Thermal habitat of flowing waters in Ontario: Growing season metrics for rivers and streams

Technical Report TR-76

Science and Research Branch
Ministry of Natural Resources

Ontario

Science and Research Technical Report TR-76

Thermal habitat of flowing waters in Ontario: Growing season metrics for rivers and streams

Isaac A. Sutton and Nicholas E. Jones

Aquatic Research and Monitoring Section, Peterborough, ON

2025

Science and Research Branch

Ministry of Natural Resources

Copies of this publication are available from info.mnrscience@ontario.ca.

Cette publication hautement spécialisée, Thermal Habitat of Flowing Waters in Ontario: Growing Season Metrics for Rivers and Streams, n'est disponible qu'en anglais conformément au Règlement 671/92, selon lequel il n'est pas obligatoire de la traduire en vertu de la Loi sur les services en français. Pour obtenir des renseignements en français, veuillez communiquer avec le ministère des Richesses naturelles au info.mnrscience@ontario.ca.

Some of the information in this document may not be compatible with assistive technologies. If you need any of the information in an alternate format, please contact info.mnrscience@ontario.ca.

Cite this report as:

Sutton, I.A. and N.E. Jones. 2025. Thermal habitat of flowing waters in Ontario: Growing season metrics for rivers and streams. Ontario Ministry of Natural Resources, Science and Research Branch, Peterborough, ON. Science and Research Technical Report TR-76. 17 p.

Abstract

Water temperature influences many physical, chemical, and biological processes in rivers and streams. The growing degree day (GDD) measures thermal energy accumulation through time and is a powerful predictor of overall ecosystem productivity and the growth and development of aquatic organisms. Current GDD estimates for Ontario's rivers and streams are derived from air temperature data and may be inaccurate due to the imperfect correlations between air and water temperature. We leveraged a large stream temperature data set and recently developed stream temperature models to model and predict growing season metrics in rivers and streams across Ontario. These models are accurate, have low bias, and represent an improvement upon existing GDD estimates based solely on air temperatures. The predictions have a variety of uses in resource management and facilitate future evaluation of ecosystem productivity in rivers and streams across Ontario.

Résumé

Habitat thermique des cours d'eau en Ontario : mesures de la saison de croissance pour les rivières et les ruisseaux

La température de l'eau influence de nombreux processus physiques, chimiques et biologiques dans les rivières et les ruisseaux. Le degré-jour de croissance (DJC) mesure l'accumulation d'énergie thermique au fil du temps et constitue un puissant indicateur de la productivité globale de l'écosystème ainsi que de la croissance et du développement des organismes aquatiques. Les estimations actuelles du DJC pour les rivières et les ruisseaux de l'Ontario sont dérivées des données sur la température de l'air et peuvent être inexactes, en raison des corrélations imparfaites entre la température de l'air et celle de l'eau. Nous avons exploité un vaste ensemble de données sur la température des cours d'eau et récemment développé des modèles de température des cours d'eau afin de modéliser et de prédire les paramètres de la saison de croissance dans les rivières et les ruisseaux de l'Ontario. Ces modèles sont précis, présentent un faible biais et constituent une amélioration par rapport aux estimations actuelles des DJC basées uniquement sur les températures de l'air. Les prédictions ont diverses utilisations dans la gestion des ressources et facilitent l'évaluation future de la productivité des écosystèmes dans les rivières et les ruisseaux de l'Ontario.

Acknowledgements

We thank the many biologists, technicians, and summer students who sampled streams and shared stream temperature data. Air temperature data was provided by Dan McKenney and colleagues from the Canadian Forest Service, Natural Resources Canada. This research was supported by funding from the ministry's Canada-Ontario Agreement on Great Lakes and the Integrated Monitoring Framework for Rivers and Streams. We appreciate thoughtful reviews from Trevor Middel and Henrique Giacomini of the Aquatic Research and Monitoring Section.

Contents

Introduction

Water temperature influences many physical, chemical, and biological processes (Caissie 2006, Webb et al. 2008). In streams, energy originates from the formation of chemical bonds through photosynthesis by primary producers (e.g., algae). Energy is transferred to higher trophic levels through the consumption of primary producers and liberated through the chemical breakdown of organic matter (e.g., algae, leaves, animal tissue) by respiration. Biochemical rates, metabolic rates, and the rates of nearly all other biological processes increase with temperature (Brown et al. 2004). The wide-ranging influence of water temperature in aquatic ecosystems has caused it to be described as an abiotic *master factor* and an *ecological resource* (Brett 1971, Magnuson et al. 1979). Relatively small changes in temperature can cause large changes in metabolic activity. For example, primary production was 20 times higher, and nutrient uptake 30 times greater, in the warmest streams across a geothermal temperature gradient (9.7–17.4 °C) in four Icelandic streams (Rasmussen et al. 2011).

Temperature plays an essential role in regulating metabolism and physiological rates in aquatic ectotherms[1] – a group that includes most aquatic invertebrate and fish species (Fry 1971, Huey and Stevenson 1979, Neuheimer and Taggart 2007). In turn, water temperature is an important control on growth in aquatic biota. Given the influence of body size on life history, demography, predator-prey interactions, and overwinter survival, it is important to understand differences in growth within and among populations (Fry 1971, Policansky 1983, Sogard 1997, Neuheimer and Taggart 2007). Productivity, the rate at which new biomass is added to an ecosystem, is directly related to biological processes such as growth and a useful quantitative metric that can provide insight into the effects of environmental change and disturbance (Brown et al. 2004, Dolbeth et al. 2012). As a result, a robust understanding of the factors influencing growth and productivity is needed to support effective resource management.

Fish growth rates increase as temperature increases up to a thermal optimum, and then decline rapidly as temperatures approach lethal thresholds (Vasseur et al. 2014, Payne et al. 2016). As a result, cumulative thermal energy exposure is a more relevant predictor of fish growth and size-at-age than calendar time (Neuheimer and Taggart 2007, Neuheimer and Taggart 2010). Degree days (DD; °C·day) are a physiologically relevant measure of an organism's "thermal history" (i.e., the cumulative thermal energy transferred to an organism from its environment). The DD has a long history in agriculture and entomology (Atkinson 1994, Bonhomme 2000), and more recent research has revealed its broad utility as a predictor of growth and size-at-age for aquatic biota (e.g., Markarian 1980, Neuheimer and Taggart 2007, Venturelli et al. 2010, Chezik et al. 2014).

Air temperature derived DD estimates are often used in studies on aquatic ecosystems due to a lack of in-situ water temperature data and evidence that air and water temperature derived DD are highly correlated in lacustrine systems (Honsey et al. 2019). However, few studies exist that evaluate the use of DD in lotic environments and recent evidence suggests that DD based on air temperature may be unsuitable for rivers and streams (Richter et al. 2024). Although incoming solar radiation is a major control on water temperature in lakes and rivers, water temperatures in lotic systems are influenced by a range of additional factors (e.g., groundwater inputs, stream

[1] Ectotherms are organisms that do not physiologically regulate internal body temperature, instead relying on heat exchange with the surrounding environment and behavioral adaptions (e.g., movement) to regulate temperature.

flow velocity, riparian shade) that make temperatures highly dynamic (Caissie 2006, Leach et al. 2023). As a result, correlations between air and water temperatures may be poor in rivers and streams, limiting the suitability of air temperature derived DD as a thermal history measure for organisms in lotic environments.

In this study, we modelled and predicted growing season length and accumulated degree days during the growing season (i.e., growing degree days; GDD) for rivers and streams in Ontario. We used a large stream temperature data set and recently developed stream temperature models (Sutton et al. 2024) to predict growing season length and GDD for the rivers and streams represented in the provincial aquatic ecosystem classification (AEC; Jones et al. 2025). Using empirical data, we also investigated correlations between air and water temperature derived GDD estimates in lotic systems. The modelled growing season characteristics have a variety of potential applications in research and management including evaluating productivity and differences in phenology.

Methods

Growing season metrics

Stream temperature records used to calculate empirical growing season metrics were extracted from a large data set compiled as part of a project to model July mean stream temperatures for Ontario (Sutton et al. 2024). This data was quality controlled to address common issues such as sensors drying during low flows, getting buried in sediment, or failing. Sites in streams influenced by lakes, dams, reservoirs, and urbanization were excluded because these features influence stream thermal characteristics (see Sutton et al. 2024 for methods and rationale). We extracted data from all sites that could be associated with an aquatic ecosystem classification (AEC; Jones et al. 2025) stream reach, excluding site-years where the time series did not extend beyond the summer months (i.e., June–August) and would not capture the full growing season. Daily mean stream temperatures were calculated from the sub-daily measurements available in the stream temperature data set, discarding days where > 20% of measurements were missing. This cut-off was applied to minimize bias and increase the likelihood of capturing daily minima and maxima.

We defined the growing season as the period from the beginning of the first week where mean weekly stream temperature exceeded and remained above the threshold temperature (T_0; see below) to last day of the first week where mean weekly stream temperature dropped below T_0. The accumulated degree days during the growing season (i.e., growing degree days; GDD) were then calculated as:

$$GDD = \sum_{i=1}^{N} T_i - T_0, \quad T_i > T_0$$

where N is the growing season length, T_i is the mean daily water temperature on the ith day of the growing season, and T_0 is a base or threshold temperature below which growth is assumed to be negligible. Chezik et al. (2014) recommended T_0 values of 0, 5, 10, and 15 °C commonly used in agriculture and entomology also be applied for aquatic ecosystems. We selected a base temperature of 5 °C for consistency with the air temperature derived growing degree days used in the AEC and because it is close to T_0 values recommended for many species in Ontario (Honsey et al. 2023).

Growing season metrics were initially calculated while ignoring gaps in the time series. We then discarded time series where missing data occurred during the growing season or where no valid growing season was found (e.g., the first or last record exceeded T_0 or daily temperatures never rose above T_0). By initially ignoring gaps, we ensured we did not exclude time series where gaps existed outside the growing season and would not affect the calculated growing season metrics.

Comparing air and water temperature derived growing season metrics

Air temperature derived growing season metrics are frequently used in investigations of aquatic ecosystems due to a paucity of water temperature data at the sites being studied (Honsey et al. 2019). Previous work in lacustrine systems showed strong correlations between growing degree days calculated using air and water temperature data. However, to our knowledge, no previous efforts have examined these correlations in lotic systems. As such, we explored the correlations between growing season metrics (i.e., season length and growing degree days) calculated using paired air and water temperature time series. We then explored how these relationships varied in relation to upstream catchment area (UCA) and base flow index (BFI) – characteristics known to influence correlations between air and water temperatures (Caissie 2006, Leach et al. 2023).

To facilitate comparison between air and water temperature based growing season metrics, we first paired each site-year of stream temperature data with air temperature data from a nearby Environment and Climate Change Canada climate station (https://climate.weather.gc.ca). Short gaps in the air temperature time series were common, so we first filled gaps up to one day long with the mean temperature of the days immediately before and after each gap. The decision to fill gaps in the air temperature time series was motivated by a desire to balance the precision of growing season estimates with potential errors introduced by pairing stream temperature sites with increasingly distant climate stations. After gap filling, we calculated growing season length and growing degree days for each air temperature time series and then assigned each site-year of water temperature data to the closest climate station with a valid growing season. The mean distance between stream temperature sites and assigned climate stations was 36.1 km (range = 2.4 to 166.5 km). Stream temperature sites were generally paired with multiple climate stations over their period of record, while within a year a single climate station was typically paired with several stream temperature sites.

Modelling growing season length and growing degree-days

Although GDD can be calculated empirically using the equation defined in the previous section, a paucity of stream temperature data makes it impossible to estimate GDD for most rivers and streams across Ontario. As such, we developed a model that exploits annual sinusoidal patterns in stream temperature to model GDD as a function of growing season length and the amplitude of the sine curve (Figure 1; Shuter et al. 1983). More specifically, GDD were modelled as $GDD = GSL + JulyT_W$ where GSL is the growing season length in days and $JulyT_W$ is July mean stream temperature in °C. We used July mean stream temperature in our models due to the availability of province-wide predictions (Sutton et al. 2024) that allow us to predict GDD in streams across Ontario and because most DD are accumulated during the summer (i.e., June–August; Figure 2), with water temperatures typically peaking in July. To account for non-independence associated with repeated sampling at many reaches, we fit a linear mixed effects model with a reach-level random intercept (Bolker et al. 2009, Harrison et al. 2018) using the *lme4* package (Bates et al. 2015) in R v4.4.2 (R Core Team 2024).

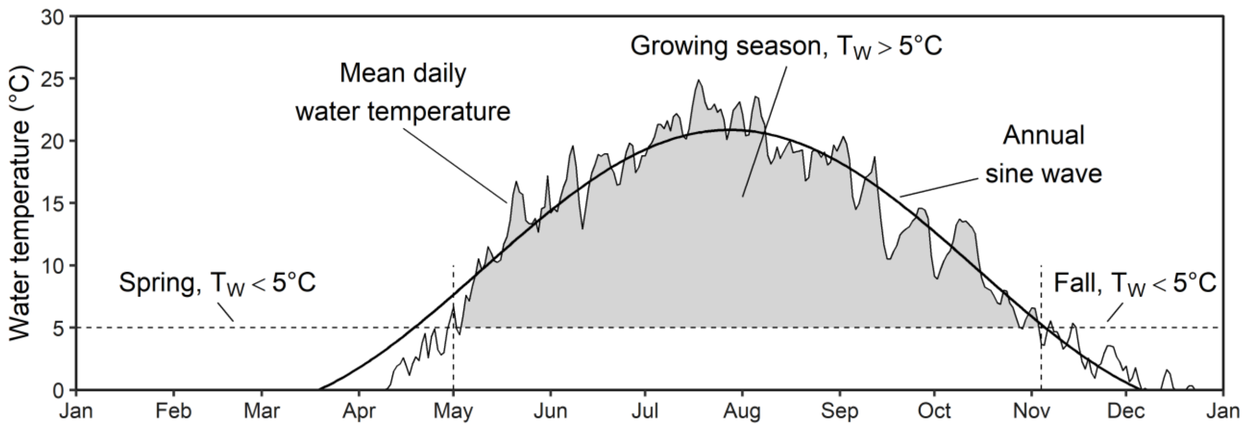

Figure 1. An illustrative example of how natural stream temperature patterns can be exploited to estimate annual growing degree days (GDD; grey shaded region). Stream temperatures (T_W) rise in the spring, peak during the summer months (typically July), and decrease in the fall. This repetitive pattern means that inter-annual variation in GDD is primarily driven by differences in growing season length and peak summer T_W. As a result, it should be possible to model GDD as a function of the growing season length and July mean stream temperature to allow estimation of GDD in streams where annual stream temperature time series are unavailable or incomplete.

To enable GDD predictions for unsampled streams, we required estimates of growing season length to pair with the predicted July mean stream temperatures from Sutton et al. (2024). As a result, we modelled growing season length as a function of mean annual air temperature based on observations that season length was most sensitive to inter-annual climatic variation (Figure 2). The mean annual air temperatures used in modelling were extracted from a gridded (60 arc-second) data set of monthly minimum and maximum air temperature provided by the Canadian Forest Service. The grids were produced using the methods described in McKenney et al. (2011) and provided historical data for each year between 1980 and 2022. We calculated mean annual air temperature by averaging the monthly minimum and maximum grids for each year. We then extracted mean annual air temperatures to each stream reach as a weighted mean proportional to the stream length overlapping each grid cell. The season length model was fit using the same linear mixed model framework and random effect structure as the GDD model.

Model performance was assessed using repeated k-fold cross-validation with 10 repeats and 10 folds. Folds were stratified by reach (i.e., all data from a reach occurred in a single fold) to avoid underestimating prediction error (Roberts et al. 2017). Predictive performance was summarized using root mean squared error (RMSE) and bias:

$$RMSE = \sqrt{\sum_{i=1}^{n} \frac{(y_i - \hat{y}_i)^2}{n}}$$

$$Bias = \sum_{i=1}^{n} \frac{y_i - \hat{y}_i}{n}$$

where y_i and $\hat{y}_i$ are observed and predicted values (GDD or GSL) for a reach and year, and n is the number of reach-year combinations.

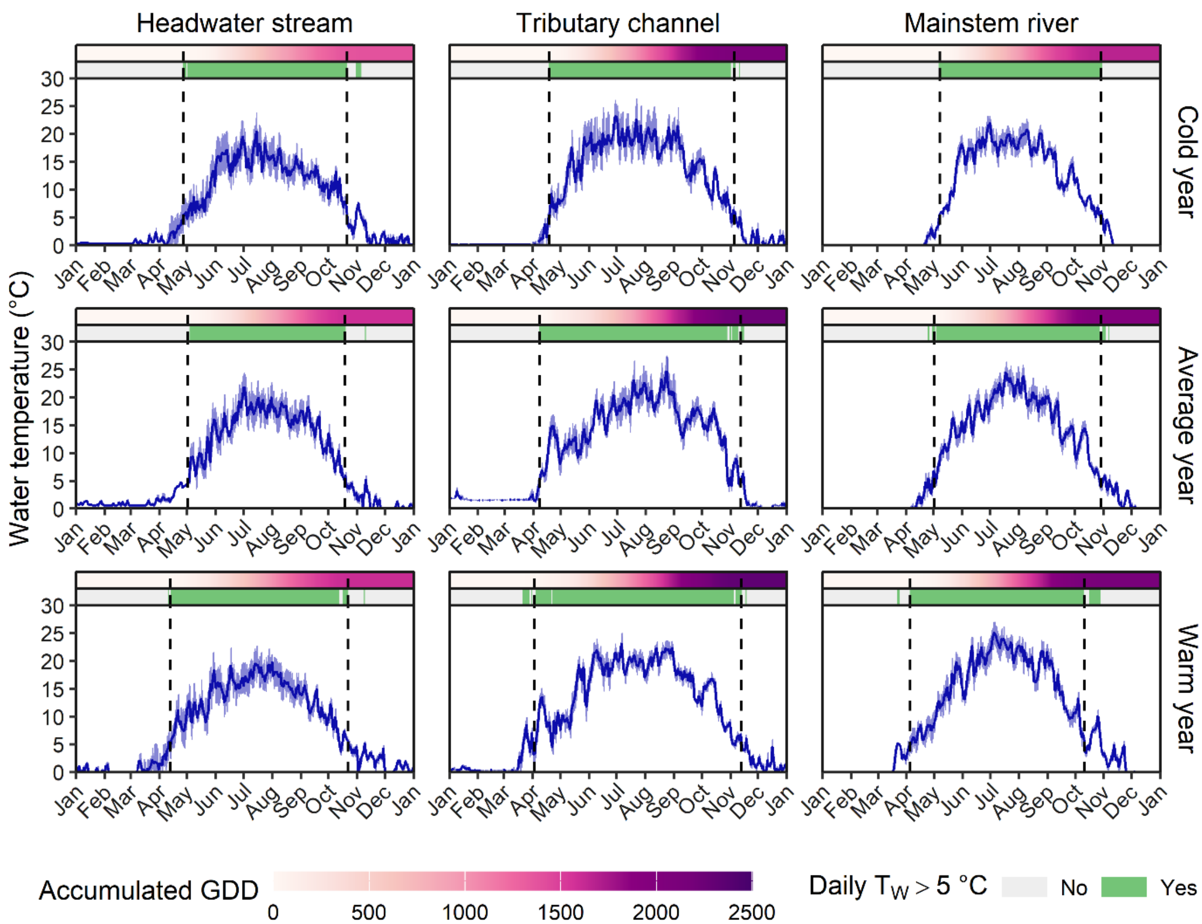

Figure 2. Annual stream temperatures (T_w), days above the threshold temperature (T_0 = 5 °C), and accumulated growing degree days (GDD) in a cold, average, and warm year at three sites: a small headwater stream (Stokely Creek in northern Ontario), a tributary of the Saugeen River in southwestern Ontario, and the mainstem of the Goulais River near Sault Ste. Marie. Daily mean (dark blue) and sub-daily (light blue) stream temperature measurements are presented for each site. The vertical dashed lines delineate the start and end of the growing season in each year.

Growing season length and GDD at unsampled reaches were predicted using the models above. We first predicted growing season length for each AEC stream reach using the air temperatures obtained from the Canadian Forest Service. We then combined these season length predictions with the July mean stream temperature predictions from Sutton et al. (2024) to predict GDD for rivers and streams across Ontario. Predictions were generated for each year between 1981 and 2010 – the same baseline period used in the July mean stream temperature models. The annual predictions were averaged to calculate mean growing season length and GDD over this baseline period.

Results

The final, cleaned, stream temperature data set contained 711 site-years of data collected from 222 reaches (231 sites) between 1997 and 2021 (Figure 3). Average record length was 3.1 years, ranging from one to thirteen years with a median of two years of data. The wide period covered by this data should make our results robust to variation driven by climatic variability (e.g., warm and wet vs. cool and dry years; Figure 2).

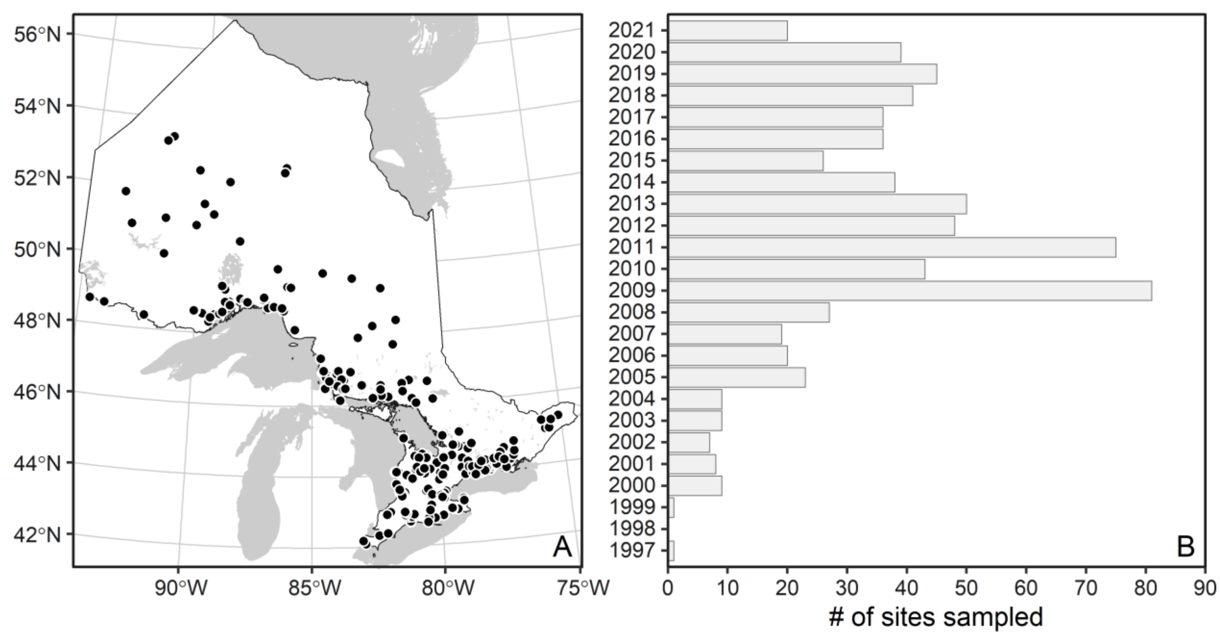

Figure 3. Temperature monitoring sites (A) and distribution of sampling effort (B) used to model growing season length and growing degree days across Ontario. Sites influenced by lakes, dams, reservoirs, and urbanization, and without useable data following quality control are not shown.

Growing season lengths calculated using stream temperature data (GSL_w) ranged between 131 and 285 days (mean = 207±28 days), while season lengths based on paired air temperature data (GSL_a) were usually shorter and ranged between 106 and 250 days (mean = 183±24 days). GDD calculated using stream temperature data (GDD_w) ranged from 883 to 3383 degree days (mean = 2054±416 degree days), while GDD derived from paired air temperatures (GDD_a) ranged from 657 and 3162 degree days (mean = 1920±405 degree days). We observed broad spatial patterns where growing season length and GDD typically increased from east to west and north to south across Ontario (Figure 4).

There was moderate correlation between growing season lengths (Pearson's r = 0.67) and GDD (Pearson's r = 0.63) calculated using air and water temperature data (Figure 5, 6). On average, growing seasons derived from water temperature data began 8 days earlier and ended 16 days later than an equivalent growing season calculated using paired air temperature data. However, these differences in growing season length did not consistently result in substantial differences in GDD, with a mean increase of 163±343 degree days when GDD were calculated using stream temperature data. Differences between GDD_w and GDD_a were not uniformly distributed across the landscape (Figure 5) and corresponded to catchment characteristics such as base flow index and stream size (Figure 6, 7). Despite the relatively small difference in GDD_a and GDD_w at most sites, sites with higher groundwater inputs often accumulated substantially fewer DD (Figure 7).

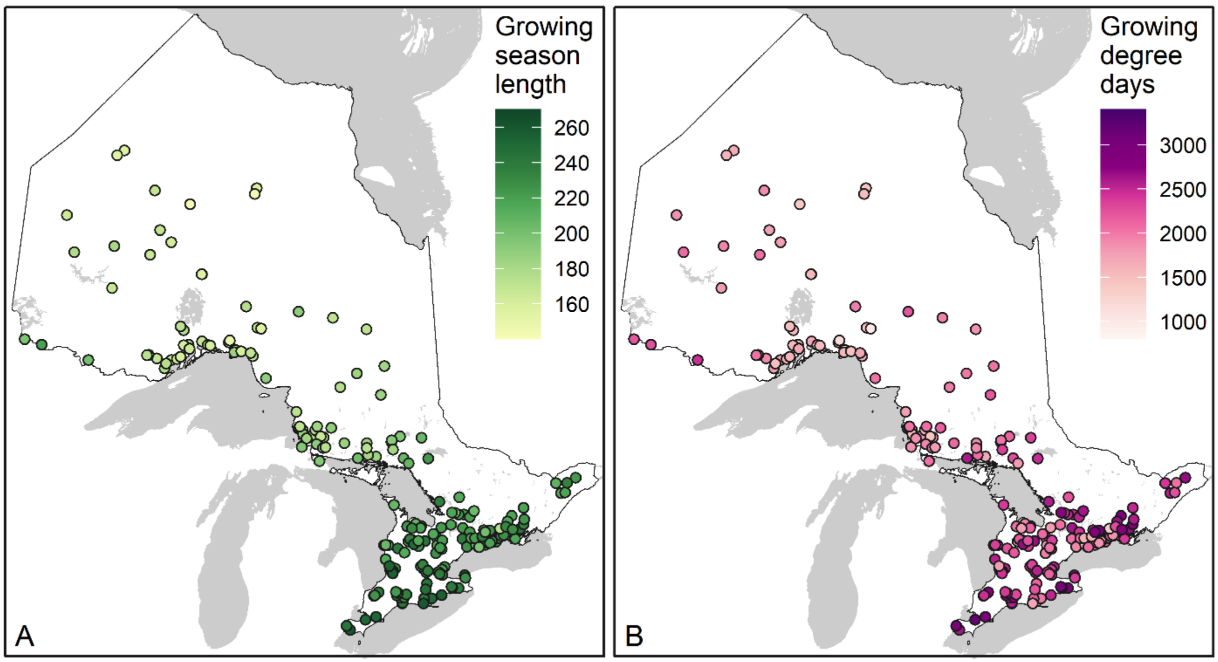

Figure 4. Mean annual growing season length (A) and growing degree days (B) calculated using water temperature records from 222 rivers and streams in Ontario sampled between 1997 and 2021 (mean record length = 3.1 years).

Growing season length and GDD were predicted with reasonable accuracy and low bias (Figure 8). Mean annual air temperatures were positively correlated with growing season length, while growing season length and July mean water temperatures were positively correlated with GDD. Over the prediction period from 1981 to 2010, predicted mean growing season lengths were between 115 and 242 days (mean = 168±27 days) (Figure 9). Over the same period, mean predicted GDD ranged between 825 and 2,728 degree days (mean = 1,608±315 degree days). As observed in the empirical data, there was a broad spatial pattern of increasing growing season length and GDD from east to west and north to south across Ontario.

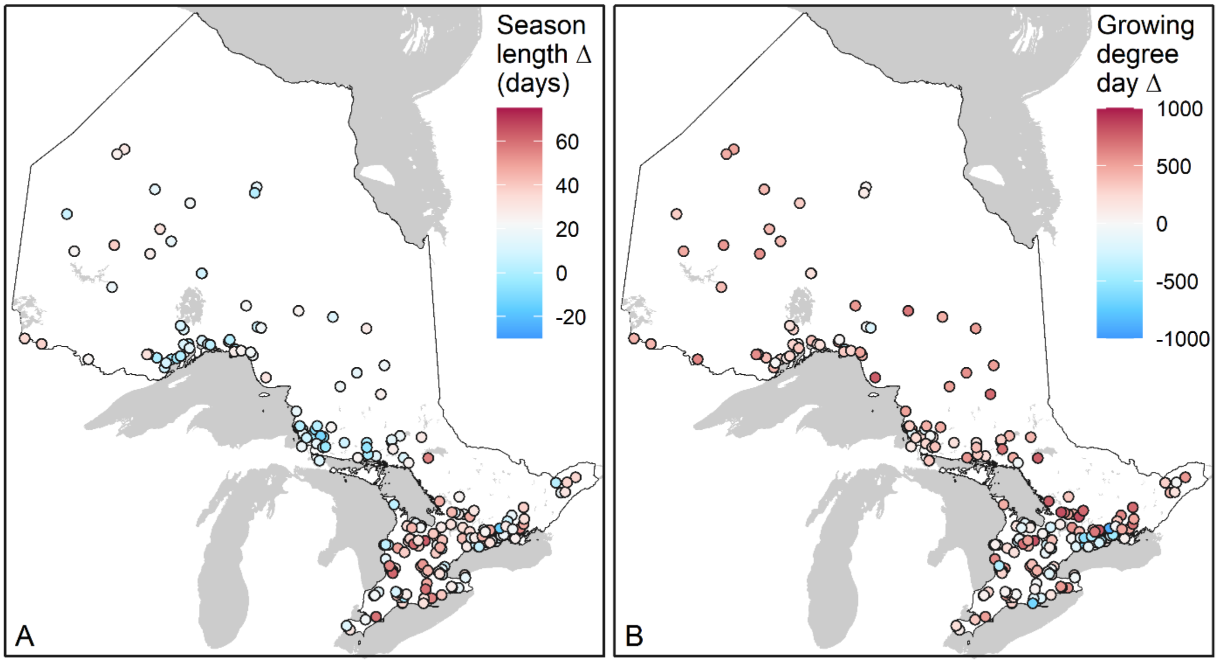

Figure 5. Differences (Δ) in growing season length (A) and growing degree days (B) derived from air and water temperature time series from 222 rivers and streams in Ontario sampled between 1997 and 2021 (mean record length = 3.1 years).

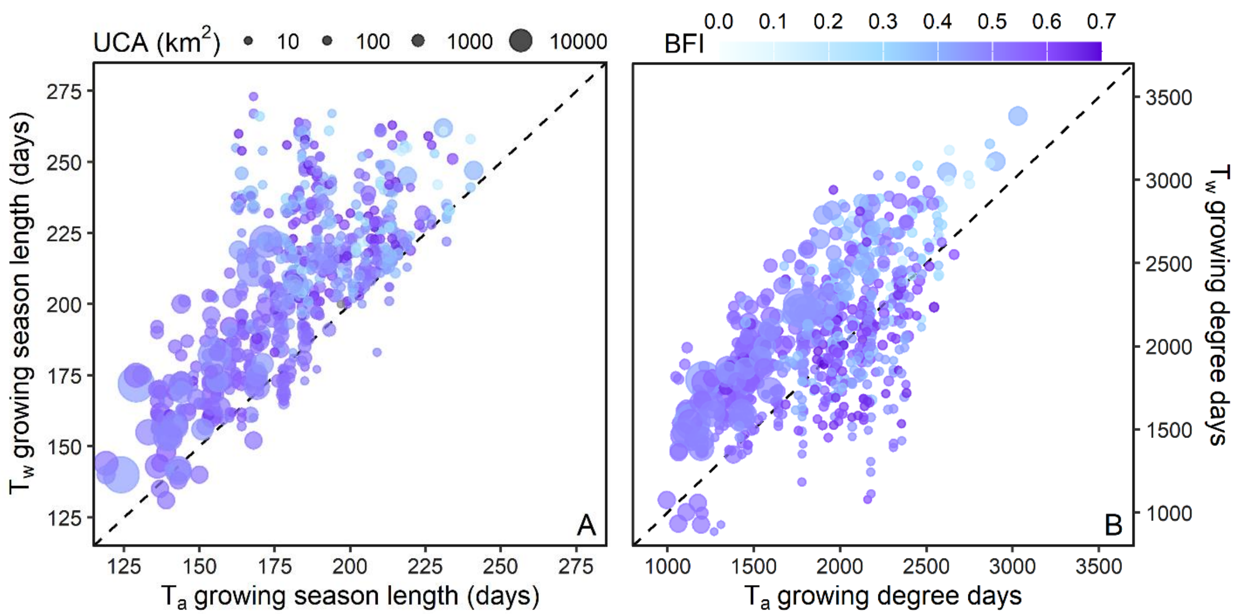

Figure 6. Observed growing season lengths (A) and growing degree days (B) calculated using air (T_a) and water (T_w) temperature time series in relation to upstream catchment area (UCA) and base flow index (BFI). Data were collected from 222 rivers and streams across Ontario between 1997 and 2021. Each point represents a single site-year of data (n = 711).

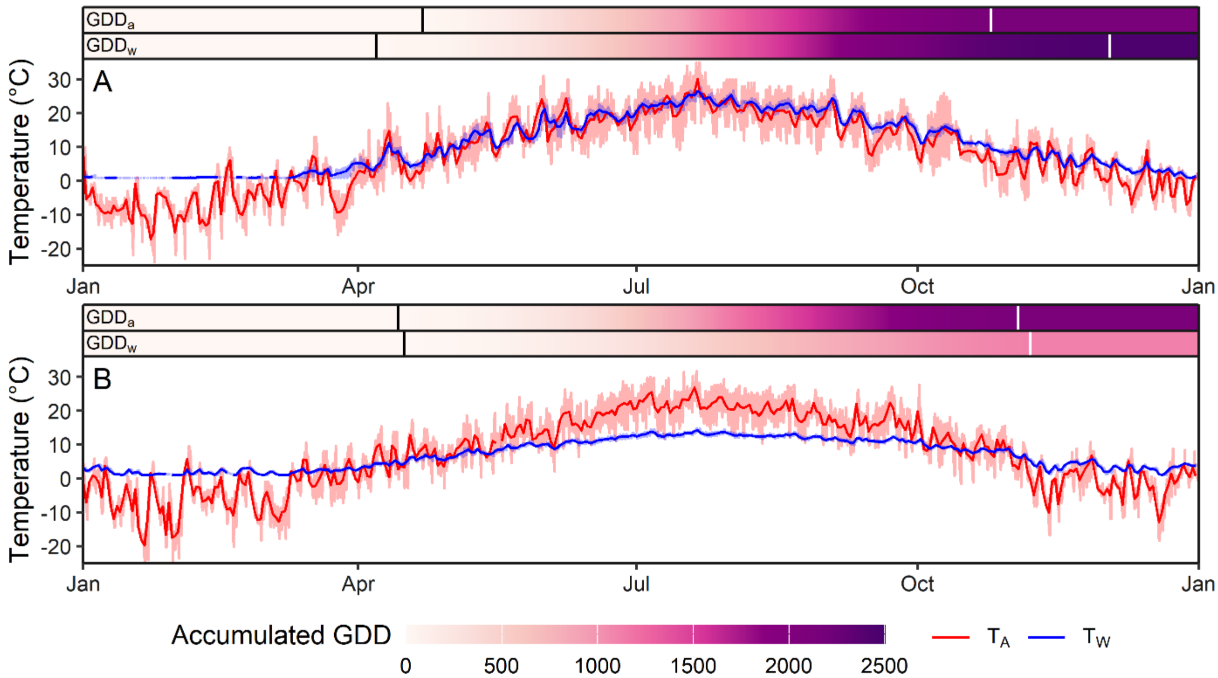

Figure 7. Annual air (T_a) and stream (T_w) temperature time series for the (A) Conestogo River and (B) Wilmot Creek. Daily (dark lines) and sub-daily (light lines) temperatures are presented at both sites in addition to cumulatively growing degree days (GDD) calculated using T_a and T_w. Solid vertical lines denote the start and end of the growing season. Air and water temperatures can become decoupled in the presence of riparian shade and/or groundwater input as seen for Wilmot Creek. This decoupling can lead to large discrepancies in GDD derived from T_a and T_w.

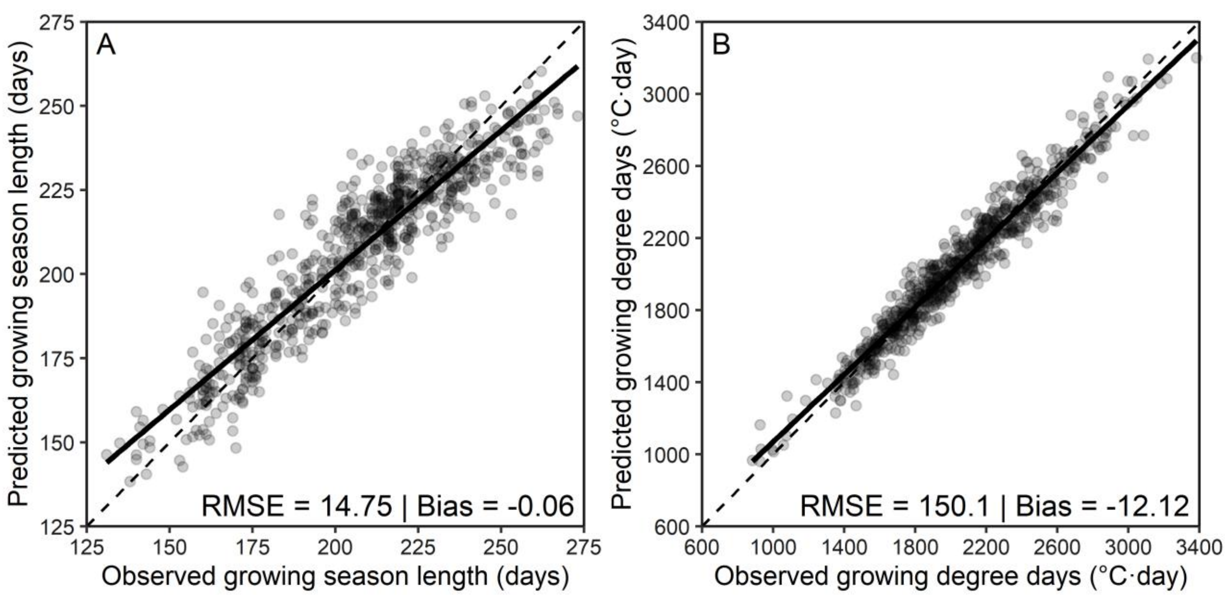

Figure 8. Observed versus predicted growing season length (A) and growing degree days (B) for the linear mixed models fit to all available data. Root mean squared error (RMSE) and bias were estimated using repeated k-fold cross-validation with 10 repeats and 10 folds.

Discussion

Temperature has been described as a *master variable* and an *ecological resource* because of its influence on aquatic ecosystems (Brett 1971, Magnuson et al. 1979). In particular, temperature plays an important role in regulating photosynthesis, metabolic rates, and, ultimately, growth in aquatic organisms such as fish (Fry 1971, Brown et al. 2004, Neuheimer and Taggart 2007). As a result, cumulative thermal energy exposure is an important predictor of growth and size-at-age. Degree days (DD) integrate temperature and time to provide a physiologically relevant measure of the thermal energy available to biota (Neuheimer and Taggart 2007, 2010). Air temperatures are often used as a surrogate for water temperatures when estimating DD in aquatic ecosystems. However, this approach may be unsuitable in rivers and streams due to the complex, dynamic, processes that shape water temperature in these ecosystems (Caissie 2006, Leach et al. 2023). Here, we used stream temperature data to model and predict growing season lengths and accumulated degree days during the growing season (growing degree days; GDD) for rivers and streams across Ontario. Our models are accurate, have low bias, and reveal considerable differences in GDD compared to air temperature derived GDD estimates. These predictions have a wide range of potential applications in research and resource management.

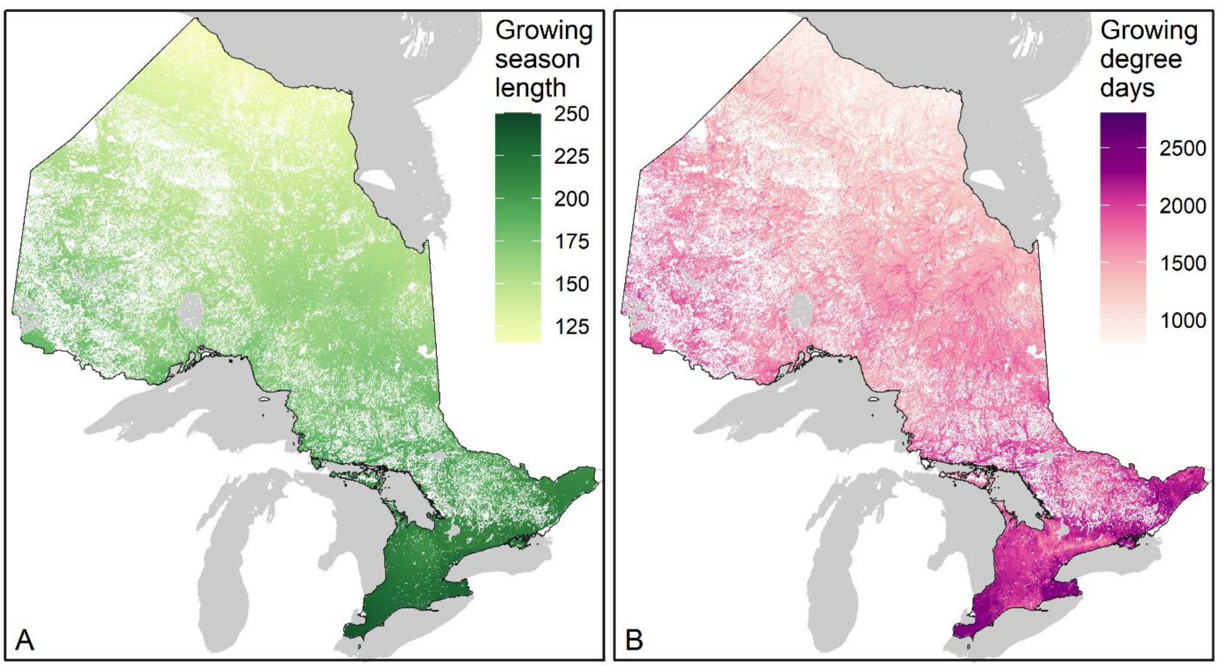

Figure 9. Mean predicted growing season length and growing degree days (GDD) between 1981 and 2010 for rivers and streams across Ontario represented in the provincial aquatic ecosystem classification (AEC; Jones et al. 2025).

Our results suggest that, with few exceptions, GDD estimates derived from air temperature data (GDD_a) underestimate GDD estimated using water temperature data (GDD_w). This finding is consistent with patterns observed in lakes, where GDD_w were consistently higher than GDD_a (Honsey et al. 2019). Exceptions to the pattern of higher GDD_w were usually smaller headwater streams where air and water temperatures can become decoupled due the influence of riparian shade and groundwater inputs (Caissie 2006, Webb et al. 2008, Leach et al. 2023). Groundwater may be a source of heat during the winter, while buffering against warming during the summer. Riparian shade (e.g., due to vegetation or topography) can reduce the amount of solar radiation reaching the stream and limit heating. Combined or in isolation, these cooling factors can result in streams that are substantially colder than the surrounding air (Figure 7B). These cold streams accumulate fewer degree days, resulting in discontinuities in the otherwise positive relationship between GDD_a and GDD_w. Similar discontinuities were not reported during previous studies on lentic environments, although there is evidence that the slope of the GDD_a- GDD_w relationship varied across lakes (Honsey et al. 2019).

A useful property of the GDD is that it provides a physiologically relevant *common currency* that facilitates comparisons within and among populations (Neuheimer and Taggart 2007, Venturelli et al. 2010). As a corollary, variation in growth that cannot be explained by variation in GDD can be attributed to other factors (e.g., water quality, food availability). A common measure used to facilitate comparisons is the thermal constant – the thermal energy needed to attain a given life history stage (Trudgill et al. 2005, Neuheimer and Taggart 2007). In fish, development is marked by changes in energy allocation from growth to other processes (e.g., reproduction) which leads to discontinuities in the relationship between growth and GDD. These discontinuities represent the thermal constant at each life history stage (e.g., emergence, maturation). Given comparable thermal constants, variability in growth and size-at-age can often be attributed to differences in the organism's thermal history. For example, chinook salmon (*Oncorhynchus tshawytscha*) eggs require roughly 516±40 °C·days to hatch, resulting in considerable variation (about 200 days) in time to emergence depending on the incubation temperature (Neuheimer and Taggart 2007). Similarly, Venturelli et al. (2010) observed that walleye (*Sander vitreus*) require between 6900 °C·days (males) and 10,000 °C·days (females) to reach maturity, with variation in GDD over time and space explaining most of the differences in calendar time to maturation (2 to 15 years) across populations. Understanding temperature-dependent variability in growth and size-at-age has important resource management implications because growth rate and body size are useful predictors of early survival for fish, ultimately influencing the timing of recruitment and number of individuals recruited to the fishery (Miller et al. 1988, Sogard 1997, Venturelli et al. 2010).

More broadly, GDD should serve as a reliable predictor of productivity. Production, in particular fish biomass production, provides a simple, easily interpreted, quantitative measure that distills varied aspects of ecosystem dynamics (e.g., abundance, growth, reproduction, mortality) into a single metric (Rypel et al. 2018, Richter et al. 2024). Fish biomass production mainly depends on the rates of biological processes (e.g., growth, reproduction, mortality) and resource availability which are, in turn, strongly influenced by temperature (Brown et al. 2004). As such, quantifying temperature-dependent variation in production is a crucial step in understanding temperature-independent factors (e.g., resource availability, water quality) shaping productivity (Neuheimer and Taggart 2007). Indeed, fish production is negatively correlated with latitude because of the influence of temperature (Rypel and David 2017) which makes it challenging to detect counter-gradient variation without first accounting for the influence of temperature (Chezik et al. 2014, Honsey et al. 2019). Although recent studies (e.g., Richter et al. 2023, 2024) found limited evidence of GDD as a predictor of productivity in rivers and streams, the use of air temperature derived GDD was a noted limitation of these efforts. Given the strong theoretical basis for GDD as predictors of growth and productivity in aquatic ecosystems, we believe further investigation is warranted and expect that our water temperature derived GDD estimates will prove useful as a predictor of productivity.

An exciting application of these predictions is in the provincial aquatic ecosystem classification (AEC; Jones et al. 2025), where expectations of aquatic productivity are currently derived from GDD based on air temperatures. These new water temperature derived predictions can replace the existing GDD data to provide a finer-grained understanding of potential aquatic productivity in rivers and streams across Ontario. Productivity is an important aspect of flowing waters with respect to harvest and ecosystem resilience. In lakes, productivity is controlled by the influence of climate, morphometry (shape/dimension), and edaphic (soil/geography) factors (Ryder 1965, Welcomme et al. 1989). Although it is challenging to generalize the morphometry of rivers and streams across Ontario, the potential productive capacity of the fluvial environment to produce biota can be approximated by combining growing degree days and conductivity, broadly akin to the morphoedaphic index (MEI) developed by Ryder (1965). The relationships between MEI and productivity likely hold true in flowing waters as well, wherein channel length, drainage area, or total floodplain area are more relevant measures than river depth (Welcomme et al. 1989).

Although our growing season models had minimal bias, systematic deviations occurred where growing season lengths were consistently overestimated at low mean annual air temperatures and underestimated at high temperatures. In Ontario, mean annual air temperatures generally increase from north to south following natural gradients in incoming solar radiation. As a result, predicted growing season lengths may be overestimated in the north – particularly for streams near the Hudson Bay coast. Similarly, growing degree days will also tend to be overestimated in the north because the predictions are derived from the modelled growing season lengths. Note that the systematic deviations do not influence the validation of the growing degree day model because the model was fit and validated with empirical growing season lengths calculated from the raw stream temperature time series.

Several other caveats should be considered when using modelled GDD in research and resource management. First, fish lengths are likely better correlated with GDD than mass due to seasonal variability in weight driven by resource availability (Neuheimer and Taggart 2007). Second, GDD may not correlate well with growth in migratory populations, when movement is restricted, or under the influence of stressors (Neuheimer and Taggart 2007, Neuheimer and Gronkjær 2012, Honsey et al. 2018). There is an implicit assumption that fish occupy habitat which is thermally optimal for growth, which may decouple the relationship between growth and estimated GDD in migratory populations where fish migrate into lakes and accumulate thermal energy outside the stream. Similarly, growth may be decoupled from GDD when fish are forced into thermally unsuitable habitat (e.g., due to in-stream barriers that limit movement into refugia). Stressors including poor water quality, land use change, and a lack of food may also reduce growth, underscoring the importance of using GDD as a thermal history measure to disentangle the influence of temperature from these temperature-independent factors. A third caveat to consider is that averaged GDD (as presented in Figure 9) are only useful for broad-scale comparisons among populations because an average does not capture each organism's unique thermal history. This lack of individual-level data prevents within-population (i.e., individual year-class) comparisons (Trudgill et al. 2005, Neuheimer and Taggart 2007). A final caveat is that our GDD estimates use a single threshold model. This approach assumes that all heat accumulated above the threshold temperature increases growth, failing to account for reductions in growth at high temperatures (Chezik et al. 2014, Honsey et al. 2018). Future work could explore two threshold models, which include an upper threshold that limits accumulation of GDD at extreme temperatures.

Conclusions

The overriding influence of temperature on growth in aquatic ectotherms makes understanding thermal history essential to evaluating within and among population differences in growth and productivity. Growing degree days are a well-supported, widely used measure of an organism's thermal history. Using a model-based approach, we predicted growing season metrics for rivers and streams across Ontario for the first time. The models are accurate, have low bias, and are an improvement over degree days estimated from air temperatures. These predictions have a range of applications in resource management and open exciting new avenues of research for future evaluation of productivity in rivers and streams across Ontario. The predictions are made available on Ontario GeoHub as part of the broader aquatic ecosystem classification data suite.

References

Atkinson, D. 1994. Temperature and organism size – A biological law for ectotherms? Advances in Ecological Research 25: 1–58.

Bates, D., M. Mächler, B. Bolker and S. Walker. 2015. Fitting linear mixed-effects models using lme4. Journal of Statistical Software 67(1): 1–48.

Bolker, B.M., M.E. Brooks, C.J. Clark, S.W. Geange, J.R. Poulsen, M.H.H. Stevens and J.S.S. White. 2009. Generalized linear mixed models: A practical guide for ecology and evolution. Trends in Ecology and Evolution 24(3): 127–135.

Bonhomme, R. 2000. Bases and limits to using 'degree.day' units. European Journal of Agronomy 13(1): 1–10.

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

Brown, J.H., J.F. Gillooly, A.P. Allen, V.M. Savage and G.B. West. 2004. Toward a metabolic theory of ecology. Ecology 85(7): 1771–1789.

Caissie, D. 2006. The thermal regime of rivers: A review. Freshwater Biology 51(8): 1398–1406.

Chezik, K.A., N.P. Lester and P.A. Venturelli. 2014. Fish growth and degree-days I: Selecting a base temperature for a within-population study. Canadian Journal of Fisheries and Aquatic Sciences 71(1): 47–55.

Dolbeth, M., M. Cusson, R. Sousa and M.A. Pardal. 2012. Secondary production as a tool for better understanding of aquatic ecosystems. Canadian Journal of Fisheries and Aquatic Sciences 69(7): 1230–1253.

Fry, F.E.J. 1971. The effects of environmental factors on the physiology of fish. Fish Physiology 6: 1–98.

Harrison, X.A., L. Donaldson, M.E. Correa-Cano, J. Evans, D.N. Fisher, C.E.D. Goodwin, B.S. Robinson, D.J. Hodgson and R. Inger. 2018. A brief introduction to mixed effects modelling and multi-model inference in ecology. PeerJ 6: e4794.

Honsey, A.E., P.A. Venturelli and N.P. Lester. 2019. Bioenergetic and limnological foundations for using air temperatures to describe fish growth. Canadian Journal of Fisheries and Aquatic Sciences 76(4): 657–669.

Honsey, A.E., A.L. Rypel and P.A. Venturelli. 2023. Guidance for selecting base temperatures when using degree-days in fish growth analyses. Canadian Journal of Fisheries and Aquatic Sciences 80(3): 549–562.

Huey, R.B. and R.D. Stevenson. 1979. Integrating thermal physiology and ecology of ectotherms: A discussion of approaches. American Zoologist 19(1): 357–366.

Jones, N.E., B.J. Schmidt, I.A. Sutton and M.S. Parna. 2025. An aquatic ecosystem classification for Ontario's rivers and streams: Version 3. Ontario Ministry of Natural Resources, Science and Research Branch, Peterborough, ON. Science and Research Technical Report TR-69. 46 p. + appendix

Leach, J.A., C. Kelleher, B.L. Kurylyk, R.D. Moore and B.T. Neilson. 2023. A primer on stream temperature processes. WIREs Water 10(4): e1643.

Magnuson, J.J., L.B. Crowder and P.A. Medvick. 1979. Temperature as an ecological resource. American Zoologist 19: 331–343.

Markarian, R.K. 1980. A study of the relationship between aquatic insect growth and water temperature in a small stream. Hydrobiologia 75: 81–95.

McKenney, D.W., M.F. Hutchison, P. Papadopol, K. Lawrence, J. Pedlar, K. Campbell, E. Milewska, R.F. Hopkinson, D. Price and T. Owen. 2011. Customized spatial climate models for North America. Bulletin of the American Meteorological Society 92(12): 1611–1622.

Miller, T.J., L.B. Crowder, J.A. Rice and E.A. Marschall. 1988. Larval size and recruitment mechanisms in fishes: Toward a conceptual framework. Canadian Journal of Fisheries and Aquatic Sciences 25(9): 1657–1670.

Neuheimer, A.B. and C.T. Taggart. 2007. The growing degree-day and fish size-at-age: The overlooked metric. Canadian Journal of Fisheries and Aquatic Sciences 64(2): 375–385.

Neuheimer, A.B. and C.T. Taggart. 2010. Can changes in length-at-age and maturation timing in Scotian Shelf haddock (*Melanogrammus aeglefinus*) be explained by fishing? Canadian Journal of Fisheries and Aquatic Sciences 67(5): 854–865.

Neuheimer, A.B. and P. Gronkjær. 2012. Climate effects on size-at-age: Growth in warming waters compensates for earlier maturity in an exploited marine fish. Global Change Biology 18(6): 1812–1822.

Payne, N.L., J.A. Smith, D.E. van der Meulen, M.D. Taylor, Y.Y. Watanabe, A. Takahashi, T.A. Marzullo, C.A. Gray, G. Cadiou and I.M. Suthers. 2016. Temperature dependence of fish performance in the wild: Links with species biogeography and physiological thermal tolerance. Functional Ecology 30(6): 903–912.

Policansky, D. Size, age and demography of metamorphosis and sexual maturation in fishes. American Zoologist 23(1): 57–63.

R Core Team. 2024. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Rasmussen, J.J., A. Battrup-Pedersen, T. Riis and N. Friberg. 2011. Stream ecosystem properties and processes along a temperature gradient. Aquatic Ecology 45: 231–242.

Richter, I.A., N.E. Jones and D.A. Jackson. 2023. Predicting riverine fish production using empirical models and the metabolic theory of ecology. Ecology of Freshwater Fish 32(3): 582–592.

Richter, I.A., D.A. Jackson and N.E. Jones. 2024. Explaining variation in stream fish productivity with biotic and abiotic variables across wadeable rivers in eastern North America. Freshwater Biology 69(6): 809–822.

Roberts, D.R., V. Bahn, S. Ciuti, M.S. Boyce, J. Elith, G. Guillera-Arroita, S. Hauenstein, J.L. Lahoz-Monfort, B. Schröder, W. Thuiller, D. I. Warton, B.A. Wintle, F. Hartig and C.F. Dormann. 2017. Cross-validation strategies for data with temporal, spatial, hierarchical, or phylogenetic structure. Ecography 40(8): 913–929.

Ryder, R.A. 1965. A method for estimating the potential fish production of north-temperate lakes. Transactions of the American Fisheries Society 94: 214–218.

Rypel, A.L. and S.R. David. 2017. Pattern and scale in latitude-production relationships for freshwater fishes. Ecosphere 8: e01660.

Rypel, A.L., D. Goto, G.G. Sass and M.J.V Zanden. 2018. Eroding productivity of walleye populations in northern Wisconsin lakes. Canadian Journal of Fisheries and Aquatic Sciences 75(12): 2291–2301.

Shuter, B.J., D.A. Schlesinger and A.P. Zimmerman. 1983. Empirical predictors of annual surface temperature water cycles in North American lakes. Canadian Journal of Fisheries and Aquatic Sciences 40(10): 1838–1845.

Sogard, S.M. 1997. Size-selective mortality in the juvenile stage of teleost fishes: A review. Bulletin of Marine Science 60(3): 1129–1157.

Sutton, I.A., N.E. Jones and B.J. Schmidt. 2024. Thermal habitat of flowing waters in Ontario: Updated models to predict current and future stream temperatures. Ontario Ministry of Natural Resources, Science and Research Branch, Peterborough, ON. Science and Research Technical Report TR-62. 33 p. + appendices.

Trudgill, D.L., A. Honek, D. Li and N.M. van Straalen. 2005. Thermal time – concepts and utility. Annals of Applied Biology 146(1): 1–14.

Vasseur, D.A., J.P. DeLong, B. Gilbert, H.S. Greig, C.D.G. Harley, K.S. McCann, V. Savage, T.D. Tunney and M.I. O'Connor. 2014. Increased temperature variation poses a greater risk to species than climate warming. Proceedings of the Royal Society B 281: 20132612.

Venturelli, P.A., N.P. Lester, T.R. Marshall and B.J. Shuter. 2010. Consistent patterns of maturity and density-dependent growth among populations of walleye (*Sander vitreus*): Application of the growing degree-day metric. Canadian Journal of Fisheries and Aquatic Sciences 67(7): 1057–1067.

Webb B.W., D.M. Hannah, R.D. Moore, L.E. Brown and F. Nobilis. 2008. Recent advances in stream and river temperature research. Hydrological Processes 22(7): 902–918.

Welcomme, R.L., R.A. Ryder and J.A. Sedell. 1989. Dynamics of fish assemblages in river systems: A synthesis. Canadian Special Publication of Fisheries and Aquatic Sciences 106: 569–577.

(0k P.R. 25 12 22)
ISBN 978-1-4868-9547-2 (pdf)