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Cyclical and stochastic thermal variability affects survival and growth in brook trout

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ABSTRACT

Directional changes in temperature have well-documented effects on ectotherms, yet few studies have explored how increased thermal variability (a concomitant of climate change) might affect individual fitness. Using a common-garden experimental protocol, we investigated how bidirectional temperature change can affect survival and growth of brook trout (*Salvelinus fontinalis*) and whether the survival and growth responses differ between two populations, using four thermal-variability treatments (mean: 10 °C; range: 7–13 °C): (i) constancy; (ii) cyclical fluctuations every two days; (iii) low stochasticity (random changes every 2 days); (iv) high stochasticity (random changes daily). Recently hatched individuals were monitored under thermal variability (6 weeks) and a subsequent one-month period of thermal constancy. We found that variability can positively influence survival, relative to thermal constancy, but negatively affect growth. The observations reported here can be interpreted within the context of Jensen's Inequality (performance at average conditions is unequal to average performance across a range of conditions). Projections of future population viability in the context of climate change would be strengthened by increased experimental attention to the fitness consequences of stochastic and non-stochastic thermal variability.

1. Introduction

Temperature affects ectotherm physiology (Angilletta et al., 2004; Pörtner and Farrell, 2008; Farrell, 2009) with consequences for individual fitness and population viability, particularly under forecasted changes in climate (Rieman et al., 2007; Wenger et al., 2011a,b). In addition to directional shifts, increased thermal variability is predicted to be a concomitant of climate change (Hanson et al., 2012; Wang and Dillon, 2014). However, considerably less attention has been directed to how variability in temperature affects fitness-related traits independently of changes to the mean (Vasseur et al., 2014; Dowd et al., 2015). This represents an important knowledge gap, given that thermal variability can represent a central determinant of ectotherm responses to environmental change (Colinet et al., 2015; Sinclair et al., 2016).

Predictions of how temperature variability might affect individuals and populations depend on how variability is quantified (Dowd et al., 2015; Bozinovic et al., 2016; Sinclair et al., 2016). Thermal variation can be manifest in various ways, e.g., cyclical vs non-cyclical; stochastic vs. non-stochastic; high-amplitude vs. low-amplitude cycles. It can also be manifest at various temporal scales (e.g., days, weeks, months, years), and at levels considered to be extreme in the context of a species' or population's thermal performance curve (Sinclair et al., 2016). This can make it challenging to study the effects of bidirectional changes in temperature under laboratory conditions in a consistent and readily comparable manner both within and among species, which might account for the paucity of such studies relative to the amount of research on directional thermal change.

Predicted responses to thermal fluctuations will also depend on the degree to which the temperature variations encompass the thermal optimum for the species, or population, under study (Morash et al., 2018). Here, the application of Jensen's Inequality (Jensen, 1909) has proven invaluable in predicting and interpreting changes in metrics of individual 'performance' (e.g., metabolic rate, growth rate) resulting from fluctuating changes in temperature (Ruel and Ayres, 1999; Denny, 2017).

Experimental work on thermal variability has largely focused on invertebrates (e.g., Kingsolver et al., 2009; Williams et al., 2012; Colinet et al., 2015). Among vertebrates, there has been some work on reptiles (Du and Ji, 2006; Les et al., 2009) and amphibians (Niehaus et al., 2012) but comparatively little on fishes (Morash et al., 2018).

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The effects of thermal variability on per capita population growth rate have been modelled for at least one endotherm (black-faced spoonbill, *Platalea minor*; Pickett et al., 2015) and experimentally explored for the green alga *Tetraselmis tetrahele* (Bernhardt et al., 2018).

Here, we examine the effects of thermal variability on two populations of brook trout (*Salvelinus fontinalis*), a fish widely distributed throughout eastern North America. For guidance regarding our laboratory levels of temperature and temperature variability, we examined water temperature data for four rivers in close proximity (< 100m to 5 km) to our study populations to ensure that our thermal experimental treatments reflected those likely to be experienced under natural conditions. According to Hanson et al. (2012), between the periods of 1951–1980 and 1981–2010, the standard deviation (σ) of global surface temperatures increased 16% during summer (June–August) and 7% during winter (December–February). However, more than 20% of the globe experienced an increase of more than 2σ in 2009, 2010, and 2011 (relative to the 1951–1980 baseline; Hanson et al., 2012). Given this information, as discussed in more detail in sections 2.2 and 2.3, our experimental value of 1.24σ can be interpreted as encompassing an empirically defensible increase in thermal variability that trout might be expected to experience under climate change.

Our primary objective is to explore how predictably cyclical and stochastic thermal variability might affect survival and growth in the early, post-hatching stage of life. Changes in water temperature are likely to be particularly important in early development, especially for fish such as trout that depend on a yolk sac for nutrition prior to the initiation of exogenous feeding (Jensen et al., 2008). Using a common-garden experimental protocol, we address a secondary objective of determining whether survival and growth responses to thermal variability are likely to differ genetically between populations of the same species.

2. Materials and methods

2.1. Study populations

The two study populations of brook trout inhabit Ouananiche Beck (46° 39.0′ N, 53° 11.0′ W) and Watern Cove River (46° 37.9′ N, 53° 9.5′ W), small rivers on Cape Race, Newfoundland, Canada (bounded by 53°16′ W, 46°45′ N, 53°04′ E, and 46°38′ S). This small, barren, coastal region is traversed by multiple short (0.27–8.10 km), low-order streams most of which contain resident trout populations that are genetically distinct from one another (Hutchings, 1993; Belmar-Lucero et al., 2012; Wood et al., 2014). Life-history differences among populations are thought to represent adaptive responses to environmentally different selective regimes, following habitat fragmentation (Hutchings, 1993, 1996; Wood et al., 2014). Phylogeographic work suggests that the populations originated from a common ancestor and have been isolated since the Wisconsin deglaciation (Danzmann et al., 1998).

2.2. Temperature

The experimental protocol subjected trout to either a constant (10 °C) or variable temperature (range: 7° to 13 °C; section 2.3), based on an empirically defensible suite of values experienced by the two source populations in the wild. The best available temperature data for Cape Race brook trout are those measured hourly over a one-year period (October 2009 to September 2010) in four separate rivers, using HOBO data loggers (Fig. 1; Table 1): Bristol Cove River, Cape Race River, Cripple Cove River, and Whale Cove River. One of our study populations (Ouananiche Beck) is a tributary of Bristol Cove River, and the other (Watern Cove River) is located 2–5 km from these four rivers. Combining data for all four rivers yields a mean of 9.59 °C and a σ of 2.41 °C for the days between 16 May and 15 June, the approximate time frame originally intended for the experiment.

Based on linear quantile-quantile plots for each dataset, the temperature data are distributed normally, meaning that 68.2% of the pooled-temperature values would fall within the range of 9.59 ± 2.41 °C. Put another way, at 1σ of the observed average mid-May to mid-June temperatures in 2010, 68.2% of the temperatures experienced by trout would be expected to fall between 7.18 and 12.00 °C (a range of 4.82 °C). For logistical reasons, the actual dates of our experiment differed slightly from the planned time period, extending from 26 April to 5 June. For these dates, the pooled temperature data for the four Cape Race rivers averaged 8.28 °C with a σ of 2.40 (Table 1). Under normality, 68.2% of the temperatures in the wild would fall between 5.88 and 10.68 °C, a range of 4.80 °C. The temperatures to which the experimental trout were exposed ranged between 7 and 13 °C. This range (6 °C) is 24% greater than that associated with 1σ for both the mid-May to Mid-June (4.82 °C) and late-April to early-June (4.82 °C) periods. Thus, the range in temperatures in our common-garden experiment can be thought of as approximating an anomaly of 1.24σ relative to 2010 conditions, an increase that falls well within the measurable increase in global surface temperatures documented by Hanson et al. (2012).

2.3. Experimental design

After one generation in the laboratory, mature adults originating from the two populations were reared and spawned at Concordia University, Montreal, in November 2015. For each population, 5 males were each crossed with 6 different females, resulting in 30 families per population. On 1 February 2016, fertilized eggs and recently hatched individuals were transported to the Aquatron Facility at Dalhousie University where they were acclimated to laboratory conditions in small, 2.8-L flow-through aquaria at 5 °C. On 26 April, trout were subjected to one of four temperature variability treatments: (1) a constant temperature of 10 °C; (2) a periodic, cyclical fluctuation of 3 °C every two days, with temperatures ranging from 7° to 13 °C; (3) a stochastic or random fluctuation of ± 3° or 6 °C every two days, with temperatures ranging from 7° to 13 °C, i.e., the ‘low-stochasticity treatment’; and (4) a treatment analogous to (iii) but with the stochastic temperature change occurring daily, i.e., the ‘high-stochasticity treatment’. The temperatures were achieved by cooling or heating ambient water provided to three separate, temperature-controlled header tanks that provided a constant flow (0.5 L min^{-1}) of water to each of the experiment tank racks. The temperature of the water in each header tank was measured daily.

Fish were randomly selected for each replicate tank from a pool of all available fish in each population. There were 5 and 7 replicates for the Watern Cove and Ouananiche Beck populations, respectively. Twenty-seven individuals were placed in each replicate tank (all tanks were identical) one week before the start of the experiment and subjected to the same photoperiod, light intensity, water flow, and food (fish were fed daily with an identical mixture of live shrimp, *Artemia* spp., and dry Corey Aquafeeds ® 0.7 mm pellets). The periodic treatment followed a cyclical pattern of 7°-10°-13°-10°-7 °C. Temperatures associated with the stochastic treatments (either 7°, 10° or 13°) were chosen randomly, using a random number generator (Fig. 2).

Three aquarium racks, each supporting sixty 2.8-L, flow-through tanks, were established at one of the three experimental temperatures. The experimental tanks were separated by rack, or temperature, and randomly allocated to a location within the rack. Temperature changes (i.e., reassignment of tank location among racks) occurred every two days for tanks associated with the constant, cyclical, and low-stochasticity treatments, and every day for those associated with the high-stochasticity treatment. Tanks were randomly allocated to a position on a rack each time a temperature change occurred. Any tank not moved to a different rack on a given day (i.e., staying at the same temperature) was randomly re-allocated to a different position on the same rack. Tanks associated with the high-stochasticity treatment were re-distributed within the same rack if they were subjected to the same

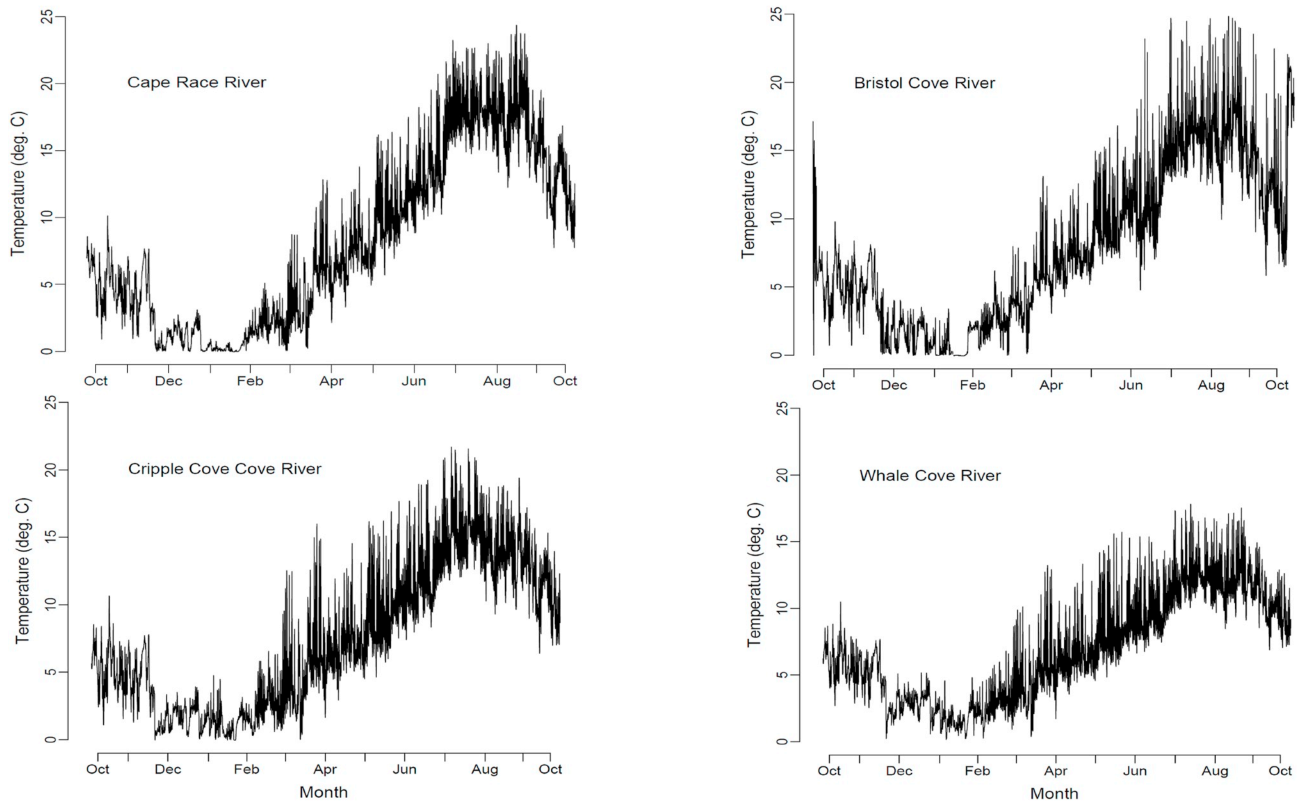

Fig. 1. Water temperature recorded hourly for one year in four rivers on Cape Race, Newfoundland, Canada.

Table 1
Water temperature data (mean; standard deviation, σ), based on hourly measurements recorded in 2010, for four rivers on Cape Race, Newfoundland. Proposed experimental dates: 16 May to 15 June; actual experimental dates: 26 April to 5 June.

Population	Temperatures during proposed experimental dates		Temperatures during actual experimental dates	
	mean	σ	mean	σ
Bristol Cove River	9.85	2.42	8.30	2.25
Cape Race River	10.50	2.29	8.67	2.46
Cripple Cove River	9.51	2.64	8.81	2.68
Whale Cove River	8.51	2.27	7.34	2.40
Pooled data	9.59	2.41	8.28	2.40

temperature for more than two consecutive days.

The duration of the experimental period was 41 days, ending on 5 June 2016. The following day, all fish were transferred to the 7 °C rack and left undisturbed for 5 weeks. Water temperatures were measured daily for each of the experimental racks to compare the nominal (intended) temperatures with the actual (measured) temperatures. For logistical reasons, actual temperature data were available daily for all three racks from days 11 through 41.

On 13 July 2016, a post-experimental monitoring period (31 days) was initiated to examine whether differences in survival and(or) growth between treatments and(or) populations during the experimental period persisted after a period of environmental constancy. Two to three replicates per treatment for each of the populations (twenty, 9-L, flow-through aquaria in total) were randomly created from the existing tanks. The experimental tanks were randomly allocated to fill one of thirty positions on a single rack. The position of all tanks remained constant until the end of the post-experimental period on 11 August 2016. Each tank

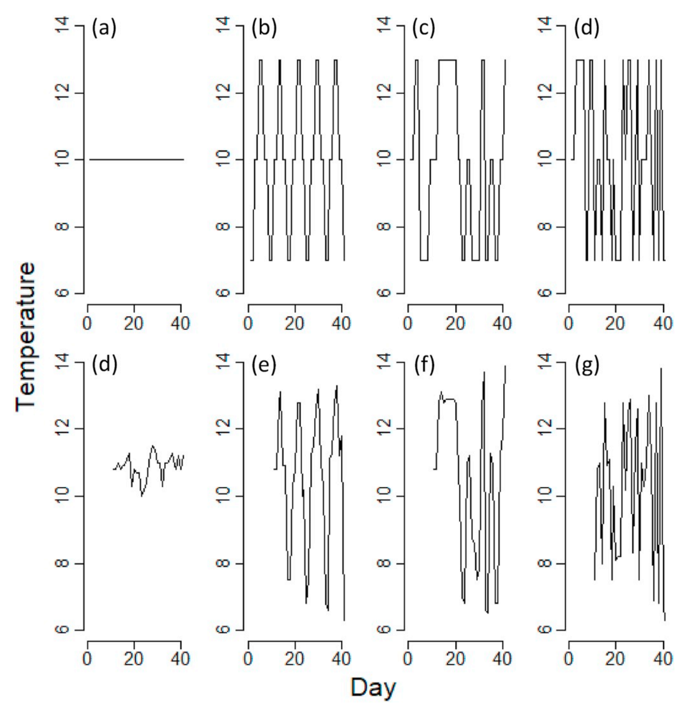

Fig. 2. Nominal (intended) daily experimental temperatures under the (a) constant, (b) cyclical, (c) low-stochasticity, and (d) high-stochasticity experimental treatments, and the actual temperatures experienced by brook trout for the (d) constant, (e) cyclical, (f) low-stochasticity, and (g) high-stochasticity treatments during days 11 through 41 of the experimental period.

experienced the same daily ambient water temperature which ranged between 13^0 and 17 °C. Fish were fed daily with an identical mixture of dry Corey Aquafeeds 0.7 mm pellets and dry 1.2 mm pellets.

2.4. Data collection and analysis

Mortalities were recorded daily for each tank during the experimental and post-experimental periods. Using a Kaplan-Meier survival analysis (Goel et al., 2010), we examined the effect of population, treatment, and replicate on time (in days) to death. A parametric model (*survreg* function in R) with a Weibull distribution and a non-constant hazard (cf. Ergon et al., 2018) with age were used to analyze the survival data.

Individual lengths were estimated from photographs (using an iPhone 7), using ImageJ 1.50i software (Schneider et al., 2012). Unanesthetized fish were collected from the tanks with a small net and placed on a white, styrofoam plate. A ruler was used as a reference in each photograph, and measurements (to the nearest 0.1 mm) were taken between the two longest points on the body. Once a clear photo had been taken of the entire body, the fish were placed back into the tanks. Length data were analyzed with a linear mixed-effects model. We examined the effect of population (fixed effect), treatment (fixed effect), number of surviving fish in each tank (fixed effect), and replicate (random effect) on total fish length. This analysis was undertaken on the data collected at the end of the experimental period (6 June 2016).

Model fitting and stepwise reduction of the models were performed with ANOVA (including all two-way interactions; none of which were significant, $p > 0.05$) and by AIC (*step* function in R). Treatment levels were combined where possible by pooling levels with similar intercept values. This was performed as a means of post-hoc analysis to determine the statistical relationships between treatments. All analyses were conducted with the survival (Therneau and Grambsch, 2000) and lme4 (Bates et al., 2015) packages in R (Version 3.3.2; R Core Team, 2016). Differences in average temperature among treatments were tested, using an ANOVA. We used the R package cvequality (Version 0.1.3; Marwick and Krishnamoorthy, 2019) to test for significant differences in the coefficient of variation (CV = σ/mean) between the cyclical, low-stochasticity, and high-stochasticity treatments, using the Feltz and Miller (1996) *D' AD* test statistic.

3. Results

During the experimental period, the actual water temperatures differed slightly from the intended nominal temperatures (Fig. 2). Nonetheless, the average (± σ) did not differ among treatments (constant: 10.89 ± 0.35 °C; cyclical: 10.53 ± 2.16 °C; low-stochasticity: 10.52 ± 2.47 °C; high-stochasticity: 10.08 ± 2.29 °C; $F_{[1,122]} = 2.649$; $p = 0.106$). Considering only the variable treatments, there were no differences in either the means ($F_{[1,91]} = 0.596$; $p = 0.442$) or the CVs (*D' AD* = 0.518; $p = 0.772$).

The number of surviving individuals declined in all four experimental treatments (Fig. 3). The constant, cyclical, and low-stochasticity treatments exhibited similar patterns of decrease during the initial three weeks, with noticeable differences in survival only becoming evident between days 20 and 30, and at the end of the experiment on day 41. A rapid decline in survival was observed among trout in the constant treatment near the end of the experimental period, such that their proportionate survival (0.75) was similar to that of trout in the high-stochasticity treatment (0.74). At the end of the experimental period, the combination of the cyclical and low-stochasticity treatments was associated with significantly higher survivorship than the combination of the constant and high-stochasticity treatments ($p < 0.01$).

At the population level, combining all treatments, survival decreased throughout the experimental period (Fig. 4). The Watern Cove population experienced significantly higher survival than the Ouananiche Beck population between days 27 and 38.

During the 30-day, post-experimental period, when all trout experienced the same, constant-temperature conditions, survival continued to decline, particularly for fish in the constant-temperature treatment. The treatments were observed to be distinctly grouped into pairs, with the combination of fish in the cyclical and high-stochasticity treatments experiencing significantly higher survival than the combination of the constant and low-stochasticity treatments ($p = 0.019$). During the post-experimental period, Watern Cove trout experienced higher mortality than those from Ouananiche Beck $p = 0.003$).

At the end of the experimental period, fish were significantly longer in the constant and low-stochasticity treatments when compared to the combination of the cyclical and high-stochasticity treatments ($p = < 0.001$; Fig. 5). Comparing populations, Watern Cove trout were significantly smaller than those from Ouananiche Beck ($p = 0.032$).

4. Discussion

The present study examined how cyclical and stochastic thermal variability, independently of changes in average temperature, can affect the growth and survival of a widespread freshwater fish. Brook trout survival early in life was lower under constant temperatures than it was under temperatures that fluctuated with regular cycles or with a relatively low level of stochasticity. There was some indication that survival was higher under regularly cyclical temperatures than under temperature regimes characterized by some level of stochasticity. Fish achieved larger sizes under the constant and low-stochasticity treatments. The common-garden experimental protocol provided an opportunity to compare growth and survival responses to thermal variability between two spatially proximate populations. The data suggest that these thermal responses differ genetically at the population level, a finding consistent with a previous thermal-acclimation study on this species (McDermid et al., 2012).

Thermal constancy did not yield higher survival probabilities than temperatures that were temporally variable. These results are similar to those reported for some reptiles. In a laboratory study on painted turtles (*Chrysemys picta*) and red-eared sliders (*Trachemys scripta*), Les et al. (2009) found that egg survival was higher at daily fluctuations (± 3 °C) around a mean of 23^0 when compared to eggs incubated at a constant temperature of 23 °C (the lower limit of viable incubation temperatures for the species). For the northern grass lizard (*Takydromus septentrionalis*), Du and Ji (2006) reported that fluctuating temperature treatments produced hatchlings with higher locomotor performance, lower mortality, and relatively large body sizes.

These findings raise interesting questions concerning the utility of rearing ectotherms at invariant temperatures (Morash et al., 2018), a practice common among laboratory studies of selection, plasticity, and physiological performance. However, from an ecological or evolutionary perspective, our findings of a relatively poor ‘performance’, as reflected by survival, in a thermally constant environment are not surprising, given that thermal fluctuations are normal for ectotherms in the wild, as amply illustrated in Fig. 1. If, as seems reasonable to assume, ectotherms are locally adapted to naturally occurring variability in temperature, it might not be surprising that they experience higher survival under conditions of fluctuating, rather than constant, temperatures similar to what they would experience in nature (cf. Dowd et al., 2015). This was the conclusion reached by Niehaus et al. (2012) on striped marsh frogs (*Limnodynastes peronii*) who found that empirical models based on temperature constancy poorly predicted the performance of this amphibian under fluctuating temperatures.

It can also be argued that expectations of higher performance under constant rather than variable temperatures very much depends on the strength of Jensen's Inequality (Jensen, 1909) which stipulates that performance under average conditions is unequal to average performance across a range of conditions (Sinclair et al., 2016; Denny, 2017). Although uncommon in the ecological literature (but see Pickett et al. (2015), Bernhardt et al. (2018), and Morash et al. (2018)), consideration of Jensen's Inequality has been prominent in the physiological literature (Martin and Huey, 2008; Denny, 2017).

Jensen's Inequality pertains to the degree to which the relationship between individual performance and a variable such as temperature

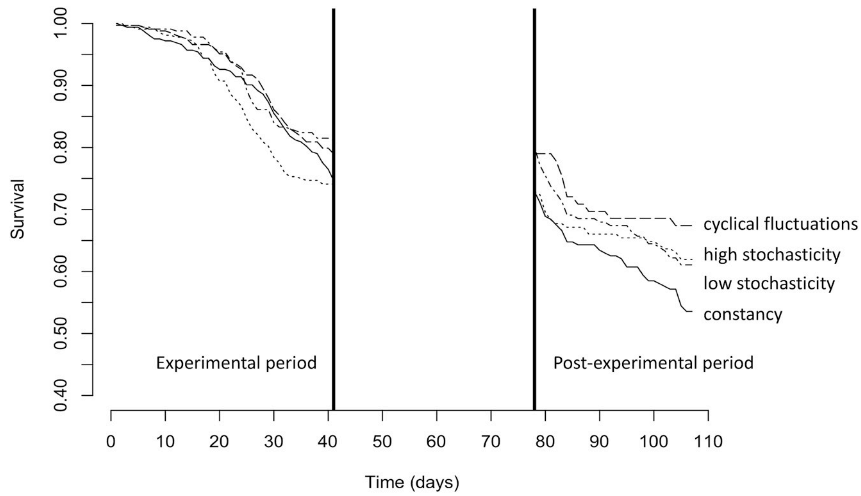

Fig. 3. Kaplan-Meier survival patterns for brook trout subjected to four thermal variability treatments during and after the experimental period.

departs from linearity (Fig. 6). Non-linear relationships between metrics of performance such as growth have been documented for many fishes, including brook trout (Farrell, 2009). For the range in temperatures examined here (7⁰–13 °C), the relationship with growth rate represents a decelerating function (sensu Ruel and Ayres, 1999, Fig. 6). According to this function, constancy at the average temperature in our experiment (~10 °C) is expected to be associated with faster growth than the average growth across the range of temperatures used in the experiment. Thus, the relationship between growth and thermal variability documented in the present study is consistent with expectations based on Jensen's Inequality. We also note, however, that the shape and position of a thermal performance curve is likely plastic and may be affected by acclimation temperature range.

Regarding survival, Farrell (2009) reported a slightly convex relationship (similar to that for growth; Fig. 6) between aerobic scope and temperature. However, it is unclear whether aerobic scope reliably reflects survival. It has been reported in juvenile Atlantic salmon (*Salmo salar*) that thermal fluctuations are associated with both increased (Beauregard et al., 2013; Oligny-Hébert et al., 2015) and reduced (Morash et al., 2018) metabolic rate, but again it is unclear whether metabolic rate is likely to be positively or negatively associated with

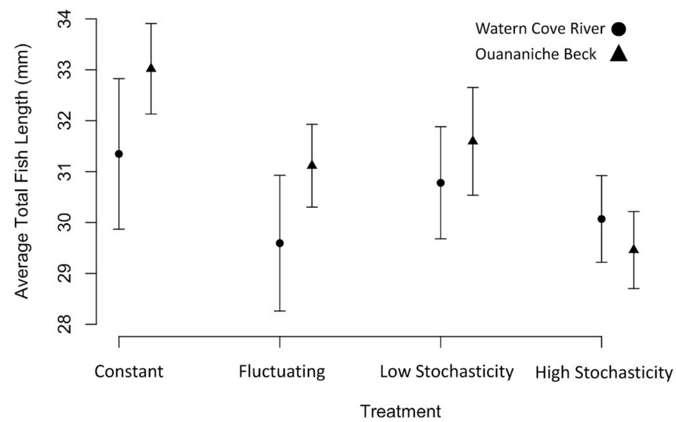

Fig. 5. Average total length (mm; ± 95% CI) of brook trout from two populations (Watern Cove River, Ouananiche Beck) subjected to four thermal variability treatments, at the termination of the experimental period.

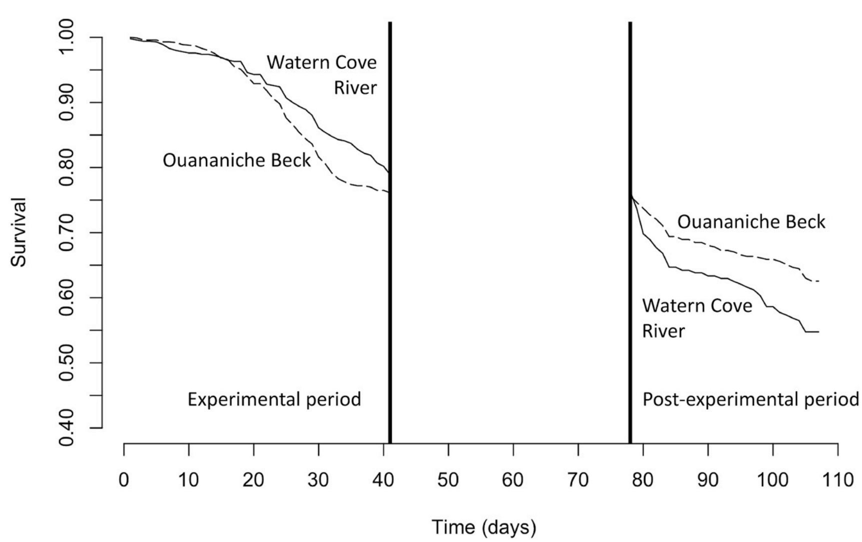

Fig. 4. Kaplan-Meier survival patterns for two populations of brook trout (Ouananiche Beck, Watern Cove River) subjected to four thermal variability treatments during and after the experimental period (data pooled within populations).

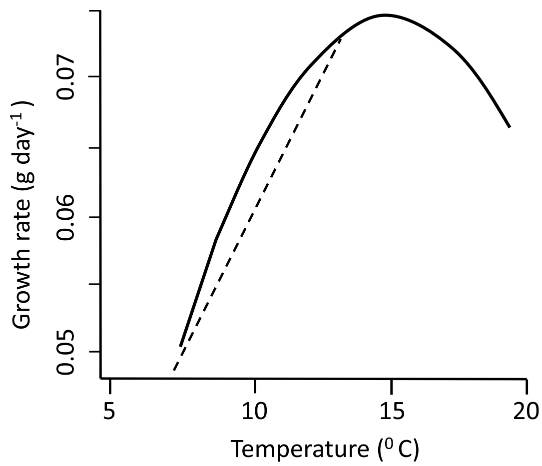

Fig. 6. Curvilinear relationship between water temperature and growth rate (solid line) in brook trout, as reported by Farrell (2009). For temperatures between 70 and 13 °C, the average growth rate (dashed line) is less than the growth rate at the average temperature of 10 °C (solid line).

survival (Burton et al., 2011).

Comparatively few studies have examined the effects of temperature variability on metrics of fitness in fishes independently of changes in mean temperature. We are aware of only three studies on survival, two of which also examined growth rate. In an uncontrolled field study on adult brook trout, Xu et al. (2010) reported positive or dome-shaped relationships between survival and temperature variability (as estimated by the CV, which was equal across our three variable-temperature treatments). In another salmonid, Hokanson et al. (1977) showed that temperature variability influenced the survival (and growth) of rainbow trout (*Oncorhynchus mykiss*) positively or negatively depending on whether the mean temperature was higher or lower than 16 °C, respectively. The work by Carveth et al. (2007) on the effects of thermal change on a southern Arizona fish (spikedace, *Meda fulgida*), while intriguing, confounded changes in temperature fluctuations with changes in mean temperature.

Relative to temperature constancy, slower growth has been reported to be associated with thermal fluctuations in several fishes (Cox and Coutant, 1981; Chadwick and McCormick, 2017; Morash et al., 2018). However, as documented by previous researchers (e.g., Morash et al., 2018; Penney et al., 2018), the influence of thermal fluctuations on developmental, physiological, and life-history traits can be conditional on factors such as population origin (Oligny-Hébert et al., 2015; present study), the degree to which thermal fluctuations occur near T_{opt} (the optimum temperature that maximizes performance; Morash et al., 2018), and other abiotic variables (Penney et al., 2018).

Notwithstanding some intriguing results and potential avenues for future research, we caution that the creation of thermally variable conditions can take many forms (e.g., cyclical vs non-cyclical; stochastic vs. non-stochastic; high-amplitude vs. low-amplitude cycles) and there can be logistical challenges in appropriately creating the intended variability. For example, upon examination of the actual temperatures experienced by our experimental fish, it was evident that trout in the cyclical treatment experienced more changes in temperature (on 20 of 40 days) than those in the low-stochasticity treatment (15 of 40 days; for comparison, those in the high-stochasticity treatment experienced a change in temperature on 27 of 40 days). As a result, trout exposed to the low-stochasticity treatment may have experienced a greater degree of temperature consistency than originally anticipated. One example of a logistical difficulty we faced was the challenge in creating the high-stochasticity treatment. In addition to experiencing a higher temporal level of thermal stochasticity, the tanks in which these fish resided were shifted every day rather than every two days. This more frequent change in tank position was necessitated by logistical constraints imposed by the temperature-control system in the laboratory. As a consequence, we are unable to conclude whether the differences between the trout in the high-stochasticity treatment and those in the other treatments were associated with differences in thermal stochasticity, frequency of tank relocation, or both (although every effort was made to shift the tanks as carefully as possible and with minimal movement of water within the tanks). Lastly, there can also be non-trivial challenges in replicating levels of thermal variability in the laboratory that are empirically defensible under natural conditions (although we have strived to do so; cf. Fig. 1).

5. Conclusions

The present study represents one of few that has explored the effects of thermal variability on metrics of fitness in an aquatic vertebrate. Within the context of our experimental protocol regarding levels of thermal constancy and variability, our results suggest that: (i) temperature variability at some level can positively influence survival relative to thermal constancy; (ii) growth rate is negatively affected by temperature variability; and (iii) common-garden experiments should incorporate empirically defensible measures of thermal variability as the baseline 'treatment' – rather than temperature constancy – for examining the effects of thermal variability on fitness. Given the challenge in determining the appropriate temporal scale at which thermal variability ought to be examined, perhaps an ideal approach would be to compare the effects of thermal variability at multiple temporal scales on fitness-related traits in a single experiment.

We conclude that the influence of stochastic and non-stochastic changes in temperature on individual fitness are not readily predictable (in part because thermal performance curves are not static) and that this field of endeavour warrants considerably more attention than it has received to date. Projections of future population viability in the context of climate change would be strengthened by increased experimental research on the fitness consequences of stochastic and non-stochastic thermal variability.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.jtherbio.2019.07.012.

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