Predicting Black Carp (*Mylopharyngodon piceus*) age at sexual maturity with water temperature

by

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Author's Declaration

I hereby declare I am the sole author of this thesis. This is a true copy of the thesis, including any required final revisions, as accepted by my examiners.

I understand that my thesis may be made electronically available to the public.

Abstract

Black Carp is one of the four invasive Asian carps in North America. It is currently considered established in the Mississippi River and has the potential to invade into the Great Lakes watershed. Black Carp is known for its ability to consume freshwater unionids, and thus could bring potential changes to the benthic ecosystems. For effective management and mitigation strategies, it is critical to understand its likely population growth rate in new environments, and to be able to predict the environmental conditions of the potential habitats it may become established in. Age at sexual maturity of the population has been identified as an important variable in determining the population establishment speed, as faster maturation typically corresponds to faster population growth.

I demonstrated that temperature metrics such as air temperature can be used to predict the age of maturity of Black Carp. Using age at maturity data and related climate metrics around the world, I found that winter duration and winter air temperature are the two best predictors of Black Carp age at maturity. This suggests that winter can play an important role in the maturation process of this invasive species. Populations experiencing longer and colder winters tend to mature later.

While temperature may be an important predictor for the speed of Black Carp invasion, water temperature data is not always available for regions of interest. Using empirical water temperature from 12 tributary locations in the Great Lakes watershed, I established a simple statistical model to predict water temperature during the growing season. I found that simple regression-based models using air temperature as input can perform better than a complex processed-based global model for estimating water temperature in the Great Lakes region.

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Chapter 1: Introduction

Importance of temperature in invasive species research

Ecological invasion refers to the process by which a species spreads and establishes reproductive populations in a novel region where it is not native (Lockwood et al., 2013). Invasive species are a pressing concern for ecosystems worldwide, often leading to decreased native species abundance (Gallardo et al., 2016), cascading effects on local food webs (David et al., 2017), and even modified habitat structure (Crooks, 2002; Crooks & Khim, 1999). As these species establish themselves in new environments, understanding the factors that affect where and how fast they can invade becomes crucial for effective management and mitigation strategies. Among these factors, temperature can play an important role.

Temperature can influence the potential geographical distribution of invasive species, as it defines the climates within which they survive and thrive (Ashcroft et al., 2011; Olyarnik et al., 2009). The physiological tolerances of species are often closely tied to temperature, affecting their metabolic rates, growth, and reproductive success (Bozinovic et al., 2011; Kelley, 2014; Payne et al., 2016). The ability of invasive species to adapt to or exploit temperature variations in novel regions can affect their establishment success and potential distribution range (Hesselschwerdt & Wantzen, 2018; Zerebecki & Sorte, 2011). Much past research has used temperature in ecological niche modeling to predict the suitable habitats for invasive species (Barbet-Massin et al., 2018; Petrosyan et al., 2023). With such models and estimated future temperature, researchers can predict where these species may become established in the future.

On the other hand, temperature can also be used to determine the speed with which these species become established in a novel region. Temperature is the primary determinant of metabolic rates, and can affect how fast invasive species grow and reproduce. In general, individuals grow faster and mature younger under warmer climates (Jobling, 1997; Kuparinen et al., 2011; Noreikiene et al., 2017). As I discuss below, with a faster growth rate and younger maturation age, populations are likely to reach a larger size and invade into new regions more rapidly.

Much past research on invasive species niche or population growth modeling used air temperature. Yet for aquatic invasive species, water temperature could be more important as it better represents the actual environment the species lives in. In this thesis, I focus on one important riverine invasive species of concern in North America, Black Carp (*Mylopharyngodon piceus*). Juveniles of this species grow and mature in the benthos of rivers or adjoining floodplains (Nico et al., 2005), where water temperature is likely to differ from air temperature.

Effects of temperature on Black Carp life history

Black Carp is one of the four invasive Asian Carp species in North America. It is a freshwater fish species native to Asia and was first introduced to North America in the 1970s as a "contaminant" in imported Grass Carp stocks. Beginning in the 1980s, private aquaculture facilities started to purposely bring Black Carp into the United States as both a food fish, and a potential biological control for zebra mussel and yellow grub (Nico et al., 2005). Currently, this species is considered established in the Mississippi River Basin (Kroboth et al., 2019; Nico et al., 2005; Whitledge et al., 2022). The current distribution extends from the Atchafalaya River to the

upper Mississippi River, and is approaching the entrance point to Lake Michigan through the Chicago Sanitary and Ship Canal (Chapman et al., 2021; Kroboth et al., 2019; Nico et al., 2005).

Similar to many other fish species, certain aspects of Black Carp's vital life history traits are affected by temperature. Having a comprehensive understanding of these effects allows us to determine how temperature can be used to estimate Black Carp potential invasion risk, and to develop management practices where required.

As ectotherms, Black Carp's growth and metabolism are controlled by temperature. It can survive in the temperature range of 0.5-38°C, but prefers an optimal temperature around 25-32°C (NACA, 1985). Hodgins et al. (2014) defined 25°C as the optimal temperature for consumption in juvenile Black Carp, while Li et al. (2020) further found the resting metabolic rate at this temperature was 2.7 times higher compared to a lower temperature (10°C). Black Carp is known to become less active and grow slower under temperatures below 15°C (Evtushenko et al., 1994; Nico et al., 2005). Throughout its wide geographical range, populations inhabiting cooler climates (e.g. Amur River, China) generally have a much slower growth rate compared to ones living in warmer climates (e.g. Yangtze River, China) (Nico et al., 2005).

Slower growth rate in cold climates leads to a later age at maturity, as individuals require a longer time to reach the size threshold for maturation. In fact, Nico et al. (2005) reported a significant relationship between latitude and age at maturity for Black Carp: individuals from northern locations mature later. As latitudinal gradients generally point to temperature gradients, it is reasonable to assume this vital trait is temperature-dependent. However, a recent analysis by Brook et al. (2023) suggested that while there is a clear relationship between air temperature and

age at maturity for the other invasive Asian carp species (Silver Carp, Bighead carp, and Grass carp), this relationship is not found for Black Carp.

In Chapter 2, I detail efforts to use different temperature metrics to predict Black Carp age at maturity. As the previous analysis by Brook et al. (2023) did not find a significant relationship between age at maturity and temperature for this species, I aimed to re-examine this relationship with a more comprehensive dataset, and incorporate a number of ecologically relevant metrics that were not used before, such as water temperature and winter duration. In addition, I investigated the effects of growing environment on Black Carp age at maturity, as common aquaculture practices, such as supplementary heating of water, may cause Black Carp in artificial environments to mature younger than populations in natural environments.

Modeling river water temperatures

While temperature controls important aspects of life history and can determine probability of invasive species establishment, there are relatively few available river water temperature records in the Great Lakes region. The United States has a monitoring system that reports real-time surface water temperatures from more than 1300 gaging stations across the country. While Canada has no publicly available national or provincial water temperature monitoring programs. Although some regional conservation authorities (such as the Grand River Conservation Authority) have temperature records online, they often focus on a few rivers in the region.

Where water temperature data is not available, there have been many attempts to predict river water temperature using other data such as air temperatures and land use type. These

prediction models can be divided into two categories: deterministic and statistical models (Benyahya et al., 2007; Caissie, 2006; Rabi et al., 2015; Zhu et al., 2018). Deterministic models (also called process-based models) calculate the thermal exchange between river and the surrounding environment to represent the physical processes simulating river temperature fluctuation (Dugdale et al., 2017; Hebert et al., 2011). While statistical models rely on the simple relationship between water temperature and other relevant meteorological variables, such as air temperature or river discharge (Benyahya et al., 2007). Different types of statistical water temperature models are explained in more detail in the introduction of Chapter 3.

In Chapter 2, I used modeled weekly river temperatures from the futureStreams database (Bosmans et al., 2022) to estimate water temperatures for each location. Yet at local scale, this global approach could lack the spatial resolution needed to capture local variability or specific conditions. In Chapter 3, I gathered empirical water temperature records from 12 different tributary locations across the Great Lakes watershed, and determined what is the best-performing simple statistical river water temperature model for each of these tributaries. I compared the predictions from these statistical models with minimal meteorological inputs to those from the more complex processed-based global model for the Great Lake tributaries.

Thesis Structure

In my thesis, I focus on predicting invasive Black Carp age at maturity with temperature in the Great Lakes region, as fish age at maturity is a critical component in determining invasion risk, and using simple models to predict water temperature in rivers that might be important for a Black Carp population. My thesis therefore consists of 2 substantive chapters, as well as this introduction and a short conclusion with some future research directions. Chapter 2 and 3 were

conceived and prepared as separate manuscripts for publication. Chapter 2 has been prepared following the format of the Ecology of Freshwater Fish Journal and Chapter 3 has been prepared following the format of the Canadian Journal of Fisheries and Aquatic Sciences. Although both chapters are distinct in their specific focus, together they demonstrate the importance of temperature in research on aquatic invasive species, and in predicting Black Carp invasion risk specifically. I will summarize these connections in the concluding chapter.

Chapter 2: Effects of temperature on Black Carp age at maturity

Overview

Black Carp (*Mylopharyngodon piceus*) is one of the four invasive Asian Carp species (Bighead Carp, *Hypophthalmichthys nobilis*; Grass Carp, *Ctenopharyngodon idella* and Silver Carp, *Hypophthalmichthys molitrix*) in North America. As benthic predators, Black Carp poses ecological risks to unionids within the Great Lakes, and could bring other changes to local benthic communities. One means of assessing invasion risk and potential impact is to determine how critical life history characteristics depend on environmental conditions in new regions. Age at sexual maturity is negatively correlated to the maximum per capita population growth rate, and thus can be used to estimate potential population growth for invasive species. Previous studies have found a significant negative relationship between age at maturity and temperature for all three other Asian Carp species, but not for Black Carp. With a more comprehensive dataset, we demonstrate that the same relationship exists for Black Carp. Winter duration is the best predictor of Black Carp age at maturity, followed by average winter air temperature. This significant relationship between age at maturity and temperature was not altered in artificial growing environments. Our results suggested that for Black Carp, temperatures in the winter months are more important for its energy accumulation and maturation, and may determine invasion risk in northern locations, such as tributaries of the Great Lakes.

Introduction

Invasive species in freshwater environments can decrease native species abundance (Gallardo et al., 2016), cause cascading effects on local food webs (David et al., 2017), and even

modify aquatic habitat structure (Crooks, 2002; Crooks & Khim, 1999). Much past research in invasion ecology has focused on identifying the niche dynamics or suitable habitats for invasive species (Jiménez-Valverde et al., 2011; Peterson, 2003). However, simply knowing where an invasive species could persist is not enough. Management responses to invasion risks are also determined by information regarding the speed at which populations of introduced individuals can increase. The potential for fast population growth suggests that greater efforts may be required. For example, many areas in eastern North America, and in particular, the Great Lakes region, are predicted to be suitable for the invasive species Black Carp (Mylopharyngodon piceus) (DeVaney et al., 2009; Nico et al., 2005). However, life history data suggests that population growth rate of this species could vary widely with location (Nico et al., 2005).

Black Carp is a freshwater fish species native to Asia and was purposely introduced to North America in the 1980s as an aquaculture species (Nico et al., 2005). Individuals escaped captivity and the species is now considered established in the Mississippi River Basin (Kroboth et al., 2019; Nico et al., 2005; Whitledge et al., 2022). The current distribution extends from the Atchafalaya River to the upper Mississippi River, and is approaching the entrance point to Lake Michigan through the Chicago Sanitary and Ship Canal (Chapman et al., 2021; Kroboth et al., 2019; Nico et al., 2005).

Black Carp may impact endangered unionid species in the Great Lakes region. As benthic predators, Black Carp is adapted for durophagy (Nico et al., 2005). It has the ability to detect and dig up fully-buried mollusks in sands, as well as targeting thin-shelled prey at nearly the extent of its mouth gape (Porreca et al., 2022). In a study of Black Carp in the Mississippi River, 60% of bivalves consumed by Black Carp were unionid mussels (Poulton et al., 2019). They also

pointed out that Black Carp can be opportunistic and feed on many other aquatic invertebrates (Poulton et al., 2019). Since there are no known native fish with the same combination of diet and morphology in the Great Lakes region, Black Carp is likely to fill an unoccupied niche, affecting the population of endangered North American unionids, as well as bringing potential changes to the local benthic communities (Nico et al., 2005).

The potential for a non-native species to establish, and the speed with which it may become established in a novel area will depend on the population growth rate of the species. Therefore, information regarding its predicted population growth rates in the new region can help managers prioritize monitoring and control responses. Age at sexual maturity is a life history characteristic that has a strong effect on population growth, and can be used to determine invasion risk (Cuddington et al., 2014). Age at maturity is negatively correlated to the maximum per capita population growth rate in teleost fish (Hutchings et al., 2012). When individuals in the population mature at a younger age, the generation time will become shorter. Consequently, there will be more new recruits in a given period of time, resulting in a higher population growth rate, given that all other relevant life history traits are constant. Conversely, if fish mature later, populations may grow quite slowly, and might be more easily controlled by management actions.

Black Carp reaches sexual maturity between 3-9 years in natural environments, depending on the geographic location and environmental conditions (Nico et al., 2005). In its native range, individuals from northern locations like the Amur River (China) become sexually mature at 8 - 9 years old (Evtushenko et al., 1994), while southern populations in the Yangtze River (China) reach maturity as early as age 3 - 4 (Bardach et al., 1972; NACA, 1985). This large geographical variation makes estimating Black Carp age at maturity in novel regions

difficult. In fact, although Black Carp has invaded many areas around the globe, very little research has been done to assess their age at maturity in these regions.

From existing literature, Nico et al. (2005) gathered data describing Black Carp age at maturity from 7 different locations. These authors found a positive relationship between age at maturity and latitude: individuals from northern regions tend to mature later. The relationship between age at maturity and latitude reported by Nico et al. (2005) is almost certainly due to differences in average temperatures or winter severity at different latitudes. Research indicates that increased temperatures promote fish growth rates, and lead to decreased size and earlier age at maturity (Berrigan & Charnov, 1994; Shapiro Goldberg et al., 2019). In contrast, fish living in cold temperatures or experiencing more severe winters consume less food, thus having less energy in total. They also need to allocate more energy towards survival, instead of reproduction. Therefore, their sexual maturation is likely to be delayed (Kjesbu et al., 2010). Many studies on different fish species across large geographical ranges have supported this negative relationship between age at maturity and temperature in both marine and freshwater ecosystems, and in controlled or natural environments (Jonsson et al., 2013; Niu et al., 2023; Ottersen et al., 2006; Shapiro Goldberg et al., 2019).

Brook et al. (2023) found a clear and strong relationship between air temperature (annual degree day and mean annual temperature) and age at sexual maturity for the other three Asian Carp species (Bighead Carp, Hypophthalmichthys nobilis; Grass Carp, Ctenopharyngodon idella; and Silver Carp, Hypophthalmichthys molitrix), but not for Black Carp. They suggested that the lack of significant relationship for Black Carp age at maturity and air temperature is likely due to its benthic-dwelling behavior, so that using water temperatures may yield better results for this

species. However, the Black Carp dataset used by Brook et al. (2023) was smaller than that available for other Asian carps (Black n=12 vs Grass n= 37, Bighead n= 18, Silver n= 20). The lack of a significant relationship between Black Carp age at maturity and temperature in Brook et al. (2023) could also simply be due to low sample size. Moreover, the data in both Brook et al. (2023) and Nico et al. (2005) included populations in both natural and artificial environments. We hypothesize that the type of growing environment can greatly affect Black Carp maturation age, as fish in aquaculture sources or ponds (artificial environments) are usually raised with abundant food or under conditions where supplementary heating of water occurs (He & Peng, 2018; NACA, 1985). If this factor is a significant predictor of Asian Carp age at maturity as well, then the relationships in previously published work for all species may not be an accurate representation of the dependence of this life history factor on latitude or temperature.

Our main objective was to determine if there was a relationship between Black Carp age at maturity and temperature which was not detected in previous work. Such a relationship could be employed to predict general trends in population growth rates across North America. In addition, we wanted to examine the impact of growing environment on age at maturity for all 4 species of Asian Carp, in order to determine the validity of previously published relationships.

We collected Black Carp age at maturity data from the published literature and addressed three hypotheses with this data. First, we examined whether the growing environment (natural or artificial) affects the relationship between Black Carp age at maturity and temperature, with the hypothesis that fish in artificial environments had younger maturation age. We also tested this idea on a subset of the other Asian Carp data from Brook et al. (2023) that contains information on the type of growing environment, in order to determine whether the previously reported

relationship for other Asian carps was affected by this factor. Second, we examined the hypothesis that temperature is a significant predictor of Black Carp age at maturity by looking for relationships between this quantity and four different air temperature metrics: annual average air temperature; average air temperature from the coldest quarter; average temperature from the warmest quarter; and base 0 annual growing degree days. Several of these temperature metrics have been previously examined for Black Carp and rejected by Brook et al. (2023); however, the larger dataset we assembled may yield more power in detecting relationships. We also examined an additional climate metric - winter duration, to represent the severity of winter. Third, we tested the hypothesis suggested by Brook et al. (2023) that water temperatures are a better predictor of age at maturity for this benthic-dwelling species, by using the metrics of annual average water temperature and average water temperature from the coldest quarter.

Methods

Black Carp age at maturity data

We compiled a larger dataset of Black Carp age at maturity values than has been previously available, by focusing on Chinese databases such as ZhiWang (https://www.cnki.net/index/) or WanfangWang (https://www.wanfangdata.com.cn/). The newly compiled data was combined with previously collected information from Nico et al. (2005) and Brook et al. (2023). Since age at maturity was reported in a number of ways, we standardized by reporting the median when the age at maturity of a population was given as a range and when multiple values were given for a single location.

In addition to age, two important ecological variables, sex and the type of growing environment were recorded for each data point. We categorized the environment into two

groups: artificial and natural. Artificial refers to fish raised in fish farms or obtained from aquaculture sources; while natural refers to wild fish populations in rivers, reservoirs and lakes.

Since most literature did not provide detailed location coordinates, several methods were used to approximate the latitude and longitude of reported data. If a specific city, region or fish farm name was given, then the latitude and longitude of that location was recorded. For populations that were identified by much broader geographic areas, like the name of a nation, province or lake, we followed Brook et al. (2023) and used an algorithm to find the geographic midpoint. This algorithm finds the center of gravity of a specific area from its most northern, eastern, southern, and western points (see equation in Appendix 1). Several populations had locations that related to a specific river. For these locations, the midpoints along the river course were found using the river's source and end.

Temperature data

Annual average air temperature, average air temperature in the warmest quarter, average air temperature in the coldest quarter, annual growing degree days using a base temperature of 0 °C (GDD0), winter duration, annual average water temperature, and average water temperature in the coldest quarter were used as predictors of Black Carp age at maturity. We obtained the first three temperature metrics from the WORLDCLIM dataset (https://www.worldclim.org; Fick & Hijmans, 2017). Daily maximum and minimum temperatures required for calculating the annual growing degree days and winter duration were retrieved from the Global temperature dataset (CPC Global Daily Temperature, 2022). FutureStreams global water temperature database (Bosmans et al., 2022) provided weekly water temperatures that were used to calculate

water temperature metrics. All three databases contain spatially extrapolated climate data, and a spatial resolution of 5 minutes (approximately 81 km^2) was used for extraction in all databases.

We calculated the annual growing degree days and winter duration using the extracted daily maximum and minimum air temperature. Base 0 annual degree days were calculated as $GDD_0 = \sum_{i=1}^{365} max\left(\frac{T_{max,i}+T_{min,i}}{2}, 0\right)$, where $T_{max,i}$ and $T_{min,i}$ are the maximum and minimum temperature for day i. We refer to winter duration as a specific period based on temperature thresholds rather than the traditional seasonal calendar. To calculate winter duration, we defined the start of winter for each year as the date when daily median temperature fell below 5°C for at least 5 consecutive days and similarly defined the end of winter as the date when daily median temperature exceeded 5°C for at least 5 consecutive days. Winter duration is the number of days during the defined winter period. If multiple periods met our selection criteria for winter, we selected the one that had the longest duration.

While we are unaware of any source of benthic water temperatures, we used modeled weekly river temperatures from the FutureStreams database (Bosmans et al., 2022) from 1986 - 2005. We then calculated the annual average water temperature and average water temperature in the coldest quarter using the biovars function in the R package dismo (Hijmans et al., 2022) so that our water temperature metrics are derived in the same way as the bioclimatic variables from the WORLDCLIM dataset. This and all other analyses were completed using R (R Core Team, 2023).

Statistical analysis

We regressed Black Carp's age at maturity with all six temperatures and winter duration separately because these metrics are all highly correlated. Because male Black Carp usually mature one year earlier than females, our analysis was completed only on the data for female fish. Based on the results from Brook et al. (2023) for other Asian Carp species, we assumed an exponentially decreasing impact of temperature on age at maturity. We examined the potential impacts of the seven metrics individually using a multiple linear regression with an interaction term for growing environment: $ln(age) = B_1 \times temp + B_2 \times environment + B_3 \times (temp \times environment) + B_0$ to find the best predictor. Best fit models were then selected using AICc. In addition, we applied the sequential Bonferroni correction to account for increased familywise Type I error rate due to running multiple analyses on the same dataset (Holm, 1979).

To determine if closely clustered points resulted in spatially autocorrelated residuals, we calculated global Moran's I (Moran, 1950) on the regression residuals between ln age at maturity and the chosen temperature metric. We also examined the local Moran's I for a range of distance classes. We observed a significant negative correlation at around 550 km for all models. Further examination revealed this correlation occurred because of two data points in close proximity (Romania (Nucet farm) and South Ukraine) which had early and late reported ages at maturity (4 and 11 years respectively). When the data point with the oldest reported age was removed, no significant spatial autocorrelation was present below 2500 km. In addition, we found that including the South Ukraine rather than the Romanian data did not significantly change our results. Therefore, we chose to conduct all analyses on Black Carp without this South Ukraine data point.

To determine whether there was an effect of growing environment on the other three invasive Asian Carp species, we acquired age at maturity data used in Brook et al. (2023). Using a subset of data from Brooks et al. (2023) that contained information regarding growing environment, we conducted the same analysis with all four air temperature metrics. The regressions were conducted on pooled data on the three Asian Carp species as Brook et al. (2023) found no species-specific effects when predicting Asian Carp maturation age with temperature. We followed the methods in Brook et al. (2023) to control the impacts of spatial autocorrelation by repeatedly subsampling at a distance of 250 km for 1000 times and recording the average value, unless otherwise noted. However, stratified subsampling was used to ensure that we had the same number of artificial or natural data points in each subsample.

Results

Data summary

We found 23 locations that reported age at maturity for Black Carp. Some of this data had been previously analyzed by Nico et al. (2005) and Brook et al. (2023), but 11 locations were newly added data sources. Seven locations (Ha'Maapil, Hukou County, South Ukraine, Taiwan, Hunan Province, Mississippi River, Yangtze River, Pingjiang County) contained Black Carp age at maturity for both sexes; the remaining locations either reported the value for one sex or contained no sex information at all. Of these locations, 11 were in natural environments and 12 were artificial. The range of ages at maturity were from 2.6 (Mississippi River, male) to 11 (South Ukraine, female) years old. The latitude of the data ranged from 23.8 °N (Taiwan) to 53.2 °N (Amur River). (Table 2.1, Figure 2.1)

Effects of growing environment

We found no significant effect of growing environment on Black Carp age at maturity. There was no effect of growing environment on the slope or intercept in a multiple linear regression with any of the four air temperature metrics, winter duration or annual average water temperature. There was a significant interaction term in a model with growing environment and mean water temperature of the coldest quarter ($p = 0.04$). However, AICc suggested that there was effectively no difference between a model with growing environment and a model without this term (AICc of simple regression model = -8.49 vs. AICc of interaction model = -7.48). Therefore, for all subsequent analysis, we used simple linear regressions with Black Carp age at maturity and temperature metrics.

We conducted the same analyses on the other Asian carps data and the 4 air temperature metrics. Over the course of 1000 subsampling trials, there was no effect of growing environment on the slope or intercept in a multiple linear regression with any of the 4 air temperature metrics for all other Asian Carp species grouped. Therefore, we concluded that, similar to Black Carp, growing environment had no effect on the relationship between age at maturity and air temperature in the other Asian carps.

Air temperatures and winter duration

In simple regression models for Black Carp, ln age at maturity decreased with annual average air temperatures, mean air temperature from the coldest quarter, base 0 annual growing degree days, and winter duration (Table 2). All four relationships remain significant after the sequential Bonferroni correction. There was no significant relationship between Black Carp age

at maturity and mean temperature from the warmest quarter (Table 2). Examination of the residuals of these models indicated no issues with spatial autocorrelation or normality when the datapoint from the South Ukraine was omitted.

Winter duration was the best predictor of Black Carp age at maturity (Figure 2.2), while mean air temperature from the coldest quarter was the best predictor among the four air temperature metrics (as indicated by the R^2) (Table 2). We noted that while these regressions are significant, there was less variance explained than what was reported by Brook et al. (2023) for other Asian Carp species. For the other Asian carps, similar to Brook et al. (2023), we found that using GDD0 was the best predictor of age at maturity even with our smaller set of subsampled data (Table 3, Figure 2.3). These species are also predicted to mature at a younger age than Black Carp under the same temperature for both metrics shown (except below -20 °C in coldest quarter average air temperature, Figure 2.3). This disparity gets greater as temperature increases.

Water temperatures

Water temperature metrics were significant predictors of Black Carp age at maturity (Table 2.2). Between the two water temperature metrics, cold quarter water temperature explained a larger portion of the variance than annual water temperature, and remains a significant predictor after the sequential Bonferroni correction. When comparing air and water temperature metrics, we found that models using water temperature were out-performed by those using air temperature either on an annual or a seasonal (cold quarter only) scale (Table 2.2).

Discussion

We demonstrate for the first time a significant decrease in Black Carp age at maturity with an increase in temperatures. Winter duration was the best predictor of age at maturity, but

other widely available metrics, in particular average cold quarter air temperature, were also good predictors. This finding suggests that winter may play an important role in Black Carp maturation. We were also able to show that the type of growing environment (natural vs artificial) is not a significant factor affecting predicted age at maturity for either Black Carp or the other three Asian carp species.

Previous analyses by Brook et al. (2023) demonstrated a strong relationship between air temperature and age at maturity for the other three Asian Carp species, but not for Black Carp. With the larger dataset we assembled, we found the same negative relationship also applies to Black Carp. Li et al. (2020) found that the resting metabolic rate of Black Carp increases with temperature, while Hodgins et al. (2014) further showed a temperature-related increase in specific growth rate in large Black carp individuals. Therefore, earlier maturation in Black Carp under warmer climates most likely occurs through increasing somatic growth to reach the size threshold for maturation (Berrigan & Charnov, 1994; Niu et al., 2023), rather than direct physiological processes enhancing gonadal development (Kuparinen et al., 2011; Niu et al., 2023; Van Der Kraak & Pankhurst, 1997).

Winter duration and average cold quarter temperature explain the most variation in Black Carp age at maturity, which suggests that winter severity may play an important role in the population growth of this species. During harsh winters with extended durations and low temperatures, Black Carp produces less total energy as it does not take in as many resources. Individuals will need to allocate a substantial proportion of this limited energy reserve towards survival. Consequently, less energy is available for gonadal development and maturation is delayed (Kjesbu et al., 2010). In addition, Black Carp maturation is also likely to be delayed by

decreased food consumption during colder winters. Hodgins et al. (2014) defined the optimal temperature for consumption to be greater than 25°C in juvenile Black Carp, and others reported that feeding drops sharply when water temperatures fall below 15°C (Evtushenko et al., 1994). No study has yet looked at the change in consumption rate under 4°C, or the minimum temperature at which individuals cease feeding. Nonetheless, a lower consumption rate is expected to slow down Black Carp growth, and extend the time to reach the critical size threshold for maturation.

The important role cold winters may play in Black Carp maturation offers valuable insights in understanding this species' reproductive potential and future management strategies. It provides a reasonable explanation for the latitudinal relationship previously reported by Nico et al. (2005). In addition, the finding suggests that if Black Carp continues to invade northwards, its ability to establish reproductive populations may be enhanced by effects of climate change on winter conditions. With shorter and warmer winters predicted under climate change (Bradshaw & Holzapfel, 2010; IPCC, 2021; Schwartz et al., 2006), Black Carp is likely to reach maturation earlier in high-latitude locations in the future.

Results for Black Carp differ somewhat from what has been reported for other Asian Carp species. Brook et al. (2023) found that temperature metrics calculated on an annual scale (base 0 annual average growing degree days) are the best predictors of age at maturity for the other Asian carps, while our results reveal that winter temperature might be a better metric for Black Carp. Other Asian Carp species generally mature 1-2 years earlier compared to Black Carp (Sleeper, 2019, also see Figure 2.3), and thus experience fewer winters before maturation.

Therefore, the cumulative effects of cold temperatures during these months are much smaller for these other species.

Water temperature was also found to be a significant predictor of Black Carp age at sexual maturity, but does not explain more variance than using air temperature as hypothesized. We believe this is because winter water temperature is generally warmer than air temperature, and as air temperature decreases below 0°C, water temperature bottoms out and becomes truncated (Mohseni et al., 1998, 1999; but also see Figure A2.1 in Appendix 2). As a result, age at maturity and water temperature are not as tightly related since water temperature is not a good proxy for winter severity. Therefore using water temperature predicts a later Black Carp age at maturity, and explains a smaller amount of variance in our analyses.

We replicated the analysis on other Asian Carp species by using a subset of data from Brook et al. (2023), for which we could identify the growing environment. Similar to Black Carp, we found no impact of environment. While it appears that growing environment does not significantly impact the predictive effect of temperature on age at maturity for any of the Asian carps in our dataset, we cannot rule out the possibility that artificial environments could have an effect that is not detectable with the available data. Our results on temperature predictors for the other three Asian Carp species are also consistent with what Brook et al. (2023) found. All temperatures except mean temperature from the warmest quarters were significant predictors of age at maturity, while base 0 annual average growing degree days (GDD0) explained the most variance. There was also no difference in the slope or intercept between our results and theirs for all three temperature-age at maturity relationships. Therefore, our results support Brook et al. (2023)'s previously established relationship between Asian Carp age at maturity and air

temperature, and further underscore the reliability of their North American prediction map that was constructed using this relationship.

As noted by other authors (Brook et al., 2023), we found that the majority of literature on Black Carp did not report the approximate population sizes from which the data were sampled, or the method used to determine the age at maturity. We have documented the methods used to determine size or sexual maturation for each location wherever such information is available (Table 2.1). In most cases, researchers estimated age using fish scale for individuals with stage 4-5 gonads from specific rivers or aquacultural sites. Of course, determining age at maturity with these (or similar) techniques requires capture and dissection of fish, and such studies are difficult to conduct on a large population scale (Whitledge et al., 2022). Additionally, factors such as the documented age of different-sized fish and the timing of sampling (whether pre- or post-spawning), are crucial for accurately determining the age at maturity in wild populations. Yet, information regarding these factors is seldom given by most literatures. Thus, all analysis of this work has the hidden and implicit assumption that the individual studies have taken these factors into consideration. However, as Black Carp invasion may become a more severe problem, we call for more research on this topic to better understand their reproductive strategy in this novel environment, their potential population distribution range, and their possible impact on the native mollusks.

In this study, we have shown that the latitudinal relationship reported by Nico et al. (2005) for Black Carp age at maturity is likely a temperature-driven relationship. With additional data, we were able to use temperature to predict the age at maturity of Black Carp similarly to the other Asian carps. Winter duration has strong effects on maturation age for this species, as

individuals experiencing longer winters need to invest more energy reserves towards survival instead of preparing for reproduction. This information would be critical to Black Carp invasion management in more northern locations like Canada, especially under climate change scenarios where winters are expected to become shorter and warmer. With abundant food, we believe Black Carp has the potential to invade the Great Lakes watershed. We can use the simple relationships reported in this contribution to predict its probable reproduction age from temperature, and thus gain information regarding likely population growth rates in new locations. Such information can be used to assess invasion risk, and establish regional management strategies as required.

Data availability

The data and code that support the findings of this study are available in a public repository: https://github.com/Eddie-Wu54/blackcarp_aam.git

Tables and figures

Table 2.1. Reported age at sexual maturity (AAM) of Black Carp. Sex is indicated as male (m) and female (f) if such information is given.

Reported Location	Environment	Age at Maturity	Calculated Coordinates	References	Reported method to determine fish AAM
Amur river, China and Russia	natural	7.75	(124.96, 53.20)	Evtushenko et al., 1994; Sokolov, 2002	NA
Biliuhe Reservoir, China†	artificial	6	(122.52, 39.85)	Yan et al., 2006	NA
Central China	artificial	6	(116.38, 32.33)	Shen, 1989	NA
Yangtze River, China	natural	4.5(f), 4(m)	(107.05, 29.74)	Li, 2001; NACA, 1985; Wu et al., 1964	Measure scale on individuals with known maturation
Daihai, China†	natural	6.5	(112.69, 40.58)	Zheng, 1964	NA
Ganjiang River, China†	natural	4.67	(115.40, 27.84)	Zhu, 2010	Measure scale on individuals with stage 4-5 gonads
HaMaapil, Israel	artificial	6.5(f), 5.5(m)	(34.98, 32.38)	Gur et al., 2000	Gonad measured
Heilongjiang province, China†	artificial	6.5	(128.07, 48.29)	Hao et al., 2007	NA
Hongshui River, China†	natural	5	(106.65, 25.17)	Wu et al., 2016	Measure scale on individuals with stage 4-5 gonads
Hongze lake, China†	natural	6	(118.64, 33.27)	Fishery Research Group, 1975	Measure scale on individuals with stage 4-5 gonads
Hukou County, China	natural	6(f,m)	(116.22, 29.74)	IHAS, 1976	Reported percentage matured in the population. No other information

Hunan province, China†	artificial	5.5(f), 4(m)	(111.37, 27.56)	Fishery Research Group, 1975	Measure scale on individuals with stage 4-5 gonads
Leninskoye, Russia	natural	8.5	(132.65, 47.93)	Gorbach, 1961	NA
Mississippi River, USA†	natural	4.55(f), 2.6(m)	(-90.01, 35.60)	Whitledge et al., 2022	Estimate age using fin rays, vertebrae, and gonadosomatic index
Northern China	artificial	7.5	(112.71, 45.94)	Shen, 1989	NA
Northern eastern China	artificial	8	(124.27, 45.52)	Shen, 1989	NA
Nucet farm, Romania	artificial	4	(25.55, 44.80)	Grozavu, 1962	NA
Pingjiang County, China†	artificial	6.5(f), 5(m)	(113.72, 28.77)	He & Peng, 2018	Measure age on individuals with stage 4-5 gonads
Shixing County, China†	artificial	4.5 (f)	(114.10, 24.79)	Zhong, 2007	No information on age; maturation determined by visual examination
South Ukraine	artificial	11(f), 9(m)	(33.67, 47.32)	Evtushenko et al., 1994	NA
Taihu lake, China†	natural	6	(120.25, 31.22)	Fishery Research Group, 1975	Measure scale on individuals with stage 4-5 gonads
Taiwan	natural	5(f), 4(m)	(121.11, 23.82)	Bardach et al., 1972	NA
Karamet-Niyaz, Turkmenistan	artificial	7.5(f)	(64.57, 37.75)	Sukhanova, 1967	Age tracked while individuals being raised in nurseries; maturation determined by gonad stage

Note. † data not previously analyzed in Nico et al. (2005) or Brook et al. (2023).

Table 2.2 Regression statistics for ln age at maturity of Black Carp and different temperature metrics.

	Slope	**Intercept**	**F value**	**p value**	**adj.R^2**
Annual average air temperatures	-0.017	1.98	$F_{20,1} = 10.34$	**0.004**	0.31
Average air temperature from the coldest quarter	-0.011	1.77	$F_{20,1} = 13.72$	**0.001**	0.38
Average air temperature from the warmest quarter	-0.015	2.14	$F_{20,1} = 1.89$	0.18	0.04
Base 0 annual growing degree days	$-6.9*10^{-5}$	2.14	$F_{20,1} = 8.92$	**0.007**	0.27
Winter duration	0.0019	1.64	$F_{20,1} = 16.31$	**$6.4*10^{-4}$**	0.42
Annual average water temperatures	-0.021	2.08	$F_{20,1} = 5.18$	0.034	0.17
Average water temperature from the coldest quarter	-0.023	1.92	$F_{20,1} = 9.77$	**0.005**	0.29

Note. Bold indicates the relationship is significant at an alpha level corrected by the sequential Bonferroni method (Holm, 1979).

Table 2.3. Regression statistics for ln age at maturity and three air temperature metrics from 1000 subsamples where data were pooled for all three other Asian Carp species.

	Slope	**Intercept**	**F value**	**p value**	**adj.R^2**
Annual average air temperatures	-0.042	2.01	$F_{36,1} = 44.61$	$1.48*10^{-7}$	0.54
Average air temperature from the coldest quarter	-0.025	1.50	$F_{36,1} = 39.99$	$4.02*10^{-7}$	0.51
Base 0 annual growing degree days	$-1.5*10^{-4}$	2.31	$F_{36,1} = 47.67$	$6.25*10^{-8}$	0.56

Note. The reported statistics represent the average over 1000 regressions. All p values are significant over 1000 regressions.

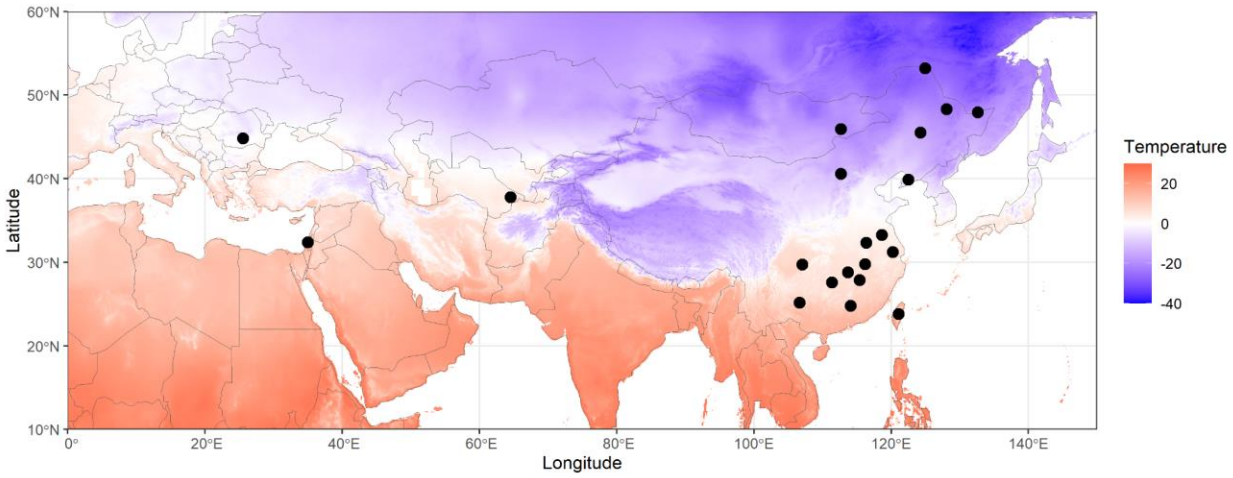


Figure 2.1. Distribution of locations that reported Black Carp age at sexual maturity and mean air temperature of the coldest quarter from 1970-2000 (obtained from the WORLDCLIM dataset; Fick & Hijmans, 2017). A data point in the Mississippi River is not shown.

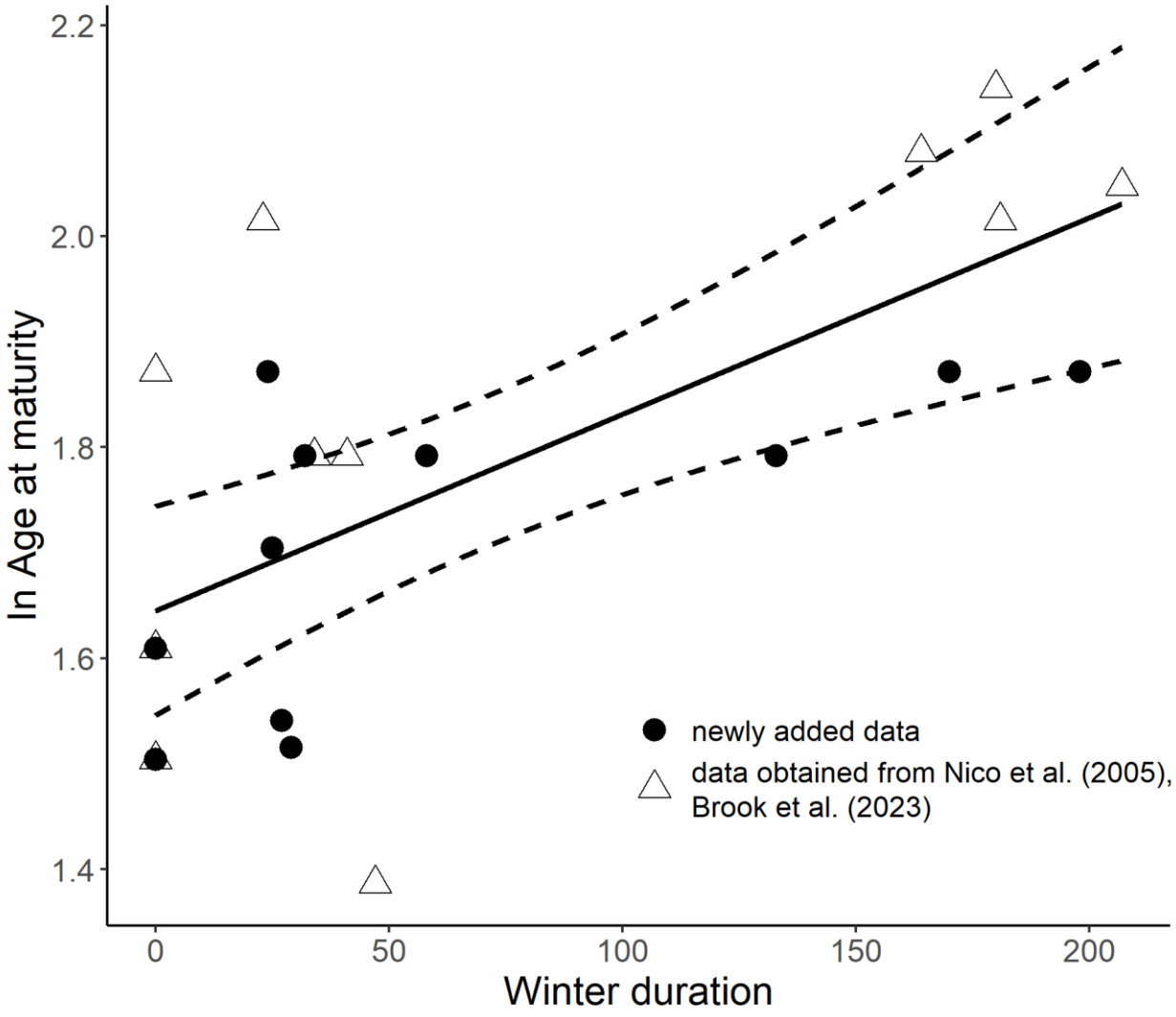


Figure 2.2. Winter duration as the best predictor of Black Carp age at sexual maturity (F20,1 = 16.31, p = 6.4e-4, adj.R2 = 0.42). Dashed lines represent 95% confidence intervals.

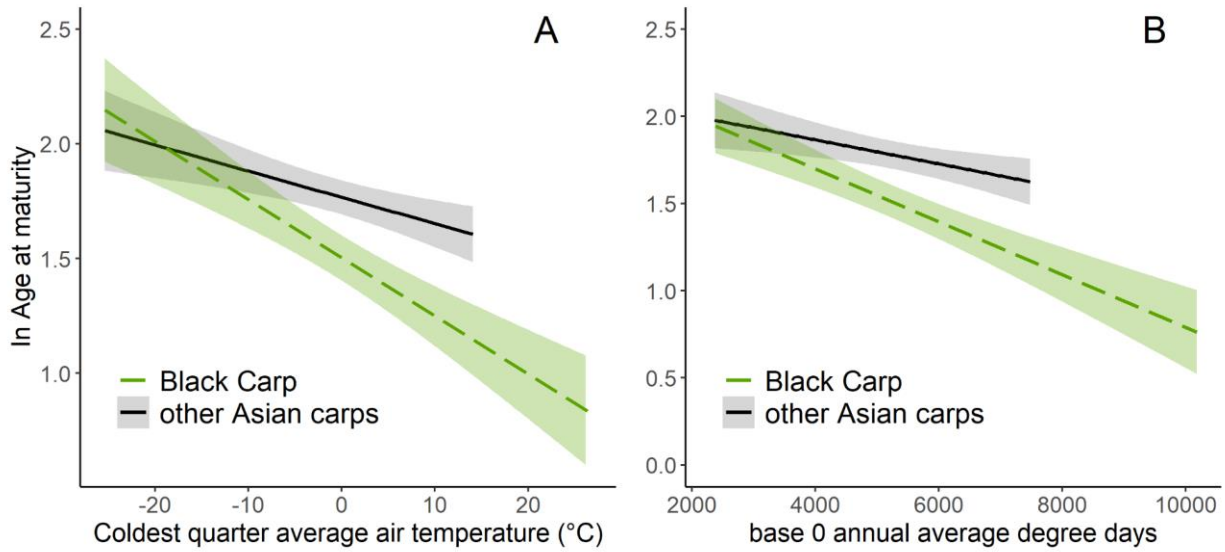


Figure 2.3. Linear regression of Black Carp and other Asian Carp species using average air temperature from the coldest quarter (A), and base 0 annual average degree days (B). Black solid lines represent Black Carp and green dashed lines represent Asian Carp. Shaded areas are 95% confidence intervals. Slope, intercept, and confidence intervals for other Asian Carp species are average values from 1000 iterations.

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Chapter 3: Use of simple statistical models to predict river water temperature in the Great Lakes region

Overview

The lack of river water temperature records has always been a problem in riverine ecosystem research. Where data is not available or complete, there have been many different approaches to model water temperature on different spatial scales. While global models can provide temperature estimates in data-limited regions, they may overlook complex local processes at smaller spatial scales. In contrast, simple statistical models applied to specific rivers, which rely on local meteorological relationships and inputs, may be a simpler solution. It remains unknown whether simple local statistical models can perform as well or even better than a complex process-based global model when predicting water temperature in Great Lakes tributaries. Using temperature records from 12 different tributary locations across the Great Lakes watershed, we demonstrate that simple local models outperform the global model at 10 out of 12 sites when estimating water temperature during the growing season. Tributary size is found to be an important factor as it constrains the applicability of linear and nonlinear models to only small rivers. The global model performed poorly at capturing temperature fluctuations at local scales, but it was still able to detect some early-season near-freezing temperature in larger rivers, indicating its limited utility in certain contexts.

Introduction

River water temperature significantly influences the distribution, survival, and reproduction of many aquatic species, making it a key determinant in the ecological function and biodiversity of riverine ecosystems (Buisson et al. 2008; Caissie 2006; Hasnain et al. 2010). Therefore, for effective management purposes, it is crucial to have water temperature for these freshwater ecosystems. However, many North American rivers, in particular tributaries of the Great Lakes Watershed, often lack complete river water temperature records, creating challenges for conducting temperature-related research in the region.

Where direct empirical records are not available, river water temperature may be predicted using other data such as air temperatures and land use type. These predictive models can be divided into two categories: deterministic and statistical (Benyahya et al. 2007; Caissie 2006). Deterministic models (also called process-based models) simulate the variation in river water temperature using the thermal exchange with the surrounding environment (Dugdale et al. 2017; Hebert et al. 2011). For example, the SHADE model takes into account the shading effects of topography and vegetation when computing the amount of solar radiation absorbed by water (Chen et al. 1998). These models normally require a large number of input variables, and their accuracy heavily depends on the quality and resolution of the input data. In contrast, statistical models of water temperature can be much simpler and use minimal inputs. Some past research has used models generated with machine learning approaches (Feigl et al. 2021; Rabi et al. 2015; Zhu et al. 2018), while other work relies on simple statistical relationships between water temperature and meteorological metrics such as air temperature and discharge (Mohseni et al. 1998; Neumann et al. 2003; Rosencranz et al. 2021).

The simplest approach to model water temperature is to apply a linear regression with air temperature as the only predictor. Given the strong correlation between the two, water temperature can be effectively estimated on a daily or weekly basis using air temperature records (Krider et al. 2013; Stefan & Preud'homme 1993). Yet, water temperature does not often respond instantaneously to the variation in air temperature, and thus air temperature at some time in the past may be a better predictor of current water temperature (Benyahya et al. 2007). Rosencranz et al. (2021) have shown that a simple linear regression model using 5 days of lagged air temperature was the best fit to predict water temperature in three Ontario rivers.

The relationship between water and air temperature is non-linear at temperature extremes, due to the density anomaly of water at low temperatures and due to evaporative cooling at high temperatures (Mohseni et al. 1998). Therefore, another approach is to apply a regression model with a sigmoid function to the water and air temperature data to capture this nonlinearity (Mohseni et al. 1998). Moheseni et al. (1998) have demonstrated that using this non-linear approach can effectively estimate weekly stream temperatures needed for fish habitat evaluation, with high accuracy and confidence for over 98% of US streams. Others later modified the non-linear model by Mohseni et al. (1998) by including other meteorological variables of interest (van Vliet et al. 2011; Webb et al. 2003), or air temperatures from preceding days (Koch & Grünewald 2010; Piotrowski & Napiorkowski 2019).

Seasonal residual model is also commonly used for water temperature modeling as it accounts for the seasonal patterns within the water temperature times series as well as the daily variation (Ahmadi-Nedushan et al. 2007). This model separates water temperature predictions into two components. The annual component represents the change in water temperatures on a

seasonal basis, while the short-term residual component captures the departure of water temperatures from the annual component (Ahmadi-Nedushan et al. 2007; Benyahya et al. 2007; Caissie et al. 1998; Cluis 1972). Much past research has suggested that seasonal residual models can perform better than other simple statistical approaches, especially at daily scales (Rabi et al. 2015; Zhu et al. 2018).

Water temperature can be modeled on different spatial scales. Some authors have used simple statistical models (Punzet et al. 2012; van Vliet et al. 2011), or more complicated deterministic models (Bosmans et al. 2022; van Beek et al. 2012; van Vliet et al. 2012; Wanders et al. 2019) to estimate water temperatures around the world. In 2019, Wanders et al. developed a dynamical 1-D water energy routing model (DynWat) that simulates river temperatures for the period 1960–2014 at a nominal 10-km and 50-km resolution. This model allows a realistic representation of water temperature at a fine spatial scale while accounting for hydrology, surface water abstraction, reservoirs, riverine flooding, and ice formation. The authors validated the model with field observations at 358 locations worldwide, and showed that the global model had a median RMSE value around 3.3°C and an average bias of only -0.3°C (Wanders et al. 2019). In 2022, Bosmans and coauthors created the futureStreams dataset using the DynWat model with different General Circulation Model (GCM) output. This dataset contains spatially extrapolated weekly predictions of river temperatures under different climate change scenarios, and from which users can directly extract water temperature forecasts for data-limited regions.

At the local scale, the DynWat model may lack the spatial resolution needed to capture local variability or specific conditions. It is possible that complex local processes (such as ground-water input) could significantly influence water temperature at a given location (Kanno

et al. 2014; Snyder et al. 2015; Westhoff & Paukert 2014), or the coarse-scale meteorological data may not provide an adequate description of local variation. In contrast to a global model some authors have used a single model to describe water temperature in a given region (McKenna Jr. et al. 2010; Rosencranz et al. 2021; Webb et al. 2003) or for a particular river (Ahmadi-Nedushan et al. 2007; Laanaya et al. 2017; Neuman et al. 2003; Zhu et al. 2018). Most regional or river-specific models take the simple statistical approach, and rely on readily available meteorological variables as input. As a result, they often provide good regional temperature estimates by being effective at capturing local geography, hydrology, and human activities.

The Great Lakes Watershed is one of the world's most diverse aquatic ecosystems. Its tributaries are home to many endangered fish and bivalve species (Jelks et al. 2008; Latta 2005). Yet, there is a notable lack of continuous and comprehensive water temperature observations for this region. The United States has a monitoring system that reports real-time surface water temperatures from the southern part of the Great Lakes (https://waterdata.usgs.gov/nwis). However, Canada has no publicly available national monitoring program for Great Lakes tributary water temperature, nor is there a provincial program in Ontario. Therefore, the ability to accurately predict water temperature from other metrics in this region becomes essential. To date, many local modeling approaches have been developed to estimate water temperature in one or a few tributaries (LeBlanc et al. 1997; McKenna Jr. et al. 2010; Rosencranz et al. 2021), but they all focused on rivers in the South. The futureStreams dataset by Bosmans et al. (2022) can provide water temperature forecasts for tributaries across the entire Great Lakes, but the validity of predictions remains to be evaluated prior to usage. In fact, if simple local models with few

meteorological inputs can perform as well or better than a complex global model it may be a simpler and easier option to guide management and research.

Our main objective was to determine if simple local statistical water temperature models with minimal meteorological inputs could perform better than a complex processed-based global model when predicting water temperature in individual rivers during the growing season. To address this objective we used empirical water temperature data from 12 different tributaries spanning across the entire Great Lakes Basin. We first determined the best simple statistical model configuration to predict river water temperature in each of these 12 tributaries. We then examined the hypothesis that simple regional models perform better than complex global models by comparing the temperature forecasts from the futureStreams dataset and our statistical models at these 12 locations.

Methods

Water temperature data

Empirical daily water temperature records were obtained for each of 12 Great Lakes tributary locations from various sources where dates of observations range from Apr 9th, 1998 to Dec 31st, 2014 (USGS 2015; Fisheries and Oceans Canada, Sea Lamprey Control Centre, unpubl. data; Table 3.1; Figure 3.1; also see Jones et al. 2017). These daily water temperature observations were checked for possible errors before use. To remove any potential artifacts caused by imputed values, we computed a rolling mean and the variance for each water temperature record over a 7 day interval. Observations with a variance smaller than 1e-10 were flagged as probably imputed and then removed.

For each tributary location, weekly modeled water temperatures were extracted from the futureStreams global river temperature dataset (referred to as futureStreams global model in later text) during the period of 1996-2019 (Bosmans et al. 2022). This dataset provides modeled temperature outputs using 5 different ISI-IMP general circulation models (GCMs), each forced with atmospheric inputs according to 4 different representative concentration pathways (RCPs) (Bosmans et al. 2022; Warszawski et al. 2014). We chose to use a GCM of GFDL-ESM2M as this circulation model is particularly strong in simulating hydrological processes. In order to compare the modeled water temperature output to empirical records during the study period, we obtained the historical reanalysis data for period 1996-2005, as well as the projection data for period 2006-2019. As the Great Lakes region has experienced a rapid annual temperature increase around 1°C since 1960 (Wuebbles et al. 2019), we selected a RCP 8.5 scenario for the projection data to represent the fast-warming conditions in the Great Lakes region at the start of the 21st century (under RCP 8.5, the Great Lakes basin is projected to warm by 4.1–5.0°C by 2100; see Xue et al. 2022).

Air temperature data

We obtained daily, empirical air temperature data from Environmental and Climate Change Canada (ECCC) for the Canadian tributary sites (https://climate.weather.gc.ca/), and from National Oceanic and Atmospheric Administration (NOAA)'s Global Historical Climatology Network daily dataset (GHCNd) for the US sites (https://www.ncei.noaa.gov). For each tributary location, the closest weather station containing a complete data record matching the water temperature data range was selected (Table A1). We then used the weathercan package (LaZerte & Albers 2018) to extract the daily mean air temperature for each selected Canadian

weather station. Since most NOAA stations within 100 km of US tributaries do not contain daily mean air temperature, we extracted the daily maximum and minimum air temperatures using the rnoaa package (Chamberlain & Hocking 2024) and from which we calculated the daily mean air temperature. Distances between selected weather stations and corresponding tributary sites range from 2.1 km to 40.4 km, and we assumed that temperature estimates are unlikely to vary significantly over this distance range.

Candidate statistical models

We fit three simple statistical models using air temperature predictors for mean daily water temperature. The first model is a multiple linear regression model which includes the air temperature of the current and previous 6 days (linear lag6). This type of model has been used previously for this region (Rosencranz et al. 2021). We also fitted a seasonal residual model (seasonal) as previous studies have indicated their generally good performance (Ahmadi-Nedushan et al. 2007). Within the seasonal residual model, the periodical annual component is computed by fitting a sinusoidal function to the daily mean times series. The residual component is modeled using a multiple regression approach with concomitant and lagged air temperature residuals from past two days (Kothandaraman 1971). Finally, we fitted a non-linear regression model (nonlinear) with a sigmoid function relating water and air temperature (van Vliet et al. 2011; Webb et al. 2003). We modified the model formulation by using the mean air temperature over the past six days, instead of the concomitant air temperature as input (Koch & Grünewald 2010). The model formulations are presented as:

$$Tw_{t,i} = a_i + \sum_{n=0}^{6} b_n \times Ta_{t-\mathrm{n},i} \text{ (linear lag6)}$$

$$Tw_{t,i} = a + b \times sin\left[\frac{2\pi}{365}(t + c)\right] + \beta_1 Ra_{t,i} + \beta_2 Ra_{t-1,i} + \beta_3 Ra_{t-2,i} + \varepsilon_{t,i} \text{ (seasonal)}$$

$$Ra_{t,i} = Ta_{t,i} - Ta_t;\ Ta_t = d + f \times sin\left[\frac{2\pi}{365}(t + g)\right]$$

$$Tw_{t,i} = \frac{\alpha}{1+e^{\gamma(\beta - T_{\bar{a},i})}} \text{ (nonlinear),}$$

where $Tw_{t,i}$ refers to the water temperature on Julian day t, at tributary location i, and $Ta_{t,i}$ is the air temperature on Julian day t at the ECCC or NOAA weather station that was paired with the tributary location.

When fitting these models, we corrected for autocorrelated errors by including an autoregressive process (AR1). To ensure that all models are valid and have predictive power with novel data, we checked for violation of model assumptions by examining the residuals for each model at each location.

Model training, testing and comparison

We modeled water temperature during the growing season in the Great Lakes region as previous research has shown that simple models can be used effectively when applied to only a certain period of a year (Rosencranz et al. 2021). To provide the best chance of a simple linear model fitting the data, we selected an important period of 112 days during the growing season that best represents a positive linear relationship between water and air temperature (Julian day 91-204; Julian week 14-29). This period was chosen to minimize the long sequences of zero temperatures in the times series, which create strong autocorrelation in the residuals that cannot be corrected. To determine the best-fitting model we created a training data set by randomly selecting a single year for each tributary location. After training, the models were tested on a

different year randomly selected for each location. Summary evaluations metrics were calculated and model assumptions checked for each location independently.

Although all three candidate models were fitted on daily data and gave daily water temperature predictions, we chose to evaluate them on a weekly scale so that the metrics could be compared to the futureStreams global model. Daily water temperature predictions from the three local models were aggregated into a weekly scale, and were matched with the weekly water temperature forecasts from futureStreams in that given year for each location.

Model performance was evaluated using metrics of: root mean square error (RMSE) (Janssen & Heuberger 1995), bias, and the Nash-Sutcliffe coefficient of efficiency (NSC) (Nash & Sutcliffe 1970), calculated as: $RMSE = \sqrt{\frac{\sum_{t=1}^{n}(P_t - O_t)^2}{n}}$; $bias = \frac{\sum_{t=1}^{n}(P_t - O_t)}{n}$; $NSC = 1 - \frac{\sum_{t=1}^{n}(P_t - O_t)^2}{\sum_{t=1}^{n}(P_t - \bar{O})^2}$, where P_t is the mean predicted temperature at week t, O_t is the mean empirical temperature at week t, and n is the total number of observations. RMSE measures the average magnitude of the error between the predictions and the actual observations, and bias assesses the systematic error direction in predictions. NSC further indicates how well the model performs compared to using a simple mean. All three metrics were also calculated with temperatures at each tributary location separately, allowing us to identify any location-specific variations in our models.

Results

Model assumptions

We found that both linear lag6 and nonlinear models fit on data from eight large rivers (defined as 16-year average discharge > 10 m^3/s; Genesee, Nipigon, Portage-Burns, St.Louis, Still, Mississagi, Saginaw, Fox River) violated model assumptions. Examination of the residuals indicated either nonlinearity, uncontrolled autocorrelation or both issues. Residuals from the seasonal model did not have these issues at any locations. However, examination of residuals suggested all model assumptions were met for 4 small rivers (defined as 16-year average discharge < 10 m^3/s; Big Creek, Big Otter, Humber, Vermilion River). Therefore, for all following analysis and comparison, the linear lag6 and nonlinear models are only applied to small rivers.

Local river water temperature models

In the four small catchments, the linear lag6 model was found to be the best among the three candidates. The nonlinear and seasonal model showed similar, but slightly inferior performance (Figure 3.2). Both linear lag6 and nonlinear models predicted water temperature with low bias and high NSC across all locations except at Big Otter River (bias=-1.29°C for linear lag6; bias=-1.59°C for nonlinear; Figure 3.3 & 3.4). The seasonal residual model had more variable errors when predicting water temperature across the four small rivers, and it tended to over or underestimate temperature by over 1°C (Figure 3.3). Its maximum and minimum prediction bias was observed at Big Otter River (bias=2.45°C) and Humber River (bias=-1.8°C).

When applied to large tributaries, the seasonal residual model was the only model that did not violate any assumptions. However, it exhibited a higher mean prediction error and bias compared to its performance on small rivers (Figure 3.2 & 3.3). This discrepancy was primarily influenced by two locations with extreme values at Still River (RMSE=4.7°C; bias=-4.22°C) and Portage-Burns Waterway (RMSE=4.67°C; bias=-4.38°C). The remaining six locations demonstrated consistent prediction errors around 3°C, bias ranging from -2.5°C to 2.5°C, and good model efficiency with an average around 0.8.

Comparison between regional and global models

We are primarily interested in whether a simple local statistical model can perform better than a complex global model for predicting water temperature in the Great Lakes region. For the four small tributaries, we found that using a simple linear lag6 model predicts water temperature with much lower and more consistent errors (mean RMSE=1.33°C; max RMSE=1.74°C) than the futureStreams global model (mean RMSE=4.15°C; max RMSE=5.25°C) (Figure 3.2). The NSC value for futureStreams fit on small rivers was also very low (mean NSC=0.27), with none of the fits over 0.7 (Figure 3.4). This suggests that the futureStreams model is not a good fit when applied to small tributaries with low water flow.

Similar to small rivers, our seasonal residual model (mean RMSE=3.13°C) also had higher average performance than the global model (mean RMSE=3.94°C) when fitted on data from large tributaries (Figure 2). It predicted water temperature with lower error and higher efficiency than the global model at 4 out of 8 locations (Fox, Mississagi, Saginaw, and Still River). Among the other 4 sites, the futureStreams model only demonstrated good performance at Genesee River and St.Louis River (RMSE < 3°C and NSC > 0.85) (Figure 2 & 4). In St.Louis

River, where futureStreams had overall best performance, it successfully estimates the near-freezing temperature during the start of the growing season (Figure 5). On the other hand, while the seasonal model is better at capturing the trend of temperature fluctuation, its predictions were bounded by the sine curve of the annual component, limiting its ability to predict temperatures below a certain threshold (Figure 5).

Discussion

We have shown that simple statistical models can give reasonable water temperature estimates during the growing season. River size is found to be an important factor when selecting the correct model formulation, as linear and nonlinear regression can only be applied to the four smaller tributaries in this study. Within these rivers, our local models outperformed the complex process-based global model with lower error and bias. In large tributaries, our local seasonal residual model still had slightly higher performance than the global model, but it failed to capture some of the near freezing temperature during early spring at certain locations.

We found that river size is an important factor in river water temperature modeling, as the applicability of many commonly used statistical models is constrained by catchment size. In small rivers, which are typically shallower and have slower water velocity, there is reduced thermal inertia and increased thermal exchange with the surrounding environment (Hockey et al. 1982; Webb et al. 2003). This dynamic enhances the influence of air temperature on water, making the water temperature more responsive to changes in the ambient environment (Webb et al. 2003). As a result, air temperature can be a strong and reliable predictor of water temperature in these settings. In contrast, in larger tributaries, higher thermal inertia resulting from greater depth and more potential for mixing leads to stronger resistance for water temperature to change.

The relationship between water and air temperature is thus much weaker and cannot be adequately captured by simple regression models.

Among the candidate statistical models, a simple regression using ambient temperature and 6 days of lagged air temperature was found to be the best model when applied to data from four small rivers during the growing season. Although linear regression is often considered to be a rather robust method when applied to weekly or monthly data (Benyahya et al. 2007; Rabi et al. 2015; Stefan & Preud'homme 1993), our results suggested that including air temperatures from proceeding days as predictors can refine the prediction to a daily scale in these small rivers. This is consistent with what Rosencranz et al. (2021) found. Using lagged temperature accounts for the non-instantaneous effects of air temperature on water, and constraining the study period to only the growing season largely addresses the problem of non-linearity at temperature extremes.

With respect to other statistical models evaluated, we found that a simple nonlinear regression with mean air temperature of the five preceding days can also provide reasonable water temperature estimates in small rivers. However, given that the water-air temperature relationship is generally linear over this period, the nonlinear model exhibited slightly inferior performance compared to linear regression, except in the Vermilion River. At this particular site, all three coefficients of the nonlinear model were found to be non-significant, indicating that this approach may not be suitable for application at this river. Similar to linear regression, the nonlinear model was first designed and has been extensively used with weekly temperature data (Benyahya et al. 2007; Mohseni et al. 1998). Our results suggested that using mean air

temperature of past days instead of ambient temperature as input can extend its applicability to daily temperature with high accuracy.

Seasonal residual models exhibited slightly worse performance compared to the other two candidates. Our result was consistent with past research (Laanaya et al. 2017; Rosencranz et al. 2021), but the performance was much poorer than that reported by others in this region (RMSE=1.68-2.15°C, Rosencranz et al. 2021; and RMSE=1.72–2.14°C, Zhu et al. 2018). At the two outlier locations (Still River and Portage-Burns Waterway), the seasonal model tends to underestimate water temperature by 2-7°C consistently throughout the study period.

The futureStreams global model was outperformed by our local models in all small tributaries, and half of the large tributaries. A comparison between empirical and predicted time series data showed that the futureStreams model struggled to capture the temperature fluctuation trends accurately. In small rivers, its predictions had errors nearly three times higher than those from simple linear regression. Given that air temperature is the dominant factor influencing water temperature in small rivers (Webb et al. 2003), a simple regression model is often sufficient to capture this relationship. In addition, the global model calculated energy balance using direct runoff, interflow, and baseflow derived from the PCR-GLOBWB hydrological model (Sutanudjaja et al. 2018; Wanders et al. 2019). Van Beek et al. (2011) found the accuracy of the PCR-GLOBWB model decreases with river size, which likely leads to the global model's underperformance in small rivers. The global model was found to have good performance in two large tributaries, Genesee River and St.Louis River. Notably, in St.Louis River, where water temperature remains around 0°C at the start of the growing season, only the global model predicts this temperature accurately.

Most statistical water temperature models in the literature do not consider the issue of autocorrelated regression residuals (Benyahya et al. 2007; Letcher et al. 2016). As the regression error at time t is likely to be related to the error at time t-1, the model assumption of independent and normal residual distribution is violated. Although these models can still give reasonable performance within the study region or river, the statistical tests of parameter significance and the confidence intervals for the predicted values are not correct. In addition, the non-independent ordinary regression residuals contain information that can be used to improve the prediction of future values. As a result, when applied to novel data, the fitted parameters will underperform. In our models, we used the AR1 term to correct for temporal autocorrelation so that the established model and coefficients can be used to estimate future water temperature in these 12 tributaries with novel air temperature input.

Among the 12 tributary locations, all four small rivers are tributaries of Lake Erie and Lake Ontario are situated below 45° latitude. It remains unknown whether the same results would apply to small rivers in more northern latitudes, as flow conditions and the freeze-off period may differ due to colder climates. We have also noticed that northern Great Lakes tributaries have fewer weather stations and less complete empirical water temperature records compared to the southern ones. At these remote locations, temperature loggers are usually installed in locations with near infrastructure such as hydrological dams or near waterfalls (in our dataset: Cameron Fall for Nipigon; Red Rock Fall for Mississagi). These locations will have different hydrological regimes than other parts of the river, and this may change the effects of air temperature on water. We encourage more temperature sampling being done at these remote northern rivers.

In this study, we compared the performance of three simple statistical models applied to individual rivers and one global model for predicting water temperature in the Great Lakes tributaries. All local models had a higher average performance than the global model when fit to data from the growing season. This finding suggests that statistical models using simple regression relationships are simpler and more accurate solutions when applied at smaller spatial scales. River size was found to be an important factor in river temperature modeling as it determined the applicability of certain models. We found that linear and nonlinear models can only be applied to small rivers, while seasonal residual models can be used across all river sizes. Although the global model demonstrated overall poor performance, it was able to model the near freezing temperature during early spring at certain locations. With novel air temperature data, future researchers can use the established models and coefficients to predict water temperature in these 12 tributaries, providing valuable insights for other water-temperature related research.

Data availability

The data and code that support the findings of this study are available in a public repository: https://github.com/Eddie-Wu54/rivertemp_GL.git

Tables and figures

Table 3.1. Summary of daily water temperature series obtained for various tributary locations in the Great Lakes Basin.

Tributary	16-year average discharge (m^3/s)	Lake	Duration	Sources
Big Creek River	7.10	Erie	2000-2009, 2012-2014	DFO, SLCC
Big Otter River	8.76	Erie	2012-2014	DFO, SLCC
Vermilion River	9.08	Erie	2012-2014	USGS Station 04199500
Humber River	7.17	Ontario	1999–2003, 2005–2009, 2011–2013	DFO, SLCC
Genesee River	83.58	Ontario	2011-2013	USGS Station 04231600
Nipigon River	404.25	Superior	1998, 2000-2010	DFO, SLCC
St.Louis River	64.49	Superior	2011-2014	USGS Station 04024000
Still River	43.78	Huron	2002, 2004, 2005, 2008	DFO, SLCC
Mississagi River	24.08	Huron	2010-2014	DFO, SLCC
Saginaw River	127.5	Huron	2012-2014	USGS Station 04157005
Fox River	126.9	Michigan	2011-2014	USGS Station 040851385
Portage-Burns Waterways	16.26	Michigan	2011-2012	USGS Station 04095090

Note. The 16-year average discharge is calculated from year 1998-2014 for each location.

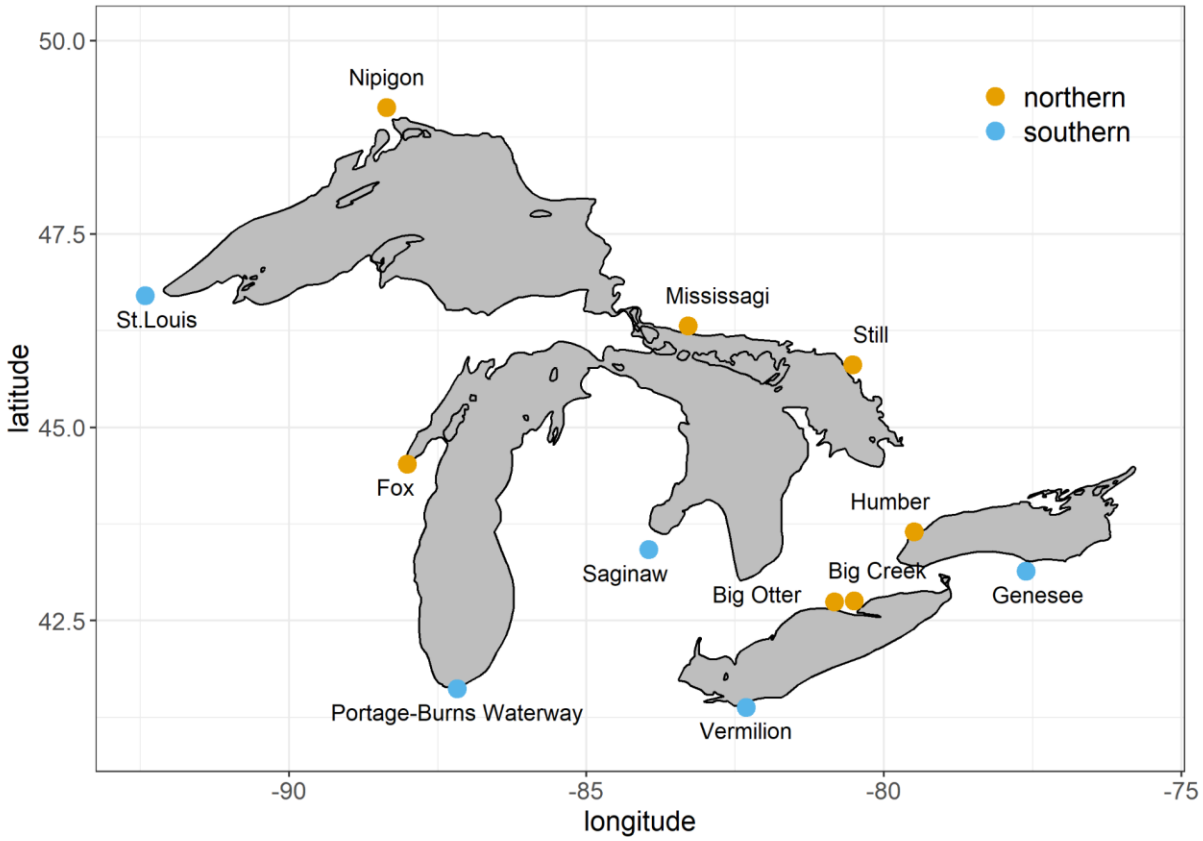


Figure 3.1. Tributary locations for which multiple years of empirical water temperature data are available in the Great Lakes region. Yellow solid points represent northern tributary locations; while blue solid points represent southern tributary locations.

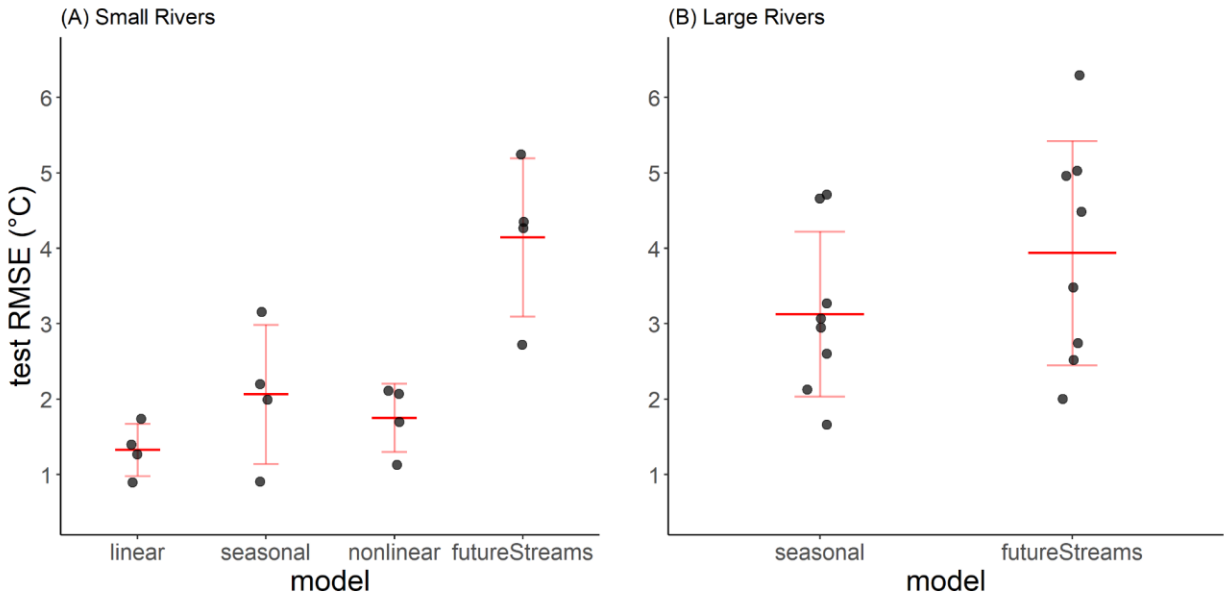


Figure 3.2. Root mean square error (RMSE) of test data for forecasted weekly mean water temperatures, for three candidate models, and the futureStreams global model. The models were fit using data from (A) four small rivers, and (B) eight large rivers. The horizontal line gives the mean, and the error bars represent the standard deviation.

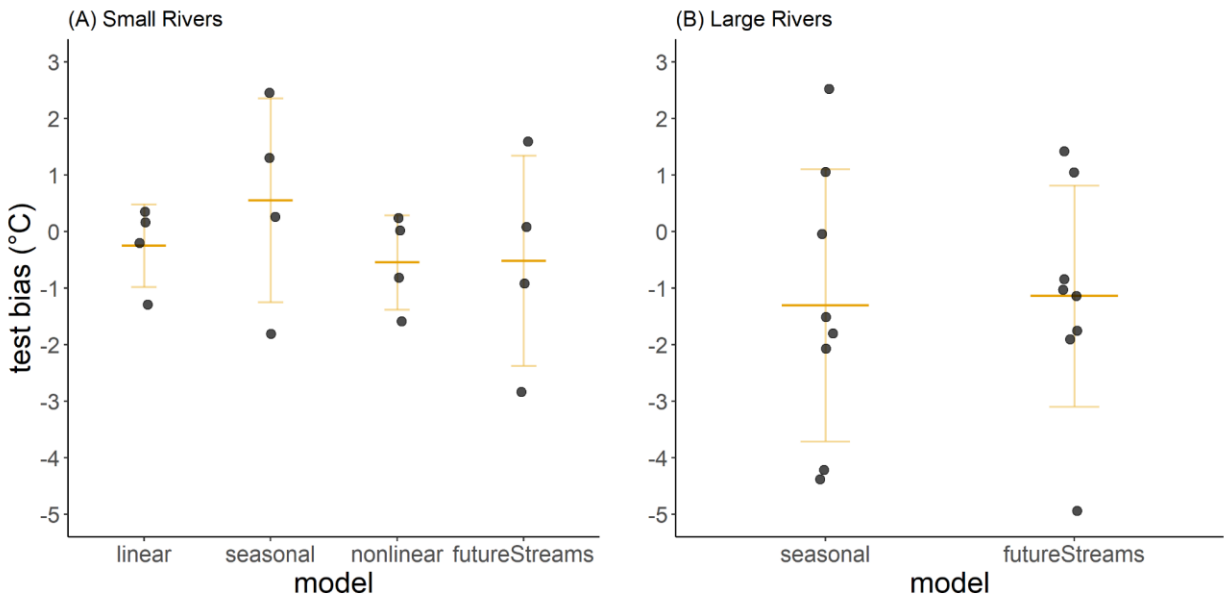


Figure 3.3. Bias of test data for forecasted weekly mean water temperatures, for three candidate models, and the futureStreams global model. The models were fit using data from (A) four small rivers, and (B) eight large rivers. The horizontal line gives the mean, and the error bars represent the standard deviation.

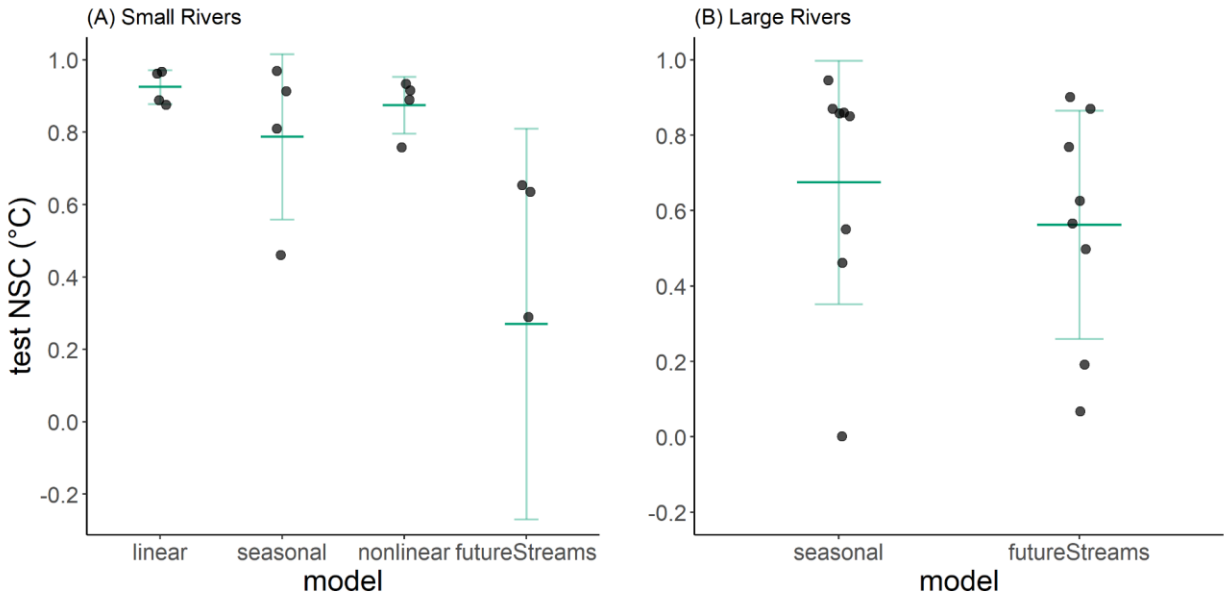


Figure 3.4. Nash-Sutcliffe coefficient of efficiency (NSC) of test data for forecasted weekly mean water temperatures, for three candidate models, and the futureStreams global model. The models were fit using data from (A) four small rivers, and (B) eight large rivers. The horizontal line gives the mean, and the error bars represent the standard deviation. An outlier for the futureStreams model at Big Otter River (NSC=-0.5) was omitted from figure panel A.

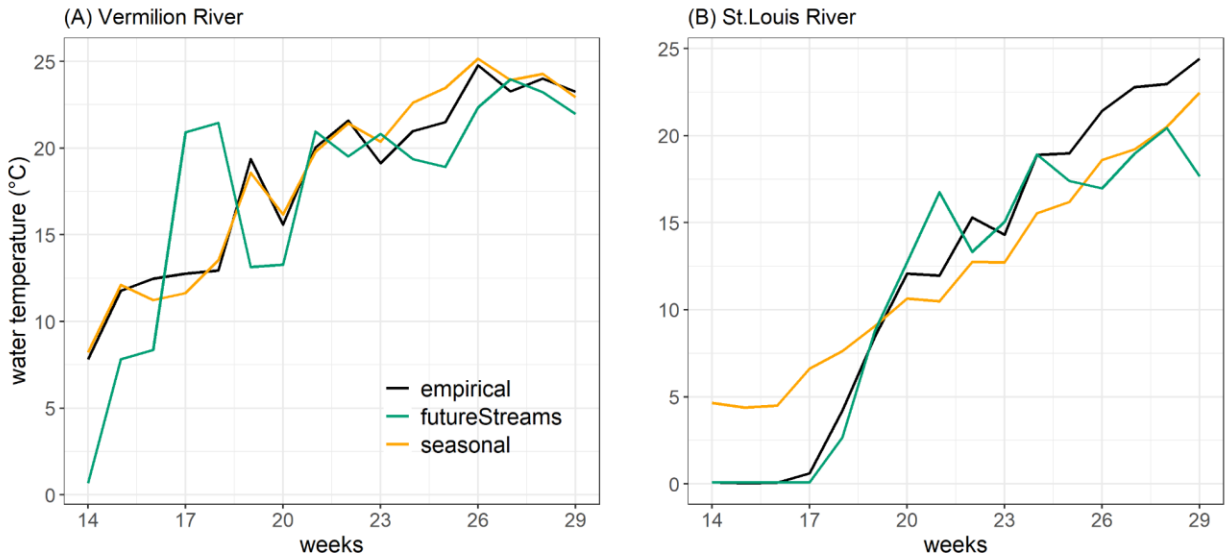


Figure 3.5. Empirical and predicted water temperatures from the seasonal residual model and global futureStreams model from week 14-29 at tributary location (A) Vermilion River year 2014 (seasonal RMSE: 0.91°C; futureStreams RMSE: 4.27°C), and (B) St.Louis River year 2013 (seasonal RMSE: 3.26°C; futureStreams RMSE: 2.73°C).

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Chapter 4: Conclusion

In this thesis, I investigated the effects of temperature on Black Carp age at maturity (Chapter 2), and developed simple statistical models to predict water temperature in the Great Lakes tributaries (Chapter 3). Black Carp is one of the four invasive Asian Carp species that has the potential to become established into the Great Lakes watershed. Being able to gain information regarding its likely population growth rate, and knowing the environmental conditions of its potential habitats is important for assessing its invasion risk.

As a previous analysis by Brook et al. (2023) did not find a significant relationship between age at maturity and air temperature for Black Carp, I re-examined this relationship with a more comprehensive dataset, and other temperature metrics that were not previously used. I found that similar to the other Asian carps, the age of maturity of Black Carp can also be predicted by simple meteorological metrics such as air temperature. Populations from northern locations mature later. I have also shown that winter duration can play an important role in predicting the maturation rate. This is likely because individuals inhabiting colder climates consume less food, grow slower, and are required to allocate more energy towards survival instead of reproduction. (Chapter 2)

As Black Carp has the potential to become established in tributaries of the Great Lakes watershed, it is important to understand the environmental conditions of these potential habitats. Since there were few available continuously logged water temperature records in the region, I developed regression-based simple statistical models to predict river water temperature in 12 different Great Lakes tributaries. I found that a simple linear regression using ambient temperature and 6 days of lagged air temperature predict water temperature with low error and

bias in small rivers, and a seasonal residual model can also give reasonable water temperature estimations in large rivers. The complex global model (Bosmans et al., 2022) did not work well in all small tributaries, and in most large tributaries. River size is also found to be an important factor as it constrains the applicability of certain statistical models to smaller streams. (Chapter 3)

My finding on the impact of temperature on age at maturity of Black carp is an important contribution for determining likely population growth rates in new locations. In addition, while I concluded that water temperature is not a better predictor of age at maturity for this species, my models of river water temperature could be useful for assessing risks for other species. Moreover, my evaluation of the futureStreams water temperature dataset reveals that simple statistical models may be a better choice for prediction, especially for small rivers.

To summarize, the findings from Chapter 2 provides a biological perspective, illustrating how temperature changes can affect the life cycles and population dynamics of invasive Black Carp. Such information becomes increasingly important as this species is more likely to become established in tributaries of the Great Lakes watershed under climate change. Meanwhile, Chapter 3 offers a practical tool for predicting water temperatures for regions with high invasion risks, enabling proactive management of these regions if required. These two chapters, though distinct in their specific focus, are interconnected through the central theme of better understanding and managing the risks of Black Carp invasion in the Great Lakes. This research framework could also be applied to other important aquatic fish species of concern, if needed.

As stated in previous chapters, there is still little research being done for Black Carp life history or population dynamics in North America. In this thesis I contributed to this area by

gathering all Black Carp age at maturity information available, developing a relationship with temperature to predict this vital trait, and creating simple statistical tools to estimate water temperature from air temperature in the Great Lakes tributaries. Future researchers are encouraged to use the relationships I found to create a Black Carp age at maturity map, or a temperature-dependent model predicting its population growth rate in the Great Lakes region. Such information is critical for informing effective management strategies and mitigating the risks associated with Black Carp invasion, especially under climate change where the northern latitudes are warming at a more rapid rate.

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Appendices

A2.1. Calculation for the midpoint of a country/province/lake

For each area , the most northern, eastern, southern and western point of the area was determined, and used in the calculation to find the midpoint as follows. The equations were derived from GeoMidpoint.com (http://www.geomidpoint.com/calculation.html).

1. Convert all coordinates to radians:

$$lat_i = lat_i * \frac{\pi}{180};\ lon_i = lon_i * \frac{\pi}{180}$$

2. Convert the lat or lon to cartesian coordinates where:

$$x_i = cos(lat_i) * cos(lon_i)$$

$$y_i = cos(lat_i) * sin(lon_i)$$

$$z_i = sin(lat_i)$$

3. Average the cartesian coordinates back to latitude and longitude:

$$Lon_{middle,i} = atan2(y_{ave,i}, x_{ave,i})$$

$$Lat_{middle,i} = atan2\left(z_{ave,i}, \left(\sqrt{x_{ave,i} * x_{ave,i} + y_{ave,i} * y_{ave,i}}\right)\right)$$

4. Convert Lat and Lon back to degrees:

$$Lon_{middle,i} = Lon_{middle,i} * \frac{180}{\pi}$$

$$Lat_{middle,i} = Lat_{middle,i} * \frac{180}{\pi}$$

A2.2. Temperature prediction of Black Carp age at sexual maturity

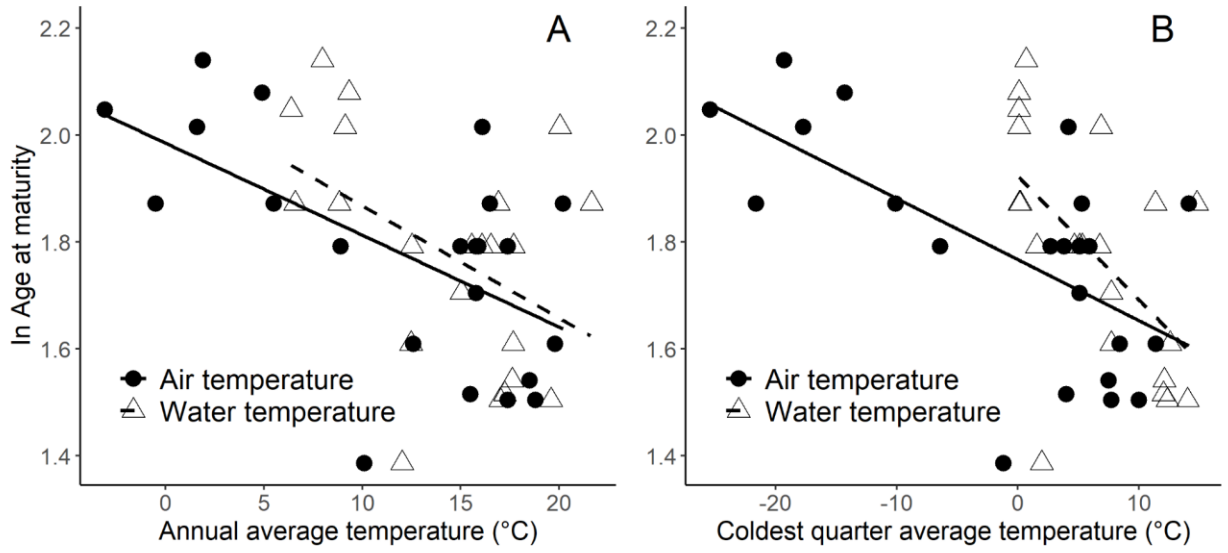


Figure A2.2. Linear regression of Black Carp using annual average temperature (A), and annual average temperature from the coldest quarter (B). Solid circles and lines represent air temperature; while empty triangles and dashed lines represent water temperature.

A3.1. Corresponding meteorological stations information

Table A3.1. Corresponding meteorological stations where air temperature information is obtained for each tributary location.

Tributary	Lake	Station name	Station ID	Duration	Sources
Big Creek	Erie	DELHI CS	27528	2000-2009, 2012-2014	ECCC
Big Otter	Erie	TILLSONBURG NORTH	27488	2012-2014	ECCC
Vermilion River	Erie	ELYRIA LORAIN CO AP	USW00004849	2012-2014	NOAA
Humber River	Ontario	TORONTO LESTER B. PEARSON INT'L A	5097	1999–2003, 2005–2009, 2011–2013	ECCC
Genesee River	Ontario	ROCHESTER GTR INTL	USW00014768	2011-2013	NOAA
Nipigon River	Superior	CAMERON FALLS (AUT)	27674	1998, 2000-2010	ECCC
St.Louis River	Superior	CLOQUET	USC00211630	2011-2014	NOAA
Still River	Huron	MONETVILLE	4125	2002, 2004, 2005, 2008	ECCC
Mississagi River	Huron	GORE BAY CLIMATE	48788	2010-2014	ECCC
Saginaw River	Huron	SAGINAW #3	USC00207222	2012-2014	USGS
Fox River	Michigan	GREEN BAY BOTANICAL	USC00473271	2011-2014	NOAA
Portage-Burns Waterways	Michigan	INDIANA DUNES NP	USC00124244	2011-2012	NOAA

A3.2. Model coefficients at 12 tributary locations

Table A3.2. Model coefficients for river water temperature models fit on daily data from 12 tributary locations independently. Linear lag6 and nonlinear regression can only be applied to the four small tributaries (Big Creek, Big Otter, Humber, and Vermilion River).

Tributary	**Model**	**Coefficients**
Linear lag6	Big Creek	a = 3.9, b_1 = 0.17, b_2 = 0.24, b_3 = 0.12, b_4 = 0.061, b_5 = 0.024, b_6 = 0.026, b_7 = 0.033
	Big Otter	a = 4.4, b_1 = 0.19, b_2 = 0.24, b_3 = 0.073, b_4 = 0.053, b_5 = 0.0075, b_6 = 0.046, b_7 = 0.086
	Humber	a = 0.88, b_1 = 0.34, b_2 = 0.26, b_3 = 0.14, b_4 = 0.09, b_5 = 0.031, b_6 = 0.078, b_7 = 0.05
	Vermilion	a = 5.2, b_1 = 0.33, b_2 = 0.14, b_3 = 0.091, b_4 = 0.095, b_5 = 0.063, b_6 = 0.039, b_7 = 0.029
Nonlinear	Big Creek	α = 27, β = 13, γ = 0.09
	Big Otter	α = 22, β = 10, γ = 0.13
	Humber	α = 30, β= 13, γ= 0.15
	Vermilion	α = 60, β = 31, γ= 0.063
Seasonal	Big Creek	a = 9.2, b = 12, c = -8900, d = 9.8, f = 8.8, g = -120, β_1 = 0.14, β_2 = 0.22, β_3 = 0.087
	Big Otter	a = 10, b = 14, c = 13000, d = 8, f = 10, g = -100, β_1 = 0.19, β_2 = 0.23, β_3 = 0.073
	Humber	a = 14, b = 12, c = -140, d = 11, f = 14, g = 620, β_1 = 0.28, β_2 = 0.23, β_3 = 0.1
	Vermilion	a = 9.9, b = 14, c = -100, d = 11, f = 13, g = -110, β_1 = 0.28, β_2 = 0.076, β_3 = 0.023
	Fox	a = 5, b = -16, c = 74, d = 7.9, f = -17, g = 800, β_1 = 0.043, β_2 = 0.087, β_3 = 0.064
	Genesee	a = 12, b = -12, c = -310, d = 13, f = 13, g = -490, β_1 = 0.088, β_2 = 0.084, β_3 = 0.076

Mississagi	a = 6.9, b = 14, c = -1200, d = 9.9, f = 14, g = -140, β_1 = -0.0033, β_2 = 0.02, β_3 = 0.026
Nipigon	a = 6.2, b = 11, c = -130, d = 9.7, f = -9.1, g = 6.4, β_1 = 0.0026, β_2 = 0.0087, β_3 = 0.0045
Portage	a = 16, b = 12, c = -140, d = 20, f = 9, g = -150, β_1 = 0.032, β_2 = 0.023, β_3 = 0.031
Saginaw	a = 7.5, b = -15, c = 2300, d = 6.5, f = 18, g = -100, β_1 = 0.25, β_2 = 0.085, β_3 = 0.032
Still	a = 12, b = 12, c = -140, d = 6.1, f = -17, g = 440, β_1 = 0.12, β_2 = 0.16, β_3 = 0.068
St.Louis	a = 7, b = 15, c = -490, d = 5.9, f = -18, g = -300, β_1 = 0.1, β_2 = 0.066, β_3 = 0.049