density and diet proportions remained constant through time, 2) due to the absence of an ontogenetic trend as seen in Jonsson and Jonsson (2003), the energy density for juvenile age classes was kept constant (4500 J·g⁻¹), 3) we used a generic consumption model developed for larvae and juvenile Coregonus albula (consumption parameters: $CA = 0.076917$, $CB = -0.61966$, $CQ = 0.08007$; Karjalainen et al. 1997) to balance the bioenergetics model. This model was selected because of the similarity in life stage and phylogeny, and because it does not allow for an optimal incidence to occur at a given temperature (i.e., exponential consumption model).
Diet proportions for Atlantic Salmon were set at 0.55 for Chironomid larvae, 0.185 for Diptera, 0.07 for Ephemeroptera, 0.066 for Trichoptera, and 0.048 for Coleoptera (Keeley and Grant 1997). These proportions were kept the same for both cohorts. In addition, energy density for the same prey orders was established, where energy density for Chironomids was set at 2580 J·g⁻¹, Diptera was 2922 J·g⁻¹, Ephemeroptera was 3368 J·g⁻¹, Trichoptera was 1704 J·g⁻¹, and Coleoptera was 7616 J·g⁻¹ (James et al. 2012; David et al. 2016). Bioenergetics simulations for LSWM and NWM rivers were done using Fish Bioenergetics 4.0 (Deslauriers et al. 2017).

**Results**

**Atlantic Salmon respiration models**

The search for Atlantic Salmon metabolic rates resulted in a total of 26 publications that satisfied our selection criteria (Table 1). A total of 938 individual standard metabolic rate values with estimates derived from a respirometry approach (i.e., measuring oxygen consumption of a fish) were extracted from the literature. The data compiled from literature included: standard metabolic rate (converted to g O₂·g⁻¹·d⁻¹), body mass (g), life stages (i.e., fry, parr, smolt or adult), salinity (ppt), and water temperature (°C) (Table 1). The dataset includes salmon covering a size range from 0.1 – 1979 g (Table 1). However, the vast majority of data were for fish measuring between 1 – 100 g (94%) and very few between 100 – 1000 g (1.2%). Studies generally focused on the 6 – 15 °C temperature range, with very few data points under 5 °C (n = 18) or above 16 °C (n= 54). Most of the fish used in the repirometry trials were of hatchery origin while only a handful of the data points came from salmon originating from the wild (five publications; Table 1). Because of the low representation of wild individuals, provenance (wild or hatchery-raised) was left out of the model.
As expected, body mass and water temperature both significantly influenced respiration rates. For the exponential respiration model, the intercept ($RA; 0.003 \pm S.E. 0.0002$), slope ($RB; -0.11 \pm S.E. 0.011$), and rate at which the function increases over relatively low water temperatures ($RQ; 0.05 \pm S.E. 0.0048$) were all determined to be significant ($p < 0.001$).

Likewise, all coefficients ($RA = 0.008 \pm S.E. 0.0002$, $RB = -0.14 \pm S.E. 0.0086$, $RQ = 5.18 \pm S.E. 0.3281$, and $RTO = 15.59 \pm S.E. 0.1816$) were determined to be significant ($p < 0.001$) for the optimal respiration model. While model parameters were significant for both models, standard metabolic rates (g O$_2 \cdot d^{-1}$) from our meta-analysis increased as a function of water temperature (°C) and decreased beyond ~16 °C regardless of body mass, reflecting more closely the behaviour of the optimal respiration model (Figure 2). Based on model criteria, the optimal respiration model performed significantly better ($AIC_{\text{optimal}} = -9185.5$ vs. $AIC_{\text{exponential}} = -8948.95$; $\Delta AIC = 236.55$). Moreover, residuals between the exponential Atlantic Salmon respiration model and meta-data were greater at lower (<10°C) and higher (>15°C) temperatures compared to the optimal respiration model (Figure 2).

Atlantic Salmon respiration model evaluation using published respirometry models

The Atlantic Salmon respiration models that followed respectively the exponential and optimal relationships with temperature were not significantly different from the four independent published models. We failed to reject the joint null hypothesis by 54.8% and 91.8% of the total number of iterations (n = 1000) for the exponential model and the optimal model, respectively, whereby the intercept and slope of the model observations differed significantly from 0 and 1 against the model predictions (Figures S1 and S2). However, probability density plots illustrated that Berg et al. (1993)’s model was found to differ by > 40% with the exponential respiration model, while Fivelstad and Smith (1991)’s model differed by ~50% with the optimal respiration model.
model (Figure 3). Interestingly, the Fivelstad and Smith (1991)’s model varied the least from Atlantic Salmon exponential respiration model (Figure 3 B), whereas the Forsberg (1994) and Grottum and Sigholt (1998) models varied the least from the Atlantic Salmon optimal respiration model (Figure 3 A).

Atlantic Salmon bioenergetics simulations for LSWM and NWM rivers

The LSWM River had higher mean daily temperatures (18.2 °C) than the NWM River (14.5 °C) and greater differences in mean daily temperatures between rivers from mid-July to mid-August were observed (differences ranged from 0.07 – 5.32 °C, across all years).

Specifically, LSWM River water temperatures ranged, on average, from 14.3 – 22.4 °C vs. 10.7 – 18.6 °C for the NWM River (Table 3). Bioenergetics growth simulations using LSWM river summer temperature profiles and empirically-derived growth rates revealed different growth trends between exponential and optimal respiration models (Figure 4). Simulations using the optimal respiration model showed a negative net energy budget at temperatures ranging between 11– 16 °C, while this negative net energy budget only occurred during the winter months for the exponential respiration model simulation. The loss of mass during the overwintering months using the exponential model can be explained by the model’s propensity of overestimating the energetic costs of metabolism at low temperatures (Figure 2). Conversely, the energetic costs of metabolism were low for the optimal respiration model simulation, enabling fish to gain mass during overwintering months. Fish grew 12% smaller in the NWM for the optimal model simulation, but grew 12% larger in the same river for the exponential model simulation (Table 3). Higher consumption estimates for both cohorts were generally observed for the exponential model simulation over the optimal model simulation. In the absence of empirical growth data for
the NWM, growth and consumption rate simulations for Atlantic Salmon remained the best available information for this river.

**Discussion**

Meta-analyses remain a powerful research-synthesis tool, combining different studies or data to assess the magnitude of the outcome across primary studies and summarize results across studies (Gurevitch et al. 2018). By sourcing metabolic rate data from 26 publications rather than synthesizing SMR model outcomes, the resulting Atlantic Salmon respiration models integrate the causes of variation among studies (e.g., water temperature and body mass), while quantifying the relationship between metabolic rates and each of the causes listed above. In other words, the pool of data used to derive models was increased, culminating in a comprehensive Atlantic Salmon respiration model that synthesizes the relationships over a greater range of mass and water temperatures and enabling a comparison of the SMR-temperature function for different published models. Meta-analyses may also help inform on where data gaps are, so that they may be accounted for or measured in future studies. The vast majority of meta-data in this study were for fish measuring between 1 – 100 g and the 6 – 15 °C temperature range, which effectively reduced the confidence in model predictions beyond these temperature and size ranges.

Previous studies place the optimum temperature for growth (maximum aerobic scope) for Atlantic Salmon in the range of 16 – 20 °C, where maximum conversion efficiency for growth energy is 42 – 58% (Elliott and Elliott 2010). While different temperature functions in the SMR-temperature curves have been proposed (Beamish 1964; Brett and Glass 1973; Kitchell et al. 1974; Claireaux and Lagardère 1999; Paakkonen et al. 2003; Niklitschek and Secor 2009; Pörtner 2010; Chabot et al. 2016; Deslauriers et al. 2017), studies have not yet fully compared
the strength of SMR-models or temperature functions. Atlantic Salmon respiration meta-data significantly increased with body mass and water temperature, following an optimal relationship where mass corrected SMR reached an optimum around ~16 °C and dropped substantially to the lethal temperature set point at 30 °C. Substantial variations for both respiration models from meta-data were observed for lower (<7 °C) and higher temperatures (>15 °C) on account of the distribution of meta-data (i.e., fewer meta-data) for certain temperatures. Greater percent differences between predictions generated by the exponential Atlantic Salmon respiration model and the four independent models were also observed for lower and higher temperatures, despite predictions for both models agreeing with published models across the same temperature range ~5 – 16 °C. These findings collectively indicated that the optimal Atlantic Salmon respiration model outperformed the exponential model, improving our confidence in this model’s ability to predict SMR across temperatures. The occurrence of a thermal optimum for the SMR relationship suggests that there may be complex homeostatic mechanisms involving the nervous and endocrine systems (e.g., failure of oxygen supply to tissues) that shape the response of metabolic rate to increasing temperatures (Schulte et al. 2015). Here, we focused on metabolic rates from the perspective of oxygen consumption and the importance of energy supply, which potentially underestimated the contribution of pathways involved in energy demand. A better understanding of the effects of temperature on both energy supply and energy demand for Atlantic Salmon will, therefore, improve our understanding of how this species responds to climate change (i.e., shape of the thermal performance curve; Schulte et al. 2015).

Water temperature is regarded as a driver affecting the physiology and behaviour of fishes, but the influence of temperature trends on juvenile Atlantic Salmon and early life-history decisions that follow are lesser known. The mechanisms controlling the onset of the parr to smolt
transition in the late spring points to a complex interaction between energy status, growth rate, size, and genetics, which also includes seasonal cues such as changes in photoperiod (day length) and temperature via its role controlling growth and developmental rates of juveniles (Stefansson et al. 2008; Fjelldal et al. 2011). Temperature tolerance in salmonids is size-specific, with evidence suggesting that adult salmon are less tolerant of high temperatures than juveniles (Fowler et al. 2009). Adult salmon in LSWM, like in other rivers, have been shown to seek out cool water refugia first over juveniles during periods of high temperatures (>30 °C) and are generally the first to die, suggesting that adults might be negatively impacted by temperature at a lower temperature on account of body size (Breau et al. 2007a; Frechette et al. 2018). For the optimal Atlantic Salmon respiration model, SMR varied as a function of body mass, with smaller individuals reaching peak respiration values per unit of body mass faster than larger individuals. As such, juvenile Atlantic Salmon (fry, parr) are likely susceptible to experiencing the detrimental effects of high water temperatures on account of compensating for increased metabolic costs due to higher energetic demands.

The Miramichi River watershed is considered a northern cold water system, but lethally high water temperatures to salmonids (>27 °C) have been reached on several occasions in the various tributaries of the system (Lund et al. 2002; Breau et al. 2007a; Caissie et al. 2012; Corey et al. 2017). While 0+ and 1+ parr have been shown to remain active at temperatures of 21 – 23 °C, which is above the temperature optimum (Breau et al. 2007b), cool water sources (<20 °C) from tributaries or groundwater seeps have played critical roles as thermal refugia for juvenile and adult Atlantic Salmon in summer months (Breau et al. 2007a). Fortunately, the Miramichi River watershed is essentially unrestricted, with a relatively low gradient and few physical barriers to up- and downstream movement, enabling juveniles to distribute themselves
throughout the watershed (Caissie and El-Jabi 1995). Furthermore, 2+ Atlantic Salmon parr inhabiting the Miramichi River were observed moving to cool water sources during high water temperatures, but younger smaller fish (young-of-the-year (YOY) or 0+ and 1+ parr) did not, exhibiting more tolerant behavioural response to high temperatures than larger older fish (Breau et al. 2011). Indeed, Magnuson et al. (1979) suggested that thermal preference displayed by salmonids with age and development reflected their genetic adaptation to predictable annual thermal conditions in their environment. Simulated Atlantic Salmon growth (cohorts 1 and 2), however, did not vary between LSWM and NWM rivers, suggesting that temperature differences (<5.3 °C) alone were insufficient to drive significant growth changes between rivers. While large and consistent simulated growth differences between rivers and cohorts were not observed, it is important to note that growth differences may exist between populations, but we were unable to evaluate them in part due to the absence of empirical growth data from the NWM. Differences between simulations (exponential vs. optimal models) led to variations in the shape of growth simulations over time for juvenile Atlantic Salmon, especially throughout overwintering periods, where simulations substantially diverged from one another. As a result, higher consumption estimates for both cohorts were observed for the exponential model simulation over the optimal model simulation. It is understood that other factors such as the physical conditioning of fish can lead to individual variation in respiration rates, and that growth rates, diet composition, and prey energy densities can influence bioenergetics outcomes. Combining this information with the use of the optimal respiration model in the context of bioenergetics modeling can produce more suitable predictions because even small differences at the individual level (e.g., ~12 % difference in growth rates) can lead to more pronounced effects at the population level.
Both LSWM and NWM rivers are major tributaries of the Miramichi River, supporting an economically important recreational Atlantic Salmon fishery (Miramichi River Environmental Assessment Committee 2007). A weakness of the study relates to the absence of comparable data to simulate bioenergetics requirements for NWM fish. However, bioenergetics models have often been converted to powerful simulation tools in fisheries science, generally for predicting consumption by predators or for projecting fish growth as a function of temperature and prey availability (Ney 1993). The optimal respiration model and the bioenergetics application (Bioenergetics 4.0) presented here should prove useful in future bioenergetics applications towards the conservation of Atlantic Salmon throughout its current range, as the quantity of food supply (i.e., total consumption) to support the growth and survival of juvenile Atlantic Salmon population may be estimated, providing information on the carrying capacity of a system (i.e., biomass per area).

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### Table 1.

Summary of the Atlantic Salmon respiration meta-data conducted using Web of Science and listed by origin of fish and life stage. The number of standard metabolic rate estimates (SMR) and a description of body mass, water temperature, and salinity are also listed.

| Origin                        | Life stage | Number of SMR estimates | Average ± SD body mass (g) | Average ± SD temperature (°C) | Salinity range (ppt) | Publication                                                                 |
|-------------------------------|------------|--------------------------|-----------------------------|-------------------------------|----------------------|----------------------------------------------------------------------------|
| Growth enhanced transgenic (1)| parr (1)   | 1                        | 8.42                        | 12.50                         | 4                    | Stevens et al. (1998)                                                       |
| Hatchery (21)                 | fry (4)    | 126                      | 3.03 ± 1.28                 | 9.45 ± 1.66                   | 0                    | Dabrowski (1986); Metcalfe et al. (1995); O’Connor et al. (2000); Cutts et al. (2002) |
|                              | parr (11)  | 437                      | 23.78 ± 16.25               | 10.66 ± 2.69                  | 0-33                 | Peterson and Anderson (1969); Higgins (1985); Maxime et al. (1989); Seddiki et al. (1996); Stevens et al. (1998); Herbert et al. (2001); Wright et al. (2001); Maxime (2002); Finstad et al. (2004); Kieffer and Wakefield (2009); Barnes et al. (2011) |
|                              | smolt (5)  | 221                      | 67.28 ± 125.91              | 11.62 ± 1.65                  | 0                    | Whitey and Saunders (1973); Higgins (1985); Maxime et al. (1989); Maxime (2002); Deitch et al. (2006) |
|                              | adult (5)  | 5                        | 1039.68 ± 570.76            | 9.3 ± 3.11                    | 33-35                | Maxime et al. (1990); Lucas et al. (1993); Lucas (1994); Penney et al. (2014) |
| Wild (5)                      | fry (1)    | 39                       | 0.44 ± 0.13                 | 13.20                         | 0                    | McCarthy (2000)                                                            |
|                              | parr (4)   | 80                       | 9.25 ± 5.29                 | 17.19 ± 3.96                  | 0                    | Baraduc and Fontaine (1955); Seppänen et al. (2009); Beauregard et al. (2013); Oligny-Hébert et al. (2015) |
|                              | smolt (3)  | 35                       | 22.17 ± 31.73               | 13.15 ± 1.38                  | 0-35                 | Baraduc and Fontaine (1955); McCarthy (2000); Seppänen et al. (2009)       |

**Note:** The numbers in parentheses indicate the number of publications sourced for the meta-analysis. Some of the publications contributed respiration estimates for more than one life-stage, which means that the numbers in parentheses in the life-stage column do not necessarily add up to those in the origin column.
Table 2. Comparison of published standard metabolic rate models, range of body size \((W)\) and temperatures \((T)\), and correlation coefficients for four published respiration models (strength of each model’s relationship with water temperature). \(U\) refers to swim speed, which for standard metabolic rates is set to 1 due to \(\text{Activity} = 1\) as per equation: \(R = RA \cdot W^{RB} \cdot e^{(RQ \cdot T) \cdot \text{Act}}\)

| Source                        | Respiration model                                                                 | Respiration unit                  | Sample size | \(R^2\) | Mass range \((W)\) | Temperature Range \((T)\) | Intercept C.I. | Slope C.I. |
|-------------------------------|----------------------------------------------------------------------------------|-----------------------------------|-------------|---------|-------------------|-------------------------|----------------|------------|
| Forsberg (1994)              | \(1.92M^{0.277}T^{0.63}10^{0.01 \cdot U}\)                                   | mg \(\text{O}_2\) \cdot kg\(^{-1}\) \cdot \text{min}^{-1} | 110         | 0.7     | 60–3500           | 5–16                    | 0.0021–0.0026  | 0.59–0.69  |
| Berg et al. (1993)           | \(62.5(M/1000)^{0.3}1.06^T\)                                                   | mg \(\text{O}_2\) \cdot kg\(^{-1}\) \cdot \text{h}^{-1} | —           | —       | 200–3300          | 6–16                    | 0.0002–0.0026  | 0.39–0.65  |
| Fivelstad & Smith (1991)     | \(10^{-0.261} \log_{10}(M/1000)+1.378^\log_{10}(T)+0.841\)                  | mg \(\text{O}_2\) \cdot kg\(^{-1}\) \cdot \text{min}^{-1} | 62          | 0.74    | 200–850           | 5–9                     | 0.0001–0.0008  | 3.01–3.65  |
| Grottum & Sigholt (1998)     | \(61.6(M/1000)^{-0.33}1.03^T1.79^U\)                                         | mg \(\text{O}_2\) \cdot kg\(^{-1}\) \cdot \text{h}^{-1} | 157         | —       | 1100–2000         | 5–15                    | 0.0013–0.0014  | 0.20–0.26  |
Table 3. Simulation results for growth (final body mass in g) and total consumption (g) for two cohorts (1: 0+ – 1+; 2: 1+ – 2+) at the end of their second growing season, using exponential or optimal respiration, for Atlantic Salmon residing in the Little Southwest Miramichi (LSWM) and Northwest Miramichi (NWM) rivers. Growth rates for LSWM were used to estimate food consumption, for which the values were used to simulate growth for fish residing in the NWM. Observed growth rates from the LSWM were used to estimate total food consumption in both the LSWM and NWM rivers.

| River                          | Water temperature (°C) | Growth (g) | Consumption (g) |
|-------------------------------|------------------------|------------|-----------------|
|                               | Tmin       | Tmax     | Mean   | cohort 1: 0+ – 1+ |             | cohort 2: 1+ – 2+ |             |                 |
|                               |            |          |        | exponential | optimal    | exponential | optimal    |                 |
| Little Southwest Miramichi (LSWM) | 14.26     | 22.4     | 18.24  | 7.71        | 7.71        | 15.31       | 15.31       | 75.769  | 62.644 | 152.688 | 119.569 |
| Northwest Miramichi (NWM)     | 10.74      | 18.56    | 14.47  | 8.714       | 7.05        | 17.14       | 13.05       | 67.85   | 68.29  | 137.89  | 130.79 |
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Figure 1. Map of the 19 Little Southwest Miramichi (LSWM) River and Northwest Miramichi (NWM) River temperature gauging stations (●) and two fish sampling sites (▲) in the LSWM (orange) and NWM (blue) sub-drainage basins, located in the Miramichi watershed (grey area), New Brunswick, Canada. Several temperature loggers on the LSWM overlap due to the scale of the map. Regional watershed and sub-drainage basin shapefiles provided by the Miramichi River Environmental Assessment Committee (MREAC).

254x190mm (300 x 300 DPI)
Figure 2. Mass corrected standard metabolic rate (g O₂·d⁻¹) from meta-data as a function of water temperature (°C). The mass corrected metabolic rates are for a 1g fish at a given temperature. The blue line and grey area correspond to the fitted loess smoothing function ± 1 S.E.M. to the meta-data (points), while the solid and dashed black lines correspond to respiration models following the exponential and optimal relationships, respectively.
Figure 3. Probability density plots illustrating the percent differences between predicted respiration values from the A) optimal and B) exponential models and respiration values generated from four published and independent respiration models: in pink, Berg et al. (1993); green, Fivelstad and Smith (1991); blue, Forsberg (1994); purple, Grottum and Sigholt (1998).

215x279mm (300 x 300 DPI)
Figure 4. Atlantic Salmon observed (boxplots) and simulated growth in the Little Southwest Miramichi using either the exponential (solid line) or optimal (dashed line) respiration models for A) ages 0+ – 1+ (first cohort), and B) ages 1+ – 2+ (second cohort). Average daily temperature profile for the LSWM is shown in grey.