Impacts of temperature on Asian Carp life history and population growth

by

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A thesis

presented to the University of Waterloo

in fulfillment of the

thesis requirement for the degree of

Master of Science

in

Biology

Waterloo, Ontario, Canada, Year

Author's Declaration

This thesis consists of material all of which I authored or co-authored: see Statement of Contributions included in the thesis. This is a true copy of the thesis, including any required final revisions, as accepted by my examiners.

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Statement of Contributions

Chapter 2: Predicting the age at maturity of Asian carp using air temperature. M.E. Brook, K. Cuddington, M.A. Koops.

While the research was my own, all authors provided valuable contributions to the research. MEB was the primary coder, analyzed the data and wrote the paper. MEB, KC and MAK contributed to data analysis. All authors contributed editorial comments to the final document.

Chapter 3: Using a temperature-dependent population model to predict the population growth rates of grass carp across North America. M.E. Brook, K. Cuddington

While the research was my own, all authors provided valuable contributions to the research. MEB was the primary coder, analyzed the data and wrote the paper. MEB and KC contributed to model development. All authors contributed editorial comments to the final document.

Abstract

Asian carp (bighead carp, *Hypophthalmichthys nobilis*; black carp, *Mylopharyngodon piceus*; grass carp, *Ctenopharyngodon idella*; and silver carp, *H. molitrix*) are a group of invasive species predicted to cause ecological and economic effects in the Great Lakes region should they invade and establish populations. They are known for their ability to consume large amounts of food, fast growth rates, and large fecundities, making them invasive species of great concern. The age at sexual maturity of the population has been identified as being an important variable in determining the likelihood of any species of Asian carp establishing a population, as faster maturation typically corresponds to faster population growth. However, there is relatively little available information about the ages at maturity of Asian carp populations in North America.

Common air temperature metrics can be used to predict the age at maturity of bighead, silver and grass carp ages at maturity across North America. Using age at maturity and temperature data from around the world, we found that annual average temperature and annual average degree days could explain 60% and 62% of the variation in ages at maturity, respectively. Both metrics predicted faster maturation in more southern locations, though annual average degree days predicted higher ages at maturity than annual average temperature did.

Using the significant relationship between air temperature and age at maturity, we constructed a temperature-dependent age-size integral projection population model for grass carp. This model predicted faster population growth in more southern locations. An elasticity analysis of the model demonstrated that adult survival rates are very important in determining grass carp population growth rates, indicating that management actions like fishing will have proportionally large effects on populations. In addition, temperature dependent growth parameters demonstrated that temperature dependent growth may dramatically change our predictions of population growth rates across different temperatures, and should be further researched. Consideration of temperature when determining population growth rates can be used to guide management priorities by indicating the areas that are most at risk of fast population growth rates, allowing additional allocation of resources in those priority locations. Our results indicate that more southern areas in the Great Lakes, like Lake Erie, are most at risk of fast population growth. Overall, we demonstrate that the inclusion of environmental conditions, like temperature, in population models can reveal important insights about population growth rates that may otherwise be overlooked.

Acknowledgements

First, I want to thank my supervisor, Dr. Kim Cuddington, for her unwavering support and guidance through my studies. Thank you for your enthusiasm throughout brainstorming sessions, debugging code, and countless manuscript drafts. Thank you also to my committee members, Dr. Marten Koops and Dr. Michael Power for their expertise and contributions to this thesis.

I want to thank the past and present members of the Cuddington lab for their encouragement during my studies, and for derailing lab meetings in the best ways. Thank you to the sources of funding for my MSc degree; the NSERC Alexander Graham Bell Canada Graduate Scholarship, NSERC discovery funds, and awards from the University of Waterloo Department of Biology.

Thank you to my friends and family, especially my Mom, Dad and brother for all their love and support through my entire time as a student. A final thank you to my dogs, who mostly did their best to be huge distractions, but were very important to my success regardless.

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Chapter 1: General Introduction

In this first chapter, I summarize the general effects of temperature on fish and age at first maturity (which I will refer to as age at maturity), as well as the effect of age at maturity on population growth rates. Focusing and expanding on these topics through the lens of a group of invasive species collectively known as Asian carp, I will summarize their invasion and potential effects on the Great Lakes, followed by a summary of their life history. While there are multiple reviews of the biology and potential invasion into the Great Lakes for grass carp (Cudmore et al., 2017; Cudmore et al., 2004); bighead and silver carp (Cudmore et al., 2012); and black carp (Nico et al., 2005), this review summarizes and, in some cases, updates the scientific knowledge. In particular, the life history section focuses on how temperature affects various aspects of Asian carp life history.

Summary of the effect of temperature on fish age at maturity

Temperature influences growth rates (Jobling, 1997), reproductive timing (Hasnain et al., 2010), development time (Tsoukali et al., 2016; Kuparinen et al., 2011), and survival (Coulter et al., 2018; Jones et al., 2017; Hasnain et al., 2010) of fish. Temperature metrics are often used to predict fish behaviour and ecology, including where they can survive or when they may spawn (Kocovsky et al., 2012; Hasnain et al., 2010). In general, as temperatures increase, growth and development rates increase up to an optimal temperature, beyond which the rate declines (Jobling, 1997). Life history traits such as mortality and growth rates can often be predicted using temperature (Weber et al., 2015; Power & Attrill, 2007).

Age at maturity is the age at which a fish reaches sexual maturity, and is important in determining the generation time in fish populations (Dillingham, 2010). Temperature affects the age at maturity of fish, with warmer temperatures generally leading to faster maturation (Kuparinen et al., 2011; Berrigan & Charnov, 1994). In general, ectotherms like fish tend to mature later, but at larger sizes, when temperatures are cold, though this pattern may not hold when food is limited (Angilletta et al., 2004; Berrigan & Charnov, 1994). Several studies have found evidence to support this trend of warmer water leading to quicker maturation in fish (Shapiro Goldberg et al., 2019; Jonsson et al., 2013; Kuparinen et al., 2011). While this pattern is not fully understood, a possible explanation is that the prolonging of maturation in favour of growth may lead to an increase in fecundity in the larger fish (Hixon et al., 2014; Angilletta et al., 2004). Other variables can also affect age at maturity of fishes, such as the availability of quality food, and adult survival (Feiner et al., 2015; Jonsson et al., 2013)

Population growth rates are extremely important for the management of endangered, harvested, and invasive species (Wang et al., 2019; Jarić et al., 2015; Hidalgo et al., 2012). More specifically, population growth rates are an important metric for determining whether an invasive species will successfully invade. Assuming that the invasive fish can overcome the biotic resistances in the invaded ecosystem, estimated population growth rates can inform managers whether populations are expected to grow or shrink over time, and at what rate. Population growth rates can also be used to predict locations where persistence or invasion is likely (e.g. Merow et al., 2014), or whether management actions are working (i.e. do they successfully decrease population growth rates?) (Fredenberg et al., 2017).

Age at maturity affects the maximum population growth rate of teleost fish, with later ages at maturity generally leading to smaller maximum population growth rates (Hutchings et al., 2012). When fish populations mature faster, the net reproductive rate (R_0; number of female offspring produced per female) increases, causing faster population growth (Jones et al., 2017).

In other words, populations that mature faster have the potential to grow faster. Age at maturity may be even more important than fecundity in determining population growth rates (Hutchings et al., 2012), and the body size of teleost fish does not appear to be correlated with maximum population growth rate (Ginzberg et al., 2010).

Given the importance of temperature on age at maturity, and age at maturity on population growth rates, temperature is likely to be an important factor affecting population growth rates in fishes. In order to examine 1) if temperature can be used to predict age at maturity in fishes and 2) how temperature could therefore affect the population growth rates of populations, I chose to focus on the group of species commonly known as Asian carp. A more detailed summary of Asian carp biology follows, but their wide ranges of age at maturity (Kolar et al., 2007; Nico et al., 2005; Cudmore & Mandrak, 2004), and the likelihood of their invasion into the Great Lakes (Cudmore et al., 2012; Cudmore et al., 2017) make them an interesting and timely species to study the effect of temperature on age at maturity and population growth rates.

Potential invasion of Asian carp in the Great Lakes

In general, most species of Asian carp were introduced to North America in the early 1970s. Grass carp (*Ctenopharyngodon idella*) were intentionally brought to North America in 1963 to be studied for their potential use in reducing macrophyte abundance (Cudmore et al., 2017). Similarly, silver (*Hypophthalmichthys molitrix*) and bighead carp (*H. nobilis*) were imported in the 1970s for use as biological agents to improve water quality through consumption of plankton, as well as for food purposes (Cudmore et al., 2012; Kolar et al., 2007). Black carp (*Mylopharyngodon piceus*) were also introduced to North America in the 1970s (Nico et al., 2005). All species of Asian carp have established reproducing populations in the Mississippi river basin, and are commonly found in rivers in Indiana and Illinois, USA (Chapman et al., 2021). Bighead, silver and black carp continue to expand their range across the United States, and grass carp have expanded into some Lake Erie tributaries (Chapman et al., 2021; Kroboth et al. 2019; USFWS, 2017; Embke et al., 2016). The Great Lakes are an area of particular concern in North America for potential further invasion of Asian carp, given their proximity to existing populations (Chapman et al., 2021), and the economic and ecosystem services that may be disrupted or altered by an invasion (Cudmore et al., 2017; Hayder & Beauchamp, 2014; Cudmore et al., 2012).

Together, bighead and silver carp are likely to cause changes to the zooplankton community in the Great Lakes, and may compete with other planktivorous fish (Cudmore et al., 2012). They have altered the zooplankton community in parts of the Illinois river (Sass et al., 2014), and have decreased the abundance of planktivorous fish where they have invaded, possibly through competition for plankton (Hayer et al., 2014; Cudmore et al., 2012, Irons et al., 2007). They are predicted to decrease planktivorous fish biomass in the Great Lakes, if invasion is successful (Rutherford et al., 2021).

Grass carp can affect ecosystems by consuming large amounts of aquatic plants in their habitat (Cudmore et al., 2017). Grass carp are predicted to severely reduce vegetation in the Great Lakes and associated wetlands (Cudmore et al., 2017; van der Lee et al., 2017). This may cause trophic effects further up the food chain, potentially impacting birds, zooplankton, and fish, as well as ecosystem services like erosion protection and nutrient cycling (Cudmore et al., 2017; Gertzen et al., 2017; Wittmann et al., 2014). There is relatively less research about the possibility of deleterious effects caused by black carp, though it has been shown that they consume both native and invasive mussels (Poulton et al., 2019).

Various measures have been enacted to prevent the further spread of Asian carp. Possession of all species of Asian carp is prohibited in Ontario and Quebec (Cudmore et al., 2017; Cudmore et al., 2012). Due to their usefulness as biological control of vegetation, triploid (functionally sterile) grass carp can be stocked in many US states (Zajicek et al., 2011), though some states still allow the use of diploid grass carp (e.g. Iowa, Missouri) (Cudmore et al., 2017). The US states directly surrounding the Great Lakes prohibit the use of diploid grass carp commercially (Cudmore et al., 2017). Despite these regulations, both diploid and triploid grass carp that originate from aquaculture have been found in the Great Lakes (Whitledge et al., 2021).

The Chicago Area Waterway System has been identified as a likely area of entry for Asian carp into Lake Michigan, specifically the Chicago Sanitary and Ship Canal (ACRCC, 2018; Cudmore et al., 2017). Electric barriers were constructed to attempt to prevent Asian carp entering Lake Michigan (Bryant et al., 2016). However, some evidence suggests that Asian carp could bypass this barrier through flooding events, or currents created by ships (Bryant et al., 2016; USACE, 2010).

There are multiple other connections that may provide entry to the Great Lakes (Cudmore et al, 2017; Cudmore et al., 2012). There are extensive efforts to manage these areas, including monitoring of adult and larval fish, monitoring eDNA, and actively fishing Asian carp (ACRCC, 2018). Once Asian carp enter the Great Lakes, they are expected to be able to reproduce and spread between them (Cudmore et al., 2017; Currie et al., 2017; Currie et al., 2012). Confirming this, a grass carp was tracked migrating from Lake Erie to Lake Huron (Harris et al., 2021).

Several models have been constructed to estimate if there is enough food available for Asian carp species to survive and grow in the Great Lakes. Between macrophytes and *Cladophora*, a type of green algae, there is expected to be sufficient food for grass carp to survive in at least some areas of the Great Lakes (Jones et al., 2017; van der Lee et al., 2017). There is also likely sufficient food for silver and bighead carp to establish in Lake Erie, and productive areas in the other Great Lakes, though there may not be enough resources in more offshore habitat (Alsip et al., 2020; Anderson et al., 2017; Anderson et al., 2015; Cudmore et al., 2012; Cooke & Hill, 2010).

Spawning is not anticipated to be a serious obstacle in the Great Lakes. There are multiple tributaries with suitable spawning habitat for Asian carp across the Great Lakes, based on factors such as river length and temperature (Heer et al., 2019; Murphy & Jackson, 2013; Cudmore et al., 2012; Kocovsky et al., 2012). Even if a given Great Lake only has a few suitable rivers for spawning, this would increase the chances of successful mating by encouraging greater aggregation of individuals (Cuddington et al., 2014).

Based on their wide temperature tolerances (Cudmore et al., 2017; Cudmore et al., 2012), temperature is not expected to be a major source of mortality for Asian carp in the Great Lakes, with the possible exception of overwintering survival of juveniles. At higher latitudes, the energy reserves Asian carp are able to obtain before winter becomes critical in determining their survival, with higher survival predicted in more southern locations (Coulter et al., 2018; Jones et al., 2017). At mid-latitudes (up to 48°N latitude), survival of overwintering for silver and bighead carp is still expected to be high (Coulter et al., 2018). However, it may be possible that cool summers and autumns in more northern locations could limit Asian carp overwintering survival.

One of the remaining questions about Asian carp's ability to invade the Great Lakes is their age at maturity. While they can mature at ages as late as 10+ years in colder climates, they can also mature as early as 2 years in more tropical, warm locations (Kolar et al., 2007; Shireman

& Smith, 1983). Cuddington et al., (2014) identified that age at maturity was an important factor affecting population growth rate for silver and bighead carp in the Great Lakes. Population growth rates were much higher when the population was modelled to mature faster, implying that later maturation decreases the likelihood of establishing a population (Cuddington et al., 2014). Despite the importance of age at maturity on the invasion, there is very limited data on the age at maturity of Asian carp in or around the Great Lakes, making it difficult to predict their relative population growth rates.

To date, a reproducing population of silver or bighead carp in the Great Lakes or associated tributaries has not been detected. There have been no silver carp caught in any of the Great Lakes, although three bighead carp have been caught in Lake Erie (Chapman et al., 2021) However, samples of bighead and silver carp eDNA have been found in Lakes Michigan and Erie, indicating there may be individuals present (Jerde et al., 2013; Cudmore et al., 2012).

Diploid (reproductively viable) grass carp have been caught in Lakes Michigan, Huron, Ontario and Erie (Chapman et al., 2021; Cudmore et al., 2017). In 2015, grass carp eggs were found in a Lake Erie tributary, confirming a spawning population (Embke et al., 2016), and larval grass carp were caught in another Lake Erie tributary in 2018 (https://www.usgs.gov/news/newly-hatched-invasive-grass-carp-found-maumee-river-ohio; accessed May 30, 2021). Further isotope analysis determined that some of the grass carp in Lakes Erie and Michigan are a result of reproduction in those tributaries, not from escaped aquaculture or intentional release (Whitledge et al., 2021). Together, this evidence indicates that there are already reproducing populations of grass carp in Lake Erie.

Asian carp life history summary

Asian carp are known to consume large quantities of food, which is part of what makes them desirable as a biological control for species such as plankton and macrophytes (Kolar et al., 2007; Cudmore & Mandrak, 2004). Bighead and silver carp are both filter feeders of plankton (Kolar et al., 2007). While both will consume zooplankton, silver carp can consume smaller organisms than bighead carp, and will more readily consume phytoplankton (Kolar et al., 2007). However, both species may also consume detritus (Zhang et al., 2016; Cudmore et al., 2012; Kolar et al., 2007)

Unlike bighead and silver carp, adult grass carp primarily eat macrophytes, and will preferentially feed on certain preferred plants (Cudmore & Mandrak, 2004). Grass carp are fairly flexible in their diets, and will also eat zooplankton, benthos, worms, etc., although this may result in poorer body condition (Cudmore et al., 2017; Cudmore & Mandrak, 2004). They will also consume the algae *Cladophora*, which is abundant in all Great Lakes except Lake Superior (Cudmore et al., 2017). Black carp consume molluscs and snails (Nico et al., 2005), though they also can consume other benthic organisms, such as insects and crustaceans, indicating their diet may be slightly flexible (Poulton et al., 2019).

Asian carp grow quickly, reaching large body sizes in their first few years of life (Kolar et al., 2007; Schrank & Guy, 2002). Grass and silver carp can reach sizes over 50 cm by age two (Chapman et al., 2013; Williamson & Garvey, 2005), and bighead and black carp can reach 50 cm in length by age 3 (Kolar et al., 2007; Nico et al., 2005). They gain weight quickly; up to 1 kg by age 1, and can gain multiple kilograms a year after that (Kolar et al., 2007; Nico et al., 2005; Cudmore & Mandrak, 2004). They can grow to lengths greater than 80 cm in adulthood, sometimes reaching sizes over 1 m (Kolar et al., 2007; Williamson & Garvey, 2005; Shireman & Smith, 1983). Asian carp are generally thought to have maximum weights of approximately 40 kg (Kolar et al., 2007; Nico et al., 2005; Shireman & Smith, 1983). We would expect that warmer temperatures would increase growth rates of Asian carp (Jobling, 1997), but there is little direct research on this matter. Temperature also affects other aspects of life history relating to growth, such as metabolism, and ingestion rates, etc. (Jobling, 1997), though there are very limited data available for grass carp.

There is relatively little mortality data for Asian carp. Egg and larval mortality is assumed to be high, as is common in highly fecund species that provide no parental care (Kolar et al., 2007). Like other fish, mortality of Asian carp typically decreases as size increases (Stich et al, 2013; Lorenzen, 1996). Because of their fast growth rates, predation is unlikely to be a significant source of mortality after their juvenile stage (Cudmore et al., 2017). Triploid (functionally sterile) grass carp annual average mortality rate ranges from approximately 0.2 to 0.4, but these measures may be inflated compared to rates in the wild, due to stocking densities and food availability (Stich et al, 2013; Kirk et al., 2000). Mortality rates of diploid grass carp from the Mississippi River ranged from 0.1 to 0.4, though these estimates include fishing mortality as well as natural mortality (Sullivan et al., 2020).

Temperature is unlikely to be a direct source of mortality for Asian carp. All Asian carp are very tolerant of extreme temperatures, surviving water as cold as 0°C up to approximately 40°C, with average optimum temperatures around 25°C (Kolar et al., 2007, Cudmore & Mandrak, 2004). This wide range allows them to survive in a variety of locations. However, it is possible that more northern locations may have summers and autumns that are sufficiently cool to decrease overwintering survival of juveniles (Coulter et al., 2018; Jones et al., 2017).

Asian carp have a wide range of ages at maturity, and can mature as quickly as 2 years up to 10 years or older (Kolar et al. 2007; Nico et al., 2005; Cudmore & Mandrak, 2004). Males tend to mature one year earlier than females (Kolar et al., 2007; Nico et al., 2005). Like other ectotherms, Asian carp age at maturity appears to be affected by temperature, with faster maturation happening in warmer climates (Kolar et al., 2007; Berrigan & Charnov, 1994). Gorbach & Krykhtin (1980) in Bogutskaya et al., (2017) used temperature data to predict the maturation of Asian carp, reporting that grass and silver carp need approximately 2865 annual degree days (base temperature assumed to be 0°C) to mature. Given the link between temperature and age at maturity, and the fact that Asian carp have a wide range of age at maturity, it is likely that North America will have a range of ages at maturity.

All Asian carp are very fecund, with the total number of eggs per individual (absolute fecundity) ranging from tens of thousands to several million for the different species (Cudmore et al., 2012; Kolar et al., 2007; Nico et al., 2005; Cudmore & Mandrak, 2004). As common with fish, absolute fecundity is related to body size, with larger individuals producing more eggs (Hixon et al., 2014; Kolar et al., 2007; Nico et al., 2005; Cudmore & Mandrak, 2004). The average relative fecundity (number of eggs relative to the weight of the fish) is approximately 100 000 eggs per kilogram (Cudmore et al. 2017; Kolar et al., 2007). Gorbach (1972) in Bogutskaya et al. (2017) reported that relative fecundity of grass carp increases with increasing body size, though this is mostly only noticeable in older/larger fish.

Spawning in Asian carp typically begins in the spring/summer, and appears to be triggered by rising hydrographs and increasing water temperature (Kolar et al., 2007). Asian carp tend to begin spawning when river temperatures reach 17-18°C, and the river must stay warm enough (above 20°C) to allow proper development of eggs and larvae (Kolar et al., 2007; Cudmore & Mandrak, 2004; Stanley et al., 1978). Aliyev & Sukhanova, (1977) in Bogutskaya et al., (2017) note that grass carp require both 800 degree days base 0°C, and water temperatures to reach 17-18°C, before spawning begins. Eggs develop best at temperatures around 20-26°C, and temperatures lower than 20°C are associated with higher egg mortality (Kolar et al., 2007; Stott & Cross, 1973). The suitability of a river to be spawning habitat for Asian carp is also dependent on water velocity and length (Kolar et al., 2007). Kolar et al., (2007) report that the river should be at least 100 km long, though it may be possible for eggs to hatch in rivers as short as 25 km (Murphy & Jackson, 2013). To ensure the current is large enough to prevent eggs from settling, which increases egg mortality, velocities should be at least 0.8 m/s (Kolar et al., 2007; Stanley et al., 1978).

Temperature affects multiple aspects of Asian carp life history, such as somatic growth rates and overwintering survival. It is less clear if fecundity is affected directly by temperature in Asian carp, and direct mortality caused by extreme temperatures does not appear to be a concern for Asian carp in the Great Lakes (Kolar et al., 2007, Cudmore & Mandrak, 2004). Temperature is important for spawning, both as a cue of when to spawn (when rivers reach a certain temperature) and in determining how long it takes for fish to mature.

Conclusion

Age at maturity has been shown to be a key factor and key unknown in Asian carp's probability of establishment in the Great Lakes (Cuddington et al., 2014). Age at maturity will likely affect the predicted time it would take to establish the population of Asian carp: i.e., at faster maturation, the population would be more likely to establish, and would take less time to reach larger population sizes. Considering that Asian carp have a wide range of ages at maturity that may be related to temperature (Kolar et al., 2007), this may be important in determining the risk of invasion of Asian carp.

Given the possible detrimental effects that Asian carp pose to the Great Lake ecosystems, it is important to have a thorough understanding of their ecology, to best make predictions about how to manage the invasion. Though it is known that the age at maturity of an invading population in the Great Lakes is likely to affect the severity and speed of the invasion, there has been no research on predicting the age at maturity of Asian carp in the Great Lakes. If the age at maturity of Asian carp could be predicted using temperature, then this relationship could be used to make more specific predictions about the population growth rates of the invading population, which would allow managers to make even more informed decisions when allocating resources. For example, a Great Lake with an early predicted age at maturity (predicted fast population growth) would be at greater risk and merit the allocation of more resources than a Great Lake with a longer predicted time to maturity.

In Chapter 2, I will detail efforts to use various air temperature metrics to predict the age at maturity of Asian carp species. Multiple air temperature variables were compared to all Asian carp species, and linear regressions were used to describe the relationship, and predict the age at maturity of Asian carp in the Great Lakes. In Chapter 3, I will incorporate the relationship between temperature and age at maturity into a temperature dependent population model for grass carp. This model will be used to make predictions of population growth rates across North America. I will also perform an elasticity analysis to determine which aspects of grass carp life history have the greatest proportional effect on their population growth rates.

Chapter 2: Predicting the age at maturity of Asian carp using air temperature

Introduction

Bighead carp (*Hypophthalmichthys nobilis*), black carp (*Mylopharyngodon piceus*), grass carp (*Ctenopharyngodon idella*) and silver carp (*H. molitrix*), known collectively as Asian carp, are an invasive group of species native to eastern Asia (Kolar et al., 2007; Nico et al., 2005; Cudmore & Mandrak, 2004). They have been introduced to countries around the world, mainly through aquaculture, and as biological control of: macrophytes (grass carp, Cudmore & Mandrak, 2004), plankton (silver and bighead carp, Kolar et al., 2007) and molluscs (black carp, Nico et al., 2005). These four species of Asian carp are all established in the Mississippi River, USA (Nico et al., 2015; Nico & Jelks, 2011; Kolar et al., 2007; Williamson & Garvey, 2005). Most evidence indicates that Asian carp will be able to establish in the Great Lakes, and will likely cause ecological effects if they invade (Alsip et al., 2019; Anderson et al., 2017; van der Lee et al., 2017; Anderson et al., 2015; Cooke & Hill, 2010). Silver and bighead carp eDNA have been detected in Lake Erie basins (Jerde et al., 2013). Grass carp are already reproducing in a tributary of the western basin of Lake Erie, and are able to migrate between lakes (Harris et al., 2021; Currie et al., 2017; Embke et al., 2016).

Asian carp tolerance of a wide range of environmental factors, high fecundity, and ability to compete with native species make them invasive species of particular concern (Wittmann et al., 2014; Irons et al., 2007; Kolar et al., 2007). In invaded areas, silver and bighead carp have altered the zooplankton community (Sass et al., 2014), and had deleterious effects in native filter-feeding fishes and sport fishes (Chick et al., 2020, Love et al., 2018; Irons et al., 2007). Wild-caught black carp in the Mississippi River consume both native and invasive molluscs (Poulton et al., 2019). Grass carp eat a relatively large quantity of macrophytes (Jones et al., 2017), and can reduce standing biomass of aquatic plants (Wittmann et al., 2014) with negative impacts on birds and native fishes (Gertzen et al., 2017; Wittmann et al., 2014).

Temperature has been previously used as a correlate of Asian carp invasion risk. Temperature was incorporated into an overwintering survival model of grass carp, which predicted higher young of the year mortality in more northern locations (Jones et al., 2017). Several bioenergetic models, which include temperature as a key variable, have also been used to predict the impact Asian carp may have on the Great Lakes (Alsip et al., 2019; Anderson et al., 2017; van der Lee et al., 2017; Anderson et al., 2015; Cooke & Hill, 2010). General patterns, like the temperature-size rule, can also be used to make generalizations and predictions about life history (Berrigan & Charnov, 1994). Based on the temperature-size rule, which predicts later maturation at larger body sizes of ectotherms in cooler temperatures, we would expect Asian carp to mature slower in cooler climates (Berrigan & Charnov, 1994).

Temperature variation may partially explain the relatively wide range of ages at maturity (approximately 2-8 years for some species) (Kolar et al., 2007, Shireman & Smith, 1983). Grass carp and silver carp have similar temperature requirements for maturation (Gorbach & Krykhtin, 1981 in Naseka & Bogutskaya, 2011), and due to similar niche occupancy, bighead carp are often assumed to have similar maturation requirements as silver carp (e.g. Kocovsky et al., 2012). Asian carp tend to mature at younger ages in tropical areas, and at older ages in more temperate areas, consistent with the temperature-size rule (Kolar et al., 2007, Berrigan & Charnov, 1994; Shireman & Smith, 1983). Furthermore, Nico et al., (2005) found that age at maturity of black carp has a linear relationship with latitude. A relationship between degree days, a cumulative measure of days above a given base temperature, and age at maturity was established for silver and grass carp in the Amur River, Russia (Gorbach & Krykhtin, 1981;

Gorbach & Krykhtin, 1980; both found in Naseka & Bogutskaya, 2011). It is not stated in the translated sources whether the degree days were calculated using air or water temperatures. This relationship has been used to estimate maturation and spawning success for new locations (Heer et al., 2019; Coulter et al., 2016; Kocovsky et al., 2012). However, the Amur River, which forms the border of Russia and China, is in a northern portion of the range of Asian carp, and it is possible that this relationship does not hold for more southern areas. Ages at maturity can also be affected by variables such as food quality, as well as adult survival (Feiner et al., 2015; Jonsson et al., 2013).

Understanding variability in age at maturity is important because the risk of Asian carp establishing in the Great Lakes may be related to their age at maturity (Cuddington et al., 2014, Jones et al., 2017), due to the influence this life history trait has on population growth rates. Population growth rates are negatively correlated to age at maturity in teleost fishes: the faster the maturation, the larger the maximum population growth rate (Hutchings et al., 2012). The age at maturity of the invading population was identified as a key knowledge gap in determining the invasive risk of Asian carp (Cuddington et al., 2014). Given the wide range of age at maturity in Asian carp, being able to predict this life history trait for new locations is important for reducing uncertainty when considering the severity of the invasion (Robinson et al. 2021).

We analyzed ages at maturity of Asian carp from around the world to determine if the trait can be predicted from air temperature data (e.g. average temperature during the warmest quarter of the year) and related metrics such as average annual temperature and annual average degree days. We then used these relationships to predict the ages at maturity of Asian carp across North America, with a particular focus in the Great Lakes.

Methods

Life history data

We created a dataset of ages at maturity of Asian carp from an exhaustive search of the published literature (Appendix 2.1). Locations are primarily from Asia and Europe, with a few measurements from populations in North America. Female Asian carp tend to mature a year later than male carp, and ultimately determine the reproductive rate of the population (Kolar et al., 2007). Therefore, when ages at maturity of both sexes were given, only the female age at maturity was recorded. If the age at maturity of a population was given as a range, or if multiple ages were given for one location, we recorded the midpoint.

Due to the varied sources and range of dates the data were gathered from, a number of potentially important variables were too sparsely available to be used in the analysis. For example, the majority of sources did not specify what type of waterbody the population inhabited, which may have impacted results. There was also limited information about the method used to age the fish across the studies, or if the given age at maturity represented the age that 50% of the population matured, or the youngest age.

Most literature sources did not provide detailed location data. When a specific location was provided (i.e. a city name), we used the latitude and longitude of that location. More often, a broad location was provided (i.e. a country name like Poland, or a geographic area like South China). For these locations, we estimated the middle of the area using the most northern, southern, eastern and western points (Appendix 2.2). This allowed us to obtain an estimate for locations where we had little data, though it assumed a uniform distribution of Asian carp in those areas. For locations given as a river name (e.g. Amur River), the midpoint of the river was determined by finding the middle of the river’s source and end. If the location was more specific (e.g. Upper Amur River, Lower Volga River), then the midpoint between the source/end and the midpoint of the river was used.

Temperature data

Air temperature is correlated with surface water temperature of rivers and lakes, and can be used as a proxy for water temperature, which is often less widely available than air temperature (Honsey et al., 2018; Erickson & Stefan, 2000; Livingstone & Lotter, 1998). Grass carp tend to be found in nearshore areas (Cudmore & Mandrak, 2004), and silver carp are found at highest abundances in shallow water (Glubzinski et al., 2021), which are habitats that are likely to have temperatures strongly correlated to air temperature.

We used average annual degree days (annual degree days); average annual air temperature (annual average); average air temperature in the warmest quarter (warmest quarter); and average air temperature in the coldest quarter (coldest quarter) as predictors of age at maturity. Annual degree days, a cumulative measure of heat, was chosen because it has been used in other Asian carp literature as a benchmark value needed to achieve maturation (Heer et al., 2019; Kocovsky et al., 2012), and has been used to analyze fish life history traits such as growth and maturation (Shapiro Goldberg et al., 2019; Honsey et al., 2018; Chezik et al. 2014a; Chezik et al. 2014b). For our analysis, we used degree day base 0°C, referred to as annual degree days, to allow comparisons between other literature (Heer et al., 2019; Kocovsky et al., 2012), and evidence that suggests Asian carp can overwinter in waters as cold as 1°C (Cudmore et al., 2017). However, Chezik et al. (2014b) demonstrated that the choice of base temperature can lead to differences in fish growth estimates, so we also investigated degree days with base temperatures of 5°C and 10°C, and determined whether the choice of different base temperature affected the predicted ages at maturity. Annual average temperature is similar to annual degree days, but is often easier to obtain. Average temperature in the warmest quarter was used as an approximate measure of the growing season for each location, while average temperature in the coldest quarter was an approximate measure of the severity of winter.

We calculated degree days for our locations using data from the Climate Prediction Center (CPC) Global temperature dataset, provided by NOAA (https://psl.noaa.gov/) (CPC Global Daily Temperature, 2020). Minimum and maximum daily temperatures from 1979 to 2019 were used, which included all the complete years available at time of analysis. Annual degree days (DD_a) were calculated as $DD_a = \sum_{c=1}^{365} DD_c$, where c is the calendar day. The accumulated degree days for day c (DD_c) were calculated as

$$DD_c = \begin{cases} \frac{T_{c,max}+T_{c,min}}{2} - T_{base} & if \quad \frac{T_{c,max}+T_{c,min}}{2} \geq T_{base} \\ 0 & if \quad \frac{T_{c,max}+T_{c,min}}{2} < T_{base} \end{cases}$$

, with $T_{c,max}$ and $T_{c,min}$ as the maximum and minimum temperatures for day c, and T_{base} as the base temperature below which degree days do not accumulate (McMaster & Wilhelm, 1997).

We used the WorldClim bioclimatic variables to get air temperatures for our remaining variables (https://www.worldclim.org; Fick & Hijmans, 2017). We downloaded annual mean temperature (BIO1), mean temperature in the warmest quarter (BIO10), and mean temperature in the coldest quarter (BIO11) at a resolution of approximately 81 km^2 (5 minutes of a degree) to account for the uncertainty in the location estimates (Fick & Hijmans, 2017).

Statistical analysis

All analyses were done in R version 4.0.0 (R Core Team, 2021). We examined each species' age at maturity relationship with all four temperature variables individually. The temperature variables were all very correlated, which prevented us from using a multiple linear regression. The lowest correlation was between the warmest quarter and coldest quarter (0.68), while all other correlations were greater than 0.75. The relationships were clearly exponential upon visual inspection, so we used a linear regression of the age at maturity data, transformed using the natural logarithm, for our analyses. To determine if the slopes were significantly different among the species that had a significant relationship with the explanatory variable, we used an ANCOVA. If the interaction term (species*temperature) was not significant in 95% of the trials, we concluded the slopes were not significantly different, and grouped the species for further analysis.

After determining which species could be grouped together, we used linear regressions on the data transformed using the natural logarithm to test the significance between the age at maturity and air temperature variables. Due to the limited sample size, we evaluated models using k-fold cross validation with 5 folds, implemented in the caret package in R (Kuhn, 2008).

To check for possible spatial autocorrelation between our locations, we performed Moran's I analysis on residuals of linear regressions between age at maturity and our air temperature variables (Paradis & Schliep, 2019). We ran two tests: one using all of our location data, and another test that subsampled our data so that only one location within an arbitrary distance of 250 km of another location was included in the dataset. We subsampled our data and ran the regressions 10 000 times to get many possible permutations of subsamples. If the Moran's I test found that there was no significant spatial autocorrelation in the residuals when the data was subsampled, we would continue to subsample the data for the remainder of the analysis.

Maturation map

We used the resulting relationships between age at maturity and the various temperature variables to predict the age at maturity of Asian carp in North America. A North America degree day map was made using data from McKenney et al., (2011). The WorldClim bioclimatic variables at a resolution of approximately 1 km^2 (30 seconds of a degree) were used to generate maps for variables other than degree days (Fick & Hijmans, 2017). We represented the uncertainty in the map using the range of the 95% confidence intervals of the regression. We also estimated the age at maturity in each of the Great Lakes using air temperature at the mouth of several tributaries that may be possible spawning habitat, as an example of how the relationship can be used to predict age at maturity (Heer et al., 2019; Kolar et al., 2007).

Results

Data summary

From the literature, we found data for 54 unique locations that reported 86 estimates of age at maturity across the four carp species. The median age at maturity across all species was 4.5, with the smallest age being grass carp with an age at maturity 1.75 years in Malacca, Malaysia, and a maximum age being black carp with 11 years in southern Ukraine. The ranges of ages at maturity across the species were relatively similar: black carp minimum was 4, black carp maximum was 11; grass carp minimum was 1.75, grass carp maximum was 10; bighead carp minimum was 3, bighead carp maximum was 10; silver carp minimum was 2, silver carp maximum was 6.375. The latitude of the data ranged from 2°N (Malacca, Malaysia), to 55°N (Moscow, Russia).

Individual species

There was a significant relationship between the log transformed age at maturity and all examined temperature variables for grass, bighead and silver carps (Appendix 2.3). The warmest quarter temperature variable had the smallest adjusted R^2 values among species (range of 0.25 to

0.37), while annual degree days had the largest adjusted R^2 values (range of 0.50 to 0.66). We transformed the age at maturity data using the natural logarithm because the relationship was clearly exponential upon visual inspection, and R^2 values were larger with the transformed data. Unlike the other species, the age at maturity of black carp did not have a significant relationship with any of the temperature variables, and was excluded from all further analysis.

Spatial autocorrelation

We were concerned about possible spatial autocorrelation in our data caused by multiple ages at maturity measures from locations close to each other. We found that subsampling our data within a distance of 250 km overall significantly decreased the spatial autocorrelation in our locations. When doing a linear regression using the entire dataset, there was significant autocorrelation in the residuals for the annual average, warmest quarter, and coldest quarter variables using the Moran's I test, though there was no significant autocorrelation for annual degree days (Appendix 2.4). However, when the data were subsampled, most of the autocorrelation in the data were nonsignificant: annual average, warmest quarter, and annual degree days did not have significant autocorrelation in the residuals in at least 95% of 10 000 trials (coldest quarter had no significant autocorrelation in more than 80% of trials) (Appendix 2.4). After determining the distance between our locations and grouping locations within 250 km of each other, we had 40 spatially independent locations. Grass carp had the most locations that were at least 250 km away from each other (n=32), followed by silver (n=17), and bighead (n=16). Therefore, for future analyses we subsampled our data so that independence assumptions were met, and ran the analyses 10 000 times. We reported model parameters as the mean values from all trials.

General relationship

Overall, there was little indication of a significant interaction between species and the predictor variable for any of the temperature metrics, indicating that the same relationship could apply for bighead, silver and grass carp. Grass carp had more locations that were greater than 250 km than the other species, so we subsampled 17 grass carp locations for each test, to prevent grass carp from biasing the results of the ANCOVA tests. Out of 10 000 ANCOVA trials, more than 98% of trials had non-significant interactions between the species and temperature. Therefore, bighead, grass and silver carp had homogeneity of slopes, and were grouped for the k-fold linear regressions. Based on the Shapiro-Wilk test, all temperature variables had normal residuals in at least 73% of trials, except for warmest quarter, which had normal residuals in only 20% of trials. For this reason, we did not continue analysis with the warmest quarter temperature variable.

All temperature variables were significant predictors of the grouped log transformed Asian carp age at maturity (Figure 2.1). Annual degree days and annual average temperature explained the most variation (adjusted R^2 of 0.62 and 0.60, respectively) (Table 2.1). We calculated the error (*observed – predicted*) for each age at maturation observation. All average model errors were close to, but slightly above 0, meaning all models slightly underestimated the age at maturity (Table 2.1). When broken down by species, the model overestimated the age at maturity of silver carp (annual average error -0.10; annual degree day error -0.097; coldest quarter error -0.15), but underestimated the ages at maturity for grass carp (annual average error 0.10; annual degree day error 0.10; coldest quarter error 0.10) and bighead carp (annual average error 0.14; annual degree day error 0.12; coldest quarter error 0.14). For all predictor variables, the largest error was found for the population of silver carp in the Mississippi River. Based on the Shapiro-Wilk test, our temperature variables had normal residuals in at least 88% of trials.

Maturation map

Using the annual degree day and annual average temperature regressions, we made maps of North America with projected ages at maturity (Figure 2.2). The more northern the location, the higher the predicted age at maturity of Asian carp. We deemed locations in the maps that predicted age at maturity larger than 11 years (the largest age at maturity found in our literature search) as areas where Asian carp were unlikely to reach maturation, and were set as null. Of course, the spread of the species will depend on many factors, and many locations coloured on the maps may not be suitable for Asian carp due to factors other than climate and maturation. As temperature decreased, the uncertainty around the estimated age at maturity increased, meaning that the estimated ages at maturation in northern locations are less precise (Figure 2.3).

We predicted the ages at maturity of Asian carp in each of the Great Lakes using our models for annual degree day and annual average temperature models (Table 2.2). Lake Superior had the largest predicted age at maturity (6.0 with annual average temperature; 6.6 with annual degree day), and Lake Erie had the smallest (4.7 with annual average temperature; 5.5 with annual degree day). Though both annual air temperature and annual degree day explained approximately the same amount of variance in age at maturity based on the adjusted R^2 values of the models, age at maturity predictions based on annual degree days were 0.75 years greater on average (Paired t-test, $t = -26.2$, $df = 9$, $p = 8.4 \times 10^{-10}$) (Table 2.2). The range of the difference between the upper and lower 95% confidence intervals of the Great Lakes prediction was slightly larger (0.29 years on average) for our annual degree day model compared to our annual average temperature model (Paired t-test, t = -12.4, df = 9, p = 5.7x10^{-7}) implying that the annual average temperature model was slightly more precise.

Degree day base temperature

The choice of degree day base can affect growth estimates (Chezik et al., 2014b), therefore, we tested whether the choice of base temperature affected the age at maturity predictions made by our grouped linear regressions. Overall, we found no significant difference between the estimated ages at maturity using a linear regression between the degree day base temperatures of 0°C, 5°C and 10°C. We used repeated measures ANOVA with the Greenhouse-Geisser sphericity correction to account for the lack of sphericity in the data. The four locations with the largest degree days (Malacca, Cuttack, Tamilnadu and Cuba) were removed from the dataset for this test to ensure normality assumptions were met. All p values were non-significant (greater than 0.3) for all 10 000 trials. This reflects the findings of Chezik et al. (2014a), who found that the choice of base temperature is generally robust at small base temperature values.

Discussion

We found that air temperature can be used to predict the age at maturity of Asian carp. As temperatures increase, there is a significant decrease in the age at maturity of bighead, silver and grass carp. Faster maturation leads to faster population growth in fishes (Hutchings et al., 2012), which means understanding the age at maturity is important for predicting and controlling invasions. Average annual degree days and average annual temperature explained approximately 62% and 60% of the variation in age at maturity, respectively. The choice of temperature variable affected the predicted age at maturity, with annual average degree days giving a longer time to maturity on average. We suggest, therefore, that easily obtained metrics like air temperature can be used to estimate the relative risk of rapid invasion in novel locations, by identifying locations of faster maturation to prioritize management.

Previous evidence collected in the Amur River indicates that silver and grass carp require approximately 2865 degree days to mature, though the source does not specify whether this was calculated using air or water temperature (Gorbach & Krykhtin, 1980 in Naseka & Bogutskaya, 2011). This value has been used as a threshold to determine if maturation in an area is possible for Asian carp. For example, this value has been used to conclude that maturation is possible in western areas of Lake Erie (Kocovsky et al., 2012), and to determine suitability of tributaries for spawning in Lake Erie (Heer et al., 2019). While both Kocovsky et al. (2012) and Heer et al. (2019) used degree days based on water temperature, we demonstrate that air temperature can also be used to predict maturation. A further advantage of our regression model is that it allows us to predict what age the fish will mature, instead of a threshold benchmark. For example, our degree day model predicts that 1487 annual degree days corresponds to maturation in 8 years, while 7559 annual degree days corresponds to maturation in 3 years. In contrast, the predictions based on annual average temperature would predict maturation in 3 years when the annual average temperature is 20.5°C. Annual average temperatures of 8.9°C would correspond to maturation in 5 years, while an average temperature of -1.8°C would correspond to maturation in 8 years.

Multiple papers have discussed the importance of understanding the age at maturity of invasive Asian carp populations (Jones et al., 2017; Cuddington et al., 2014). Jones et al. (2017) found that all possible ages at maturity (2 to 8 years) of grass carp were projected to have a net reproductive rate (R_0) above 1 in the Great Lakes, with faster maturation corresponding to larger R_0 values, and therefore faster population growth. If we assume that a given population size is required for a species to be firmly established in a new region, then the age at maturity of Asian carp will affect how long it takes a population to establish, with faster maturation likely leading to less time until establishment (Cuddington et al., 2014), assuming that the Asian carp could survive and overcome other biotic resistances necessary for invasion. Our results indicate a range of ages at maturity across the Great Lakes, and therefore a range of risk of establishment. This means the population of Asian carp in more southern lakes, like Lake Erie, would likely grow and establish populations faster than in other lakes, and will require different management actions and strategies.

Despite the large amount of variance explained by the model, both annual degree days and average annual temperature overestimated the age at maturity expected in the Mississippi river. The measured age at maturity is approximately 2 years for silver carp (Williamson & Garvey, 2005; Appendix 2.1), while the predicted age was 4.1 (95% CI of 3.7 and 4.7) for our annual average model, and 4.7 (95% CI of 4.1 and 5.3) for our annual degree day model. However, there are multiple ways researchers may classify the age at maturity of a population. Some researchers consider age at maturity to be the age where approximately 50% of the cohort is mature (e.g., Gorbach, 1961), while other studies report the youngest age of mature fish found (though most papers did not specify). The age at maturity from Williamson and Garvey (2005) in the Mississippi was based on only 6 mature fish, so it is possible that the age at maturity of the population as a whole is higher (it is unlikely that maturation is faster than 2 years, given that the only measurement of faster maturation was that of 1.75 from Malaysia). Other North American locations did not deviate as much from the predicted age of maturity. The average error of the other locations in North America was -0.18 for both annual average and annual degree days, while the Mississippi location had an error value for those variables of -0.73 and -0.79, respectively.

The Mississippi river connects to a likely point of entry for Asian carp into the Great Lakes (Cudmore et al., 2012), so understanding discrepancy between our model predictions and the data will be important in determining the age at maturity of the invading population. It is possible that harvesting of Asian carp in the Mississippi (ACRCC, 2018) has over time shifted the population to mature at smaller, younger sizes (Feiner et al., 2015). Another possible explanation is that abundant food resources in the Mississippi are driving the early maturation of Asian carp. Both food and temperature contribute to growth rates in fish (Jobling, 1997). The Mississippi has high concentrations of phosphorus, even compared to other rivers like the Yangtze River (Rabouille et al., 2008). This nutrient loading could partially explain why the age at maturity of Asian carp is lower than predicted in that area, as higher concentrations of phosphorus can increase zooplankton growth rates (Elser et al., 2001). Furthermore, increasing temperature also increases productivity of aquatic environments (Lewandowska et al., 2012), so it may be difficult to separate the effects of food and temperature on the age at maturity of Asian carp.

We note that unlike bighead, grass and silver carp, age at maturity of black carp did not have a significant relationship with any of our temperature variables (Appendix 2.3), despite the fact that Nico et al. (2005) found that there was a significant relationship with latitude. This could be because, unlike the other species of Asian carp, black carp tend to stay near the bottom of waterbodies (Glubzinski et al., 2021; Nico et al., 2015; Cudmore & Mandrak, 2004). Because of their benthic nature, air temperature may not be appropriate to approximate the temperatures they experience. Analysis using water temperature may have better results, given that air temperature is correlated with surface water temperatures, and therefore may not be sufficiently correlated with benthic water temperatures (Honsey et al., 2018).

Using temperature to model life history traits is relatively common for other species. Temperature dependent models have been made for maturation and development rate (Quinn, 2017, Adams et al., 2001), embryonic development (Du et al., 2007, Escribano et al., 1998), and growth rates (Gotthard et al., 2000) in arthropods (Quinn, 2017, Gotthard et al., 2000, Escribano et al., 1998), reptiles (Du et al., 2007), and plants (Adams et al., 2001). Being ectotherms, fish are a good candidate for these types of models, as they are dependent on the water temperature surrounding them (Jobling, 1997). While fish bioenergetic models incorporate temperature, for example in the form of temperature dependent consumption rates that account for maximum and optimal feeding temperatures (Anderson et al., 2017; Anderson et al., 2015; Cook & Hill, 2010), we demonstrate that temperature can be used to make predictions about life history without the need for a complicated bioenergetic model. While there are some models that use temperature to predict early life history in fish (e.g., egg development rates, Keller et al., 2020, Tsoukali et al., 2016, Petereit et al., 2008, Geffen et al., 2006, Pepin, 1991), there is relatively little research creating models to predict life history such as growth and maturation (though see Raimondo, 2012; Power & Attrill, 2007). We encourage more models relating environmental variables like temperature to life history traits of fishes as a method of prediction.

Table 2.1. Results of 10 000 k-fold linear regressions. Slopes, intercepts, and adjusted R^2 are mean values. The mean error represents the error of the final, averaged model.

	Slope	Intercept	Adj R^2	Mean Error
Annual Average	-0.044	2.0	0.60	0.056
Coldest Quarter	-0.026	1.5	0.57	0.045
Annual Degree Days	-1.6×10^{-4}	2.3	0.62	0.054

Table 2.2. Predicted age at maturity of Asian carp in the Great Lakes. The air temperature at the mouth of tributaries for each lake was used to make the estimate. Chosen tributaries are rivers that may be suitable for spawning. Upper and lower 95% confidence intervals are given in brackets.

	Latitude (decimal degrees)	Longitude (decimal degrees)	Annual average age estimate (95% CI)	Annual degree day age estimate (95% CI)
Superior				
Ontonagon River[a]	46.8764	-89.3272	5.9 (5.1 – 6.9)	6.6 (5.6 – 7.7)
Nemadji River[a]	46.7035	-92.0257	6.0 (5.2 – 7.0)	6.6 (5.7 – 7.8)
Michigan				
Sheboygan River[a]	43.7489	-87.7024	5.2 (4.6 – 6.0)	6.1 (5.3 – 7.1)
Grand River[a]	43.0579	-86.2512	5.0 (4.4 – 5.7)	5.9 (5.1– 6.8)
Huron				
Saginaw River[a]	43.6473	-83.8495	5.2 (4.5 – 5.9)	5.8 (5.1 – 6.7)
Black River[a]	43.0053	-82.4191	5.1 (4.4 – 5.8)	5.8 (5.1 – 6.7)
Ontario				
Etobicoke Creek[b]	43.5848	-79.5412	5.1 (4.5 – 5.8)	5.8 (5.1 – 6.7)
Humber River[b]	43.6315	-79.4706	5.1 (4.4 – 5.8)	5.8 (5.1 – 6.7)
Erie				
Maumee River[a]	41.7091	-83.4405	4.7 (4.2 – 5.4)	5.5 (4.8 – 6.3)
Vermillion River[a]	41.4264	-82.3642	4.7 (4.2 – 5.4)	5.5 (4.8 – 6.3)

[a] Kolar et al., 2007

[b] Heer et al., 2019

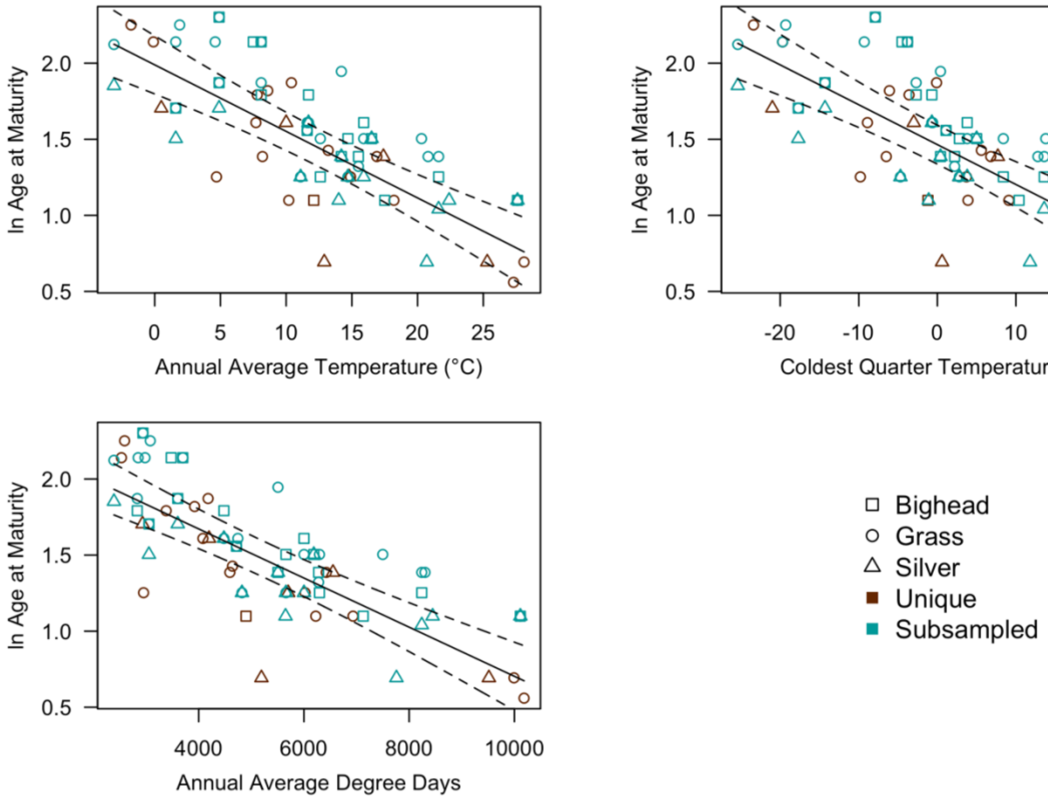

Figure 2.1. Linear regressions of grouped species. Solid black regression lines represent the mean slope and intercept, while dashed lines show 95% confidence intervals. Brown symbols are locations that were at least 250 km from any other locations, while blue symbols show locations within 250 km of at least one other location, and were therefore subsampled to avoid possible spatial autocorrelation.

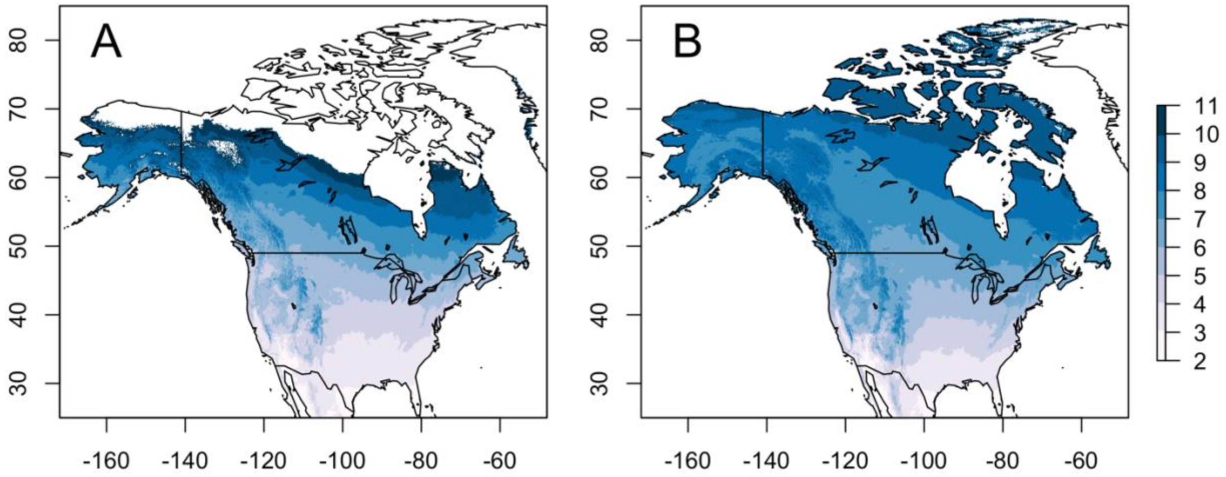

Figure 2.2. Predicted age at maturity (years) in North America, based on average annual temperature (panel A) and annual degree days (panel B). Ages over 11 were excluded.

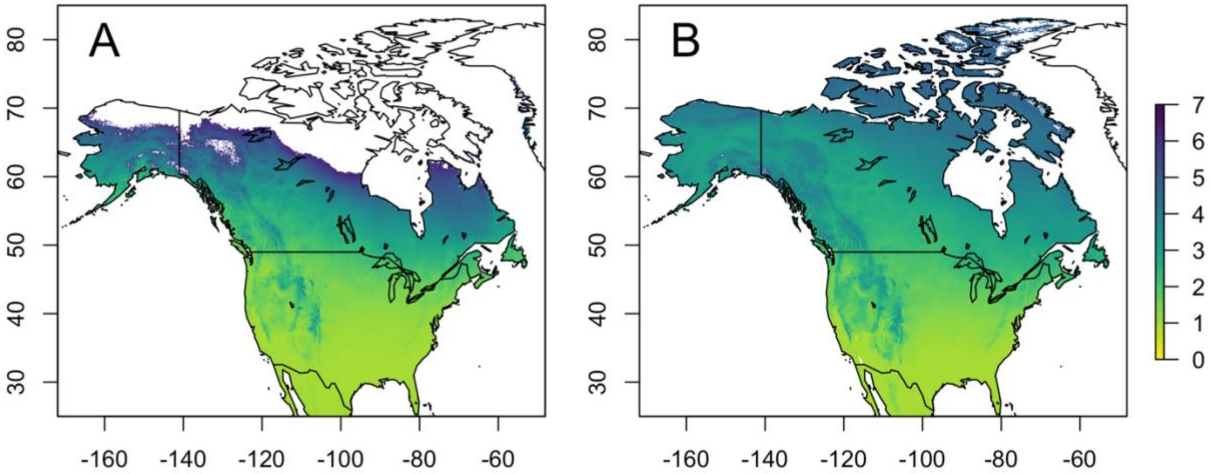

Figure 2.3. Uncertainty (in years) of annual average model (panel A) and annual average degree days model (panel B), represented by the difference between the upper and lower 95% confidence intervals in years.

Chapter 3: Using a temperature-dependent population model to predict the population growth rates of grass carp across North America

Introduction

Models that predict population growth rates are an important tool in managing invasive species. Population growth rates can be used to predict the persistence of invasive populations (Merow et al., 2014), time until establishment (Cuddington et al., 2014), and to assess if management actions will have the intended impacts on populations (Fredenberg et al., 2017). Knowing the predicted population growth rate of populations of invasive species allows managers to prioritize locations for management actions. For example, if a population was expected to grow faster in one location than another, actions could focus on the location with fast growth first, as there is less time to act before the invasive population reaches a large size.

Age at maturity (the average age at which an individual reaches sexual maturity) exhibits a significant effect on population growth rates in fishes (Wang et al., 2019; Carlson & Simpfendorfer, 2015; Hutchings et al., 2012). Maximum population growth rates significantly increase as age at maturity decreases (Hutchings et al., 2012), meaning that populations with later ages at maturity have smaller growth rates (Wang et al., 2019; Carlson & Simpfendorfer, 2015). Wang et al., (2019) found that age at maturity explained approximately 75% of the variance in population growth rates for freshwater fishes. Age at maturity is known to be affected by variables such as food concentration, temperature and survival (Feiner et al., 2015; Jonsson et al., 2013).

Ectotherms like fish tend to grow faster, but mature earlier and at smaller sizes in warm climates compared to cool (Angilletta et al., 2004; Berrigan & Charnov, 1994). Jonsson et al., (2013) found that Atlantic salmon (*Salmo salar*) matured faster in warmer temperatures compared to colder temperatures. Temperature can predict the age at maturity of a group of species known as Asian carp, implying that population growth rates will be faster in warmer locations that have earlier maturation (Chapter 2). Because of the effect of age at maturity on population growth rates, temperature may have strong influences on population growth rates, suppressing growth of populations in cooler locations.

Air temperature can be used to predict the age at maturity of grass carp (*Ctenopharyngodon idella*), with faster maturation in warmer locations (Chapter 2). Grass carp are a species of Asian carp which were introduced to North America for macrophyte control (Cudmore et al., 2017). They are voracious consumers of plants, with fast somatic growth rates, high fecundity, and can grow to sizes over a metre long (Cudmore et al., 2017; Shireman & Smith, 1983). They are already reproducing in Lake Erie, and may be starting to expand to other Great Lakes (Harris et al., 2021; Whitledge et al., 2021; Embke et al., 2016). The age at maturity of the invading population is not currently known, and there are few empirical studies of age at maturity of grass carp in North America. However, a threshold value of 2865 degree days (assumed to be base 0°C, though this is not specified in the source) needed to reach maturity has been used to estimate the suitability of rivers for spawning in Asian carp (Heer et al., 2019; Kocovsky et al., 2012; Gorbach & Krykhtin, 1980 in Naseka & Bogutskaya, 2011). However, Asian carp can likely mature in locations with fewer degree days (i.e. colder areas) (Chapter 2).

To test how severely temperature may affect the population growth rate of grass carp in North America, we constructed an age-size integral projection population model (IPM) where the age at maturity was determined by degree days. IPMs are similar to matrix models, but instead of classifying the population into discrete stages, IPMs express life history as continuous functions (Easterling et al., 2000). These smooth functions make IPMs useful in incorporating environmental variables, such as temperature (e.g. Vindenes et al., 2016; Dalgleish et al., 2011). We used this model to map the estimated population growth rates across North America. We also investigated how temperature dependent growth may affect population growth rate predictions by simulating a theoretical relationship between degree days, growth rate and maximum size, and incorporating it in the model.

Methods

Grass carp life history

In North America, grass carp have been, and continue to be, stocked in their triploid (sterile) form for use in biological control of macrophytes (Cudmore et al., 2017). This can make it difficult to find life history data relating to wild, diploid grass carp. When possible, we used data from wild, diploid populations, as there can be differences between diploids and triploids in terms of resource allotment for growth (Aydin, 2021; Ihssen et al., 1990), and high stocking densities, combined with the corresponding reduction of food availability, may affect mortality (Stich et al, 2013; Kirk et al., 2000).

Most wild grass carp live to be approximately 11-15 years of age (Sullivan et al., 2020; Shireman & Smith, 1983). The oldest grass carp caught in the Mississippi river was 13 years of age (Sullivan et al., 2020), and grass carp live approximately 13-15 years in the Amur River (Shireman & Smith, 1983). However, older fish have been caught, notably an age 33 fish (Cudmore & Mandrak, 2004), and a stocked triploid population had individuals as old as 23 years (Caves et al., 2021). Adult survival may be affected by food availability, as grass carp are voracious eaters (Kirk & Socha, 2003), or fishing mortality. Mortality rates in stocked, triploid grass carp increased from 0.22 in 1994 (Morrow et al., 1997) to 0.38 in 2002 (Kirk & Socha, 2003), possibly due to a reduction in food (Kirk et al., 2000) in the Santee Cooper reservoir system. Stich et al., (2003) found that mortality was approximately 50% in age-1 triploid grass carp. In wild diploid populations from the Mississippi River, annual mortality rates ranged from 0.4 downstream, to 0.1 in the more sparsely populated upstream (Sullivan et al., 2020), though these estimates incorporate fishing mortality as well as natural mortality.

Grass carp are generally thought to grow quickly as juveniles, rapidly reaching large sizes up to a metre in length (Shireman & Smith, 1983). Sullivan et al., (2020) calculated von Bertalanffy equations for populations of grass carp in the Mississippi river, but all other known sources of von Bertalanffy fitted curves come from stocked triploid populations (Table 3.1). Overall, growth rates (k) and maximum sizes (L_{inf}) varied widely through the different populations (Table 3.1).

Grass carp are highly fecund fish, averaging up to hundreds of thousands of eggs per kilogram (Table 3.2). The general pattern of smaller relative fecundities in more southern locations may be related to the body size at maturation of the fish in the various locations. In warmer climates, fish tend to mature faster, but at smaller sizes (and therefore likely a lower fecundity) (Angilletta et al., 2004; Berrigan & Charnov, 1994). Limited data were available on the hatching success rate of eggs, but it is believed to be approximately 65% (Naeem et al., 2011; Verigin et al., 1978 in Bogutskaya et al. 2017). Survival of individuals in the first year is expected to be low (Shireman & Smith, 1983), and given the presence of piscivorous fish is estimated to be 0.02% (Rottman, 1977). Grass carp have a wide range of ages at maturity, spanning 2 to 10 years, which can be predicted using temperature (Chapter 2).

Temperature data

We used degree days base 0°C to predict temperature impacts on age at maturity and fecundity (see Appendix 3.2 for additional explanation). Degree days are a cumulative measure of temperature experienced through the year above a base temperature (Chezik et al. 2014a). Our degree day estimate is based on air temperature, which is correlated with surface water temperature (Honsey et al., 2018) in shallow systems. Using air temperature as a proxy for water temperature may be inappropriate for fish species that inhabit deeper benthic habitats, or lakes with stratification, but grass carp are known to be found in near-shore, shallow areas (Cudmore & Mandrak, 2004). Using our population model, we mapped the population growth rates of grass carp across North America, using a degree day map from McKenney et al., (2011). We used 2000 degree days and below as a cut-off of where grass carp could grow (based on data from Chapter 2 which indicated that no grass carp were found in locations with fewer than 2000 degree days).

Model description

To model how temperature may affect the population growth rate of grass carp, we parameterized a deterministic, density independent integral projection model (IPM). For more general summaries of IPMs, see Merow et al, (2014), and Rees et al., (2014). All analyses were conducted in R version 4.0.3 (R Core Team, 2021). The IPM model was constructed using the “ipmr” package (Levin et al., 2021). We conducted elasticity analysis on all of our parameters, paying particular attention to the parameters that were chosen arbitrarily due to limited data (detailed below).

Our model expresses the above discussed life history (such as growth, reproduction and survival) of grass carp as continuous functions with explanatory variables of either length in mm (z), or age in years (a). Length and age are therefore the “state variables” in our model.

New recruits (age 0) are added to the population using the equation

$n_0(z', t+1) = \sum_{a=0}^{M} \int_L^U F_a(z', z)\, n_a(z, t) dz$, where *t* refers to time, $F_a(z', z)$ is the reproductive kernel (group of equations) that controls reproduction related variables (e.g. fecundity, probability of reproducing, etc.), and $n_a(z,t)$ is the length distribution of the population at age *a* and time *t*. The equation is integrated over the length variable. M is the maximum age of the population. *L* and *U* are the lower and upper limits of the integral, representing the minimum and maximum possible lengths of individuals. The choice of some model parameters (e.g. maximum age, upper limit) can affect the final predicted population growth rate. The numbers must be realistic, but if they are too small, they may artificially increase or decrease the population growth rate estimates (Appendix 3.1). We used a maximum age of 20 years, which is biologically realistic (Appendix 3.1 Figure 3; Sullivan et al., 2020; Shireman & Smith, 1983), and produces a stable model output that is not sensitive to changes in the parameter (will not artificially decrease population growth rate estimates). Our upper limit was chosen to equal 1100 mm, for similar reasons; the value is biologically realistic (Sullivan et al., 2020), and allowed for stable population growth rate values (Appendix 3.1 Figure 2). Our lower limit is 0 mm.

Reproductive kernel

The reproduction kernel, $F_a(z', z)$ is composed of multiple functions and probabilities. It contains the probability of maturing, *pm(a)*, fecundity *b(z)*, hatching success *hp*, survival of juveniles *hs*, and the size distribution of the juveniles *Rs(z')*:

$$F_a(z', z) = pm(a) * b(z) * hp * hs * Rs(z').$$

The probability of maturation *pm(a)* was derived using the age at maturity and temperature relationship derived from literature data (Chapter 2). Using the estimated age at maturity and uncertainty around that estimate, we derived a relationship between the degree days and the parameters (α_m and β_m) of the logistic equation $pm(a) = \frac{1}{1+e^{\beta_m(a-\alpha_m)}}$ (See Appendix 3.2 for additional detail). The relationship between the parameters of the logistic equation and degree days was used to obtain specific equations given the number of degree days (Appendix 3.2 Figure 6). However, the regressions which determine the parameters are only suitable for locations with fewer than 5000 annual degree days (Appendix 3.2 Figure 5). It is also important to note that we modeled the variance around the inflection point, representing the variance within the population, using the variance among locations (Chapter 2), due to limited data available on within-population variance. The difference in equations based on degree days is shown in Figure 3.1A, where the Upper Mississippi River (approximate location of Sullivan et al., 2020 sampling sites), Lake Erie and Lake Superior are compared.

Our models assumed that grass carp spawn every year after maturation. The relationship is for female Asian carp, as male Asian carp tend to mature one year earlier than females (Chapter 2). Therefore, the *pm(a)* function models female probability of maturation, with the assumption that males are already mature, and that the probability of spawning of the population is determined by the female probability of maturation.

Because of the wide range of relative fecundities likely caused by varying sizes at maturity, we created a model that predicted relative fecundity (eggs per kg), based on the degree days in each location (Appendix 3.2). Based on the temperature-size rule (Angilletta et al., 2004; Berrigan & Charnov, 1994), we expect that individuals that mature faster at smaller sizes will have smaller fecundities. There is evidence of the relationship between relative fecundity and body weight for grass carp (Shireman & Smith, 1983), which is the relationship our degree days is approximating (given inadequate length data for each location). Therefore, the relative fecundity parameter, f, in our model was determined by degree days, with larger relative fecundities in colder locations (Appendix 3.2 Figure 8).

To convert our length variable, z, into weight, we applied length-weight relationships using the mean of the parameters from Wanner & Klumb (2009), as well as data parametrized from raw data from Sullivan et al., (2020). The slopes (β_w) are 2.87, 2.77 (Wanner & Klumn, 2009) and 2.78 (Sullivan et al., 2020); with a mean value of 2.81. The intercepts (α_w) are -4.59, -4.33 (Wanner & Klumn, 2009) and -4.32 (Sullivan et al., 2020); with a mean value of -4.41. Combined, this gave us the equation for our fecundity equation: $b(z) = f * \frac{10^{\beta_w * log_{10}(z) + \alpha_w}}{1000}$, where f varies by degree days (Figure 3.1B demonstrates fecundity values at locations with varying degree days: the Upper Mississippi River, Lake Erie and Lake Superior).

We used a hatching success (hp) of 65%, representing the ratio of eggs that were successfully fertilized and hatched (Naeem et al., 2011; Verigin et al., 1978 in Bogutskaya et al. 2017). Assuming the presence of predation, we used a juvenile survival (hs) value of 0.02% from Rottman (1977). The size distribution of age-0 recruits was represented as a normal distribution where $Rs(z') \sim N(\mu_r, \sigma_r)$. It was modelled using the size of 2-month olds, which have a mean size of 52 mm (μ_r) and a standard deviation of 21 mm (σ_r) (Shireman & Smith, 1983).

Growth kernel

The growth and survival of individuals equal to or greater than one year is given as $n_a(z', t+1) = \int_L^U P_{a-1}(z', z)\, n_{a-1}(z, t) dz$, where z refers to size, t refers to time, a refers to age, and $n_a(z,t)$ is the size distribution of the population at age a and time t. $P_a(z',z)$ is the kernel that controls the growth and survival of the population. The integral has the same upper (U) and lower (L) limits: 1100 mm and 0 mm. $P_a(z',z)$, includes the survival function $s(a)$, and the normal probability distribution that controls the length of the population $G(z',z)$: $P_a(z',z) = s(a) * G(z',z)$.

The survival probability $s(a)$ is given by a logistic equation based on the data from Stich et al., (2003): $s(a) = \frac{max_s - min_s}{1+e^{\beta_s(a-\alpha_s)}} + min_s$. We used a value of 50% mortality at age 1 for the inflection point (α_s) (Stich et al., 2003). The steepness of the curve (β_s) was one of the few parameters arbitrarily chosen for the model. We used a value of -2 as a moderate value that caused the shape of the curve to not be particularly steep or shallow (Figure 3.1C). We also used a minimum survival (min_s) probability of 0.1 for the youngest adult fish (Shireman & Smith, 1983). Given the wide range of annual mortality rate estimates discussed in the life history section, we evaluated our model using two possible maximum survival rates max_s: 0.9 and 0.6 reported in Sullivan et al., (2020). Grass carp are fished in the Mississippi River, which means that both the 0.9 and 0.6 estimates of mortality include both natural and fishing mortality (Sullivan et al., 2020).

The population length distribution is controlled by the normal distribution where $G(z', z) \sim N(\mu_g, \sigma_g)$. The mean of the distribution, μ_g is the growth increment (how much a fish is expected to grow) based on its currently length z, added to its current length: $\mu_g = z + g_{inc}(z)$. $g_{inc}(z)$ is the expected growth increment based on the von Bertalanffy equation, where max_g is the maximum growth increment, and L_{inf} is the maximum size: $g_{inc}(z) = max_g - \frac{max_g}{L_{inf}} * z$ (Figure 3.1D; Appendix 3.2). To parameterize these functions, we used data from Sullivan et al., (2020) and fit the von Bertalanffy equation, using the nls function in R, and then used the von Bertalanffy function to get the parameters max_g and L_{inf}. At very large sizes (equal to and greater than L_{inf}), the growth increment was set to 0.1 mm (min_g), to represent very limited growth at large sizes (Figure 3.1D). Sullivan et al., (2020) separated populations into upstream and downstream populations. However, due to the comparatively wider geographic range we are considering, we grouped their data to calculate these parameters.

To minimize shrinkage in the model (when size z_{t+1} is smaller than size z_t), the standard deviation of the normal distribution decreased as fish increased in length: $\sigma_g = \frac{g_{inc}(z)}{d_g}$, where d_g was chosen arbitrarily to equal 4 (See Appendix 3.2, Figure 11). At large sizes (when the growth increment is very small), the standard deviation was set to 5mm (σ_{min}), to reflect that sharp increases in growth are unlikely at large sizes. A summary table of parameter values is provided in Table 3.3.

Calculating population growth rates

To get the population growth rate for any deterministic combination of parameters, the model is discretized by converting the smooth kernels into iteration matrices (Doak et al., 2021) using the midpoint rule approach, where the range from L to U is divided into n size bins with equal widths (Rees et al., 2014). The number of bin sizes can be chosen by starting at a small number of bin sizes and increasing the number of bins until the results stabilize (Rees et al., 2014; Appendix 3.1). Our model used 150 mesh points, chosen after testing a number of possible mesh points for the best stability (Appendix 3.1 Figure 1). The value of each function at these midpoints creates an iteration matrix for the model, which is functionally the same as classic matrix models (Doak et al., 2021). The dominant eigenvalue of this large matrix is equivalent to the discrete time population growth rate (λ) of the population, when the population is at its stable size distribution.

We conducted an elasticity analysis on all of our parameters to test the effect each parameter had on our population growth rate. Elasticity analysis can be used to determine which parameters are a good candidate for management actions (e.g. a higher elasticity for juvenile survival than adult survival indicates actions that targeted juveniles versus adults may be more effective), and to see how the arbitrarily chosen parameters (min_g, d_g, σ_{min}, min_s, and β_s) affected the predictions of the model. We calculated elasticities of our parameters by changing each of our parameters by ±10%, one at a time, and estimating a new λ. The sensitivity of a parameter *x* is given by: $sensitivity_x = \frac{\lambda_{x\pm10\%} - \lambda_{original}}{x_{\pm10\%} - x_{original}}$. However, the sensitivity can vary widely depending on the magnitude of the parameter value. Therefore, we scaled the sensitivities by the value of the parameter as: $elasticity_x = sensitivity_x * \frac{x_{original}}{\lambda_{original}}$, to get the elasticities, which are proportional, and can be compared between parameters of different magnitudes. Larger magnitudes of elasticities correspond to parameters that have larger proportional effects on the population growth rate. We calculated elasticities with the degree days of different locations (Upper Mississippi River - 4280; Lake Erie - 3560; Lake Superior - 2330), to see if elasticities varied across temperatures. For each location, we calculated the elasticities at each maximum adult survival value (0.9 and 0.6), using ± each parameter of 10%. The elasticity at each degree day was a mean of the trials at that temperature.

We calculated confidence intervals for our population growth rates using latin hypercube sampling (McKay et al., 1979) in the package lhs (Carnell, 2021). Latin hypercube sampling ensures that the margins of distributions are represented in the sampling, as opposed to random sampling, which is biased towards the mean (McKay et al., 1979). We were able to find actual variance measures for parameters max_s, max_g, L_{inf}, α_w, β_w and *f*. For all other parameters we used a variance with the value of: $var_x = parameter_x * 0.2$. All parameters were represented as normal distributions, except for non-normal, probability parameters min_s, max_s, min_g, *hp* and *hs*, which were expressed as a uniform distribution with minimum and maximum values of parameter ± variance. The confidence intervals were calculated on 1000 samples.

Simulating temperature dependent growth parameters

To approximate how temperature-dependent growth parameters k and L_{inf} in the von Bertalanffy equation ($L_t = L_{inf}(1 - e^{-k(t-t_0)})$ may affect the model, we simulated a relationship for these parameters using the minimum and maximum measured growth rates found in the literature (Table 3.1). We made the smallest k value (0.17) equivalent to a relatively small number of degree days (2500), and the largest k value (0.615) equivalent to 5000 degree days (the warmest area permitted in the population model), based on the assumption that fish grow faster in warmer environments (Appendix 3.3 Figure 1; Jobling, 1997). Because L_{inf} values tend to be large when k values are small (Weber et al., 2015), we set the smallest L_{inf} value (810 mm) to the largest number of degree days (5000), and the largest L_{inf} value (1297 mm) to 2500 degree days (Appendix 3.3 Figure 2).

Results

Population growth rate predictions

As expected, we found that the population growth rate predicted by our model increased with the number of degree days (Figure 3.2). However, the population growth rate was not particularly sensitive to variation in temperature. A change of 1000 degree days changed λ approximately 2.5%. We found that the confidence intervals around the values were narrow and did not dramatically change with increasing degree days (Figure 3.2), and on average were ± 0.0071. The model with a higher adult survival ($max_s = 0.9$) had higher λ values compared to the model with lower adult survival ($max_s = 0.6$). Maximum adult survival had dramatic effects on the λ predictions, with a change of maximum survival of 0.1 leading to an approximate 16% change in λ prediction (Figure 3.3). At 2330 degree days, λ is equal to 1 at a maximum survival value of 0.66; but this value decreases to 0.64 at 3560 degree days, and further decreases to 0.62 at 4280 degree days (Figure 3.3).

The model with high adult survival predicted that the λ value would be greater than 1 for all of North America (Figure 3.4). However, when adult survival was lower, λ values were predicted to be less than 1 (Figure 3.4). Population growth rates estimates were larger in more southern regions for both models.

Using our model, the threshold value of 2865 from Gorbach & Krykhtin, (1980) in Naseka & Bogutskaya, (2011) has a λ value of 1.3 (high adult survivorship) and 0.94 (low adult survivorship). For comparison, 5000 annual average degree days, which corresponds to an age at maturity of approximately 4.5, gives a predicted λ of 1.4 (high adult survivorship), and 0.99 (low adult survivorship). An age at maturity of 6 (degree day of 3175) has an approximate predicted λ of 1.3 (high adult survivorship), and 0.95 (low adult survivorship). These differences in population growth rates may seem slight, but can have drastic effects on population size. The doubling time, the number of years it takes for a population to double in size, of a population with a λ of 1.1 is approximately 7 years. However, a population with a λ of 1.2 has a doubling time of only 4 years, and a λ of 1.4 has a doubling time of 2 years.

Elasticities

We found that the slope and the intercept of the length-weight equation had extremely high elasticities compared to the other parameters (mean elasticities of 1.9 and -1.0 respectively), possibly due to the $\log_{10}$ transformation of the variables as part of the equation $b(z)$. However, we have relatively high confidence in our parameter values for this equation, as both Wanner & Klumb (2009) and Sullivan et al., (2020) had very similar parameter values. The other parameters that had high elasticities were maximum survival (max_s), mean value of 0.83; the maximum size (L_{inf}), mean value of 0.18; the age at maturity (α_m), mean value of -0.18; and the age where the probability of survival is 50% (α_s), mean value of -0.18 (Figure 3.5).

The parameters that were arbitrarily chosen for the model all had relatively low elasticities, implying that our arbitrary selection of those parameters did not have a large effect on the predicted population growth rates. The slope of the logistic equation for the survival function (β_s) had a mean elasticity of -0.049; the minimum survival probability min_s had an elasticity of 0.067; and the parameter reducing the standard deviation in the growth distribution d_g had an elasticity of -0.00071 (Figure 3.5). The minimum growth increment (min_g) the minimum standard deviation (σ_{min}) both had elasticities less than 0.0001.

The number of degree days affected the elasticities of several of the parameters (Figure 3.5). The maximum survival of the adults (max_s) was less elastic (affected the population growth rate less) in warmer areas, as elasticity decreased from 0.85 with 2330 degree days (corresponding to Lake Superior) to 0.81 with 4280 degree days (corresponding to the Upper Mississippi River). On the other hand, the inflection point in the survival function (α_s) was more elastic in warmer temperatures, with a decrease in elasticity from -0.20 with 4280 degree days to -0.16 with 2330 degree days. The age at maturity (α_m) was determined by degree days, and did not appear to have a general trend with temperature (Figure 3.5).

Temperature dependent growth parameters

We found that adding temperature dependence to the growth rate *k* and L_{inf} values changed our prediction of the population growth rate (Figure 3.6). When only *k* was temperature dependent, the predicted λ was smaller than the model with a static *k* in colder locations. However, at high degree days the model with a temperature dependent *k* value predicted a larger population growth rate than a static *k*. When both L_{inf} and *k* were temperature dependent, the population growth rate was larger than the model with static values when degree days were greater than approximately 2500 (Figure 3.6). These results indicate that temperature dependent growth parameters can make a difference when predicting whether a population size is predicted to grow or decrease over time.

Discussion

Our temperature dependent integral projection model suggests that population growth rates of grass carp are expected to be faster in more southern, warmer regions of North America (Figure 3.4), as decreasing ages at maturity caused faster growth. Our model with a high (0.9) maximum adult survival predicted population growth rates greater than 1 throughout North America (range of approximately 1.3-1.4, indicating that grass carp populations would be able to grow even in relatively cold locations) (Figure 3.4). However, with a higher adult mortality (0.6 maximum adult survival), our model predicted that populations would be unlikely to persist long-term (approximate North American range of 0.92-0.99). It is clear that adult survival rates are an important factor in whether northern locations are sufficiently cold to prevent population growth in various locations in North America. At moderate values of adult survival (approximately 0.6 - 0.7), the number of degree days can determine whether the population is expected to grow or not (Figure 3.3).

Our maximum adult mortality parameters of 0.9 and 0.6 come from the Upper Mississippi River, where grass carp are fished (Sullivan et al., 2020). Therefore, our parameters include both natural mortality and fishing mortality. This likely explains why our predictions of population growth rate were less than 1 when adult survival was set at 0.6; when adult survival is decreased to that level, grass carp populations are not expected to grow (in locations with fewer than 5000 degree days). Furthermore, maximum adult survival is a very elastic parameter (Figure

3.5), and so relatively small changes to this value will have proportionately larger effects on population growth rates compared to other parameters. For example, the population growth rate in the Upper Mississippi River (annual degree days are approximately 4280) is expected to be 0.98 at a maximum survival of 0.6. At a maximum survival of 0.7, this increases to 1.1. This small change in adult survival may translate to the difference between the population being expected to grow ($\lambda > 1$) or decrease over time ($\lambda < 1$).

It is possible that natural adult survival of grass carp itself varies across North America. Weber et al., (2015) found that common carp (*Cyprinus carpio*) mortality decreased with increasing latitudes. If grass carp follow the same trend, this would imply that λ would naturally increase as latitudes increase. However, elasticity of adult survival was slightly larger in colder temperatures (0.85) than warmer temperatures (0.81) (Figure 3.5). This indicates that management actions like fishing may be even more effective at decreasing grass carp population growth rates in cooler, more northern environments. Overall, management actions that increase adult mortality like fishing are likely to be an effective method at decreasing grass carp population growth rates.

It is important to note that just because a population is not expected to survive in the long term (λ value < 1) does not mean that the population cannot cause ecological effects. For example, if grass carp temporarily established a population in a new location, those adults could still affect the ecosystem by consuming large amounts of macrophytes, even if they are not expected to grow or persist in the long-term. Furthermore, grass carp are relatively mobile (Currie et al., 2017), so an established population could be a source of grass carp to cause effects elsewhere, even if the population does not grow in the areas the fish migrate to.

Some important parameters were found to have relatively little influence on the population growth rate. Juvenile survival (*hs*) had a mean elasticity value of 0.10 (Figure 3.5), suggesting that management actions targeting juvenile survival will have proportionally less effect on the population growth rate than targeting a parameter like maximum adult survival. Furthermore, the elasticity of juvenile survival slightly decreased in cooler temperatures (elasticity of 0.092 with 2330 degree days; elasticity of 0.11 with 4280 degree days), so targeting juvenile survival may have even less of an effect in cooler climates.

Gorbach & Krykhtin, (1980) in Naseka & Bogutskaya, (2011) state that grass carp require approximately 2865 annual degree days to mature. Our model with high survivorship found that grass carp populations would likely still be able to mature and grow in locations with fewer degree days than that threshold. Conversely, our model with lower survivorship found that these populations would not grow in many environments despite having more than 2865 degree days. The threshold value of 2865 from Gorbach & Krykhtin, (1980) in Naseka & Bogutskaya, (2011) has a predicted λ of 1.3 (high adult survivorship) and 0.94 (low adult survivorship) in our models. Overall, our results indicate that the use of a threshold value of degree days to determine if a population could grow is strongly affected by assumptions made about the mortality of the adult population, and should be used cautiously.

There are other factors relating to temperature that may affect grass carp population growth rates. Overwintering survival of Asian carp has been shown to be higher in more southern, warmer locations (Coulter et al., 2018; Jones et al., 2017). Periods of shorter growing seasons combined with longer winters can prevent juvenile young of the year fish from storing sufficient energy reserves to survive the winter, increasing mortality in juveniles (Jones et al., 2017; Shuter et al., 1980). Jones et al., (2017) found that mortality of young grass carp caused by overwintering was generally higher in more northern Great Lakes like Lake Superior, compared to more southern Lakes, and in some northern locations was predicted to be as high as 100% mortality. Though juvenile survival is not a particularly elastic parameter, large enough juvenile mortality may be sufficient to decrease the population growth rate below 1 in more northern locations in North America without any management actions required.

We did not directly include density-dependence in our model due to our interest in modelling the initial population surge following invasion. However, some evidence suggests that grass carp are strongly affected by density dependence (Caves et al., 2021; Cudmore & Mandrak, 2004; Shelton et al., 1981). In areas of higher density, grass carp average sizes decreased (Caves et al., 2021; Shelton et al., 1981). Sullivan et al., (2020) found that grass carp had a higher annual mortality rate (0.4) in the downstream Mississippi River where the catch per unit effort was higher than upstream, which had an annual mortality rate upstream of only 0.1. If this difference in mortality rates is due to density related effects, then we would expect adult survival to decrease as the population grows, slowing the population growth rates and possibly limiting population size.

The lack of data regarding temperature and grass carp growth rates led us to simulate the possible effects of temperature dependent growth parameters for k and L_{inf}. Our results indicate that including temperature dependence in these values can change the predicted population growth rates at different degree days (Figure 3.6). At low degree days, incorporating temperature dependent growth caused λ to be smaller than we would otherwise expect. However, at higher degree days, our λ values were larger than the static model when we incorporated temperature dependent growth. This was especially noticeable when both k and L_{inf} were temperature dependent. Though our results are only a simulation, they demonstrate that temperature dependent growth parameters might have important impacts on grass carp population growth rates. Our research highlights the need for more data investigating the relationship between grass carp somatic growth and temperature.

The predicted population growth rates from the model with low adult mortality (range of approximately 1.3-1.4) were roughly in the middle compared to other models for grass carp: 1.7 (Jones et al., 2017); 1.23 (Erickson et al., 2017), though our model with higher adult mortality predicted values that were noticeably lower than the other literature values (range of approximately 0.92-0.99). For comparison, non-native lake trout in the western United States had a λ value of 1.23, though population growth rates declined to values of 0.61–0.79 under suppression efforts (Fredenberg et al., 2017). Our model incorporated size-specific and degree day dependent fecundity, where Jones et al. (2017) used a flat value, which may contribute to the differences in λ, though they used a similar mortality value (0.63) as we did for our higher mortality model (0.6). Our growth distribution severely restricted growth above our maximum size L_{inf}, which prevented any extremely large, fecund fish from entering the model, which may have decreased our population growth rate predictions (Hixon et al., 2014). Furthermore, all of the values for relative fecundity that we found in our literature search had a relative fecundity of at least 41 000 eggs/kg, which is much higher than the value of 5 000 eggs/kg used by Erickson et al., (2017), even after accounting for fertilization success of 65%. The range of fecundities in grass carp is wide (Table 3.2), and further exploration of factors that affect fecundity (e.g., food quality) may be useful in predicting fecundities more specific to locations of interest.

Our results highlight the need for monitoring and action to manage the invasion of grass carp in the more southern, warmer areas. For the Great Lakes, our findings indicate that Lake Erie is most at risk of fast population growth (Figure 3.4). This prediction is significant especially in light of the evidence suggesting there is already a reproducing population present there (Whitledge et al., 2021; Embke et al., 2016). We also indicate that maximum adult survival is very important in controlling the population growth rate of grass carp, and that survival may be even more important in colder locations (Figure 3.5). This relationship indicates that management actions that contribute to reductions in adult survival are likely an effective management strategy for limiting the spread of grass carp, due to the high elasticity of the parameter.

Our results demonstrate that considering the environment that fishes live in can affect the predictions made about the growth or persistence of their populations. This is relevant for invasive species, but also endangered or important harvested populations (Wang et al., 2019; Jarić et al., 2015; Hidalgo et al., 2012). Incorporating environmental conditions into population models allows predictions to be made about how climate change or other stressors may impact populations. By not accounting for environmental conditions, managers may not be getting accurate predictions about population growth rates.

Table 3.1. Table of fitted parameters for the von Bertalanffy equation ($L_t = L_{inf}(1 - e^{-k(t-t_0)})$) for grass carp, organized by ploidy status of the population.

Location	L_{inf} (mm)	k	t_0 (mm)	Ploidy	Source
Lake Gaston	1292	0.17	NA	Triploid	Caves et al., (2021)
Lake Gaston	1297	0.1352	-1.52	Triploid	Stich et al., (2013)
Santee-Cooper Reservoir	1044	0.615	0.59	Triploid	Morrow et al., (1997)
Upstream Upper Mississippi River	916	0.38	0	Diploid	Sullivan et al., (2020)
Downstream Upper Mississippi River	810	0.42	0	Diploid	Sullivan et al., (2020)

Table 3.2. Relative fecundities of grass carp. When the source paper provided a range, we used the midpoint. Fecundities are sorted from largest to smallest.

Relative fecundity (eggs/kg)	Location	Source
233 000	Ili River Delta, Kazakhstan	Karpov et al., 1989[a]
130 000	Dagestan, Russia	Abdusamadov, 1989[a]
112 000	Middle Amur River, Russia	Shireman & Smith, 1983
91 400	Kapchagay Reservoir, Kazakhstan	Karpov et al., 1989[a]
88 000	Lake Balkhash, Kazakhstan	Karpov et al., 1989[a]
85 528	Texas, USA	Elder & Murphy, 1997
82 000	Cuttack, India	Shireman & Smith, 1983
62 532	Faisalabad, Pakistan	Naeem et al., 2011
41 000	Malaysia	Shireman & Smith, 1983

[a] in Bogutskaya et al., 2017

Table 3.3. Summary of parameters for IPM model.

Process	Symbol	Parameter Value	Units	Source
Probability of maturing: *pm(a)*	α_m	Degree day dependent	year	Appendix 3.2 Figure 6
	β_m	Degree day dependent	-	Appendix 3.2 Figure 6
Fecundity: *b(z)*	f	Degree day dependent	eggs/kg	Appendix 3.2 Figure 8
	α_w	-4.41	-	Sullivan et al., (2020); Wanner & Klumb (2009)
	β_w	2.81	-	Sullivan et al., (2020); Wanner & Klumb (2009)
Hatching success: *hp*	hp	0.65	-	Verigin et al. (1978) in Bogutskaya et al. (2017); Naeem et al. (2011)
Juvenile survival: *hs*	hs	0.0002	-	Rottman (1977)
Juvenile size: *Rs(z')*	μ_r	52	mm	Shireman & Smith (1983)
	σ_r	21	mm	Shireman & Smith (1983)
Growth: *G(z',z)*	max_g	161	mm	Sullivan et al. (2020)
	min_g	0.1	mm	
	L_{inf}	813	mm	Sullivan et al. (2020)
	d_g	4	-	
	σ_{min}	5	mm	
Probability of survival: *s(a)*	min_s	0.1	-	
	max_s	0.9 OR 0.6	-	Sullivan et al. (2020)
	α_s	1	year	Stich et al. (2013)
	β_s	-2	-	

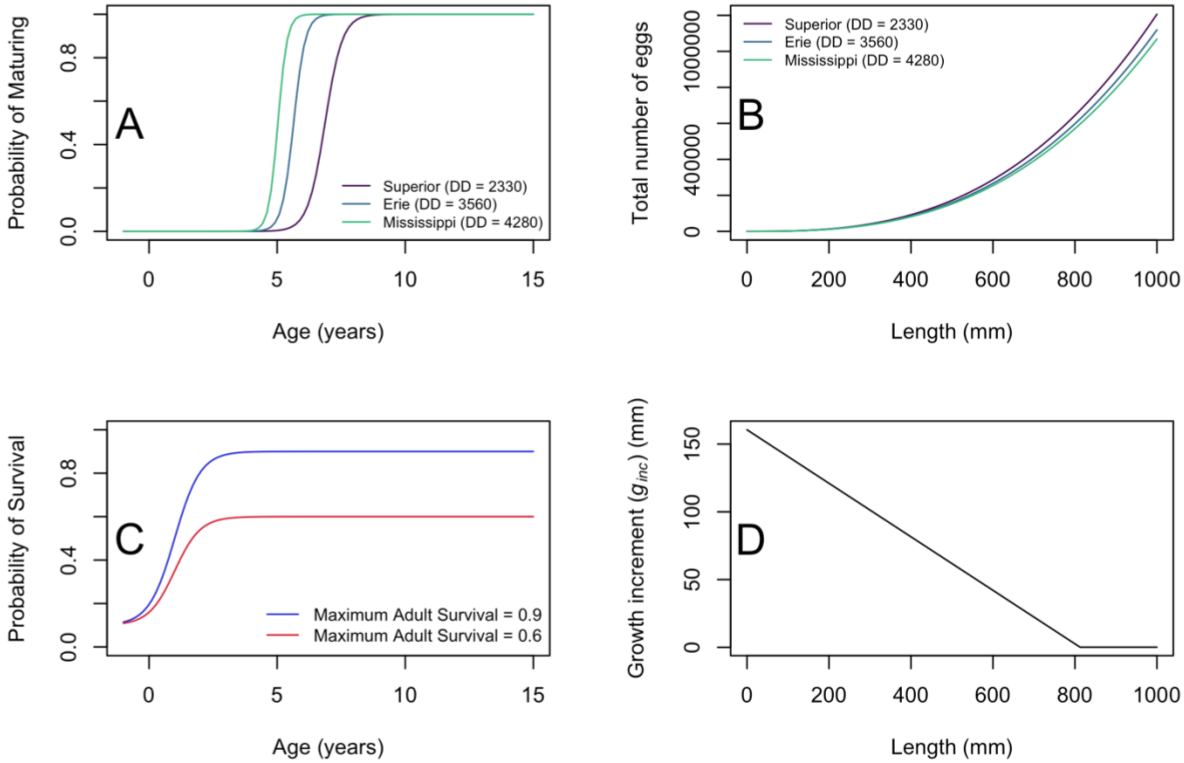

Figure 3.1. Growth, fecundity, survival and probability of reproducing equations used in the age-size IPM. Panel A shows the probability of reproducing, *pm(a)*; panel B shows the size-specific fecundity, *b(z)*; panel C shows the probability of survival, *s(a)*; and panel D shows the equation for the growth increment $g_{inc}(z)$. The degree days (DD) of the locations are shown in brackets.

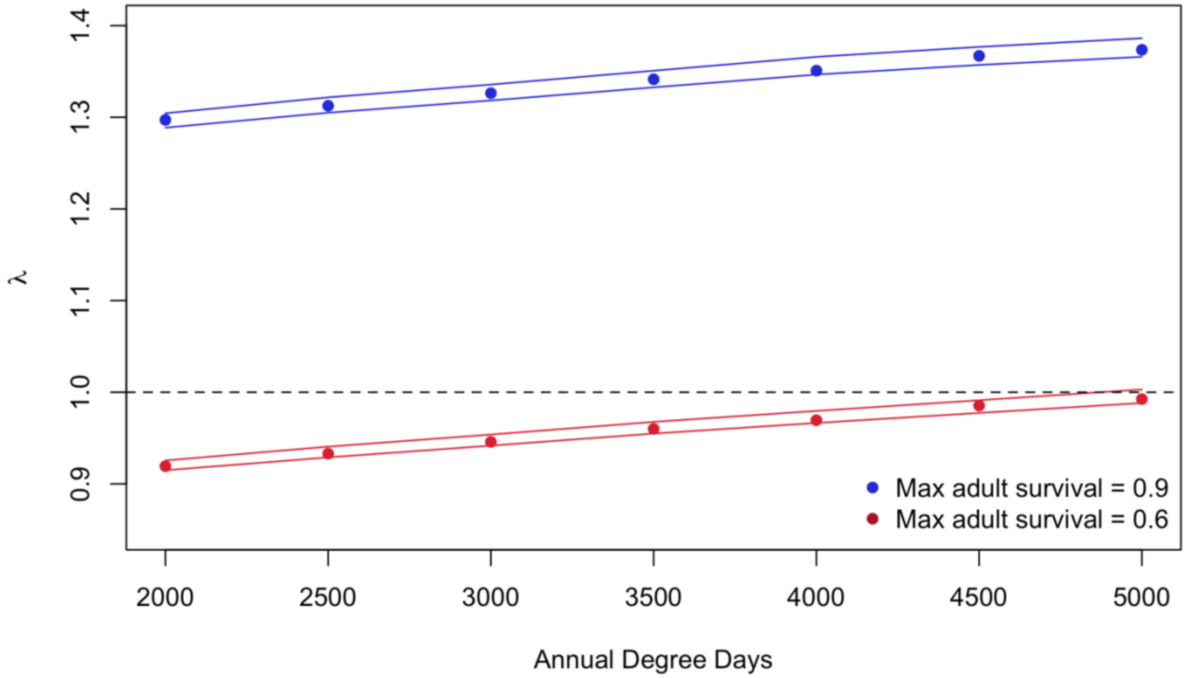

Figure 3.2. The relationship between the annual degree days and the predicted population growth rate with a maximum survival value of 0.9 and 0.6. Lines represent 95% confidence intervals. As annual degree days increase, so does the predicted population growth rate. Population growth rates above 1 are populations that are expected to grow over time. All λ values were greater than 1 for the model with a higher adult survivorship, but λ values were less than 1 when adult survivorship was smaller.

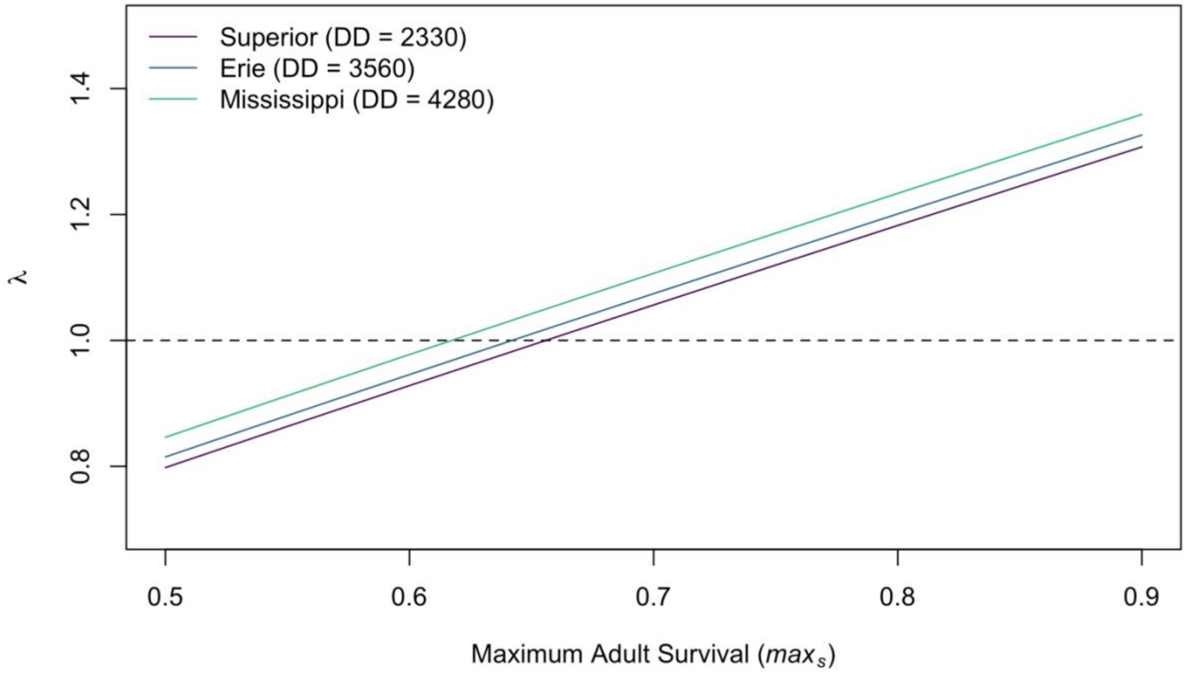

Figure 3.3. Effect of different maximum adult survivals for locations with different degree days. At higher degree days (DD) like the Upper Mississippi River, the population growth rate becomes greater than 1 at smaller adult survival values, compared to colder areas. For example, at a maximum adult survival of 0.65, a population in the Mississippi River would be expected to grow, but a population in Lake Superior would not.

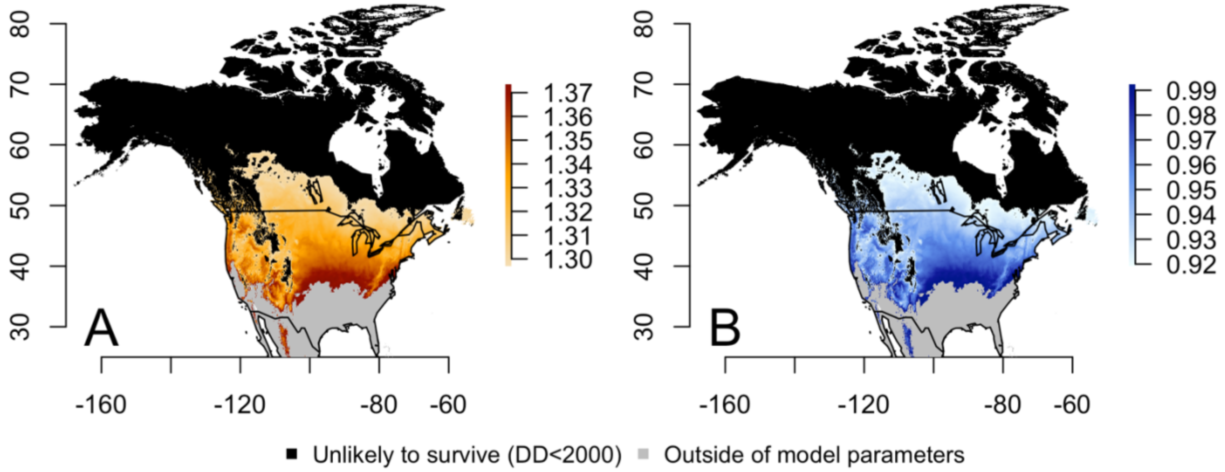

Figure 3.4. Map of North America showing the predicted population growth rate with a maximum adult survival value (max_s) of 0.9 (panel A) and 0.6 (panel B), for locations with fewer than 5000 annual average degree days (DD). The population growth rate is predicted to be faster in more southern locations. We used 2000 degree days as an upper cut-off for grass carp survival.

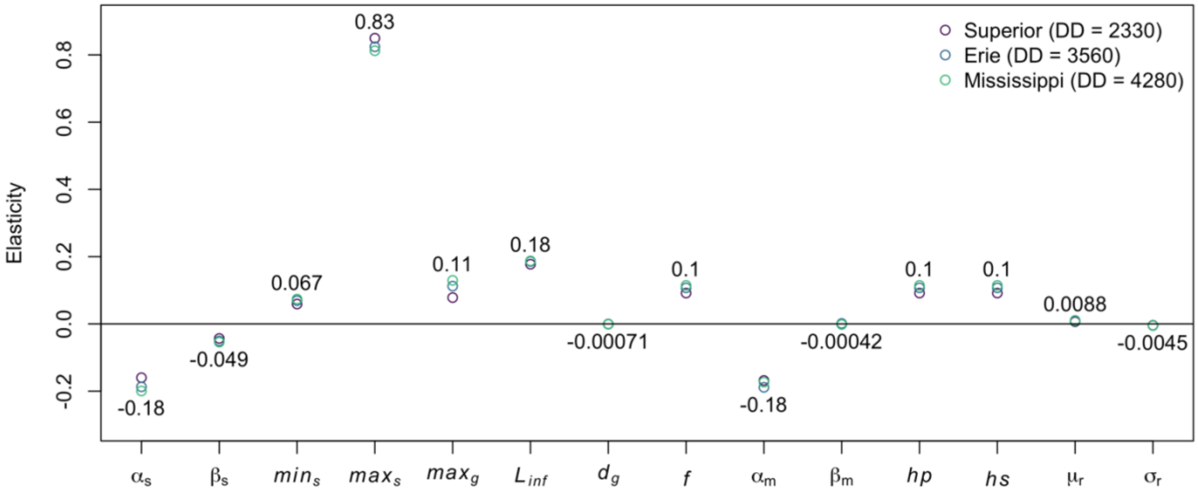

Figure 3.5. Elasticities of model parameters at various degree days. The intercept and slope of the length-weight relationship (α_w and β_w) are not included to better show the distribution of the other parameters. The parameters min_g and σ_{min} had mean elasticities less than 0.0001, and were therefore not included on the graph. The values shown for each parameter represent the mean elasticities across the three locations with different degree days (DD).

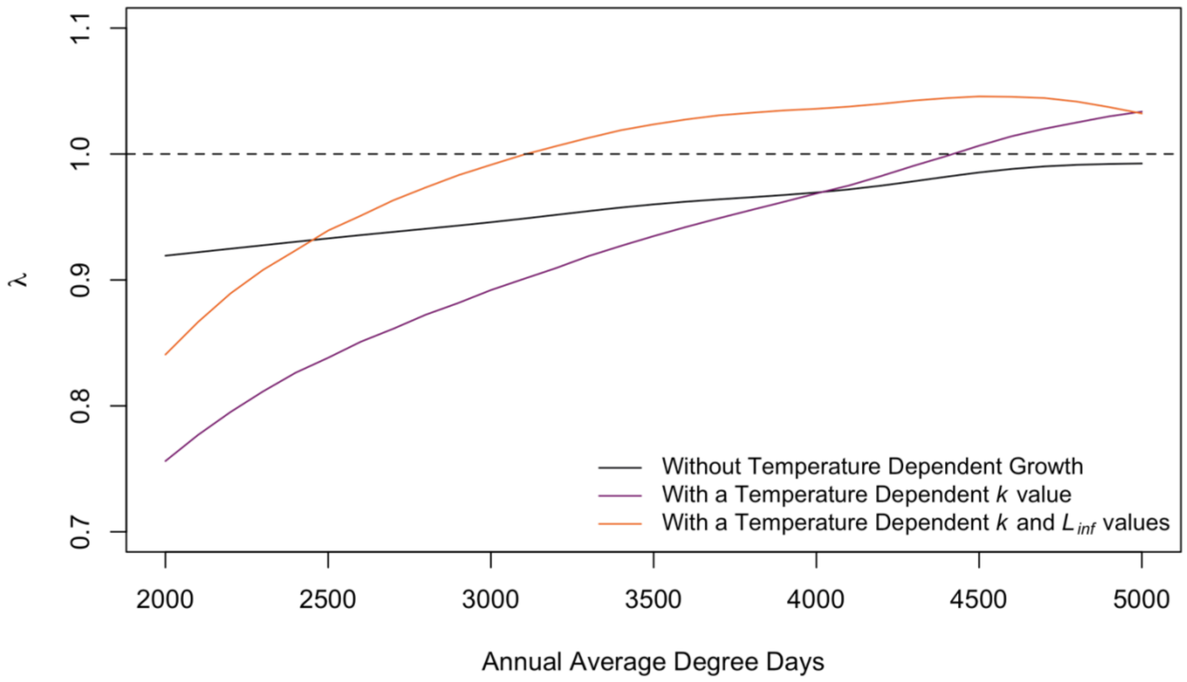

Figure 3.6. The relationship between λ and annual degree days when a temperature dependent growth rate *k* and temperature dependent L_{inf} value is included in the model, and when it is not. This shows the results from the model with maximum survival of 0.6; results were similar with a maximum survival of 0.9.

Chapter 4: Conclusion

Summary of thesis

In this thesis, I investigated the effects of temperature on life history traits in Asian carp, and considered the potential consequences of these thermal dependencies to effects on population growth rates. Asian carp are a group of invasive species which are likely to invade the Great Lakes (or, in the case of grass carp, have likely already begun to invade (Whitledge et al., 2021; Embke et al., 2016)). I determined that air temperature could be used to predict ages at maturity of Asian carp across the world (Chapter 2). Using this relationship between temperature and age at maturity, as well as a relationship between fecundity and temperature, I predicted population growth rates of grass carp across North America. I confirmed the hypothesis that faster maturation would lead to faster population growth rates (Chapter 3).

Despite the importance of age at maturity in determining population growth rates (Wang et al., 2019; Hutchings et al., 2012), there is little age at maturity data available for Asian carp in North America. To attempt to predict ages at maturity of Asian carp in the Great Lakes area, I compared ages at maturity of Asian carp from across the world to the temperature data from their locations. I found that the age at maturity of silver, bighead and grass carp can be predicted using easily obtained air temperature measurements (Chapter 2). Based on this relationship, Asian carp are predicted to mature later in colder locations. This result matches general biological trends like the temperature-size rule, which states that ectotherms tend to mature faster, at smaller body sizes, in warmer locations (Angilletta et al., 2004; Berrigan & Charnov, 1994).

Based on the general relationship between age at maturity and population growth rates (Wang et al., 2019; Hutchings et al., 2012), I predicted that locations with faster maturation would also have faster population growth rates. I constructed a population model for grass carp where the probability of maturation was determined by degree days (Chapter 3). The population model predicted faster population growth rates in warmer locations. Based on the elasticities of the model parameters, I determined that adult survival is a very important parameter in determining population growth rates of grass carp. The importance of adult survival on population growth rates indicates that management actions that decrease adult survival, like fishing, are likely to be effective in controlling the population invasion. When I incorporated temperature dependent parameters for growth rate and maximum size, I found that the predictions of population growth rates changed; either predicting larger or smaller population growth rates, depending on the degree days. My model demonstrates the importance of considering environmental variables like temperature when modelling invasive fish, species at risk, and when making climate change predictions.

Implications for future research

In this thesis, I contribute to the body of literature that explicitly connects temperature to life history of ectotherms. In fish, it is common to use threshold metrics for survival and reproduction, such as upper lethal temperature and optimum spawning temperature (Hasnain et al., 2010). While temperature has been connected to egg development in fish (e.g. Keller et al., 2020, Tsoukali et al., 2016), there are relatively fewer papers connecting temperature to growth and maturation as smooth relationships, encompassing sublethal and non-optimal impacts. Because of the importance of temperature to fish, particularly for traits like growth (Jobling et al., 1997), I encourage more studies to link temperature to life history in fishes across a wider range of temperatures, instead of using “hot” and “cold” treatments.

To more accurately predict grass carp growth rates in the Great Lakes, more field studies should be conducted analyzing life history traits in the grass carp population in Lake Erie

(Whitledge et al., 2021; Embke et al., 2016). In particular, it is extremely important to get an estimate for adult survival. It would be useful to understand the natural mortality of the Lake Erie population to allow managers to estimate how much additional fishing mortality would be required to stop population growth. Furthermore, more general experiments determining the relationship between temperature, grass carp growth rates, and maximum size would be useful in determining accurate estimates of population growth rates across the Great Lakes region.

A possible source of grass carp mortality related to temperature is overwintering mortality (Coulter et al., 2018; Jones et al., 2017). Temperature can be an extremely important factor in determining whether young of the year fish survive; fish must reach large enough sizes to have energy to survive the winter (Shuter et al., 1980). Based on a relationship between temperature and the growth of young grass carp, Jones et al., (2017) found that overwintering survival was expected to be lower in more northern locations. Incorporating this relationship into my degree day dependent population model would allow more robust estimations of locations grass carp could survive.

Overall, when there is a direct relationship between temperature and life history, temperature can be incorporated smoothly into population models to make location specific predictions and inferences. Raimondo (2012) noted that if constant parameters are used, instead of temperature dependent parameters, that there can be large differences in fish population size estimates. Therefore, the inclusion of temperature in population models can reveal relevant insights about population growth rates that might otherwise be overlooked.

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Appendix 2.1 Table of ages at maturity of Asian carp

Appendix 2.1 Table 1. Table of ages at maturity used in our analyses. Species and locations are listed by alphabetical order. Specific sources were given when possible; if the primary source could not be found, the article that references it was listed.

Species	Age at Maturity	Location	Source
Bighead	4	Amu Darya River	Mitrofanov et al., 1992[a]
	4.5	Balyktchy fish farm, Uzbeckistan	Komrakova & Kamilov, 2001
	5	Central and Eastern China	Peirong, 1989
	4.5	Central China	Jennings, 1988
	3	Cuttack, India	Alikunhi et al., 1963
	8.5	Dnieper River	Mitrofanov et al., 1992[a]
	3	Israel	Jennings, 1988
	8.5	Kiev, Ukraine	Jennings, 1988
	4.75	Krasnodar, Russia	Jennings, 1988; Mitrofanov et al., 1992[a]
	3	Missouri River, USA	Schrank & Guy, 2002
	10	Moscow, Russia	Jennings, 1988
	6.5	North Eastern China	Peirong, 1989; Jennings, 1988
	5.5	Northern China	Peirong, 1989
	6	Romania	Jennings, 1988
	3.5	Southern China	Jennings, 1988
	3.5	Taiwan	Jennings, 1988
	6	Terek River	Abdusamadov, 1987
	4	Turkmenistan	Jennings, 1988
Black	7.17	Amur River	Nico et al., 2005
	6	Central and Eastern China	Peirong, 1989
	6.5	Ha'Maapil, Israel	Gur et al., 2000
	6	Hukou county, China	Nico et al., 2005
	8.5	Leninskoye, Russia	Gorbach, 1961
	8	North Eastern China	Peirong, 1989
	7.5	Northern China	Peirong, 1989
	4	Nucet fish farm, Romania	Nico et al., 2005
	11	Southern Ukraine	Nico et al., 2005

Table 1 cont.

Species	Age at Maturity	Location	Source
Black	5	Taiwan	Nico et al., 2005
	7.5	Turkmenistan	Nico et al., 2005
	4.33	Yangtze River	Nico et al., 2005
Grass	3	Alabama	Shireman & Smith, 1983
	7	Amu Darya River	Abdullayev & Khakberdiyev, 1989[b]
	8.36	Amur River	Mitrofanov et al., 1992[a] ; Shireman & Smith, 1983 ; Gorbach & Krykhtin, 1981[a] ; Gorbach & Krykhtin, 1980[a] ; Makeyeva, 1963[a] ; Gorbach, 1961
	3.5	Arkansas	Shireman & Smith, 1983
	5	Balkhash Lake	Karpov et al., 1989[b]
	3.5	Balyktchy fish farm, Uzbeckistan	Komrakova & Kamilov, 2001
	8.5	Central Russia	Shireman & Smith, 1983
	4.5	Central and Eastern China	Peirong, 1989
	4	Central and Southern China	Shireman & Smith, 1983
	3	Cuttack, India	Alikunhi et al., 1963
	4.5	Dor, Israel	Shireman & Smith, 1983
	6.5	Hungary	Opuszyński, 1972
	4	Kapchagay Reservoir, Kazakhstan	Karpov et al., 1989[b]
	8.5	Khabarovsk, Russia	Gorbach & Krykhtin, 1988[b]
	8.5	Kiev, Ukraine	Shireman & Smith, 1983
	4.75	Krasnodar, Russia	Shireman & Smith, 1983
	9.5	Leninskoye, Russia	Gorbach, 1961
	8.5	Lower Amur River	Shireman & Smith, 1983
	6.17	Lower Volga River	Mitrofanov et al., 1992[b]; Shireman & Smith, 1983 ; Martino, 1974[b]
	1.75	Malacca, Malaysia	Shireman & Smith, 1983
	10	Moscow, Russia	Shireman & Smith, 1983; Opuszyński, 1972
	3	Nepal	Shireman & Smith, 1983
	6.5	North Eastern China	Peirong, 1989
	5.5	Northern China	Peirong, 1989
	6	Poland	Shireman & Smith, 1983
	6.5	Romania	Opuszyński, 1972

Table 1 cont.

Species	Age at Maturity	Location	Source
Grass	3.5	South Central Russia	Shireman & Smith, 1983
	4	Southern China	Peirong, 1989; Opuszyński, 1972
	4.17	Southern Yangtze River	Shireman & Smith, 1983
	4	Sunchow, China	Shireman & Smith, 1983
	3.5	Syr Darya River	Mitrofanov et al., 1992[b]
	4.5	Taiwan	Shireman & Smith, 1983
	2	Tamilnadu, India	Shireman & Smith, 1983
	5	Terek River	Abdusamadov, 1987
	5	Terek River (Dagestan region)	Abdusamadov 1989[b]
	3.75	Turkmenistan	Mitrofanov et al., 1992[b] ; Shireman & Smith, 1983
	9.5	Upper Amur River	Shireman & Smith, 1983
Silver	4	Amu Darya River	Abdullayev & Khakberdiyev, 1989[a]
	6.38	Amur River	Mitrofanov et al., 1992[a] ; Gorbach & Krykhtin, 1981[a] ; Gorbach & Krykhtin, 1980[a]
	3.5	Balyktchy fish farm, Uzbeckistan	Kamilov & Komrakova, 1999
	3.5	Central and Eastern China	Peirong, 1989
	4.5	Central China	Kolar et al., 2007
	2	Cuba	Bagrov & Chertikhin, 1985[a]
	3	Cuttack, India	Alikunhi et al., 1963
	3	Guangdong, China	Peirong, 1989
	2	Guangxi, China	Peirong, 1989
	5.5	Heilongjiang, China	Peirong, 1989
	3.5	Jiangsu, China	Peirong, 1989
	2	Middle Mississippi River	Williamson & Garvey, 2005
	5.5	North Eastern China	Peirong, 1989
	4.5	Northern China	Kolar et al., 2007; Peirong, 1989
	2.83	Southern China	Kolar et al., 2007; Peirong, 1989
	5	Southern Russia	Kolar et al., 2007
	3.5	Syr Darya River	Kamilov & Salikhov, 1996[a]
	5	Terek River	Abdusamadov, 1987
	3	Uzbekistan	Kamilov, 1986[a]
	4	Yangtze River	Kolar et al., 2007

[a] in Naseka & Bogutskaya, 2011; [b] in Bogutskaya et al., 2017

Appendix 2.1 References

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Appendix 2.2: Calculation for the midpoint of a country/large area.

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

   $\mathrm{lat}_i = \mathrm{lat}_i * \frac{\pi}{180}$

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

   $x_i = \cos(\mathrm{lat}_i) * \cos(\mathrm{lon}_i)$

   $y_i = \cos(\mathrm{lat}_i) * \sin(\mathrm{lon}_i)$

   $z_i = \sin(\mathrm{lat}_i)$

3. Average the cartesian coordinates back to latitude and longitude

   $\mathrm{Lon}_{\mathrm{middle}} = \mathrm{atan2}(y_{ave}, x_{ave})$

   $\mathrm{Lat}_{\mathrm{middle}} = \mathrm{atan2}(z_{\mathrm{ave}}, (\sqrt{x_{ave} * x_{ave} + y_{ave} * y_{ave}}))$

4. Convert Lat and Lon to back to degrees

   $\mathrm{Lon}_{\mathrm{middle}} = \mathrm{Lon}_{\mathrm{middle}} * \frac{180}{\pi}$

   $\mathrm{Lat}_{\mathrm{middle}} = \mathrm{Lat}_{\mathrm{middle}} * \frac{180}{\pi}$

Appendix 2.3: Outcome of individual species regressions.

Appendix 2.3 Table 1. Outcome of regressions on individual species. For species with spatially autocorrelated locations (within 250 km), the numbers represent an average of all possible regressions. All regressions except black carp were significant. Significant p values ($p < 0.05$) are bolded.

	Black	Bighead	Grass	Silver
Annual Average				
Slope	-0.016	-0.040	-0.043	-0.030
Intercept	2.0	2.1	2.1	1.7
P value	0.17	**0.0015**	**4.2×10^{-8}**	**8.7×10^{-4}**
Adjusted R^2	0.097	0.49	0.63	0.50
Warmest Quarter				
Slope	-0.0054	-0.042	-0.58	-0.057
Intercept	2.0	2.6	2.9	2.7
P value	0.80	**0.030**	**2.1×10^{-4}**	**0.0055**
Adjusted R^2	-0.092	0.25	0.36	0.37
Coldest Quarter				
Slope	-0.0011	-0.025	-0.026	-0.018
Intercept	1.8	1.6	1.5	1.3
P value	0.12	**0.0028**	**4.9×10^{-8}**	**8.0×10^{-4}**
Adjusted R^2	0.15	0.45	0.63	0.51
Annual Degree Days				
Slope	-7.4×10^{-5}	-1.4×10^{-4}	-1.6×10^{-4}	-1.1×10^{-4}
Intercept	2.2	2.3	2.4	2.0
P value	0.17	**4.0×10^{-4}**	**1.2×10^{-8}**	**9.6×10^{-4}**
Adjusted R^2	0.10	0.58	0.66	0.50

Appendix 2.4: Moran's I spatial autocorrelation tests

When using the entire dataset, the p values for the Moran's I spatial autocorrelation test were as follows:

Annual average: 0.031

Warmest quarter: 0.0063

Coldest quarter: 4.9×10^{-4}

Annual degree days base 0°C: 0.53

When the data were subsampled so that only locations at least 250 km apart were included within the same analysis, the autocorrelation decreased. The following represents the percentage of Moran's I test p values that were not significant ($p > 0.05$), out of 10 000 trials:

Annual average: 99.85%

Warmest quarter: 99.76%

Coldest quarter: 83.93%

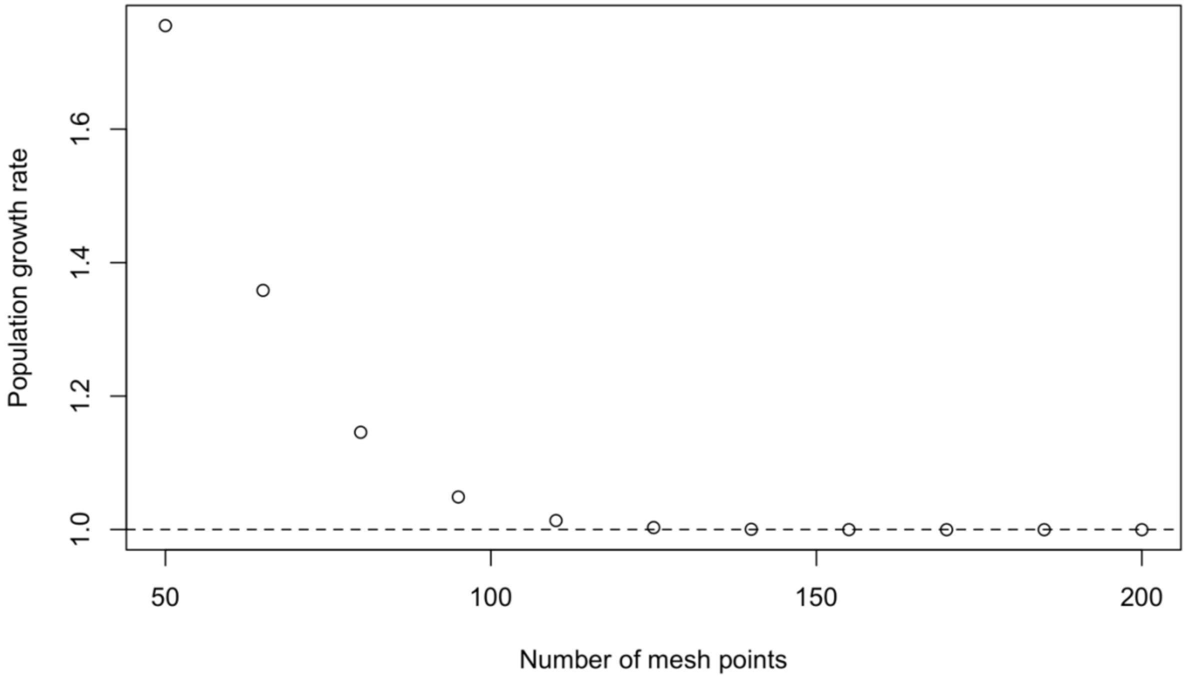
Annual degree days base 0°C: 97.84%

Appendix 3.1: Diagnostics for IPM model

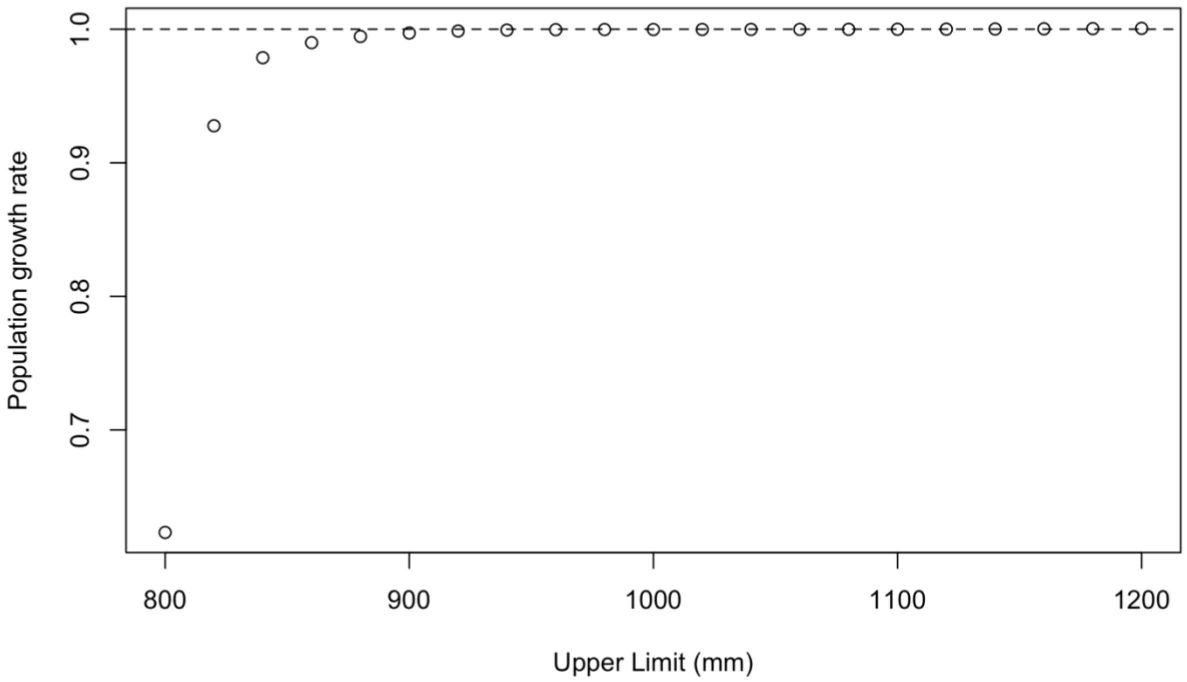
The appropriate number of mesh points and the upper limit of the integral, can be determined by testing the model that only includes the growth distribution *G(z',z)*. With no mortality or addition of new recruits, the λ value should be stable at 1 (population is not expected to change over time). If the λ value does not equal 1, then the values of mesh points and upper limit should be adjusted.

As the number of mesh points increased, the λ value formed an asymptote to 1 (Appendix 3.1 Figure 1). Similarly, as the upper limit *U* increased, the λ value formed an asymptote to 1 (Appendix 3.1 Figure 2). Based on these diagnostic graphs, we chose 150 mesh points, with a upper limit of 1100 mm as stable values for our model.

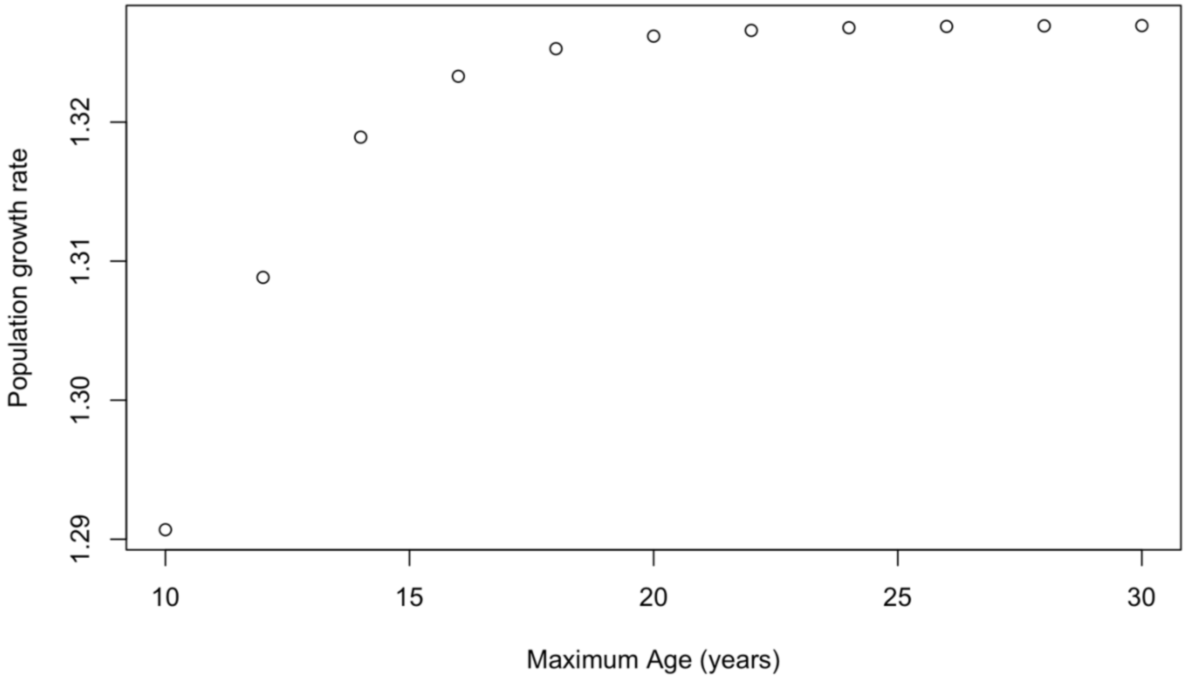
Using our chosen values for upper limit and mesh points, we determined the appropriate value for maximum age *M*. In this case, the population growth rate does not asymptote to 1 (because the model now includes mortality and reproduction), but should roughly asymptote to the population growth rate as maximum age increases. However, grass carp in the wild do not typically live longer than 15 years (Sullivan et al., 2020; Shireman & Smith, 1983), so the maximum age value should be relatively close to this to be realistic to the data available. Based on our diagnostic data combined with biological data, we chose a maximum age of 20 years (Appendix 3.1 Figure 3).



Appendix 3.1 Figure 1. The effects of the number of mesh points on the predicted population growth rate.



Appendix 3.1 Figure 2. The effect of the upper limit *U* on the population growth rate.



Appendix 3.1 Figure 3. Plot of how maximum age affects the predicted λ value.

Appendix 3.2: Parameterizing functions of our IPM model

Probability of maturation

To parametrize our degree-day dependent function for the probability of maturing, we started with the relationship between degree days and age at maturity from Chapter 2 (Appendix 3.2 Figure 1). Using this relationship, we obtained the degree day associated with an age at maturity from 2-11 (in an interval of 0.1), and obtained the standard deviation for each estimate using the 95% confidence intervals. In a normal distribution, 95% of the data falls within 1.96 ± the standard deviation. Therefore, with the range of the upper and lower confidence intervals, the standard deviation around each age at maturity was estimated using as: $\sigma = \frac{CI_{upper} - CI_{lower}}{2*1.96}$, where CI_{upper} and CI_{lower} represent the upper and lower 95% confidence intervals.

These means and standard deviations were then used to make a distribution of possible ages at maturity for each age, with 50 000 randomly generated ages (e.g. Appendix 3.2 Figure 2). These distributions of ages at maturity were compared to a simulated population of grass carp of 50 000 individuals with a mean age of 6 years and a standard deviation of 4 years (Appendix 3.2 Figure 3).

By comparing each distribution of age at maturity to the age distribution of the fish population, we were able to make a distribution of mature or immature individuals in the population for each age at maturity. A random fish age from the fish distribution (Appendix 3.2 Figure 3) was paired with a random value from an age at maturity distribution (Appendix 3.2 Figure 2). If the fish age was greater than the age at maturity, it was considered mature (1), otherwise it was considered immature (0) (Appendix 3.2 Figure 4). These distributions were fit to generalized linear models using the glm function for each age, and the parameters α and β

from the equation $p(a) = \frac{1}{1+e^{\beta(a-\alpha)}}$ were collected for each trial, where *p(a)* was the probability of maturation for each trial, and a is the age in years (Appendix 3.2 Figure 4).

The parameters for the logistic regression were then plotted against the degree days that correspond to the given ages at maturity (Appendix 3.2 Figure 5). We noticed that while parameter α followed an exponential pattern, the shape in the relationship between degree days and parameter β appeared to shift around 5000 degree days. When we only considered locations with fewer than 5000 degree days, we were able to use a linear regression of the value of the parameters transformed using the natural logarithm to predict their value based on the degree days (Appendix 3.2 Figure 6).

Fecundity

To determine the relationship between the relative fecundity of grass carp and degree days, we used Climate Prediction Center (CPC) Global temperature dataset (https://psl.noaa.gov/) (CPC Global Daily Temperature, 2020) to get the degree days at each location from Table 3.2. We used minimum and maximum daily temperatures from 1979 to 2019 in our calculations. We calculated annual degree days (DD_a) as $DD_a = \sum_{c=1}^{365} DD_c$, where c is the calendar day. The degree day for day c (DD_c) was calculated as

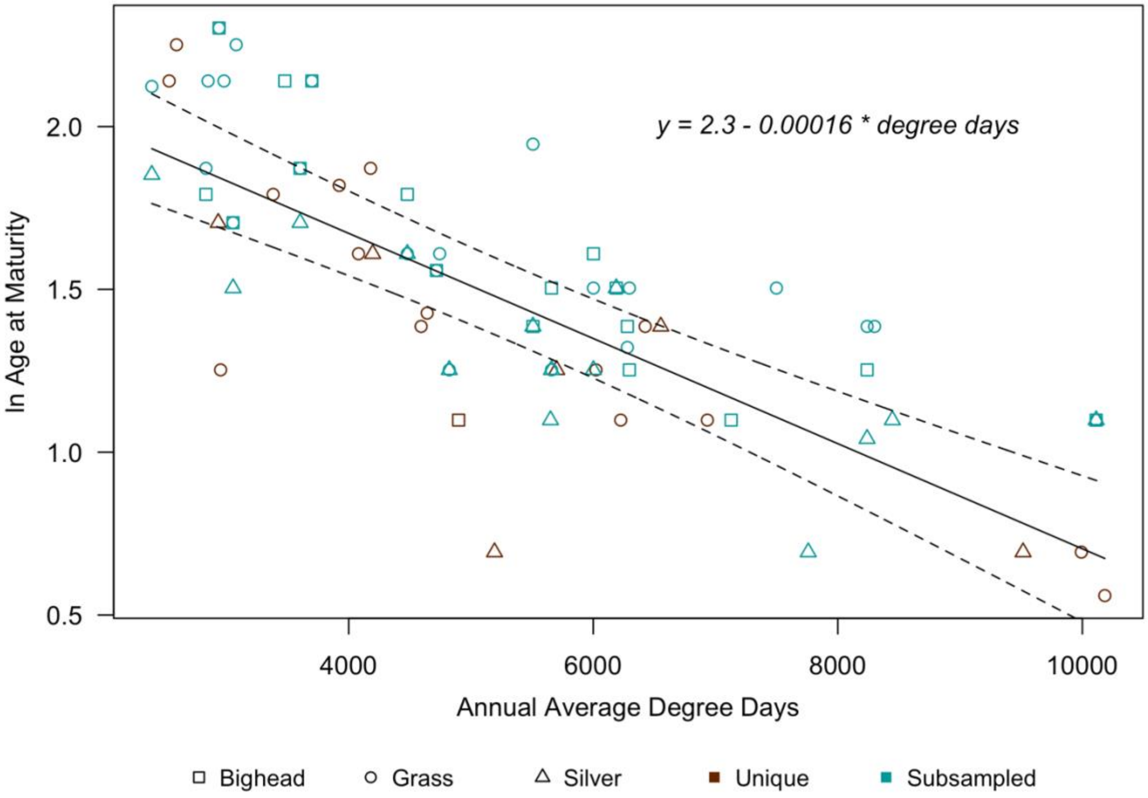
$$DD_c = \begin{cases} \frac{T_{c,max}+T_{c,min}}{2} - T_{base} & if \quad \frac{T_{c,max}+T_{c,min}}{2} \geq T_{base} \\ 0 & if \quad \frac{T_{c,max}+T_{c,min}}{2} < T_{base} \end{cases}$$

, with $T_{c,max}$ and $T_{c,min}$ as the maximum and minimum temperatures for day c, and T_{base} as the base temperature, which we set as 0 (McMaster & Wilhelm, 1997). Due to difficulty in delineating between the locations Ili River Delta and Balkhash Lake, we used the location for Balkhash Lake for both locations (the Ili River Delta enters into Balkhash Lake). The location with a relative fecundity of 233 000 eggs/kg (Ili River Delta) was an outlier compared to the rest of the data (Appendix 3.2 Figure 7), and was excluded from further analysis. When the outlier was excluded, the relative fecundities had a significant relationship with annual average degree days (Appendix 3.2 Figure 8), which allowed us to use degree days to predict the relative fecundity for different locations.

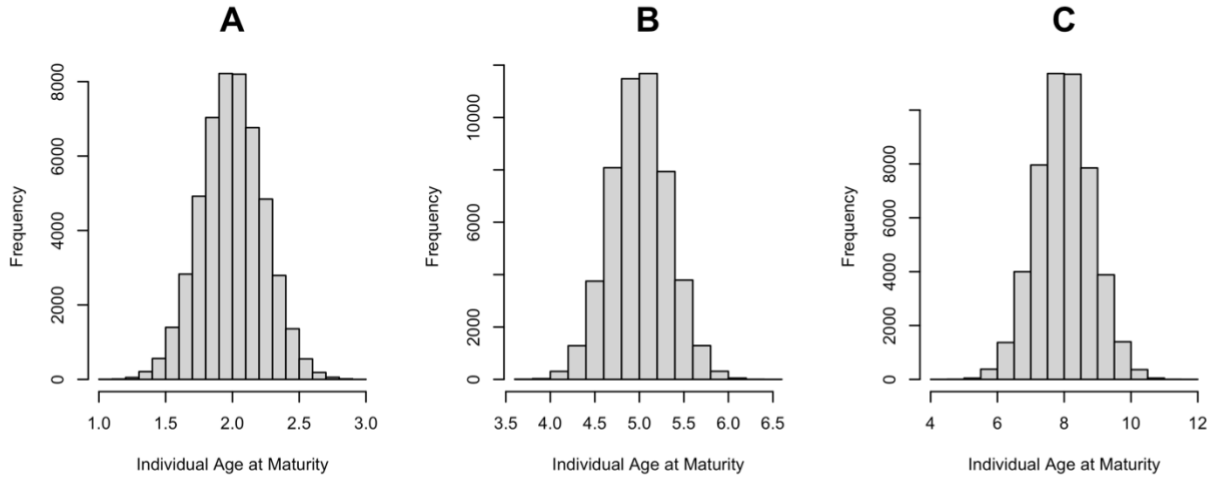
Growth Distribution

Our growth distribution was derived from fitting the von Bertalanffy equation ($L_t = L_{inf}(1 - e^{-k(t-t_0)})$) to data from Sullivan et al., (2020) (Appendix 3.2 Figure 9). Like in Sullivan et al., (2020), we fixed the t_0 parameter at 0. Using this equation, we calculated how much a fish was expected to grow in one year, based on their initial length (Appendix 3.2 Figure 10). Based on this relationship, the growth increment becomes negative when length exceeds L_{inf}, so for our model we set the yearly growth increment to 0.1 mm when the fish was equal to or exceeded L_{inf}. The mean of our normal distribution (μ_g) was the growth increment added to the current length: $\mu_g = z + g_{inc}(z)$.

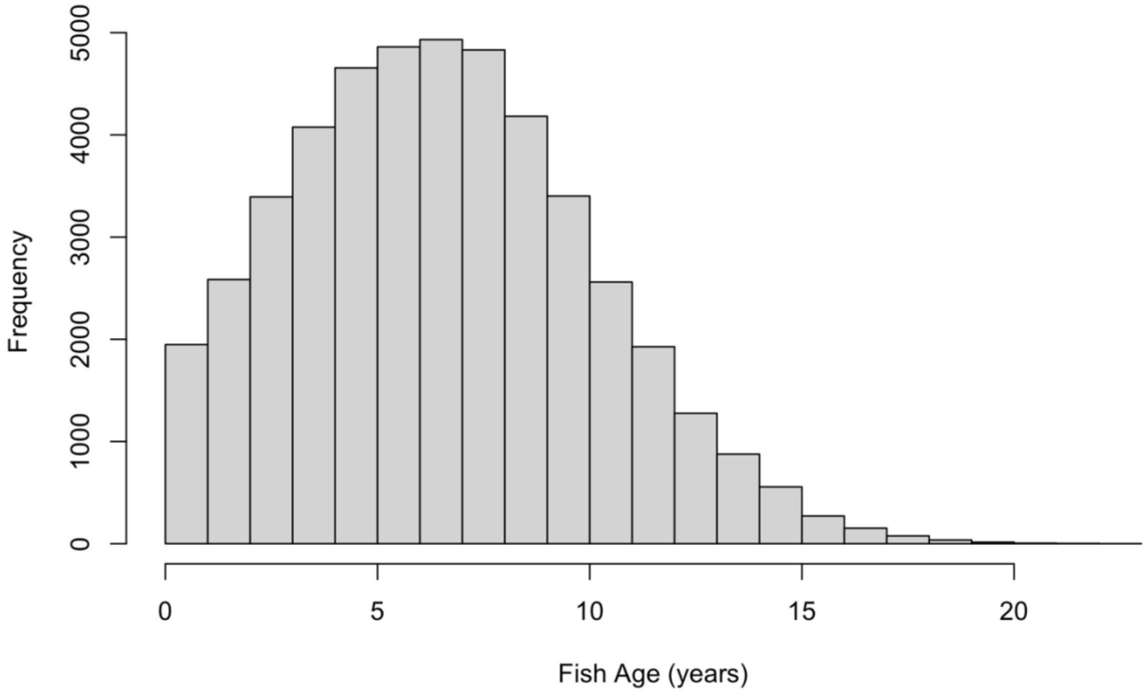
To decrease possible shrinking (when length at time t is greater than length at time $t+1$) in our model, the standard deviation of the normal distribution (σ_g) decreased as fish length increased according to the equation $\sigma_g = \frac{g_{inc}(z)}{d_g}$, where g_{inc} is determined by the functions in Appendix 3.2 Figure 10, and d_g is a division factor that we set to 4. This ensured that as fish grew, they were unlikely to shrink. When fish reached large sizes (small growth increments), we set the standard deviation to 5 mm. Appendix 3.2 Figure 11 shows several example distributions at various sizes. At large sizes, some shrinking is possible, but ultimately the fish is unlikely to change sizes by very much.



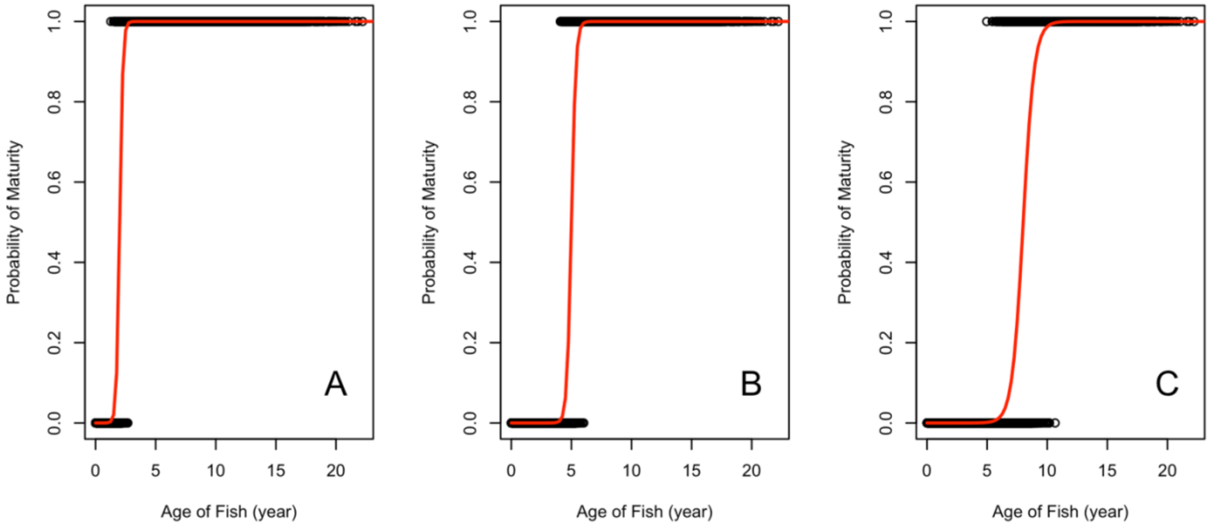
Appendix 3.2 Figure 1. Relationship between annual average degree days and age at maturity of Asian carp (taken from Chapter 2).



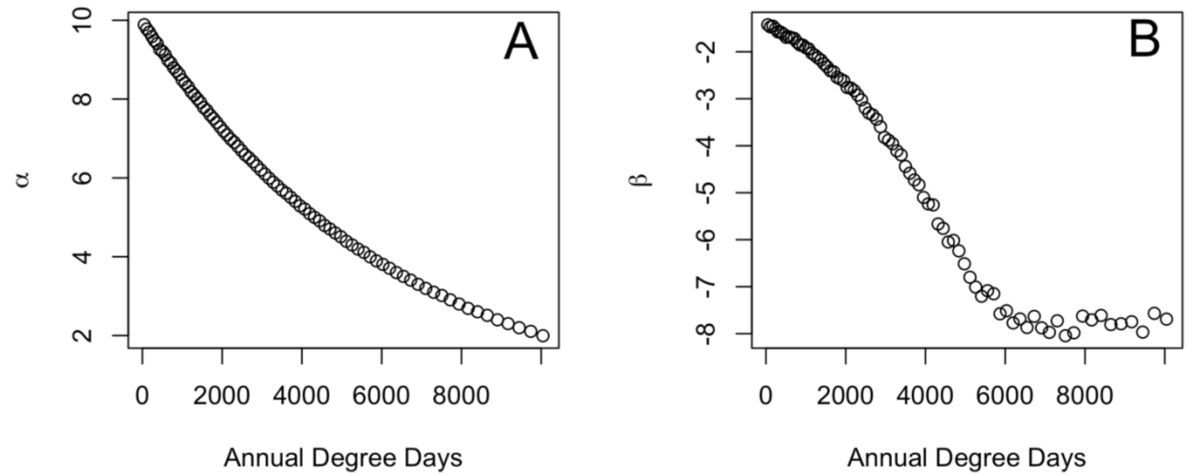
Appendix 3.2 Figure 2. Example histograms of distributions of possible ages at maturity for an age at maturity of 2 (panel A), an age at maturity of 5 (panel B), and an age at maturity of 8 (panel C). As age at maturity increased, the standard deviation also increased.



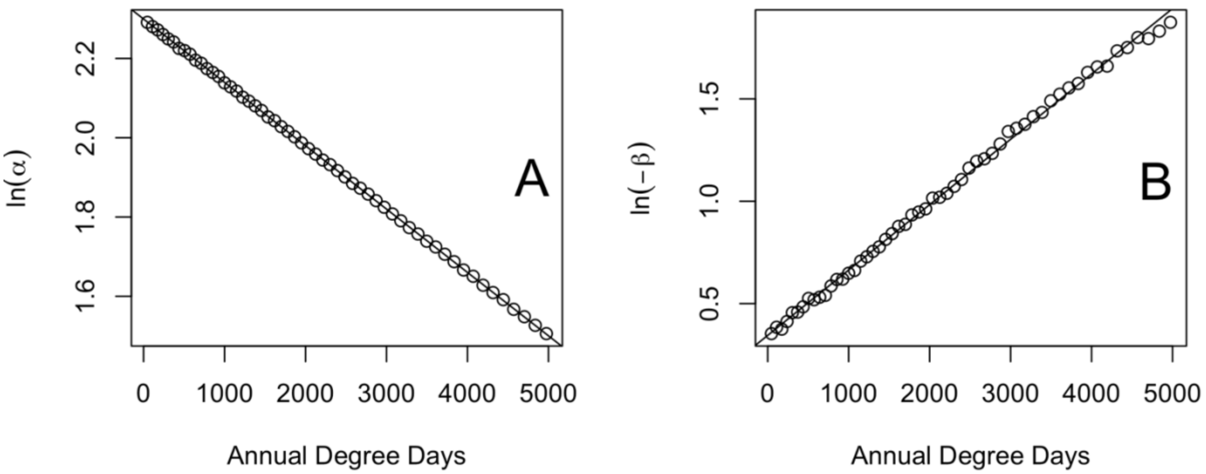
Appendix 3.2 Figure 3. Histogram of a simulated fish population of 50 000 individuals, created with a mean age of 6 with a standard deviation of 4. Fish that were less than 0 years in age were excluded.



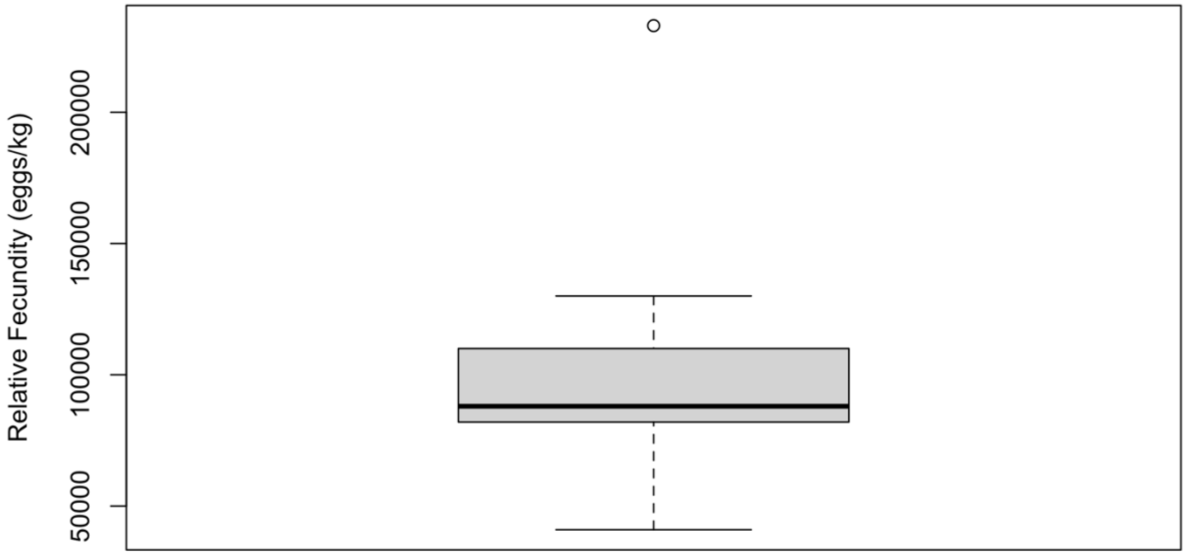
Appendix 3.2 Figure 4. The maturation status of mature (1) and immature (0) individuals from the simulated population with an age at maturity of 2 (A), age at maturity of 5 (B), and age at maturity of 8 (C). Examples of fitted generalized linear models of simulated data were shown in fitted curves.



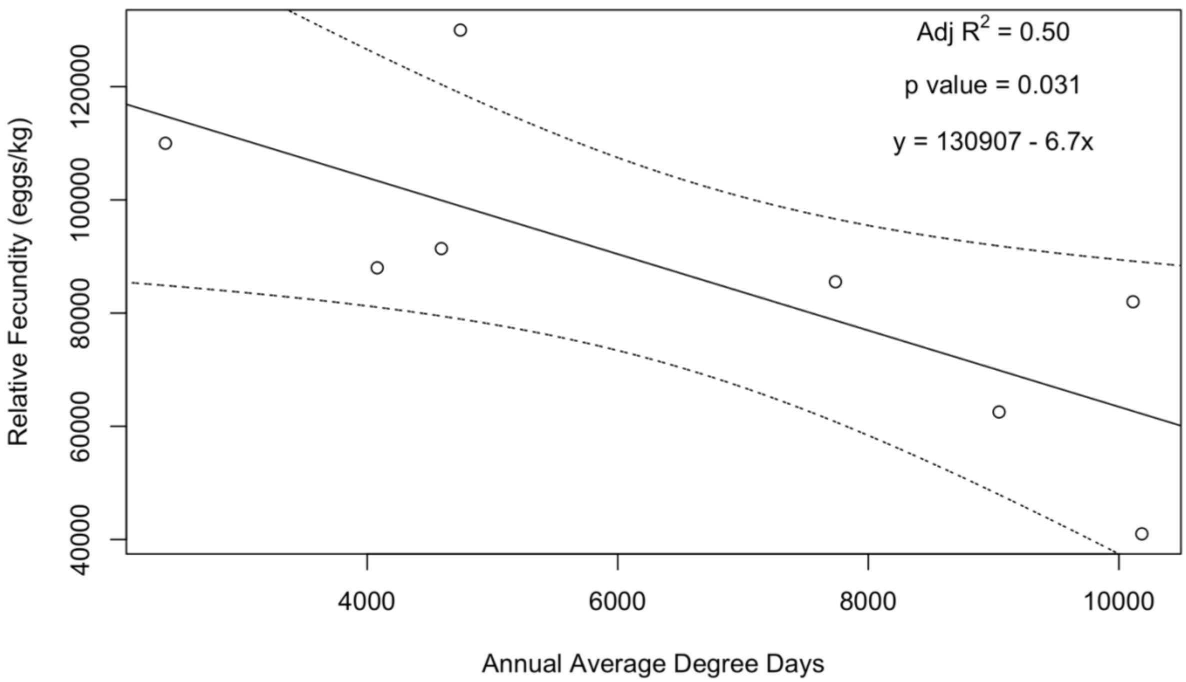
Appendix 3.2 Figure 5. The relationship between the parameters *α* (panel A) and *β* (panel B) across all degree days. Parameter *α* is equivalent to the age at maturity of the population.



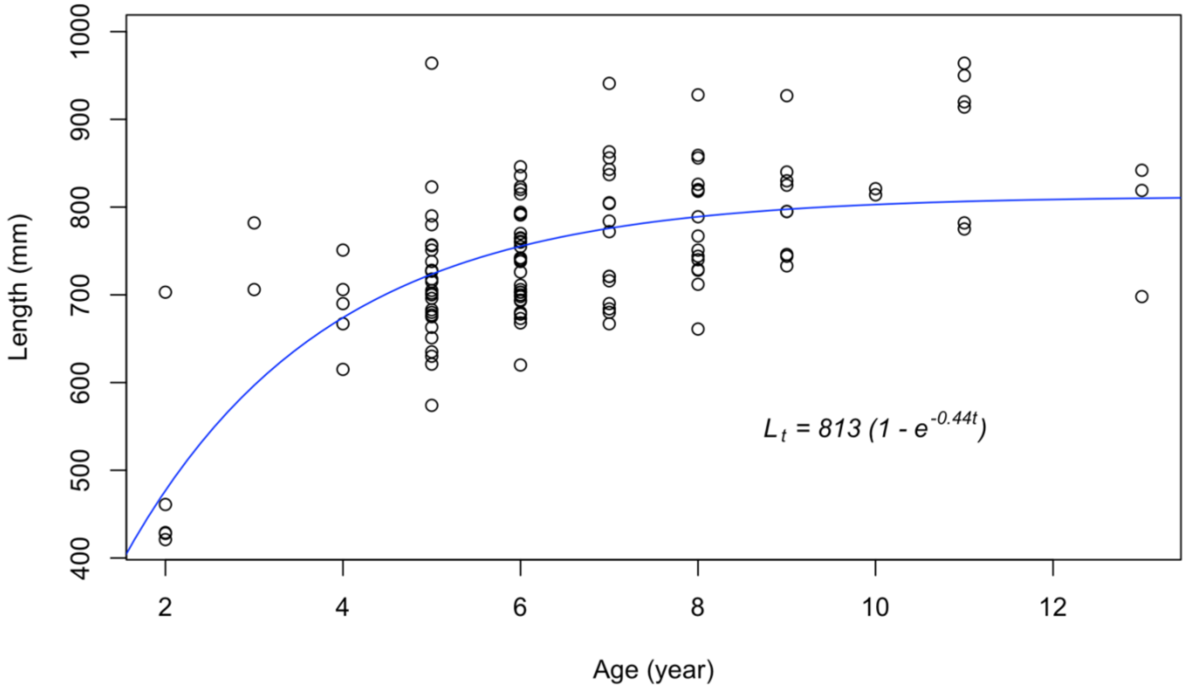
Appendix 3.2 Figure 6. The relationship between the ln value of the parameters *α* (panel A) and *β* (panel B) with degree days fewer than 5000.



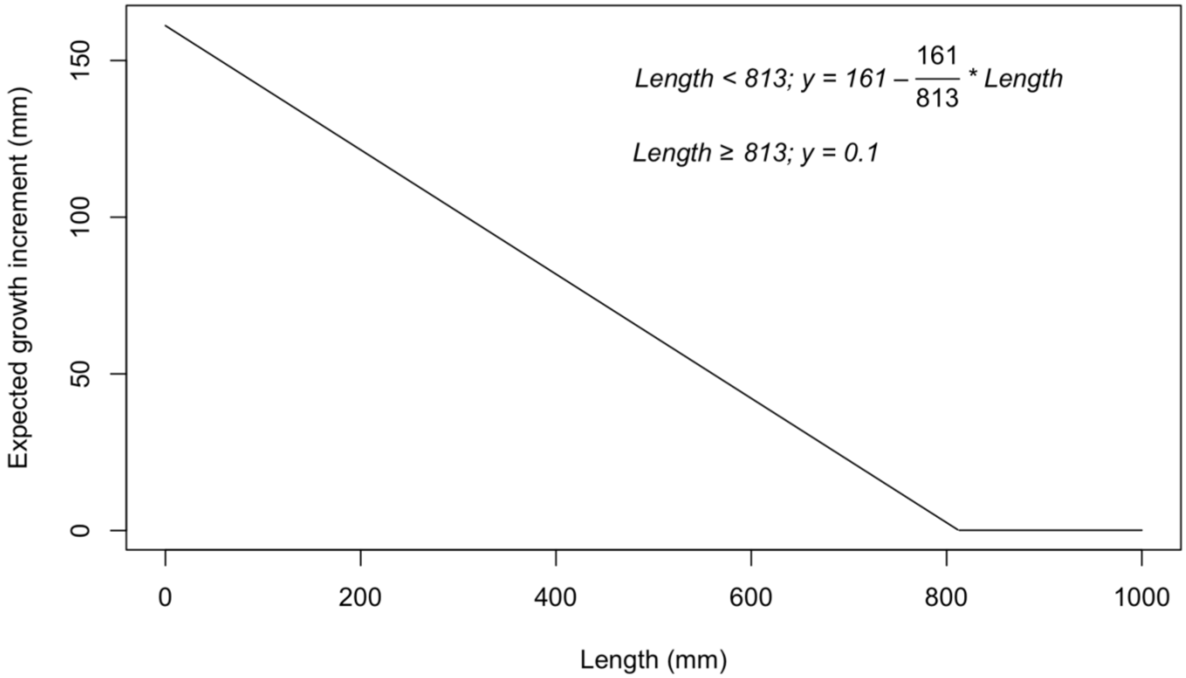
Appendix 3.2 Figure 7. Boxplot of relative fecundity data from Table 3.2.



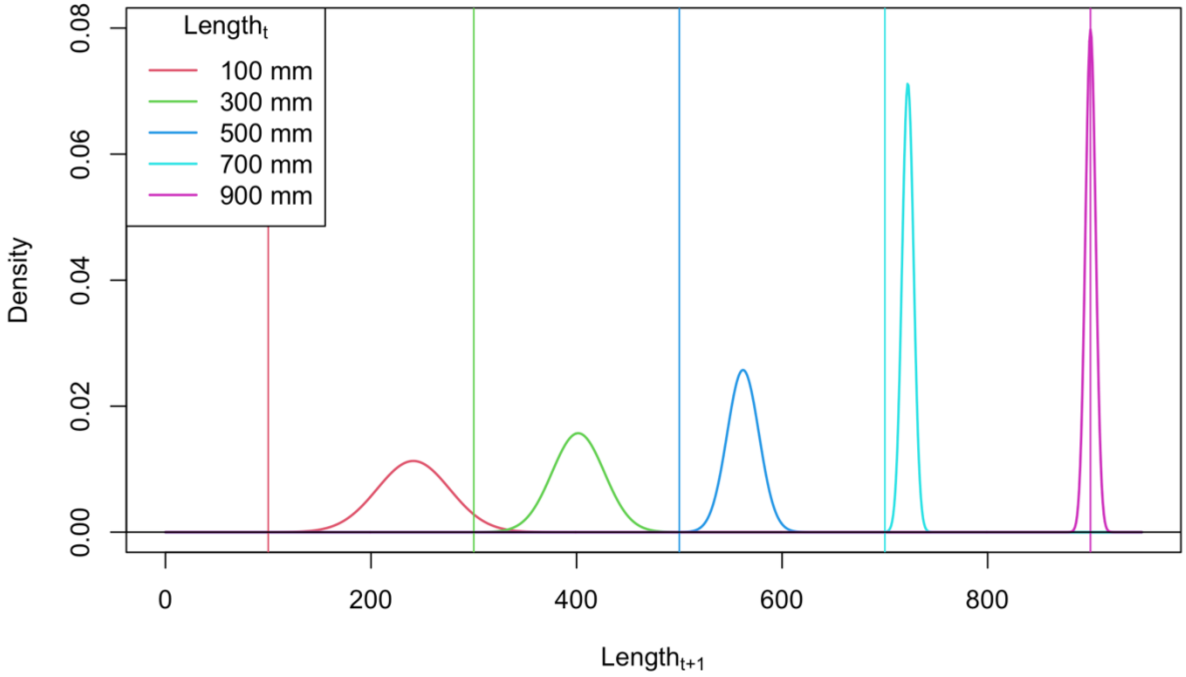
Appendix 3.2 Figure 8. Linear regression of relative fecundities and annual degree days. Regression line is shown as a solid line, with dotted lines representing 95% confidence intervals. Annual average degree days significantly predicted relative fecundities (p value = 0.031), and explained about 50% of the variance in relative fecundities (Adjusted R^2 value of 0.50).



Appendix 3.2 Figure 9. Fit von Bertalanffy equation to raw data from Sullivan et al., (2020). L_{inf} is equal to 813 mm, and k is equal to 0.44.



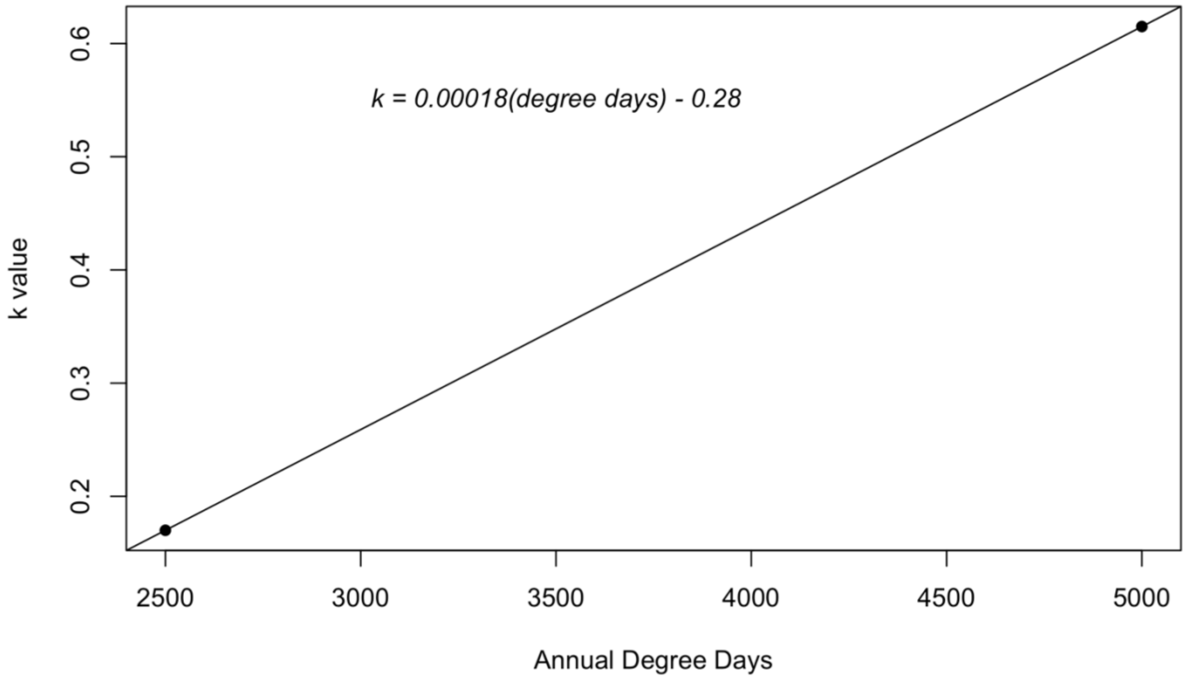
Appendix 3.2 Figure 10. Plot demonstrating the expected growth increment in the next year, based on the current length.



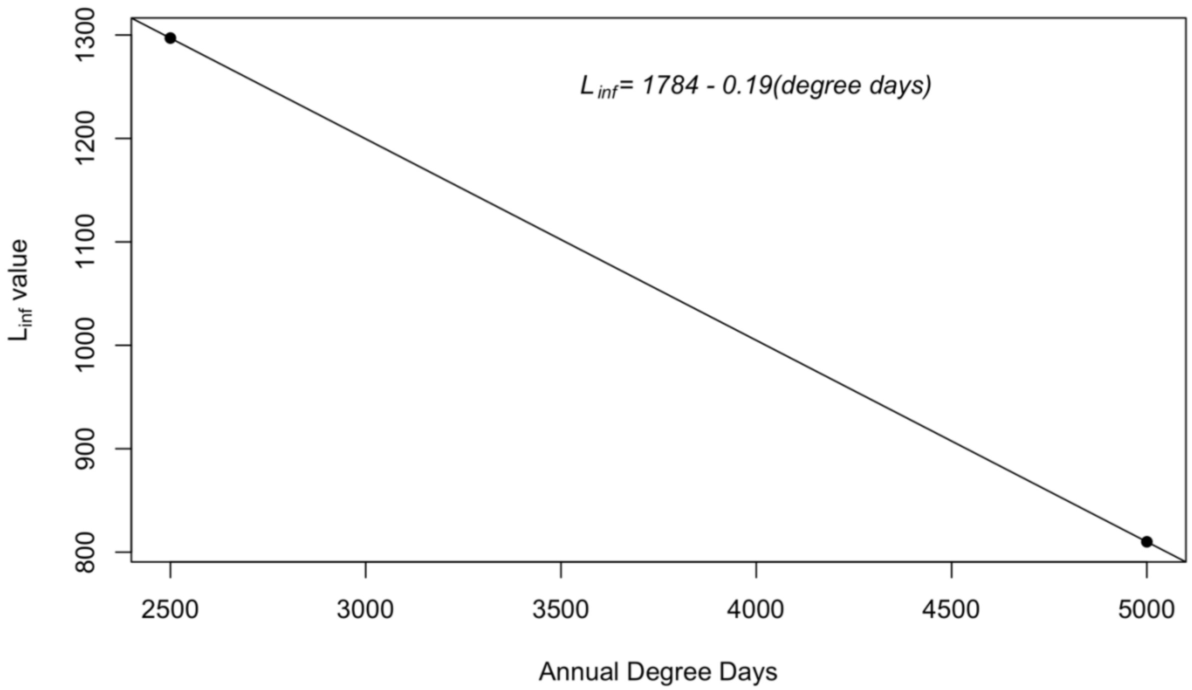
Appendix 3.2 Figure 11. Example growth distributions at multiple lengths. Initial lengths at time t are shown as vertical lines. At small sizes, the distribution of lengths at time t+1 do not overlap with the initial size. At large sizes (greater than L_{inf}), there is an equal chance of some growth or some shrinking, but it is unlikely change by a large amount either way.

Appendix 3.3: Simulating a relationship between temperature and growth parameters

Our simulated values for a temperature dependent *k* value and a temperature dependent L_{inf} value are shown in Appendix 3.3 Figure 1 and Appendix 3.3 Figure 2. We assumed an approximately inverse relationship between *k* and L_{inf}, where when *k* is small, L_{inf} is large (Weber et al., 2015).



Appendix 3.3 Figure 1. Hypothetical relationship between the growth rate *k* and annual degree days. The smallest *k* value of 0.17 was assigned to 2500 degree days base 0°C, and the largest *k* value of 0.615 was assigned to 5000 degree days base 0°C.



Appendix 3.3 Figure 2. Hypothetical relationship between the maximum size L_{inf} and annual degree days. The smallest L_{inf} value of 810 mm was assigned to 2500 degree days base 0°C, and the largest L_{inf} value of 1297 mm was assigned to 5000 degree days base 0°C.