

The effect of environmental conditions on Atlantic salmon smolts' (*Salmo salar*) bioenergetic requirements and migration through an inland sea

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Abstract The timing of the juvenile Atlantic salmon ocean-entry is considered a critical stage in the species' life-history. Entry into the ocean at suboptimal times can have negative survival impacts on entire smolt cohorts. Previous studies have identified smolt residency time in the Bras d'Or Lakes as highly variable and correlated with body condition. This study combines energetic modelling using Dynamic Energy Budget (DEB) theory with acoustic telemetry to mechanistically link smolt bioenergetics to their migration strategy within the Bras d'Or. This study examines two main questions: 1) what is the relationship between smolts' bioenergetics and

smolts' migration strategy, and 2) what effect would warmer water temperature have on smolts' energetic requirements? Simulation results indicate that smolts requiring more food are more likely to exit the Bras d'Or during the observation period. The results also suggest higher lake temperature would result in faster depletion of smolt energy reserves, which is predicted to favour smolts migrating to the ocean sooner.

Keywords Atlantic salmon · Dynamic Energy Budget theory · Acoustic telemetry · Migration · Climate change · Food availability · Temperature

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Introduction

Atlantic salmon (*Salmo salar*) are highly valued in Atlantic Canada due to their ecological, cultural, and economic worth (Thorstad et al. 2012; Minister's Advisory Committee on Atlantic salmon 2015). Atlantic salmon populations have been declining since the 1960s (Parrish et al. 1998), primarily due to overfishing and the construction of dams that blocked migration (Dunfield 1985). Even after the mitigation of these practices, declines continued (Parrish et al. 1998). Recent synchronous declines occurring in populations across eastern North America (Friedland et al. 1993) have been hypothesized to be the result of a common stressor across the species range (Mills et al. 2013). Low ocean survival was identified as an important driver of the decline (Friedland et al. 1993, 1998; Chaput 2012; Jonsson and Jonsson 2004). Numerous factors have

been hypothesized as the cause of low survival in the North Atlantic Ocean including predation (Hansen and Quinn 1998) and unfavorable climatic conditions (Kennedy and Crozier 2010; Mills et al. 2013; Friedland et al. 2014).

The smolt migration to sea has been identified as a key life-history stage for Atlantic salmon, characterized by high mortality affecting yearly recruitment (Klemetsen et al. 2003; Kennedy and Crozier 2010; Friedland et al. 2014). Ocean-entry timing may be a particularly critical component of post-smolt survival (Friedland et al. 1998, 2003; Hvidsten et al. 2009; Kennedy and Crozier 2010; Friedland et al. 2014). Previous studies have highlighted the importance of smolts entering the marine environment during an optimal “smolt window” (McCormick et al. 1998; Hansen et al. 2003) that may coincide with optimal marine conditions, including peaks in marine productivity (Jonsson and Jonsson 2004) and favourable oceanographic conditions (Moriarty et al. 2016). Smolts migrating too early or too late, hence missing the “smolt window”, would have a lower chance of survival (Hvidsten et al. 2009).

In preparation for their ocean migration, juvenile Atlantic salmon (parr) undergo a transformation, during which the parr restructure their osmoregulatory physiology and morphology for ocean-entry, becoming smolts (McCormick and Saunders 1987; Thorstad et al. 2012). Following smoltification, Atlantic salmon respond to a number of environmental cues to begin downstream migration, the most significant of which are: river temperature and water flow (McCormick et al. 1998; Riley 2007; Thorstad et al. 2012). In some populations, water temperature is the primary initiating factor (Jonsson and Ruud-Hansen 1985; Zydlewski et al. 2005; Thorstad et al. 2012), and can explain ~90% of year-to-year variation in the timing of the smolt migration (Jonsson and Ruud-Hansen 1985). Due to the importance of temperature for the initiation of their migration, deviations from long-term thermal averages caused by climate change may alter the timing of smolts' downstream migration and the subsequent timing of ocean-entry (Friedland et al. 2003; Kennedy and Crozier 2010; Otero et al. 2014). Changes in the timing of smolts' downstream migration associated with warmer temperatures has been observed in the Bush River, Northern Ireland (Kennedy and Crozier 2010) as well as rivers draining to the Gulf of Maine, Nova Scotia (Friedland et al. 2003), and throughout the North Atlantic (Otero et al. 2014). Warmer temperatures in the Gulf of Maine

have been associated with decreases in post-smolt survival, hypothesized to be the result of poor synchronization between smolt ocean-entry and favourable ocean conditions (Friedland et al. 2003).

Smolts may pause their ocean-entry in the estuaries of their home river, in some cases for extended periods (Brawn 1982; Crossin et al. 2016). While estuarine residency has been hypothesized to facilitate acclimatization to salt water (Gudjonsson et al. 2005), some studies suggest that smolts are already physiologically adapted to salt water before initiating their downstream migration (Moore et al. 1995). However, estuarine residency may provide other survival or growth benefits (Dempson et al. 2011; Halfyard et al. 2013; Crossin et al. 2016). Brawn (1982) observed marked inter-individual variation in estuary residency times, with some smolts exiting after 7 days while others suspended their migration and resided up to 108 days within the estuary following exit from their home river. Acoustic telemetry studies conducted by Halfyard et al. (2013) within the Bay of Fundy, and Dempson et al. (2011) in a Newfoundland fjord, concluded that the probability of an individual smolt surviving until they reached the ocean increased with residency time within the estuarine habitat, up to an optimal threshold. A recent study by Crossin et al. (2016) examined the correlates of inter-individual variation in potential fitness-linked characteristics, particularly the influence of body condition (mass relative to length), to estuarine residency times within an extended estuary, the brackish-water Bras d'Or Lakes, Nova Scotia, Canada. While some acoustically tagged smolts were detected exiting the lakes to the ocean a few weeks after exiting their home rivers, others remained resident in the estuary for up to 2 months. These varied residency tactics were correlated with body condition, with poorer condition smolts exiting the Bras d'Or Lakes more quickly than those in better condition. Crossin et al. (2016) suggested that due to food limitations within the Bras d'Or, poor condition smolts were presumably unable to sustain growth and survival, necessitating their directed migration to sea to find adequate food resources. By contrast, smolts in higher body condition could remain within the Bras d'Or longer, channeling body reserves towards growth in an environment where they were likely to experience lower predation than in the adjacent ocean (Brönmark et al. 2008; Crossin et al. 2016). The current study builds on the work completed by Crossin et al. (2016) and provides evidence derived from bioenergetics that supports the hypothesis.

Previous studies have considered the univariate effect of temperature (Jonsson and Ruud-Hansen 1985; McCormick et al. 1998; Riley 2007), food availability (Lans et al. 2011; Vainikka et al. 2012), or body condition (Crossin et al. 2016), on smolt migration. This study simultaneously examined the influence of external (food availability and temperature) and internal (body condition) drivers of the growth, and survival of smolts migrating through the Bras d'Or estuary. This was achieved through the use of a Dynamic Energy Budget (DEB, Kooijman 2010) model, which allowed the investigation and prediction of individual bioenergetics under different environmental scenarios. The DEB model was created using Dynamic Energy Budget theory that is based on fundamental principles of biology, as well as physics, and chemistry (Sousa et al. 2010), making it applicable to most organisms after species-specific calibration (Kooijman 2010). The DEB model can be used to relate smolt migration (as determined from acoustic telemetry) to smolt energy budgets under different environmental conditions. Using this combination of tools, this study aimed to answer two primary questions 1) what was the relationship between smolts' bioenergetics and smolts' migration strategy, and 2) what effect did warmer water temperature have on smolts energetic requirements.

Materials and methods

Study site

The Bras d'Or Lakes form is an oceanographically unique inland sea located in Cape Breton, Nova Scotia (Centroid: 45°51'37" N 60°46'44"W; Fig. 1). The Lakes consist of two major basins separated by a single strait, and several smaller basins and embayments connected by narrow straits and channels (Yang et al. 2007). These basins collectively make up a total surface area of 1200 km² with a maximum depth of 280 m (Petrie and Bugden 2002). Unrestricted access to the NW Atlantic Ocean (Sydney Bight) occurs through two channels (Great Bras d'Or and Little Bras d'Or). Tidal flow can be strong within the two ocean channels, reaching 2.8 m.s⁻¹, and 1.1 m.s⁻¹ in the Barra Strait (McMillan et al. 2012), but is generally well less than 1 m.s⁻¹ within the rest of the lakes (Yang et al. 2007). The seabed composition varies throughout the Bras d'Or Lakes, and may consist of bedrock, cobble, gravel, sand or

mud depending on location, depth, and proximity to the shore (Shaw et al. 2002; Tremblay et al. 2005).

The watershed of the Bras d'Or Lakes drains a region more than twice the area of the Lake's water surface. Fresh water inflow from the large rivers ranges from 56 to 140 m³ s⁻¹ (Gurbutt and Petrie 1995), and buoyancy forcing contributes significantly to the hydrodynamics (Yang et al. 2007). As a result of these inputs the water is brackish, with an average salinity of 20–23 ppt (Strain and Yeats 2002), and so the Bras d'Or Lakes actually form a large, complex estuary. The vertical structure of the water column reveals a surficial layer of brackish waters flowing seaward and a deep, more saline, layer flowing landward (Yang et al. 2007). Little mixing occurs between these layers, except sometimes in the winter months (Petrie and Bugden 2002). The Middle River originates within the Cape Breton Highlands, located 450 m above sea-level, and flows south into Nyanza Bay and out into the St. Patrick's Channel and the Bras d'Or Lakes (Amiro et al. 2006). The Middle River supports one of the largest Atlantic salmon populations in Eastern Nova Scotia. Similar to other Atlantic salmon populations in North America, the Eastern Cape Breton stock has experienced substantial declines leading to the stock being designated as endangered by the Committee on the Status of Endangered Wildlife in Canada (COSEWIC 2010).

Dynamic energy budget model

The standard DEB model used in this study was modified from Filgueira et al. (2016). The model (Table 1) follows the original notation from Kooijman (2010), in which $[\]$ indicates quantities represented as per unit structural volume, $\{ \}$ indicates quantities that are represented as per unit surface-area of the structural volume, and a dot over the symbol (e.g. $\dot{p}G$) indicates a rate or a dimension per time. Dynamic Energy Budget theory describes the allocation of energy by using three state variables: reserves, structure, and maturity/reproduction (Fig. 2). In brief, the DEB model includes the most relevant energy fluxes: a fraction of the food ingested from the environment is excreted as waste and the remainder is assimilated and stored in reserves. From reserves, a fixed fraction of the energy (κ) is allocated to structural maintenance of body structures and to growth. The remainder of the energy ($1-\kappa$) is allocated to maturity maintenance and development/reproduction. All physiological rates in DEB have been corrected according to the extended Arrhenius law

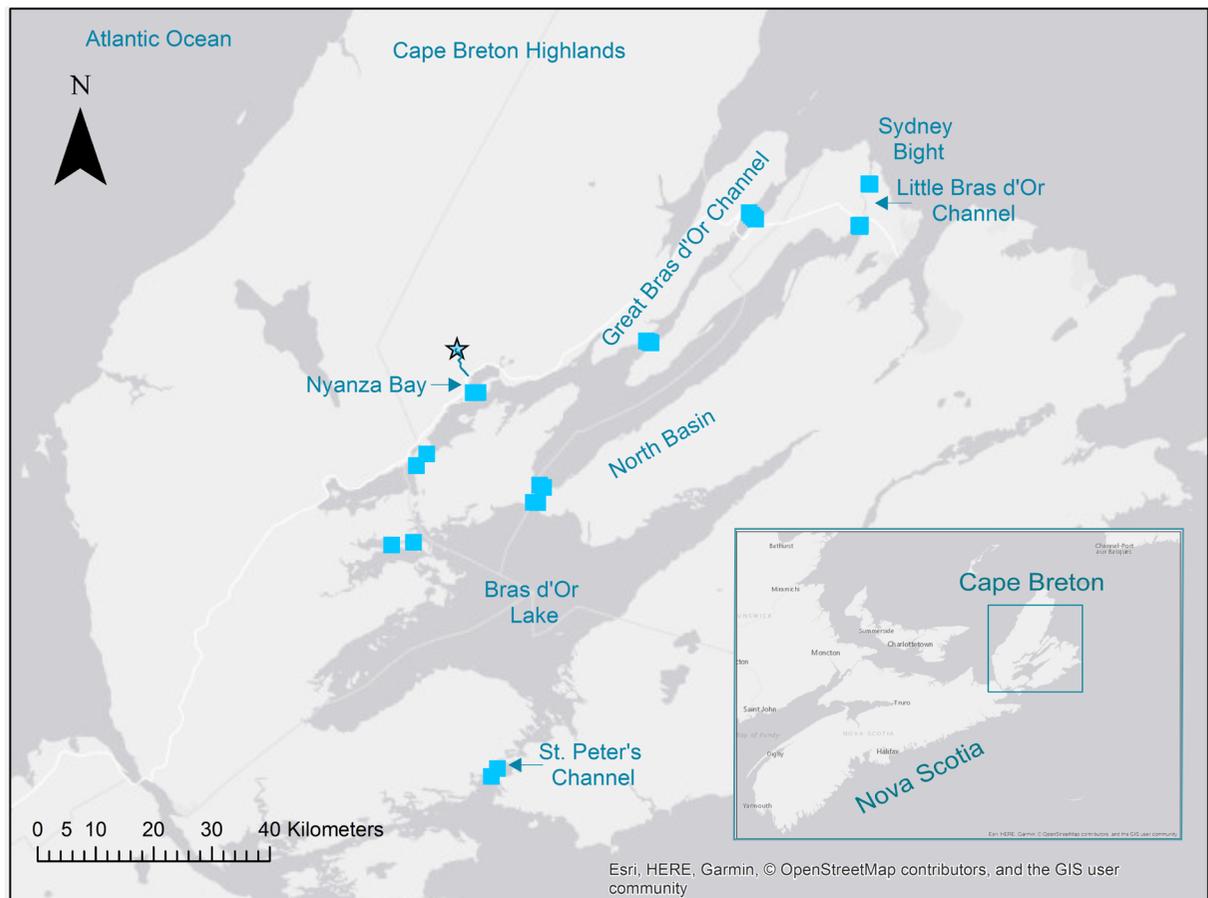


Fig. 1 Aerial map shows the majority of Cape Breton Island with the The Bras d'Or lakes crossing through the centre – Map depicts key basins and channels that may be used by smolts during their migration,

as well as The Ocean Tracking Network's Bras d'Or Acoustic receiver array (■) and the Middle River smolt tagging site (★), figure created using ArcGIS

(Kooijman 2010; Table 1). In this study the DEB model has been parameterized for the juvenile stage (parr and smolt) of Atlantic salmon. The model was not extended to the adult or the embryo stage due to data restrictions. Two modifications from Filgueira et al. (2016) were carried out to adapt the model to this specific study. First, given the focus on the juvenile stage, volume threshold at puberty (V_p) was excluded from the original model. Second, lower boundary tolerance range (T_L , online resource 1) and the rate of decrease at the lower boundary (T_{AL} , online resource 1) were incorporated into the model, which improves the model performance at low temperatures (Filgueira et al. 2016). The DEB model was constructed in Similie (Simulistics Ltd). The model was calibrated using the data set collected for this study, Middle River Hatchery 2016, an existing dataset Rowe and Thorpe (1990), and optimisation tools (online resource 1). The shape coefficient (δ), that describes how a specific

length translates to the structural body volume, was directly estimated based on the allometric relationship of wet weight and length from Middle River smolts at the Margaree Fish Hatchery, the smolt wheel operated on the Middle River between 2012 and 2016, and smolts tagged in 2012, 2013, and 2016. This approach assumes the density of the structural volume equals 1 g cm^{-3} . The shape parameter was estimated to allow 5% of the observed weights to fall below the fitted curve, assuming that wet weight includes not only structure but also reserves and reproduction (Rosland et al. 2009). As stated in Rosland et al. (2009) the structural mass should lie below the observed mass. Allowing for 5% below the curve, accounts for potential measurement errors. The parameterization of maximum length (L_m) for adult Atlantic salmon was based on field data collected during adult tagging on the Middle River (Bordeleau et al. 2018).

Table 1 State and forcing variables, parameters for *Salmo salar* and equations for the standard DEB model

Symbol	Value	Units	Definition
<i>State and Forcing variable</i>			
E		J	Reserve energy
V		cm ³	Structural volume
E_H		J	Cumulated energy invested in development
E_R		J	Reproduction buffer energy
T		K	Absolute temperature
f			Scaled functional response
$c(T)$			Temperature correction factor
<i>Parameters</i>			
$[\dot{p}_M]$	11.6	Jcm ⁻³ d ⁻¹	Volume-specific somatic maintenance rate
$\{\dot{p}_T\}$	0	Jcm ⁻² d ⁻¹	Surface-specific somatic maintenance rate
$[E_G]$	5500	Jcm ⁻³	Volume-specific cost for structure
\dot{v}	0.19	cmd ⁻¹	Energy conductance
κ	0.9		Fraction of reserves to growth and maintenance
T_A	6000	K	Arrhenius temperature
T_1	293	K	Reference temperature
δ	0.207		Shape coefficient
lm	110	cm	Maximum observed length
$\{\dot{p}_{Am}\}$	$L_m[\dot{p}_M]/\kappa$	Jcm ⁻² d ⁻¹	Maximum surface area-specific assimilation rate
g	$\dot{v}[E_G]/\kappa\{\dot{p}_{Am}\}$		Energy investment ratio
$[E_m]$	$\{\dot{p}_{Am}\}/\dot{v}$	Jcm ⁻³	Maximum reserve density
T_L	280	K	Lower boundary tolerance range
T_{AL}	160,416	K	Rate of decrease at the lower boundary

Equations

$$\frac{d}{dt}E = \dot{p}_A - \dot{p}_C$$

$$\frac{d}{dt}V = \frac{1}{[E_G]} \dot{p}_G = \frac{1}{[E_G]} (\kappa \dot{p}_C - \dot{p}_S)$$

$$\frac{d}{dt}E_H = (1 - \kappa) \dot{p}_C - \dot{p}_J \text{ if } V < V_P, \text{ else } \frac{d}{dt}E_H = 0$$

$$\frac{d}{dt}E_R = 0 \text{ if } V < V_P, \text{ else } \frac{d}{dt}E_R = (1 - \kappa) \dot{p}_C - \dot{p}_J$$

with $\dot{p}_A = c(T)f\{\dot{p}_{Am}\}L^2$

$$\dot{p}_C = c(T)\{\dot{p}_{Am}\}L^2 \frac{ge}{g+e} \left(1 + \frac{L}{gL_m}\right)$$

with $e = \frac{[E]}{[Em]} = \frac{E}{V} \frac{\dot{v}}{\{\dot{p}_{Am}\}}$ and $L = V^{1/3}$

$$\dot{p}_S = c(T)(\{\dot{p}_M\}L^3 + \{\dot{p}_T\}L^2)$$

$$\dot{p}_J = c(T)\left(\frac{1-\kappa}{\kappa}\right) \min(V, V_P) [\dot{p}_M]$$

$$c(T) = \exp\left(\frac{T_A - T}{T_1}\right) \times s(T)/s(T_1)$$

$$s(T) = \left(1 + \exp\left(\frac{T_{AL} - T}{T_L}\right)\right)^{-1}$$

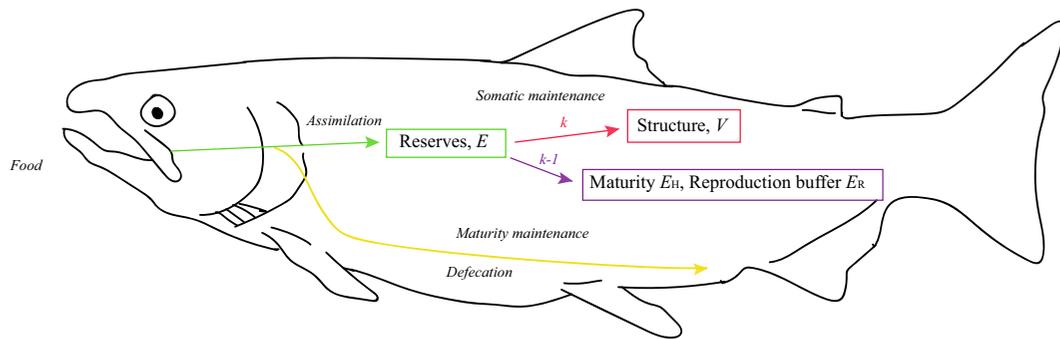


Fig. 2 Standard DEB model diagram depicting state variables and the allocation of energy between them (Outline retrieved from Fauntleroy Watershed, 2017)

Volume-specific somatic maintenance rate ($[\dot{p}_M]$), volume-specific cost for structure ($[E_G]$), fraction of reserves devoted to growth and maintenance (κ), and energy conductance (\dot{v}) were estimated using PEST (Model-independent Parameter Estimation, Watermark numerical computing, <http://www.pesthomepage.org>). PEST is an optimisation tool that uses the Gauss - Marquardt - Levenberg algorithm to estimate the optimal parameter value that minimizes the discrepancy between observed and simulated results. The optimal parameters were selected from the range 0.4–0.95, 4000–7000, 5–90, 0.001–0.2, 0–500,000 for κ , $[E_G]$, $[\dot{p}_M]$, \dot{v} and T_{AL} , respectively. PEST was used to estimate these parameters using a dataset collected for this study (Hatchery 2016, online resource 1). The Hatchery 2016 dataset consisted of weight measurements of parr taken from May to August 2016 by Margaree Fish Hatchery staff. During this time, parr average weights measurements were determined by weighing a net full of parr from the Middle River pond, counting the number of parr in the net and then calculating average weight. More detailed measurements of growth were taken from a random sample of 100 Middle River parr at the Margaree Fish Hatchery bi-weekly from September to November 2016. Each parr was individually anesthetized using MS-222 and then weighed and measured (fork length). Temperature was recorded at the Margaree Fish Hatchery and parr were fed ad libitum by Margaree Fish Hatchery staff throughout the observation period, until the last 17 days when feed was reduced. Following the initial parameterization of the model, PEST and the Rowe and Thorpe (1990) dataset were used to estimate the lower boundary tolerance range (T_L) and the rate of decrease at the lower boundary (T_{AL}).

The original DEB parameter, scaled functional response (f) is directly related to food availability within the environment following a Holling Type II response: $f = \frac{X}{X + X_K}$ (Kooijman 2010). In this equation, X represents the food density in the environment and X_K represents the time and energy an organism must allocate to searching for food. If, f tends to 1, an individual does not need to spend time and energy searching for food, and conversely if f tends to 0, an individual must spend a significant amount of energy on searching for food in the environment. Therefore, f can be understood as a proxy of food availability where $f=0$ represents no food available in the environment and $f=1$ represents food available ad libitum in the environment (Saraiva et al. 2011; Kearney 2012). Given the absence of direct measurements of food density (X) in the Middle River and Bras d'Or lakes, the functional response (f) was simplified as a scale from 0 to 1, directly representing food availability in the environment. In terms of energy consumption, this implies that under $f=0$ the consumption rate of an individual is negligible and under $f=1$, the individual would consume energy at its maximum rate.

The sensitivity of the model parameters was calculated by increasing and decreasing the value of each parameter by 10% and calculating the percent change in simulated smolt weight and length at the end of the simulation. Testing the sensitivity of each parameter is important for understanding the influence of small parameter differences on the performance of the model.

Validation

The DEB model was validated by applying the estimated parameters to four independent datasets, two from the

literature (Rowe and Thorpe 1990; Imholt et al. 2011) and two from the Margaree Fish Hatchery (Hatchery 2015 and Hatchery 2013; see Table 3, online resource 1). For each dataset, initial observed weight and length were input into the model along with forcing variables (food availability and temperature) for the study period. The model was then run for the number of days observed in the original dataset. After the simulation was complete, simulated growth was compared to observed growth. The agreement between observed and simulated data points for all independent datasets was evaluated using a reduced major axis regression (RMA) (Duarte et al. 2003). The significance of the RMAs' regression slopes and intercepts was tested using an ANOVA and ANCOVA in order to compare the slopes and intercepts to 1 and 0, respectively.

Acoustic telemetry

Tagging datasets were available from 2012 and 2013 (Crossin et al. 2016) and one additional year (2016) was completed for this study. In 2012, 2013 and 2016, a total of 114 smolts ($n = 14, 50$ and 50 , respectively) were captured using a rotary screw trap positioned in the Middle River. All fish were anaesthetised, weighed ($+0.1$ g) and measured (fork length) before acoustic transmitters (V9-4 \times in 2012 or V8-4 \times in 2013 and 2016) were surgically inserted into the abdominal cavity (Vemco Ltd., NS, Canada) using standard operating procedures from Lacroix et al. (2005). Following tagging, fish were given time to recover in an oxygenated tank filled with cold ambient water before being released back into a sheltered section of the river. Only fish that were larger than 12.8 cm were tagged, due to the larger body size being better suited to accommodate the acoustic tag. Transmitters accounted for $\sim 11\%$ of the fish body weight in 2012, $\sim 8\%$ in 2013, and $\sim 8\%$ in 2016. Once initiated, transmitters had a battery life of ~ 74 days (in 2012 and 2013) and ~ 104 days in (2016). Fish handling and surgical procedures followed the guidelines outlined by the Canadian Committee on Animal Care, approved by Dalhousie University Animal Care Committee (Dalhousie University Animal Care Protocol 14–105) and Cape Breton University Animal Care Committee (Permits # ACC-2011-10; ACC#1213–16).

To monitor smolts' movement, a total of 30 VR2-W acoustic receivers (Vemco Ltd., NS, Canada) were used to detect the migration and residency of tagged smolts

throughout the Bras d'Or estuary. Lines of receivers (gates) were positioned across channels in order to determine the transit of tagged fish amongst geographic sections of the estuary, and to monitor the exit of fish to the ocean either through the Little or Great Bras d'Or channels (Fig. 1). Receivers within these exits did not exceed 0.39 km from each other or 0.34 km from shore. Receiver efficiencies were measured by calculating four different indices: 1) The probability of the receiver picking up a fixed tag or mobile tag; 2) The probability that the gate would detect a smolt that was detected nearby by another receiver; 3) The probability receivers would pick up signals from sentinel tags, pinging at known intervals and distance from the receiver located in problem areas; and 4) Range testing using sentinel tags. A more detailed description of these techniques can be found in Crossin et al. (2016). Detection efficiencies varied between 82.4 and 96.6% during the time of migration. These detection efficiencies are considered good, similar to other arrays in comparable environments, and demonstrate a high capability of the arrays to detect tagged smolts. The lowest receiver efficiencies occurred in shallow, narrow, winding channels during times of high water turbulence (see Supplementary Data in Crossin et al. 2016).

Smolts that were not detected after the Nyanza Bay array or displayed detections indicating mortality, such as being detected at one receiver continuously for days/months, were excluded from further analyses ($n = 43$) as they were assumed to be dead (alternatively, transmitters might have been expelled). For fish that were detected through freshwater ($n = 71$), our measure of "Bras d'Or days detected" started at the day of tagging and ended at the last day they were detected within the Bras d'Or Lakes. Some of these fish ($n = 24$) were not detected leaving the system, in which case days detected ended at the time of last detection on a Bras d'Or Lakes receiver. For fish that were detected leaving the system to enter the Atlantic Ocean ($n = 47$), Bras d'Or residency period ended at the time of last detection at a receiver situated at one of the exits from the Bras d'Or to the ocean.

Body condition was calculated following the procedure outlined in Schulte-Hostedde et al. (2005), body mass was regressed against body length, a natural log was applied, and the resulting residuals were used as a measure of body condition. Body condition of tagged smolts was subsequently divided into quartiles based on their condition: lowest, low, high, highest ($-0.183, -0.032, 0.003, 0.040$).

Simulations

The DEB model was run for each tagged smolt using wet weight and length at tagging as input variables, and sea surface temperature (SST) and inferred food availability as forcing variables. The number of days to run the simulation was determined by the number of days each smolt was detected within the Bras d'Or, which was determined from the acoustic telemetry records. Daily satellite images of SST were retrieved for the Bras d'Or for 2012, 2013, and 2016 from Ocean Colour Web (level-3, global, daily, 4Km standard mapped images (SMI) of MoDIS-Aqua SST (11 μm , daytime); <http://oceancolor.gsfc.nasa.gov/>). Spatially-averaged temperature for the waters delimited by 46.2107 N \rightarrow 45.8591 N \rightarrow 61.2254 W \rightarrow 60.3765 W was assumed to represent the average temperature conditions for the Bras d'Or. Note that the spatial resolution of the satellite product was not fine enough to extract SST for the specific basins that form the Bras d'Or. Satellite SST data was validated by CTD casts within the Bras d'Or during 2016 (online resource 2). Three sets of simulations were carried out to investigate: 1) food requirements of tagged smolts and minimum food availability in the Bras d'Or Lakes, 2) the effect of food availability on growth, and 3) the effect of warming sea temperatures on smolts' body reserves.

Food availability and migration

Simulations were run to determine the minimum food availability that smolts would require in order to survive during their observed residency period within the Bras d'Or Lakes. The DEB model was run for each individual assuming that no food is present in the system ($f=0$) to determine the number of days until the reserves of each smolt would be depleted. The depletion of reserves was used as an indicator of mortality (hereafter referred to as "days until reserve depletion"). The number of days each tagged smolt remained within the Bras d'Or was determined from the acoustic tracking records (hereafter referred to as "days detected"). Each individual's days detected was then subtracted from their days until reserve depletion. Positive values represented individuals that could have survived during their stay in the Bras d'Or system without eating, and negative values represented individuals that would have needed to feed to survive. Subsequently, new simulations were

run to determine the minimum food availability required to explain the survival of individuals that could not have survived without feeding. This was achieved by running the model for the individuals that required food, with food availability starting at 0.05 and increasing by increments of 0.05 simulating low (0.05) and increasing levels (0.10, 0.15...1.0) of food availability in the environment until the individual smolt could survive for the number of days it was detected. The minimum food availability that could explain the survival of all individuals was assumed to be the minimum food availability that must have been present within the Bras d'Or during the smolts' out-migration.

The effect of food availability on growth rate

The effect of food availability on the growth of three different body condition smolts was simulated using idealized individuals. DEB models were initialized for 14.0 cm smolts (mean length of tagged smolts) with weights that were representative of low, medium, and high condition smolts based on the allometric length-weight relationship. Each condition simulation was run with food availabilities ranging from 0.0 to 1.0, increasing by increments of 0.05, and daily SST temperatures averaged over 2012, 2013, and 2016 for May, June, July, and August. Growth rate was then calculated using the following equation: $\mu = \ln(W_2/W_1)/(t_2-t_1)$ from Larsen et al. (2014), where W represents weight and t represents time.

The effect of increased temperatures on smolt survival

To assess the possible impact of a warming sea temperatures, the model was run for each smolt with the actual temperatures experienced in the Bras d'Or Lakes during migration, as well as with three scenarios where temperature were respectively +1 $^{\circ}\text{C}$, +2 $^{\circ}\text{C}$, and +3 $^{\circ}\text{C}$ higher each day than the actual temperatures on the same days during the study. Food availability was set at 0 for all temperature simulations, representing the lowest possible food availability. The model was run until the reserves of each smolt were depleted (reserves = 0), which was used as an indicator of mortality.

Results

Calibration and validation

The estimation of the shape coefficient (δ), calibration of volume-specific somatic maintenance rate ($[\dot{p}_M]$), volume-specific cost for structure ($[E_G]$) fraction of reserves to growth and maintenance (κ), energy conductance (\dot{v}), lower boundary tolerance range (T_L), and rate of decrease at the lower boundary (T_{AL}) using PEST showed a good agreement between observed and simulated growth of Hatchery 2016 smolts (Fig. 3a and b).

Three independent datasets were used to assess the predictive capacity of the DEB model: Imholt et al. (2011) and Middle River Hatchery data from

2013 and 2015. The RMA regression comparing observed and predicted data points from all validated datasets (Fig. 3c and d) resulted in an intercept and slope not statistically different from 0 and 1, respectively, demonstrating that predicted and observed growth were in agreement.

The results of the sensitivity test (Table 2) identified the shape coefficient as the most sensitive parameter in the model. When the shape coefficient was increased or decreased by 10% it caused a 25% change in final weight. However, the extensive ($n = 2565$) size measurements dataset used in the estimation of this parameter reduces its uncertainty. The DEB model was not as sensitive to other parameters, including but not limited to: kappa (κ), energy conductance (\dot{v}) and Arrhenius temperature (T_A ; Table 2).

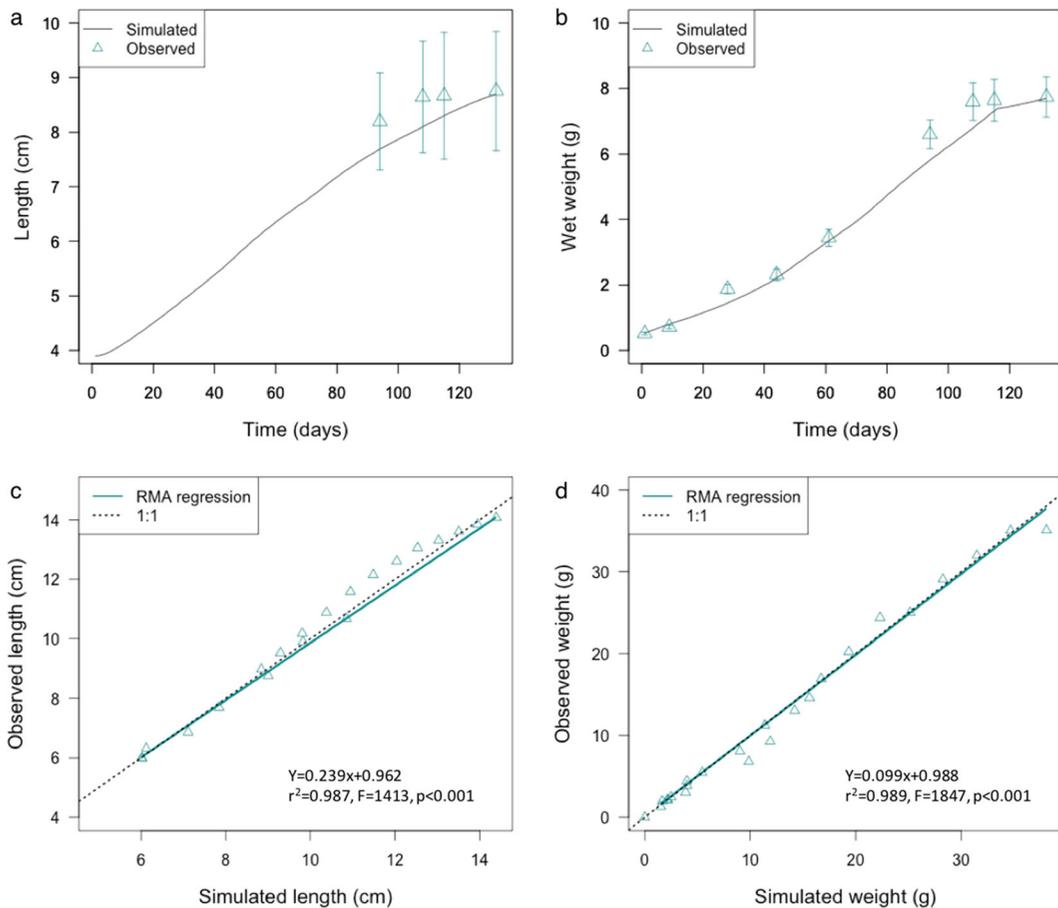


Fig. 3 Simulated (—) and observed (Δ) growth represented by length (a) and wet weight (b) from the Hatchery 2016 dataset; RMA regression (—) for wet weight (c) and length (d) comparing observed versus predicted data points for all validated data sets:

Rowe and Thorpe (1990), Imholt et al. (2011), and Hatchery data from 2013 and 2015 and a 1:1 regression line (—), figures created using R studio

Table 2 Sensitivity test results – percent change in weight and length that occurred after each parameter was increased and decreased by 10%

Parameter	Percent change weight (+10%)	Percent change weight (–10%)	Percent change length (+10%)	Percent change length (–10%)
κ	–0.8	–0.8	–0.9	3.1
$[E_G]$	–4.9	–11.4	3.79	15.6
$[\dot{p}_M]$	3.3	16.9	–5.3	–14.7
\dot{v}	–0.22	0.9	–2.3	–5.2
T_A	1.26	6.7	–2.9	–5.3
T_{AL}	–0.87	0.5	–0.9	0.5
T_L	–1.48	–0.5	–0.9	0.5
δ	–2.1	24.6	2.7	–25.5
%DW	–0.87	8	–0.3	–5.5
g to J	–0.87	–1.8	–0.9	3.1
l_m	3.7	–1.7	–1.7	–2.6

Food availability and migration

Differences in both means and variance in the number of days until reserve depletion (simulated by the model) were observed across body condition groups. On average, smolts with higher body condition could survive longer without food than smolts with lower body condition (Fig. 4a). Highest-condition smolts also showed the lowest variation in the number of survival days, with a range from 34 to 54 days. Lowest-condition smolts exhibited the greatest survival variation, with a range of survival from 0 to 35 days.

Smolts' food availability requirements while traveling through the Bras d'Or were assessed (Fig. 4b). Based on DEB predictions, food availability within Bras d'Or would not have needed to be very high in order to meet the needs of smolts during the period they stayed within the lakes. The majority of smolts (69%) would not have required any food during the time they remained within the Bras d'Or Lakes system. Other smolts (31%) would have required food in varying amounts between $f=0.05$, (low food availability); and 0.15, (higher food availability). Therefore, a minimum food availability of 0.15 would have been enough to guarantee the survival of all tagged smolts for the amount of time they were detected within the Bras d'Or. These food requirement values represent the level of food availability that had to be within the Bras d'Or to

explain the survival of the smolt for the entirety of their migration. Food availability is represented on a scale of 0 to 1 representing increasing food availability from none to ad libitum. Smolts either had a food availability of 0.0, 0.05, 0.10, or 0.15, representing low to higher food availability requirements for individual smolts.

Body condition was found to be inversely proportional to food availability requirements (Fig. 4c). The percentage of smolts that required little or no food increased with increasing body condition when the low, medium and high body-condition groups were compared. Smolts requiring the highest food availability within the Bras d'Or (0.15) were all in the lowest body-condition group (Fig. 4c).

The percentage of smolts that exited the Bras d'Or increased with food availability requirements (Fig. 4d). Smolts that did not require food, were the most likely to have stayed; whereas, smolts that required the greatest amount of food (0.15) were the least likely to have stayed within the Bras d'Or (Fig. 4d).

The effect of food availability on growth rate

The modelled growth rate of smolts was directly related to food availability in the environment (Fig. 5). When food availability was between 0 and approximately 0.15 growth did not occur, suggesting that between food availabilities of 0.0 and 0.15 the energy assimilated from the environment by smolts is mostly used to pay maintenance costs. As food availability increased above 0.15, growth rate increased linearly. The highest growth rate was achieved when food availability was equal to 1 ($f=1$ represents food available ad libitum in the environment). Growth rate was inversely related to body condition; that is, low condition smolts showed the highest growth rate at all levels of food availability and high-condition smolts showed the lowest.

The effect of increased temperatures on smolt survival

The effect of three increased sea temperature scenarios on smolts' survival was assessed. Increasing daily water temperatures by +1 °C, +2 °C, and +3 °C reduced the number of days smolts could survive without food, with +1 °C causing the least and +3 °C the greatest reductions in survival days (Fig. 6). The greatest reduction in the number of days an individual smolt could survive without food compared to current temperature regimes was 10 days and occurred in the +3 °C scenario.

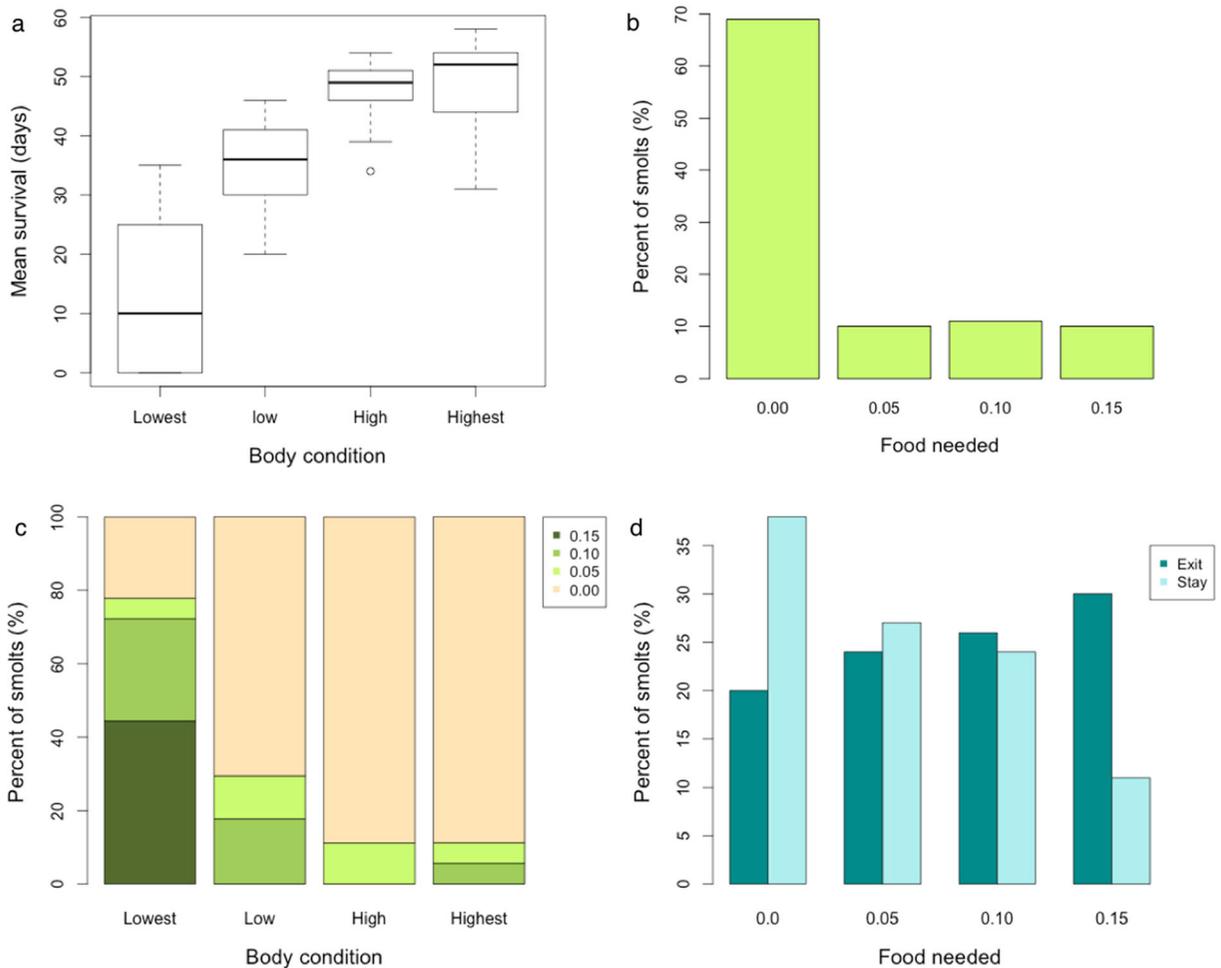


Fig. 4 **a** Boxplots comparing average number of days smolts can survive without food in quartile body condition: lowest, low, high, and highest **b** The number of smolts that would have required 0.00, 0.05, 0.10, or 0.15 food availability within the Bras d’Or in order explain their survival **c** The percentage of smolts in each body condition quartile (lowest, low, high, highest) that required

0.00 (orange), 0.05 (light green), 0.10 (medium green), and 0.15 (dark green) food availability in the Bras d’Or to explain their survival **d** Percentage of smolts that stayed (light teal) and exited (dark teal) the Bras d’Or Lakes that required 0.00, 0.05, 0.10, and 0.15 food availability to explain their survival, figures created using R studio

Discussion

Crossin et al. (2016) hypothesized that smolts with poor body condition left the Bras d’Or Lakes sooner than those with higher body condition due to their higher bioenergetic/feeding requirements that could not be met in the nutrient-poor Bras d’Or system. Using the Atlantic salmon DEB model and acoustic telemetry records, this study developed mechanistic models to assess the validity of the Crossin et al. (2016) hypothesis. Two main questions were addressed. The first examined the relationship between smolts’ bioenergetics and smolts’ migratory strategy. Results indicated that food requirements of individual smolts influenced the migratory

tactics employed during their migration. Smolts with higher food requirements were more likely to leave the Bras d’Or system for the ocean during the time of observation. The second question focused on the effect increased water temperature could have on smolts’ energetic requirements. Model simulations assessed the extent to which temperature rises would result in a more rapid depletion of the smolt’s body reserves over 1 °, 2 °, and 3 °C, respectively.

This knowledge provides valuable insights into the influence of energetic/feeding requirements and temperature on smolts’ energy budget and migratory tactics within the complex Bras d’Or system as well as other sites where Atlantic salmon migrate. Previous studies

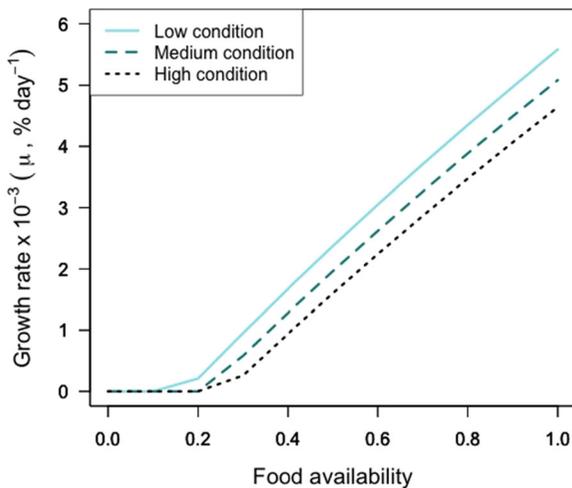


Fig. 5 Predicted growth rate for smolts of low (—), medium (---), and high (····) body conditions with different environmental food availabilities (0.00, 0.05, 0.10, 0.15), figure created using R studio

with Atlantic salmon in the Bras d’Or system and elsewhere have looked at the isolated effects of factors such as water temperature (Jonsson and Ruud-Hansen 1985; Zydlewski et al. 2005), body condition (Crossin et al. 2016), and food rations (Lans et al. 2011; Vainikka et al. 2012) on smolt migration behaviour. This study assessed the combined effects of these factors using a mechanistic approach by modelling the smolt’s energy budget throughout their migration; observing how differences in body condition, feeding requirements, and

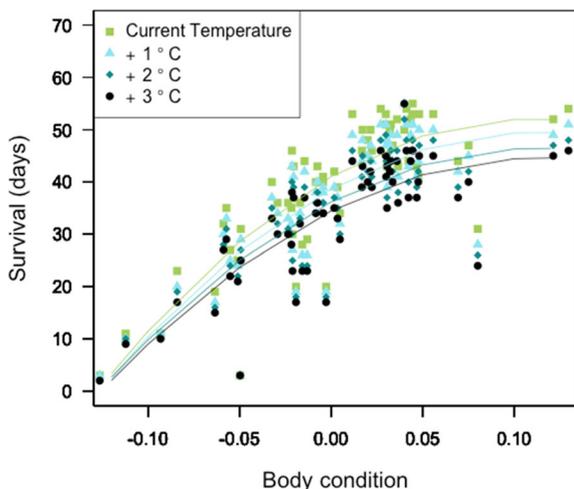


Fig. 6 The effect of body condition and temperature: current (■), +1°C (▲), +2°C (◆), +3°C (●) on the number of days smolts can survive without food, trend lines are only used for visual purposes, therefore, equations were not displayed, figure created using R studio

temperature impacted smolts’ energetic costs. Results provided evidence to support Crossin et al. (2016) hypothesis that the timing of smolts leaving for the ocean is related to their food requirements. This is also consistent with other experimental studies that have found reduced food rations have hastened the migration of smolts (Lans et al. 2011; Vainikka et al. 2012). Furthermore, this study provided predictions for how future increased water temperatures in the Bras d’Or could alter smolts’ energetic requirements and migration.

Food availability has been hypothesized to be one of the reasons for the evolution of diadromous migration, allowing smolts to take advantage of two habitats with differing benefits and costs (Gross et al. 1988). Smolts migrating to ocean environments that have higher food availability allows them to feed and grow rapidly, with benefits for both survival (larger fish are less predator vulnerable) and reproduction (Gross et al. 1988). Alternatively, freshwater environments, although comparatively nutrient-poor, offer a safer habitat for juveniles (Brönmark et al. 2008). Smolt migration is influenced by this trade-off between predation risk and feeding opportunities (Brönmark et al. 2008).

The effect of food ration manipulation on salmonid parr migration has been examined in several empirical studies. In juvenile Atlantic salmon, reduced food rations the year before migration lead to increased likelihood of smoltification and faster out-migration speed, but with no apparent benefit on longer-term survival (Lans et al. 2011; Vainikka et al. 2012). Similar findings have been obtained in anadromous brown trout (*Salmo trutta*), where reduced food rations led to an increase in the number of brown trout juvenile smolting and migrating to sea (Wysujack et al. 2009; Davidsen et al. 2014; Jones et al. 2015). Related to food availability, body condition also has been found to influence migratory behaviours. Crossin et al. (2016) found that body condition was correlated with the variability in residency duration within the Bras d’Or. Lower body-condition smolts exited the Bras d’Or system sooner than higher body-condition smolts. The current study builds on the results of Crossin et al. (2016) by modelling a smolt’s energy budget throughout their seaward migration and by providing mechanistic evidence to support the hypothesis that the bioenergetic needs of smolts constitute a predictor of variability among smolts in individual exit timing (Crossin et al. 2016). Due to the trade-off between food availability and predation, smolts with higher food requirements may adopt the riskier strategy

of exiting the Bras d'Or sooner in order to reach areas of higher food availability more quickly (Gross et al. 1988; Crossin et al. 2016). By contrast, smolts with higher body reserves may stay within the Bras d'Or in order to take advantage of a lower risk of predation (e.g., Brönmark et al. 2008; Crossin et al. 2016).

Time series data are providing evidence that rising water temperatures are causing changes in the timing of seaward migration of Atlantic salmon. Otero et al. (2014) examined the time of migration in rivers across the North Atlantic over the past five decades. Their findings showed that the timing of smolt migration has advanced at a rate of 2.5 days per decade. Changes in the timing of smolt migration due to higher water temperatures also has been observed in Bush River, Northern Ireland (Kennedy and Crozier 2010) and rivers connecting to the Gulf of Maine, Nova Scotia (Friedland et al. 2003). These findings coincide with the DEB models' prediction that warmer water temperatures may lead to more rapid depletion of body reserves, and given the other findings from this study, hasten smolt migration within the Bras d'Or and possibly across the species range.

The timing of smolts' migration is particularly relevant because of its relationship with survival. Although this study did not specifically examine the effect that an advancement in migration may have on the Bras d'Or population, previous studies assessed the effect migration timing has on the survival of other Atlantic salmon populations (Friedland et al. 1998, 2003; Hvidsten et al. 2009; Kennedy and Crozier 2010; Friedland et al. 2014). During the optimal "smolt migration windows", smolts enter the ocean at times when they would most likely encounter favourable conditions for survival (McCormick et al. 1998; Hansen et al. 2003). Smolts entering the ocean outside of the "smolt window" can have reduced survival chances (Hvidsten et al. 2009) due to adverse conditions (Byron et al. 2014; Renkawitz et al. 2015; Moriarty et al. 2016).

The effect that increased water temperature may have on the timing of the smolt migrations is difficult to assess without controlling other environmental factors. Oxygen saturation may negatively impact smolts during their migration (Jonsson and Jonsson 2009; Remen et al. 2013). Increasing temperature could also influence the production of important prey types positively or negatively within the Bras d'Or, which might in turn alter the residency of smolts within the lakes. These issues were not addressed in this study but may prove beneficial topics for further research.

Our parameterization is based on some direct measurements and mathematical optimization, a common method to estimate and reduce uncertainty in ecological modelling (e.g., Lika et al. 2011). However, the addition of empirical datasets such as, starvation experiments, specific measurement of percent dry weight, and additional growth records of Middle River juveniles would be beneficial in further reducing model uncertainty. The DEB model was used to assess smolt mortality based on the depletion of the state variable reserves. Reserve depletion is probably a conservative indicator of mortality due to the ability of organisms to draw on structural tissues for energy past the point of reserve depletion. Although the number of days until depletion may be lowered, the response (higher temperature lead to quicker reserve depletion) would not be affected. The index used for food availability (0–1) should be understood as a qualitative scale ranging from no food to plenty of food. Therefore, the addition of a quantitative proxy for food availability that is directly related to Atlantic salmon diet could further validate the findings of this study and improve the model's predictive ability.

Certain limitations were posed by the acoustic telemetry technology, principally its inability to distinguish among smolts that may have stayed in the Bras d'Or, and smolts that may have died in the Bras d'Or or possibly evaded detection. We do not, however, believe that these limitations would be likely to fundamentally change our conclusions. The gates had high detection efficiencies (82.4%–96.6%) which reduced the likelihood of smolts passing by undetected. Although there is uncertainty associated with smolts that could be dead within the Bras d'Or instead of residing within the lakes; even excluding the stay group, and solely observing the exit group (which has a lower level of uncertainty, due to high gate efficiencies) we can still make the same association between food requirements and migration. As food requirements increase a higher percentage of smolts exit to the ocean. This allows us to make the same conclusion, food requirements impact migration, and the higher food requirements an individual has the more likely they are to exit.

The results of this study show how food availability and temperature could affect the energy budget of smolts travelling through the Bras d'Or estuary and influence their residency time within the lakes. We provide mechanistic evidence to support the empirical hypothesis proposed by Crossin et al. (2016) that low-condition smolts exit the Bras d'Or sooner than high-

condition smolts because of their higher food requirements. The results of the increased temperature scenarios also suggest that warming lake temperatures may cause a more rapid use of body reserves by smolts, which could in turn lead to a higher percentage of smolts exiting to the ocean more rapidly due to their higher food availability requirements.

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