Influence of temperature on the growth and performance of non-native goldfishes (*Carassius* spp.)

Jessamine Trueman

Department of Biology

McGill University

January 2021

A thesis submitted to McGill University in partial fulfillment of the requirements of the degree of Master of Science in Biology

Table of Contents

Abstract

The impacts and invasion success of non-native aquatic species are expected to change with climate warming, particularly in north temperate regions. Goldfish (*Carassius auratus*) and Prussian carp (*C. gibelio*) are non-native species that can rapidly invade and alter inland water ecosystems. The goldfish is already well-established in the Great Lakes, and its abundance is increasing, whereas the Prussian carp has been established in western Canada since at least the mid-2000s and is spreading in Alberta and Saskatchewan; invasions of both these fishes could plausibly be facilitated by warmer temperatures. To understand how climate warming can affect the performance of *Carassius* populations, we measured growth rates and maximum feeding rates across a range of temperatures for individuals from four latitudinally-distributed populations of goldfish and one population of Prussian carp in North America. Despite some populations having a more recent introduction, a countergradient pattern in growth and a latitudinal pattern in feeding rate was observed in the goldfish populations and the Prussian carp population. These results suggest that *Carassius* species are able to rapidly adapt or acclimate to new and changing thermal environments.

Résumé

Les impacts des espèces aquatiques non indigènes sont appelés à changer avec le réchauffement climatique, en particulier dans les régions tempérées du nord. Le poisson rouge (*Carassius auratus*) et le carassin argenté (*C. gibelio*) sont des espèces non indigènes qui peuvent rapidement envahir et altérer les écosystèmes lacustres et fluviaux. Les poissons rouges sont déjà bien établis dans les Grands Lacs et leur abondance est en croissance, tandis que le carassin argenté est établie dans l'ouest du Canada depuis au moins le milieu des années 2000 et il se propage en Alberta et en Saskatchewan. L'invasion de ces deux poissons pourrait être facilitée par des températures plus chaudes. Pour comprendre comment le réchauffement climatique peut affecter la performance des populations de *Carassius* spp. d'Amérique du Nord, nous avons mesuré les taux de croissance et les taux d'alimentation maximaux d'individus exposés à différents régimes thermiques chez quatre populations de poissons rouges situées le long d'un gradient latitudinal et d'une population de carassins argenté . Bien que certaines populations Nord-Américaines aient été introduites plus récemment, nous avons observé que le taux d'alimentation moyen est positivement corrélé à la latitude tandis que le taux de croissance moyen est négativement corrélé avec le gradient latitudinal. La population de carassins argenté suit les modèles latitudinaux établis par les populations de poissons rouges. Ces résultats suggèrent que les carassins sont capables de s'adapter ou de s'acclimater rapidement à des environnements thermiques nouveaux ou changeants.

Acknowledgements

This project could not have been completed without the hard work and commitment of many people and organizations who deserve thanks and recognition. I want to start by thanking my supervisor, Anthony Ricciardi, for his guidance and support which has helped me grow as a scientist and as a person. Thank you to my committee members, Jennifer Sunday and Andrew Hendry for their feedback and encouragement. Thank you to Fond de recherches Québec – Nature et technologies, the McGill Biology department, and the Redpath Museum for providing me with financial support for my research.

I'd like to thank John Armstrong, the parks supervisor of the Special Areas Board in Alberta for providing me with a place to stay, assisting me with sampling for fish and for helping me to gather important data from the other side of the country. Thank you to the staff of the Cold Lake Fish Hatchery for their help in collecting Prussian carp in Alberta, and to Tys Theijsmeyer for his advice on goldfish in Cootes Paradise Marsh.

I am very grateful to all the members of the Ricciardi lab for their support and advice the past two years. Thank you to all the undergraduate assistants who have helped me, but especially Nicole Moore, Hélène Pfister and Phillipe Hénault for putting in countless hours in the field, in the lab and at home and for always keeping a positive attitude in the face of inclement weather and setbacks. I am especially appreciative of my fellow graduate student, Heather Reid for all her help in the field, and to Heather and Gen D'Avignon for all of their help with animal care and running experiments during COVID restrictions. The teamwork, patience and moral support they both provided made the process infinitely easier.

Finally, I'd like to thank Joe Culpepper, my partner, for his steadfast support, advice and encouragement throughout this entire process.

Contribution of Authors

Study concept and design: Trueman and Ricciardi

Acquisition of data: Trueman

Analysis and interpretation of data: Trueman

Drafting of manuscript: Trueman

Critical revision: Trueman and Ricciardi

General introduction and literature review

Non-native species can have substantial impacts on native flora and fauna (Gallardo et al., 2016; Kessel et al., 2011; Strain and Johnson, 2013; Strecker et al., 2006). The rate at which new species are introduced around the globe is accelerating and is several orders of magnitude higher than the prehistorical rates (Ricciardi, 2007). Freshwater ecosystems, in particular, are quite susceptible to invasions, in part because they are major centres of human activity and thus receive higher propagule pressure (Dudgeon et al., 2006; Strayer and Dudgeon, 2010). For example, owing largely to intense shipping traffic and other human activities, more than 180 invaders are established in the Great Lakes-St Lawrence basin – the most invaded freshwater ecosystem in the world (Ricciardi, 2006). The growing number of non-native species in the Great Lakes and other urbanized watersheds adds to other stressors, including climate change, that are already straining ecosystems and threatening their integrity (Allan et al., 2012)

1. Context dependencies complicate non-native species risk assessment

Burgeoning numbers of invasions make it impossible to manage or prevent every new potential threat. However, not all non-native species are equivalent in impact. Some, like the zebra mussel *Dreissena polymorpha*, colonize rapidly and often become superabundant, altering nutrient cycles (Nalepa and Schloesser, 1992), causing drastic reductions in native mussel species (Ricciardi et al., 1998), and damaging infrastructure (Connelly et al., 2007; Ludyanskiy et al., 1993); whereas other species remain relatively limited in their abundance and distribution, or have minimal impact. Risk assessments must identify which species are likely to be the most successful and have the largest impacts, and should be prioritized for management. A major challenge to this goal is the context-dependent nature of invasions (Ricciardi et al., 2013).

Climate change is projected to substantially alter the composition, abundance, and impacts of invaders in temperate ecosystems like the Great Lakes (Pagnucco et al., 2015; Woodward et al., 2010). Surface waters of the Great Lakes are expected to warm considerably over the next few decades. A decade ago, Trumpickas et al. (2009) reported that summer surface temperatures (measured in T_{max}: the 20th warmest temperature of the year) ranged between 15°C for Lake Superior and 23°C for Lake Erie, and projected that they would be between 18.2°C and 24.9°C by the period of 2041-2070 (Trumpickas et al., 2009). These elevated temperatures should create conditions more hospitable to non-native species originating from southern climates, increasing their probability of establishment (Hellmann et al., 2008) and possibly their impacts: a meta-analysis found that the trophic impacts of non-native aquatic species increased as the ambient water temperature approached their physiological optima (Iacarella et al., 2015). Therefore, it is crucial to consider emerging temperature contexts when assessing risks of invasion and targeting species for management.

2. *Carassius spp*. as model invaders

The *Carassius* group includes several fishes with invasion histories and which may benefit from climate warming in temperate regions. While details of the phylogeny of the genus are still being debated, five species are generally accepted to be valid: the common goldfish (crucian carp) *C. auratus*, crucian carp *C. carassius,* Prussian carp (gibel carp or silver crucian carp) *C. gibelio*, gengorobuna *C. cuvieri*, and ginbuna (Japanese silver crucian carp) *C. langsdorfii* (Rylková et al., 2013). *Carassius gibelio, C. cuvieri*, and *C. langsdorfii* were considered by some researchers as subspecies of *C. auratus* (Apalikova et al., 2008; Shimizu et al., 1993); however, these four taxa have been confirmed as distinct species by cytochrome b mtDNA analysis in two different studies (Kalous et al., 2012; Rylková et al., 2013).

The crucian carp *C. carassius* can be distinguished morphologically from its congeners through several traits including the convex margin of its dorsal fin, its possession of 23-33 gill rakers (whereas other species have 37-53), and having a white peritoneum (in contrast to other species have a black peritoneum; Kottelat and Freyhof, 2007; Rylková et al., 2013). Moreover, both *C. cuvieri* and *C. carassius* are the only species that are exclusively diploid. The only reliable way of distinguishing *C. langsdorfii*, *C. gibelio* and *C. auratus* might be cytochrome b analysis (Rylková *et al*., 2013). All five *Carassius* species have been introduced outside of their native range (Beatty et al., 2017; Jang et al., 2002; Jeffries et al., 2017; Kalous et al., 2013; Lusková et al., 2010a; Rylková et al., 2013), although in some regions their biogeographic history is unclear; there is debate as to whether *C. carassius* is native or non-native in much or all of Europe (Sayer et al., 2020).

In North America, at least two non-native *Carassius* species currently pose an invasion threat to aquatic ecosystems. The common goldfish (*C. auratus*) has established populations throughout North America, including the Great Lakes, over the past two centuries (Halas et al., 2018; Nico et al., 2018; Scott and Crossman, 1973). Until relatively recently, it was generally perceived to be innocuous (but see Richardson et al. 1995 and Roy 1992). The Prussian carp (*C. gibelio*), which is highly invasive in western Europe (Lusková et al., 2010a; Ribeiro et al., 2015), is an emerging invader in Canada, where it is spreading rapidly in Alberta and Saskatchewan (Docherty et al., 2017).

Goldfish and Prussian carp can be visually distinguished only by their colouring (Kottelat and Freyhof, 2007), although this an unreliable trait for identifying fishes in general. Since

Prussian carp is often misidentified as goldfish or as other *Carassius* species (Elgin et al., 2014), the global distribution of each species is unclear. For accurate risk assessment, it is important to determine to what extent the two species differ in physiology and ecological impacts.

2.1 Comparative reproduction and genetics

The ploidy of *Carassius* species is also a subject of debate. Most of the literature describes the different species of the *Carassius* species complex as diploid, triploid, and tetraploid (Apalikova et al., 2008; Liasko et al., 2011; Lusková et al., 2010a; Shimizu et al., 1993), but some studies have revealed that *Carassius* species are actually composed of tetraploid, hexaploids, and octoploids (Liu et al., 2017; Luo et al., 2014, 1999).

Ploidy affects the reproductive mode of various *Carassius* species. Hexaploids can reproduce by gynogenesis (Liasko et al., 2011; Mada et al., 2001), thereby forming clonal lines of females. Gynogenetic females use the sperm of closely-related cyprinids to trigger the division of their eggs. Hexaploid males also exist and can reproduce bisexually with hexaploid females (Jiang et al., 2013; Liasko et al., 2011; Lusková et al., 2010a). In Europe, the first populations of *C. gibelio* were composed of only hexaploid females, but since the apparition of mostly tetraploid males in the population in the 1990s (either naturally or through introduction), their contribution to the reproductive pool is causing a demographic augmentation of the tetraploids in the population (Liasko et al., 2011; Lusková et al., 2010a). Previously, *C. auratus* was assumed to be only tetraploid, but in the last decade hexaploid individuals have also been discovered (Rylková et al., 2013; Takada et al., 2010; Xiao et al., 2011). In Europe, *C. auratus* populations seem to be either almost entirely tetraploid, or almost entirely hexaploid, and the distribution of each group is clustered (Rylková et al., 2013), which suggests that the hexaploid fish were introduced independently of the tetraploids. Gynogenetic reproduction has not yet been reported from goldfish populations in North America or Australia, so it is possible that only tetraploid, sexually reproducing goldfish were introduced in these locations. However, given that the ploidy of goldfish on these two continents has not been investigated, it is possible that there are triploid individuals in these populations as well.

Genetic background and ploidy in *Carassius* can affect life history traits and competitive abilities. Hexaploid gynogenetic fish seem to have great colonizing potential because of their higher overall condition (measured by the protein concentration in their blood; Vetesník et al., 2013) and the numeric advantage of asexual reproduction. Nonetheless, they tend to have a higher annual energy intake (Vetesník et al., 2013) and less effective oxygen intake at the gills (Sezaki et al., 1991) than tetraploids, which could lead to long-term competitive disadvantages if tetraploids appear in the system.

2.2 Invasion histories of goldfish and Prussian carp

The goldfish is native to central China (Rylková et al., 2010) and was domesticated in the early Sung dynasty (Balon, 2004). It was introduced to Europe, beginning in Portugal, as early as 1611, and then it was transported to England by 1691 and to France by 1755 (Balon, 2004). The species is thought to have been brought to North America in the late 17th century (De Kay and Seward, 1842), which would make goldfish the first recorded introduction of a non-native fish to the continent (Nico and Fuller, 1999). It is unclear exactly when goldfish were introduced into the Great Lakes watershed. The earliest record of goldfish being introduced into states that border the Great Lakes was in 1878 (Emery, 1985); by 1888 goldfish were found frequently in the canals of Hamilton County, Ohio (Battle, 1940), so they were likely introduced to the Great

Lakes basin within that decade. Goldfish are now well established in the Great Lakes–St. Lawrence watershed (Halas et al., 2018), and the abundance of populations in western Lake Ontario and Lake Erie has been increasing rapidly in recent years (Craggs, 2016; Hessenauer and Wills, 2016).

There is some dispute about the native range of Prussian carp. Some sources consider it to be a non-native species throughout Europe (Lusková, 2004), whereas others consider it to be native to central Europe (Kottelat and Freyhof, 2007). Rylková et al. (2013) offered a convincing argument that the native range of Prussian carp was originally in northern East Asia and that the species likely underwent a natural post-glacial range expansion from East Asia through Siberia into central Europe. Thus, it is unclear whether Prussian carp first invaded Europe via the Danube River in Romania in 1920, or if they are native to the region (Bănărescu, 1964; Vasile, 2019). What is clear is that in 1954, Prussian carp were introduced to Hungary for aquaculture and subsequently escaped into the Körös and Tisza rivers (Holčík and Žitňan, 1978). Prussian carp entered the middle Danube from the Tisza River and began to expand its range upstream (Holčík and Žitňan, 1978). By the 1970s, Prussian carp had spread into other watersheds, including the Dyje and Morava rivers (Lusková et al., 2010a). It is now genetically confirmed as present in at least 17 European countries (Rylková et al., 2013) as well as in the Middle East (Jawad et al., 2012; Khosravi et al., 2020).

Prussian carp were recently discovered in the Bow River and Red Deer River basins in Alberta in 2006, and in the South Saskatchewan River basin in 2012; these are the first reported occurrences of the species in North America (Elgin et al., 2014). Prussian carp are now widespread and abundant in Alberta (Docherty et al., 2017) and have migrated along the South Saskatchewan River basin as far as Saskatoon, Saskatchewan (Liebenberg, 2020).

2.3 Physiological tolerances

C. auratus and *C. gibelio* are particularly well adapted to physico-chemical conditions that will be promoted by climate change (e.g. warm surface temperatures, increasing salinity, summer hypoxia; (Rahel and Olden, 2008). This may give them a physiological advantage over many native species.

Salinity

In goldfish, tolerance to salinity appears to be based on age; larval fish have limited survival at 4 ppt, whereas YOY goldfish can survive and grow in salinities at least as high as 9ppt (Altinok and Grizzle, 2001; Murai and Andrews, 1977). Salinity tolerance among juvenile and adult goldfish varies across populations, with >80% survival at 10-20 ppt (Küçük, 2013; Schofield et al., 2006). In the laboratory, 33% of adult Prussian carp can survive for 3 months at 15ppt (Elger and Hentschel, 1981), but self-sustaining populations of Prussian carp occur in brackish bodies of water like Shira Lake (15 ppt) (Rogozin et al., 2011) and the Black Sea (18 ppt) (Abramenko, 2000). In the wild, goldfish do not seem to be able to maintain self-sustaining populations in brackish water, although they have been found in estuaries and appear to tolerate salinities up to 21 ppt (Beatty et al., 2017, Henderson and Bird, 2010; Martinho et al., 2007; Tweedley et al., 2017). The lack of self-sustaining populations of goldfish in brackish water may be due to the lower salinity tolerance of juvenile goldfish. Further study of the salinity tolerance of these two species is necessary to understand the differences.

Temperature

Published studies characterize Prussian carp and goldfish as warmwater species with a preference for temperatures near 28°C (Table 1). Goldfish can tolerate temperatures spanning 0.3°C to 43.6°C (Ford and Beitinger, 2005). The tolerance range of Prussian carp is not known, but they have a chronic lethal maximum of 38-39°C (Table 1).

Hypoxia and Desiccation

Both species exhibit a high tolerance for hypoxia (McNeil and Closs, 2007; Suzuki and Kanzaki, 1974; Yao et al., 2020). Goldfish can tolerate dissolved oxygen (DO) levels as low as 0.2–0.8 mg/L in 25°C water (McNeil and Closs, 2007). Prussian carp tolerate DO concentrations as low as 1.5 mg/L in experimental conditions (Yao et al., 2020), but their lower tolerance limit has not yet been specifically tested. Both *Carassius* species are able to survive hypoxia because they have evolved an anaerobic metabolic pathway using alcohol dehydrogenase to produce alcohol as an end product, which is released as waste via the gills (Fagernes et al., 2017). Furthermore, goldfish and Prussian carp are tolerant to several hours of desiccation, with goldfish being able to survive 7 hours out of water (Nakamura, 1995) and Prussian carp able to survive for at least 5 hours out of water (pers. obs.).

2.4 Ecological impacts

Using FISK (Fish Invasiveness Screening Kit – a scoring system designed to conduct risk assessments for non-native fish; Copp et al., 2009) and generic impact scoring systems, *Carassius* spp. have been scored as among the non-native species with the highest impact potential in Europe (Almeida et al., 2013; Veer and Nentwig, 2015). Such impacts include ecosystem engineering, hybridization, disease transmission, and native species declines.

Ecosystem engineering

Introductions of goldfish and Prussian carp are often followed by increases in suspended sediments (turbidity) and concomitant declines in submerged plants (Crivelli, 1995; Richardson et al., 1995). These changes are associated with their feeding activities: both species take up sediment while capturing benthic prey and then spit out the inedible particles into the water column. Plants can be uprooted by the sediment disturbance and are negatively affected by loss of light transparency owing to increased turbidity (Richardson et al., 1995). The per-capita effect of goldfish is such that turbidity generation increases linearly with their abundance (Gonzalez et al., 2008; Richardson and Whoriskey, 1992). However, a few larger goldfish can have twice the effect of many smaller goldfish, even where both groups are of equivalent biomass (Richardson and Whoriskey, 1992). Furthermore, consumption of zooplankton by goldfish and Prussian carp can be substantive enough to cause trophic cascades; released predation pressure on phytoplankton promotes algal blooms, and thus higher turbidity, in lentic systems (Crivelli, 1995; Paulovits et al., 1988). The turbidity effects of goldfish and Prussian carp are less pronounced in rivers, likely because the water current flushes suspended sediment downstream (Ruppert et al., 2017).

Hybridization

Goldfish can hybridize with crucian carp *Carassius carassius* and common carp *Cyprinus carpio* (Hänfling et al., 2005; Haynes et al., 2012). Prussian carp/crucian carp hybrids have also been reported from the Iberian Peninsula and the Baltic Sea (Ribeiro et al., 2015; Wouters et al., 2012). In the UK, where non-native crucian carp are considered a cultural heritage species targeted for conservation (Copp and Sayer, 2020), hybrids of goldfish and crucian carp have been found in all sympatric populations, and consequently, pure crucian carp are declining in such areas. However, backcrossing and introgression of goldfish DNA into crucian carp has occurred in only a few populations (Hänfling et al., 2005). With common carp and goldfish hybrids, some F2 generation and backcrossing has been detected, which could increase genetic diversity in both non-native species and facilitate their invasion (Haynes et al., 2012). For example, goldfish are susceptible to cyprinid herpesvirus 2 and carp are susceptible to cyprinid herpesvirus 3, but their hybrids are resistant to both viruses (Hedrick et al., 2006). Herpesviruses can be used to control non-native populations (Haynes et al., 2012); therefore, resistance to both viruses gained through backcrossing could render goldfish more difficult to control. Prussian carp are also susceptible to cyprinid herpesvirus 2 (Wang et al., 2012) and are capable of hybridizing and backcrossing with common carp (Balashov et al., 2017), so resistance genes likely pass between these two species.

Disease transmission

Introductions of goldfish and Prussian carp often bring pathogens, including monogenean flatworms, trematodes, cestodes, parasitic copepods, myxozoans, various other protists, and viruses, some of which are also non-native taxa (Daghigh Roohi et al., 2014; Davydov et al., 2012; Faillace et al., 2017; Fletcher, 1998; Lewisch et al., 2015; Magalhães, 2006; Martínez-Aquino and Aguirre-Macedo, 2019). Both goldfish and Prussian carp carry commensal organisms that could be pathogenic to resident fishes and amphibians; for example, goldfish carry FV3 ranavirus that can be transmitted to frogs, and Prussian carp are vectors of carp edema virus disease (Faillace et al., 2017; Matras et al., 2019).

Declines in native species

Goldfish compete with various species for food. In laboratory studies, there were indications that goldfish have a competitive advantage over crucian carp and tench (*Tinca tinca*) when food is limited (Magalhães and Jacobi, 2013; Busst and Britton, 2015, 2017; Guo et al., 2017). Goldfish can also contribute to declines in newt and salamander populations through competition for food, preying upon their eggs and interfering with their reproduction (Roy, 1992; Monello and Wright, 2001; Winandy and Denoël, 2013). In the wild, goldfish presence has been associated with a decline in native poolfish (*Empetrichthys latos)* and cichlids (Deacon et al., 1964; Magalhães and Jacobi, 2013), although further study is needed to determine if such declines are caused by antagonistic interactions.

In North America, Prussian carp are considered likely competitors for space and food with native cyprinids, sunfishes, and suckers (Docherty et al., 2017), and indeed following their introduction there have been declines in the abundance of native fishes (Ruppert et al., 2017). Prussian carp have a tendency to become very abundant. For example, in the Dyje River floodplain the species reached densities of 1358 kg/ha, and 0+ fish can reach densities of 45-84 fish/m of shoreline; this large increase in abundance coincided with reductions in native cyprinid populations such that *T. tinca* and *C. carassius* became rare in the pools, oxbows, and woodland lakes (Lusková et al., 2010b). These declines may be the result of competition for food or reproductive interference by Prussian carp, but could also be coincident responses to changes in resources or environmental conditions in the river.

Reproductive interference by Prussian carp has been documented, including, for example, gynogenetic reproduction in which the sperm of other cyprinids is parasitized. Furthermore, Prussian carp can progressively increase their spawning duration to encompass the spawning periods of multiple native fish species, resulting in a decline in spawning, gonadosomatic index and catch per unit effort of native fishes, and a rapid increase in catch per unit effort for Prussian carp (Tarkan et al., 2012).

3. A population-based approach to studying non-native species

Traits of non-native populations can differ from those of conspecific populations in their native range (Bastlová, and Květ, 2002; Erfmeier and Bruelheide, 2005; Zou et al., 2007) as well as across the non-native range (Evangelista et al., 2019; Latorre et al., 2018; Liu et al., 2016; Saulic et al., 2013), owing to phenotypic plasticity (Liu et al., 2016) or contemporary evolution (Evangelista et al., 2019). Emerging invasive populations are capable of rapid adaptation in new environments (Prentis et al., 2008). Recognizing that interpopulation trait variation can be substantial, a valuable but underexploited approach for predicting a non-native species' response to projected future conditions is to collect individuals from multiple conspecific populations from areas where they experience different conditions and test them in a common new environment. This approach can reveal a range of trait values that are possible for the species.

4. Research objectives

For the purposes of risk assessment and management prioritization in an era of climate change, it is necessary to understand the extent to which goldfish and Prussian carp can respectively perform under elevated temperatures. This study will compare the optimal growth temperature and maximum feeding rate of two size classes of juvenile goldfish and Prussian carp at a range of temperatures representative of summer surface temperatures in temperate lakes. Measurements of growth rate can reveal physiological optima, as well as habitat conditions conducive to high abundance. A high growth rate increases the likelihood of overwinter survival in juveniles experiencing their first winter (Conover, 1990), and determines how quickly older juvenile fish will escape predation by gape-size limited predators (Urban, 2007). Higher growth rates likely lead to higher survivorship, which, in turn, can result in a larger reproductive population over time. Maximum feeding rate can indicate how rapidly a fish can reduce prey populations and therefore how intensely they may compete with other species. Since goldfishes generate turbidity and uproot macrophytes through their feeding activities (Richardson et al., 1995), maximum feeding rate might be a proxy indicator for the extent to which they can potentially alter habitat conditions.

My objectives were to use these two metrics of performance and impact to address the following questions:

1. **How does the relationship between growth rate and temperature vary across latitudinally distributed populations?** Here I tested two competing hypotheses. First, I hypothesize that goldfish respond to a cold climate and shorter growing season by maximizing their growth at cooler temperatures, in which case individuals from higher latitudes will have a lower optimal growth temperature compared to those from lower latitudes (Gilchrist, 1995). Alternatively, goldfish could exhibit countergradient variation in growth rate, in which juvenile goldfish from higher latitudes will have a higher overall growth rate to compensate for a shorter growing season (Conover, 1990).

2. **How does the relationship between growth rate and temperatures differ between non-native temperate populations of Prussian carp and goldfish?** Here, I compared one population of Prussian carp to three populations of goldfish to determine whether the traits of the Prussian carp population differ significantly from the trait range of goldfish populations. When Prussian carp and goldfish populations were genetically identified in Europe, goldfish populations were located primarily in southern countries with warmer climates, whereas Prussian carp were found across a broad range of latitudes (Rylková et al., 2013). Therefore, I hypothesized that Prussian carp are better able to adapt or acclimatize to temperate climates, and therefore they should have a higher growth rate than goldfish at cooler temperatures.

3. **What is the relationship between maximum feeding rate and source population, ambient temperature and growth rate?** I determined whether maximum feeding rate has a consistent relationship to growth rate over a set of populations and species. In bioenergetics models, the relationship between maximum feeding rate and temperature is typically modal (Árnason et al., 2009); the initial increase in feeding rate reflects increasing metabolic demands (Cuenco et al., 1985) and the subsequent decline in feeding rate is correlated with reduced attack rates (Englund et al., 2011), which could be attributed to the rising oxygen demands of active foraging. The temperature at which feeding rate is highest occurs at a temperature ~2-3 degrees higher than the optimal growth temperature (Cuenco et al., 1985; Jobling, 1993). However, in these models it is assumed that food is not limited, which results in a higher optimum growth temperature than when feeding is more restricted (Jobling,

1993). In this case, since feeding rate is restricted to 1% of body mass/day, I hypothesized that the optimum growth temperature will be lower, and therefore the maximum feeding rate for a given population will peak, at an ambient temperature 4-6 degrees higher than the optimum growth temperature.

Table 1. Documented measures of thermal tolerance and optima for goldfish (*C. auratus*) and Prussian carp (*C. gibelio*). Abbreviations: OGT= Optimal growth temperature, FTP= final temperature preferendum, OS = optimal spawning temperature, OE= optimal egg development temperature, CTmax= Critical thermal maximum, ULT = upper lethal temperature. Temperatures in brackets denote acclimation temperature. Age and source population for fish are included when information was available.

Species	**OGT**	**FTP**	**OS**	**OE**	**CTmax**	**ULT**
C. auratus	25°C (Audige 1921) juvenile 28°C (Kestemont 1995) larvae	25-29°C (15°C), 29-32°C (20°C) (Roy and Johansen 1970) 40-60mm, pet store 26.0°C-29.7°C (20-22°C) (Reynolds et al. 1978) 40-70mm, pet store 28.1 (Fry 1947) juvenile 24-27°C (Reutter and Herdendorf 1974) adult 24.7-27°C (25°C), 19.2°C (15°C) 6.8-7.9°C (5°C) (Nelson and Prosser 1978) 80-100mm	17-24°C (Gillet et al. 1977) 3-4 years	24-28°C (Battle 1940) Lake Erie	43.6°C (35°C) (Ford and Beitinger, 2005) pet store 36.2°C (17°C), 39.2°C (27°C) (Weatherley, 1970) juvenile, pet store	41°C (Ford and Beitinger 2005) 36.2 (17°C), 39.2 (27°C) (Weatherley, 1970) 29°C (5°C), 41°C (40°C) (Brett 1944)
C. gibelio		27°C-28°C (18-22°C) (Golovanov 2013) Rybinsk Reservoir, 0+ and 1+	15-19°C, 22°C (Alabaster and Lloyd 2013) 12-14°C (Paschos et al. 2004) Greece 13.5-29.4°C (Sasi 2008) Anatolia 11.7 -22°C (Kirankaya and Ekmekci, 2013) Anatolia	20.5°C (Saat and Veersalu, 1996) Estonia		38-39°C (1°C/day increase) (Golovanov 2013) Rybinsk Reservoir, 0+ to 1+

Materials and methods

1. Fish and temperature collection

Fish collection, care, and use for growth and feeding experiments was approved by McGill University's Facility Animal Care Committee (protocol number #2018-8004) following the Guide to the Care and Use of Experimental Animals (Canadian Council on Animal Care 1993). Fish were obtained from goldfish and Prussian carp populations at 5 North American locations (Figure 1). Wild goldfish were collected using fyke and seine nets from populations in Lac des Battures (45.45533, -73.554347) on Nun's Island, Montreal, Quebec, and Cootes Paradise Marsh (43.275392, -79.895289) in the western end of Lake Ontario, Hamilton, Ontario. Wild Prussian carp were collected using fyke, seine and gill nets from Blood Indian Creek Reservoir in southern Alberta (51.248879, -111.209328). Goldfish were driven from Hamilton, Ontario to McGill University in coolers. Oxygen levels were maintained with battery powered aerators, and temperature was checked every 2 hours with a thermometer and reduced when necessary with the addition of ice packs to the water in short intervals (no more than 15 minutes). Prussian carp were packed in a double layer of 3-mm thick plastic bags filled with 3 parts ambient air and one part clean, 18°C water, placed in coolers and transported by airplane from Calgary to Montreal. The total time between packaging at the field site and arrival at the McGill University facility was 30 hours. Prior to transport, Prussian carp were subjected to a 48-hour starvation period to minimize the amount of waste produced during transport. Uniodized salt and Seachem Prime were added to the water at concentrations of 5 ppt and 0.05 ml/L respectively, to reduce stress and the buildup of free ammonia during transport.

Additional goldfish were purchased from two pet stores in Montreal. One population originated from Mt. Parnell Fisheries near Mercersburg, Pennsylvania (39.898493, -77.897507).

The other originated from the Tampa region; the pet store was unwilling to specify the farm from which they came, and the Tampa area does not have any large-scale goldfish producers in the area (Dr. Matthew DiMaggio, University of Florida, personal communication) – however, there is a large-scale farm nearby in Eustis, which is called Blackwater Creek Koi Farms (28.910012, -81.449404). It seems likely that the Tampa fish originated from here. We were able to confirm that the Mt. Parnell population was raised in outdoor ponds. The standard practice in the Tampa area is to raise fish in outdoor ponds ("Tropical Fish Farming in Florida," 2021), and this was the case for goldfish at Blackwater Creek Koi Farms (Rick Gann, Blackwater Creek Koi Farms Inc., personal communication).

Two size classes were collected for each population: a small size class measuring 20-60mm and a larger size class measuring 70-130mm. The small size class was assumed to represent young-of-the-year (YOY), based on reported length-at-age information from the literature (Balik et al., 2004; Lorenzoni et al., 2007; Mugiya and Tanaka, 1992) and owing to the timing of their appearance in the middle of the growing season. The larger size was assumed to represent juveniles that are likely age-1, again based on published studies (Balik et al., 2004; Lorenzoni et al., 2007). However, since we did not verify age using otoliths, we will refer to the two groups as the small and large size classes. At Cootes Paradise Marsh, only fish in the large size class were collected; at the time of sampling in August 2019 no small fish were found, and plans to return to collect them from Cootes Paradise Marsh were cancelled in the summer of 2020 owing to the COVID-19 pandemic. The pet store goldfish were examined because they offered an opportunity to increase the range of the latitudinal gradient in populations. Pet store goldfish also represent potential sources of invasions in the Great Lakes-St Lawrence system, and wild-caught populations have been established for multiple years in this watershed.

We selected one population from each latitude. While it would be beneficial to capture variation in growth and feeding from multiple populations within each latitudinal band, we made the assumption that variation would be greater across latitudes than within. Previous studies on freshwater fish have found significant latitudinal patterns in growth rate both when replication within latitudes was included (Power and McKinley, 1997; Rypel, 2012; Weber et al., 2015) and when there was no replication between latitudes (Yamahira and Conover, 2002).

Ambient temperatures for the growing season were collected for the three wild populations using HOBO MX2201 temperature loggers set at 1m depth. The temperature loggers in Blood Indian Creek Reservoir were stolen in May and replaced with new loggers in early July; the stolen loggers were returned by the end of the summer, so some data was available for May temperatures. As we were unable to obtain temperatures directly from the aquaculture facilities for Tampa and Mercersburg, we used temperatures from the closest USGS monitoring location. For Mercersburg, data were obtained from site 01563200 on the Rays Branch of the Juniata River, where it enters Raystown Lake. For Tampa, data were obtained from site 02264000 on Cypress Creek in Orlando, FL, which was chosen because it is the closest stream gage to Eustis that measures temperature and most closely matches the annual temperature range reported by Blackwater Creek Koi Farm. Annual temperatures taken from rivers tend to differ from temperatures taken from lakes and ponds, because they are influenced by different hydrological processes. However, both lakes and rivers do reflect changes in ambient air temperatures; so in the absence of pond temperature data, river temperatures were used as an approximation of seasonality and temperature in these areas.

2. Growth experiments

Growth experiments were conducted for both size classes to measure performance relative to temperature – which is particularly important for the small size class, as they are dependent on the vegetated littoral zone for food and shelter and thus less able to seek thermal refuge if temperatures range too far outside their optimum. Feeding rate experiments were conducted only on the larger size class, as these were expected to have a greater trophic impact. For all experiments, 6 replicates were tested for each temperature, for a total of 24 fish tested in each population. Experiments were conducted at four temperatures: 18°C, 22°C, 25°C, and 28°C; the first three of these temperatures were chosen based on projected T_{max} surface water temperatures for Lake Superior, Lake Huron, Lake Erie, and Lake Ontario, for the period of 2041-2070 (Trumpickas et al., 2009). The final temperature of 28°C is included to account for the fact that average summer surface temperatures are likely to be higher in shallow marshes, ponds, and the littoral zones of lakes and wetlands – the preferred warm weather habitats for goldfish and Prussian carp (Lorenzoni et al., 2007; Petering and Johnson, 1991; Specziár et al., 1997). Water temperatures for individual tanks varied depending on the position of the tank within the temperature-controlled chamber. Temperature within the tanks did not vary greatly on a temporal scale, so water temperatures were taken once a week and the average temperature was determined from three weekly measurements over the course of the growth period.

After collection from the wild, fish were placed in aquaria in one of four temperature-controlled chambers with a controlled photoperiod (12L:12D). For a minimum of 7 days, the fish were held at a temperature close to the ambient temperature they had experienced prior to collection, to acclimate them to the new environment. After this initial acclimation period, the water temperature was either increased or reduced by 1–2°C/day until fish reached their treatment temperature for the experiment; this incremental rate allows fish to acclimate to new temperatures with minimal stress and mortality (Cocking, 1959). After the treatment temperature was reached, fish were allowed to acclimate for 3 weeks at this temperature before trials began.

After acclimation, each fish was weighed (live mass, to the nearest 0.01g) and then placed in either an individual 19L tank (small fish) or a 76L tank (large fish). Fish remained in their individual tanks for 3 weeks and were fed pellet food at 1% of body weight per day during this period. At the end of the 3-week period, mass was recorded again and the specific growth rate was calculated following methods in (Froese, 2006).

A daily ration of 1% body weight per day was chosen based on previous studies indicating that juvenile fish tend to consume about 0.5–3% of their body weight in food per day (Du et al., 2006; Rybczyk, 2006; Specziár, 2002). We chose a percentage that was on the lower side of this range to account for the fact that a significant portion of wild goldfish and Prussian carp diets is made up of detritus, plants and algae (Richardson et al., 1995; Specziár et al., 1997; Yalcin Ozdilek and Jones, 2014), which are fairly low in protein compared to the pellet food. A small pilot study with Lac des Battures and Cootes Paradise Marsh fish at higher temperatures confirmed that growth would occur with this daily ration.

3. Feeding experiments

After growth trials were completed, the fish were subjected to feeding trials. Individual fish were acclimated to a new 76L tank with no substrate for 48 hours during which they were starved for 24 hours to standardize hunger levels, and then presented with chironomid larvae (*Chironomus* spp., stored in a freezer and subsequently thawed in water for 15min prior to use) for 1hr. The mean mass of each chironomid larvae was 0.003g. At the end of the trial, fish were removed to a recovery tank and the remaining larvae were counted and subtracted from the initial total to determine the number of prey consumed.

The number of larvae provided to each population of fish was initially computed based on a ratio of larvae consumed to the mass of fish, derived from a pilot study with pet store goldfish, where the maximum feeding rate for goldfish at 25°C was determined from a functional response curve. The largest ratio of larvae to mass of fish (~8 larvae/g of fish) was extracted from the functional response experiment. This ratio was multiplied by the mass of the largest fish in a population to determine the number of larvae to be offered to all fish undergoing trials; the rationale for this method is that the amount of food eaten by a fish relative to its mass declines as mass increases, although a linear relationship can be approximated over a small range of mass (Elliott, 1975, 1976). The largest ratio of larvae eaten to mass of fish was typically found in smaller fish, so when that ratio was applied to larger fish within the population, their maximum feeding rate was marginally overestimated. At the same time, since the ratio is multiplied by the mass of the largest fish, the number of larvae used also marginally overestimated the maximum feeding rate of smaller fish.

When this method was applied to the first population tested, the Prussian carp, they were given 150 larvae each, and each fish left at least 50 larvae uneaten, so it was assumed that they were satiated. However, when the first half of the Pennsylvania pet store population was tested with 150 larvae per individual, about one-third of the fish tested consumed all 150 larvae. Therefore, fish within the remaining Pennsylvania pet store population were subsequently given 250 larvae per fish; in this case, each fish left at least 50 larvae uneaten. The first half of this population was held in their individual tanks at temperature and they were tested with 250 larvae two weeks later. An ANCOVA with mass and date as explanatory variables was used to determine that the fish that were tested twice did not differ significantly in the number of larvae eaten relative to the fish that were tested once.

The Pennsylvania pet store fish consumed the largest number of larvae at 22°C, so a new ratio of larvae consumed per gram of fish was derived from the average number of larvae eaten and the average mass of the fish tested at 22°C. This new ratio (14 larvae /g fish) was used to determine the number of larvae offered to the Cootes Paradise, Nun's Island, and Tampa populations. All fish tested in these three populations left at least 50 larvae uneaten, so it was assumed that they had eaten to satiation.

4. Statistical analysis

Variation in growth rate across latitudinally distributed populations (Question 1) and between species (Question 2)

HGAMs (hierarchical generalized additive models) were fit to the data for questions 1 and 2, using the "mgcv" function within the R package mgcv. A Gaussian error distribution with identity link function was used to construct models for questions 1 and 2. Mass, temperature, and population were initially considered as covariates for both models, and species was also considered as a covariate for the model for question 2. Smoothness parameters were estimated with restricted maximum likelihood (REML).

Models were selected by comparing deviance explained, adjusted R^2 and AIC values (Akaike, 1987).

Relation of growth rate to feeding rate across temperatures and populations (Question 3)

A multivariate additive model was constructed with both growth rate and feeding rate as the response variables, using the mgcv package and a multivariate Gaussian distribution with identity link function. The covariates included for growth rate were temperature and population, and for feeding rate they were temperature, population and mass. Models were selected using deviance explained, adjusted R^2 and AIC values. All analyses were conducted in R (version 3.6.3).

Figure 1. Map of collection sites for wild goldfish (Lac des Battures and Cootes Paradise Marsh), Prussian carp (Blood Indian Creek Reservoir) and aquaculture sites for pet store goldfish (Mercersburg, Pennsylvania and Tampa, Florida).

Results

1. Variation in growth rate across latitudinally distributed populations

For both size classes, population and temperature had significant effects on growth rates (Tables 2 & 3, Figs. 2a & b). For the larger size class, mean growth rates for Cootes Paradise Marsh, Lac des Battures and Mercersburg did not differ significantly and were higher than that of the Tampa population. The effect of temperature on growth rate varied significantly between populations and growth was non-linear for all populations except Cootes Paradise Marsh (Table 2, Fig. 2a).

For the smaller size class, mean growth rate was highest in the Mercersburg population and lowest in the Lac des Battures population (Table 3, Fig. 2b). Again, the effect of temperature on growth rate varied significantly between populations. Temperature had a linear negative effect on growth rate for the Mercersburg population, and a non-linear effect on growth rate for the Lac des Battures and Tampa populations.

2. Variation in Prussian carp growth rate

For the larger size class, species, initial mass and temperature all had significant effects on growth rate, with the relationship of growth rate and temperature differing between populations (Table 4, Fig. 3a). Goldfish populations had significantly lower mean growth rates than Prussian carp (Table 4, Fig. 3a), while the effect of temperature on mass-adjusted growth rate varied significantly between populations. Growth was non-linear for all populations except Cootes Paradise Marsh. The highest growth rate within the measured temperature range occurred near 18°C for the Prussian carp and for goldfish populations from Cootes Paradise Marsh and Mercersburg. Growth rate for the Lac des Battures population was highest at 22°C.

The effect of mass on growth rate was non-linear, with intermediate values having a moderately higher growth rate.

For the smaller size class, the model indicated that population, initial mass and temperature all had significant effects on growth rate (Table 5, Fig. 3b). The ‘species’ variable was removed from the model because it did not have a significant effect nor improve the AIC score. Mean growth rate was highest in the Mercersburg population and lowest in the Prussian carp population. The mass-adjusted effect of temperature on growth rate varied significantly between populations. Temperature had a linear negative effect on growth rate for the Prussian carp and Mercersburg populations, and a non-linear effect on growth rate for the Lac des Battures population. Growth rate was highest at 18°C for the Prussian carp and Mercersburg populations, while the Lac des Battures population experienced the highest growth rate near 22°C. The effect of mass on growth rate was non-linear, and fish with lower initial mass had a higher growth rate.

3. Relationship between growth and feeding rates across populations and temperatures

Growth rate was significantly affected by population and by temperature, whereas feeding rate was significantly affected by population, temperature and mass (Figure 4, Table 6). The correlation between the two response variables, feeding rate and growth rate, was 0.00052. Mean growth rate was highest for the Prussian carp population, and lowest for the Tampa goldfish population. The relationship of growth rate to temperature varied by population, and was non-linear for all populations except that of Cootes Paradise Marsh.

Mean feeding rate was highest for the Mercersburg population and lowest for the Prussian carp population, and its relationship to temperature varied by population. The Lac des

Battures and Prussian carp populations had a positive, linear relationship between feeding rate and temperature, whereas the Tampa population had a negative, linear relationship between feeding rate and temperature. The relationship was non-linear (and varied greatly) for the Mercersburg population, and was not significant for the Cootes Paradise Marsh population. Across all populations, feeding rate was positively and linearly related to fish mass.

4. Temperature data

Temperature were coolest and the growing season was shortest in Blood Indian Creek Reservoir, where the Prussian carp were collected. Growing season length and average temperatures increased from north to south (Appendix: Figure A1), with temperatures 18°C and above occurring from early July to late August in Blood Indian Creek Reservoir, from late May to early September in Lac des Battures, from at least early June to mid-September in Cootes Paradise Marsh, and from early June to late October in Mercersburg. In Orlando, temperatures above 18°C occurred starting in February and lasting until late November.

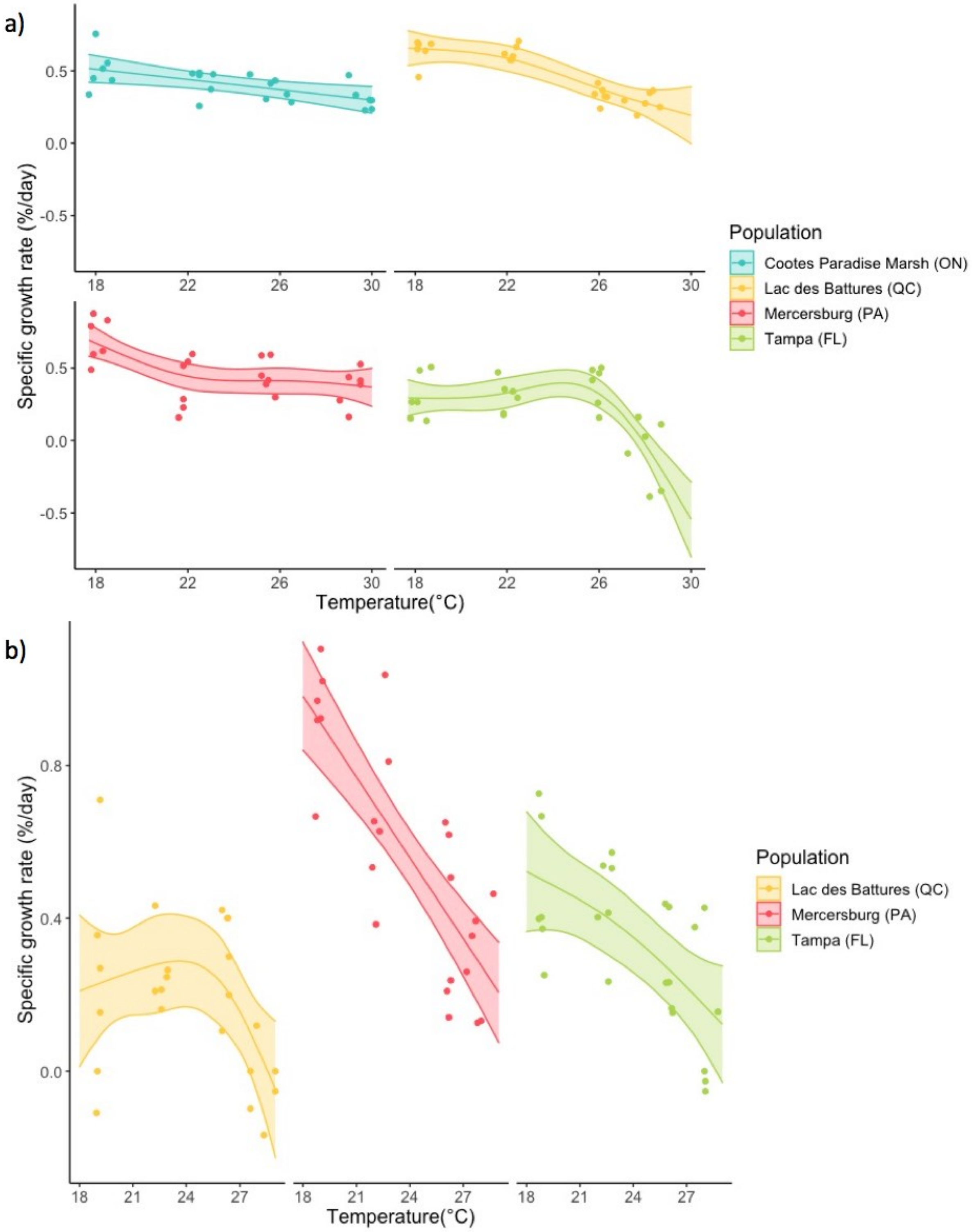

Figure 2. Growth rate functions and partial residuals for the a) large size class and b) small size class from North American goldfish populations across a latitudinal gradient. Shaded regions represent the 95% confidence intervals.

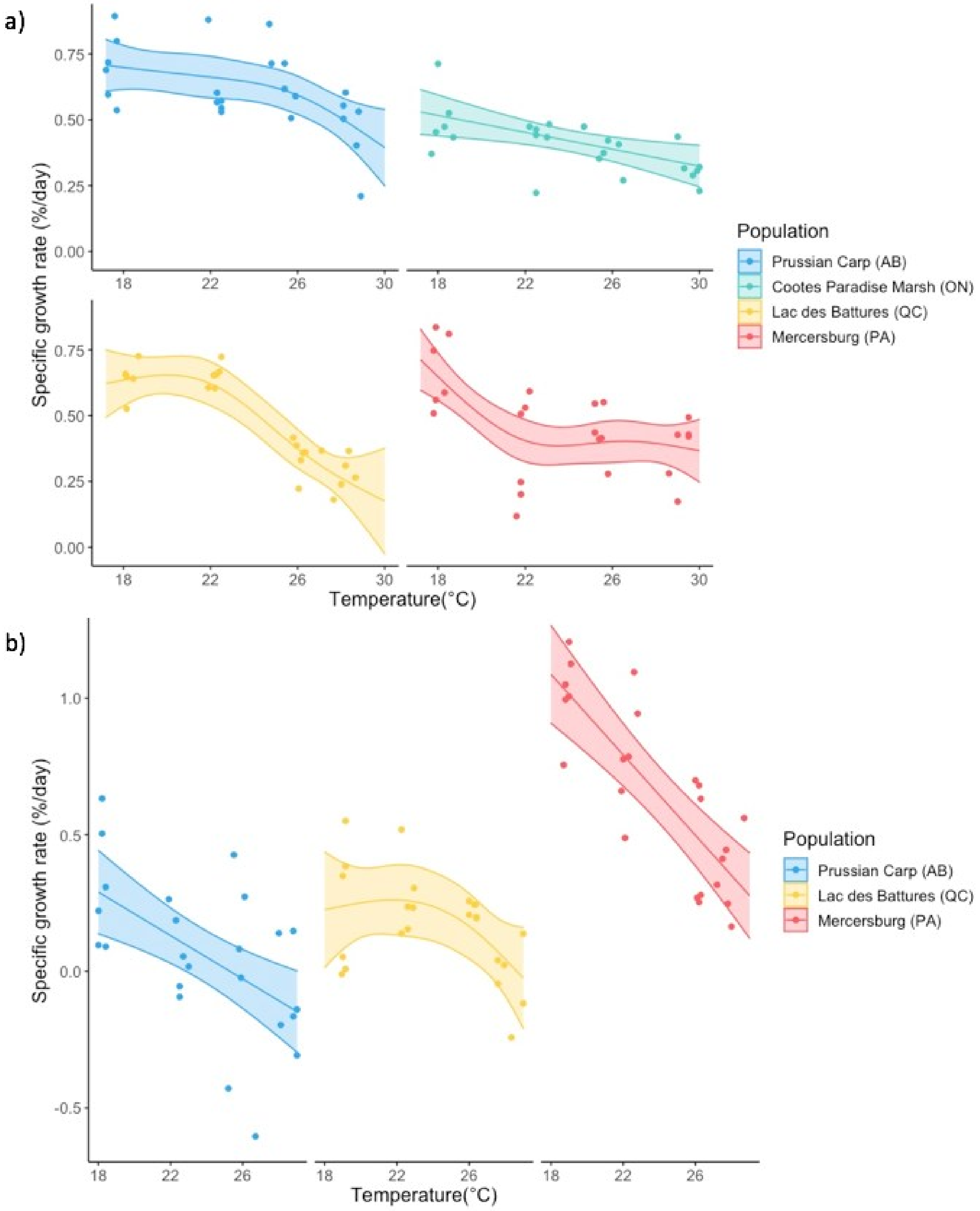

Figure 3. Mass-adjusted growth rate functions and partial residuals for the a) large size class and b) small size class from the temperate Prussian carp and goldfish populations. Shaded regions represent the 95% confidence intervals.

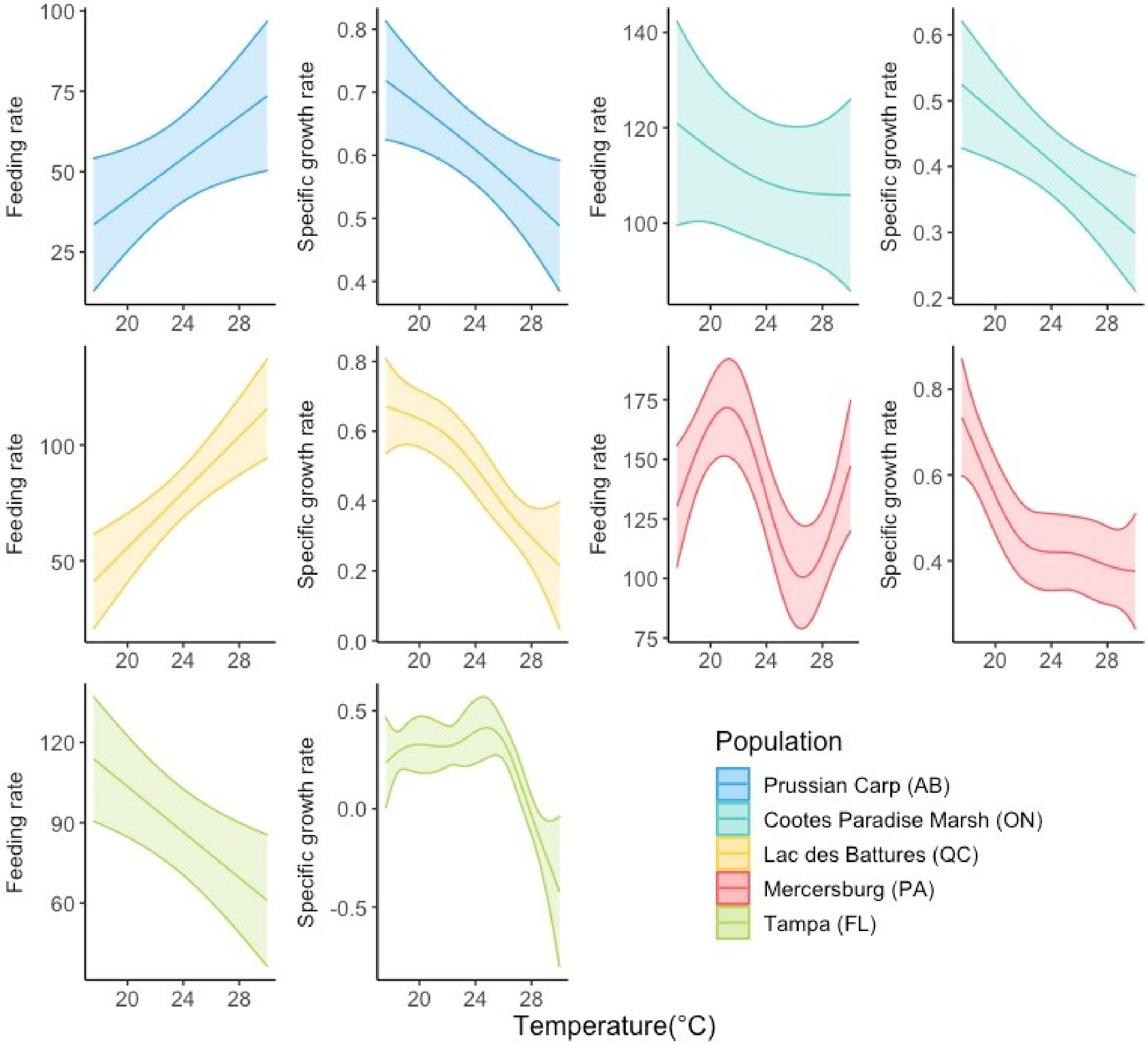

Figure 4. Growth rate and mass-adjusted feeding rate functions for the large size class of all populations. Feeding rate units are in number of bloodworms/hour and growth rate units are in %/day. Shaded regions represent the 95% confidence intervals for each function.

Table 2. Summary of GAM model (identity link, restricted maximum likelihood, thin plate smoothing splines) fitted to latitudinal goldfish population growth rates for the large size class. Adjusted R^2 for this model is 0.621. Degrees of freedom is abbreviated as df. There are separate smooth terms that describe the relationship of temperature to growth rate for each population. The effective degrees of freedom are a measure of how flexible or rigid a smooth term is, with 1 representing a perfectly linear relationship and higher numbers representing increasingly flexible smooth terms. The p value for each smooth represents a zero effect test and it is <0.05 when the relationship between the x and y variable is significantly different from a line with a slope of 0.

Parameter	Estimate	Standard error	*t*	*P*
Cootes Paradise Marsh (ON) (Intercept)	0.409	0.027	15.344	<0.0001
Lac des Battures (QC)	0.057	0.038	1.491	0.1397
Mercersburg (PA)	0.065	0.038	1.718	0.0895
Tampa (FL)	-0.222	0.038	-5.785	<0.0001
Smooth terms	**Effective df**	**Reference df**	***F***	***P***
Temp: Cootes Paradise Marsh (ON)	1.000	1.000	7.854	0.006292
Temp: Lac des Battures (QC)	1.960	2.338	14.305	<0.0001
Temp: Mercersburg (PA)	2.268	2.627	7.826	<0.000608
Temp:Tampa (FL)	2.980	2.840	14.803	<0.0001

Table 3. Summary of GAM model (identity link, restricted maximum likelihood, thin plate smoothing splines) fitted to latitudinal goldfish population growth rates across temperatures for the small size class. Adjusted R^2 for this model is 0.625. Degrees of freedom is abbreviated as df. There are separate smooth terms that describe the relationship of temperature to growth rate for each population.

Parameter	Estimate	Standard error	*t*	*P*
Lac des Battures (QC) (Intercept)	0.195	0.037	5.346	<0.0001
Mercersburg (PA)	0.371	0.052	7.186	<0.0001
Tampa (FL)	0.138	0.052	2.680	0.00934

Smooth terms	Effective df	Reference df	*F*	*P*
Temp: Lac des Battures (QC)	2.229	2.613	2.703	0.04052
Temp: Mercersburg (PA)	1.000	1.000	45.417	<0.0001
Temp:Tampa (FL)	1.368	1.633	8.720	0.00322

Table 4. Summary of GAM model (identity link, restricted maximum likelihood, thin plate smoothing splines) fitted to growth rates of temperate goldfish and Prussian carp populations for the large size class. Adjusted R^2 for this model is 0.589. Degrees of freedom is abbreviated as df. There are separate smooth terms that describe the relationship of temperature to growth rate for each population. In addition there is a smooth term for the relationship of the mass of the fish to the growth rate, and a smooth term that acts as a random effect for population.

Parameter	Estimate	Standard error	*t*	*P*
Goldfish (Intercept)	0.450	0.022	20.662	<0.0001
Prussian carp	0.156	0.045	3.476	0.000813
Smooth terms	**Effective df**	**Reference df**	***F***	***P***
Temp: Cootes Paradise Marsh (ON)	1.000	1.000	8.251	0.005167
Temp: Lac des Battures (QC)	2.325	2.678	17.815	<0.0001
Temp: Mercersburg (PA)	2.460	2.784	7.282	0.000229
Temp: Prussian carp (AB)	2.022	2.360	5.304	0.003887
Mass of fish (g)	2.476	2.800	4.488	0.024418
Population	1.135	2.000	1.361	0.091227

Table 5. Summary of GAM model (identity link, restricted maximum likelihood, thin plate smoothing splines) fitted to growth rates of temperate goldfish and Prussian carp populations for the small size class. Adjusted R^2 for this model is 0.589. Degrees of freedom is abbreviated as df. There are separate smooth terms that describe the relationship of temperature to growth rate for each population. In addition, there is a smooth term for the relationship of the mass of the fish to the growth rate.

Parameter	Estimate	Standard error	*t*	*P*
Prussian carp (AB) (Intercept)	0.031	0.053	0.578	0.566
Lac des Battures (QC)	0.112	0.061	1.830	0.072
Mercersburg (PA)	0.690	0.102	6.729	<0.0001

Smooth terms	Effective df	Reference df	*F*	*P*
Temp: Prussian carp (AB)	1.000	1.000	13.639	0.000461
Temp: Lac des Battures (QC)	1.794	2.175	2.469	0.079958
Temp: Mercersburg (PA)	1.000	1.000	34.761	<0.0001
Mass of fish (g)	1.489	1.794	3.936	0.018363

Table 6. Summary of multivariate normal GAM model (restricted maximum likelihood) fitted to growth rates and feeding rates across temperature for all populations (large size class). Degrees of freedom is abbreviated as df. This model explains 67.10% of the deviance in the data. There are two response variables: growth rate and feeding rate. For each response variable there are separate smooth terms that describe the relationship of temperature to growth rate for each population. For the feeding rate response variable there is also a smooth term for the relationship of the mass of the fish to the feeding rate.

	Parametric coefficients				Nonlinear effects				
Parameter	Estimate	Standard error	*z value*	*P*	Parameter	Effective df	Reference df	$\chi2$	*P*
Growth rate									
Blood Indian Creek Reservoir (AB) (Intercept)	0.608	0.025	23.905	<0.0001	Temp: Blood Indian Creek Reservoir (AB)	1.111	1.211	8.664	0.007478
Cootes Paradise Marsh (ON)	-0.197	0.036	-5.482	<0.0001	Temp: Cootes Paradise Marsh (ON)	1.000	1.000	8.624	0.003319
Lac des Battures (QC)	-0.134	0.036	-3.701	0.000215	Temp: Lac des Battures (QC)	1.859	2.251	33.854	<0.0001
Mercersburg (PA)	-0.132	0.036	-3.634	0.000279	Temp: Mercersburg (PA)	2.408	2.818	23.109	0.000112
Tampa Bay (FL)	-0.409	0.039	-10.613	<0.0001	Temp:Tampa Bay (FL)	3.443	4.041	48.510	>0.0001
Feeding rate									
Blood Indian Creek Reservoir (AB) (Intercept)	53.437	6.766	7.897	<0.0001	Temp: Blood Indian Creek Reservoir (AB)	1.000	1.000	5.221	0.022323
Cootes Paradise Marsh (ON)	58.195	8.066	7.214	<0.0001	Temp: Cootes Paradise Marsh (ON)	1.280	1.495	1.511	0.473184
Lac des Battures (QC)	24.247	8.403	2.886	0.003908	Temp: Lac des Battures (QC)	1.000	1.000	19.196	<0.0001
Mercersburg (PA)	80.981	8.550	9.472	<0.0001	Temp: Mercersburg (PA)	2.862	2.985	18.899	0.000501
Tampa Bay (FL)	35.071	12.983	2.701	0.006909	Temp:Tampa Bay (FL)	1.000	1.000	8.782	0.003044
					Mass (g)	1.000	1.000	22.466	<0.0001

Discussion

1. Variation in growth rate across latitude

Goldfish from high-latitude populations were hypothesized to have either a higher overall growth rate or a lower optimal growth temperature than goldfish from low-latitude populations. The larger size class from these populations seem to exhibit both patterns. Overall, mean growth rate in the larger size class appeared to follow countergradient variation and had a positive relationship with latitude. The three high-latitude populations had higher mean growth rates than the Tampa population. Countergradient variation is predicted to occur when populations at high latitudes experience a shorter growing season than those at low latitudes (Conover and Present, 1990). A higher growth rate at high latitudes is necessary to attain a similar size to fish in lower latitudes that have a longer growing season. In juvenile fish, selection pressure to attain a large size at the end of the growing season is likely due to size-selected overwinter mortality (Conover, 1990) and perhaps also to escape predation by gape-limited predators (Urban, 2007) .

The low-latitude Tampa population maintained a high growth rate from 18°C to 25°C, but rapidly declined at warmer temperatures. The large-size goldfish from high-latitude populations had a higher growth rate at cooler temperatures, but sustained moderate growth at warmer temperatures. This indicates some adaptation, or acclimation, to cooler temperatures in high-latitude populations. However, high-latitude goldfish likely sustain growth at all temperatures in the range measured because temperatures can vary widely during the growing season (Appendix: Figure A1) and fish need to be able to maintain growth throughout the entire short season. By contrast, the Tampa population experiences temperatures within a range where growth is possible for 11 months of the year (Appendix: Figure A1). At Blackwater Creek Koi Farms, the annual temperature range that the goldfish experience is between 10°C and 27°C.

Based on temperatures from Cypress Creek, there is only short period of the year where temperatures are above 25°C, so the goldfish may adapt behaviourally to seek out ideal growing temperatures, and avoid these temporary warm temperatures that impose higher metabolic costs.

Countergradient variation in growth rate is not immediately evident in the smaller size class from these populations. Goldfish from the high-latitude (Lac des Battures) population had the lowest mean growth rate, whereas those from the mid-latitude (Mercersburg) population had the highest mean growth rate, and the subtropical (Tampa) population fell in between. In the field, high-latitude populations have exhibited low growth rates in some studies (Modde and Scalet, 1985; Villeneuve et al., 2005), possibly due to lower temperatures or lower food availability. In this experiment, although all populations experienced the same temperature and food rations, the growth rate was lower for the high-latitude population. At first glance, it would appear that younger goldfish from higher latitudes have a lower growth efficiency – that is, they are less efficient at converting the energy they consume into somatic tissue. This would be surprising, because if this size class exhibits countergradient variation in growth like the larger size class, then high-latitude populations would be expected to have a higher growth efficiency (Billerbeck et al., 2000). However, this effect could be related to the ration that the fish were given; 1% of body weight in food rations is a fairly restricted ration for this size of fish (El-Shamy, 1978), and fish at higher latitudes may be able to compensate for a low growth efficiency during the growing season by increasing their consumption rate. In fact, there may be a trade-off occurring here. Billerback et al. (2000) suggest that fish that have high growth efficiency when food is abundant would be favoured in the north, where they can take advantage of peak phytoplankton blooms in spring and late summer. In southern locations, peaks in productivity are less pronounced and temperatures are adequate for growth year-round, so southern fish could be better adapted to food-limited situations. While this hypothesis was not supported in the system studied by Billerback et al. (2000), it offers an explanation for the trend in mean growth rate being reversed for the two size classes: 1% of body mass per day of a high protein food is a reasonable ration for larger juvenile fish, but very limited for small fish (El-Shamy, 1978; Lantry and Stewart, 1993). For example, Rodde et al. (2020) found that populations of sea bass that grew faster on high rations lost more weight on low rations. In both the Billerback et al. (2000) and Rodde et al. (2020) studies, growth efficiency effects were similar across multiple size classes. Assuming this relationship of growth efficiency and ration holds true for the goldfish, we would expect that if ration was increased for the smaller size class, then the Lac des Battures population would have the highest growth rate; similarly, if ration for the larger fish was reduced, the Lac des Battures population would have the lowest growth rate.

The highest growth rate for the Lac des Battures population occurred at 23-24°C, according to our model. Growth rates were fairly high from 18°C to 23°C, before declining and becoming negative near 28°C. Growth rate was highest at 18°C and negatively correlated with temperature for the Mercersburg and Tampa populations. The negative correlation was steeper in the Mercersburg population. It is surprising that the growth rate of the low-latitude Tampa population peaked at a cooler temperature than the high-latitude Lac des Battures population, since this is contrary to the hypothesis that high-latitude populations will have the highest growth rate at low temperatures. This is also the opposite of the trend seen in the larger size class, where growth rate peaked at 22°C for Lac des Battures and at 25°C for Tampa. It should be noted that young goldfish are less mobile than older juvenile goldfish and tend to remain in the warm waters of the littoral zone for most of the growing season, whereas older juvenile goldfish move in and out of the littoral zone depending on the conditions (pers. obs.).

The optimal spawning temperature for goldfish is reported as 17–24°C (Gillet et al., 1977). Goldfish spawning occurs during the spring season in central Florida, and 25–50mm fish are available by April (Rick Gann, Blackwater Creek Koi Farms, personal communication). Goldfish take about 50 days before fish start to reach a length of 30mm (Mugiya and Tanaka, 1992), which suggests that spawning begins as early as mid-February. In Lac des Battures, spawning likely takes place from May to July; the timing of appearance of 20–30mm YOY goldfish in early July corroborates this timeline (personal observations). While goldfish are batch spawners, the largest reproductive effort tends to occur during the first spawning event (Becker, 1983). In Tampa, most fish would hatch in mid-February to March, and young goldfish would experience temperatures in the range of 18–24°C for 3 months before temperatures began to consistently remain above 25°C in late June. We observed a threshold between 26°C and 28°C, where growth was consistently positive at 26°C, but half of the population experienced negative growth at 28°C. Blackwater Creek Koi Farms confirmed that water temperatures range between 10°C and 27°C during the year, so temperatures above 27°C are outside of the range of experience and thus could be difficult for these fish to handle. By contrast, in Lac des Battures, the largest spawning event would take place in early to mid-May. In May and June, temperatures rise rapidly and remain between 22°C and 25°C for most of the short growing season before dropping rapidly below 15°C by the end of September (Appendix: Figure A1). It is advantageous for the young fish in Lac des Battures to be able to grow more rapidly at warmer temperatures, which they experience most frequently in the littoral zone where food is abundant. In Mercersburg, peak spawning likely also occurs in May, when temperatures reach 17°C (Appendix: Figure A1). Temperatures reach 30°C in Pennsylvania during the summer and do not drop below 18°C until the beginning of November. Growth rates in the Pennsylvania population remain high (above 0.5% per day) up to about 24°C. There is a long period of the growing season during which temperatures are between 18 and 24°C, allowing an opportunity for rapid growth. Moderate growth still occurs during the warmest part of the growing season when temperatures are above 25°C.

2. Growth rate of Prussian Carp

Prussian carp were hypothesized to have a greater ability to adapt to temperate climates than goldfish, and thus would exhibit higher growth rates at cool temperatures. Prussian carp and temperate goldfish populations had their highest growth rates at cooler temperatures, suggesting that these populations are adjusted to temperate climates, although it is unclear from these experiments whether the change in growth rate is due to environmental cues during development or to genetic adaptation. Growth rates for the larger size class of Prussian carp remained fairly high for all temperatures tested, and the mean growth rate was significantly higher than for the temperate goldfish populations, suggesting that the Prussian carp population was more efficient in converting the same energy ration into somatic growth. If so, this could translate into an advantage in the wild, where faster growing fish would escape gape-limited predators earlier in their lifespan.

However, our Prussian carp population originated from a location that was 6° higher in latitude than the most northern goldfish population we tested (Lac des Battures). This suggests the alternate possibility that the observed differences in overall growth rate could be due to countergradient variation; the shorter growing season in Blood Indian Creek Reservoir could select for a faster growth rate for predator evasion before temperatures drop too low. Further experiments should compare growth rates of sympatric populations of goldfish and Prussian carp.

For the smaller size class, Prussian carp had the lowest overall mean growth rate, followed by Lac des Battures and Mercersburg, respectively, although the difference in growth rate between Prussian carp and Lac des Battures was not significant. It might appear that young Prussian carp are less efficient in converting a restricted ration of food into somatic growth compared to the goldfish populations; however, when factoring in latitudinal differences, mean growth rate in the Prussian carp follows the trend seen amongst the smaller size class of goldfish populations from different latitudes.

Young Prussian carp had their highest growth rate at 18°C, and according to the model growth became negative at temperatures warmer than ~26°C. This is not surprising, given that temperatures in the littoral zone of Blood Indian Creek Reservoir, the site of the source population, exceeded 20°C for only about a month of the growing season and peaked at an average daily temperature of 23°C (Appendix: Figure A1). However, it is surprising that the larger size class was able to grow well at 28°C, a temperature that they do not experience in the reservoir. Overall, there does not seem to be a clear difference between the Prussian carp and goldfish populations in either size class that cannot be explained by differences in latitude and climate.

3. Relationship between growth and feeding rate across populations and temperatures

We hypothesized that the peak in feeding rate would occur at a temperature 4–6 degrees higher than the peak in growth rate. The rationale is provided by various studies indicating that the temperature at which feeding rate is maximal occurs at a higher temperature than that for optimal growth, and growth optimum occurs at a lower temperature when feeding is restricted (Cuenco et al., 1985; Jobling, 1993; Oyugi et al., 2012), which should widen the gap between the two measurements. The results from some of the populations fit this hypothesis, although the gap between the two optima was at least 10°C. For both the Lac des Battures and Prussian carp populations, there was a negative correlation between feeding rate and growth rate, and their optimum growth temperature was likely at 18°C or below, whereas the peak for maximum feeding rate was at 28°C or higher. However, the hypothesis was not supported by the other populations. For the goldfish from Cootes Paradise Marsh, feeding rate did not change significantly from 18°C to 28°C, but there was a shallow but significant decline in growth rate, suggesting that the Cootes Paradise population was tolerant of a broad range of temperatures. Feeding rate for the Tampa population declined from 18°C onward, which suggests that the peak maximum feeding rate occurred at 18°C or lower; however, growth rate increased slightly from 18°C to 25°C before declining sharply, suggesting that the optimal growth temperature would be higher than that of the peak feeding rate for this population, contrary to what is typically reported in the literature. The lack of a relationship between growth and feeding rates, as well as the multiple peaks in feeding rate, for the Pennsylvania population are intriguing and suggest that further exploration of how metabolic rate and oxygen demand change with temperature for this population is merited.

The differing relationships between feeding rate and growth rate in these populations could be explained by the length of the growing season and the seasonality of food availability at different latitudes. Although fish at higher latitudes are expected to perform best at cooler temperatures, they must remain active foragers during the period of peak productivity in late spring and summer. The higher temperatures drive increased metabolism and therefore increased feeding rates to maintain growth. The steady feeding rate across all temperatures for the Cootes Paradise Marsh population suggests that this population may not experience as large an increase in metabolic energy demand with increasing temperatures, likely because they encounter warm temperatures more frequently than higher latitude populations and need to be active at those temperatures to continue growing throughout the summer.

In Florida, temperatures are high enough that growth can occur for 11 months of the year, and yet feeding rate for the Tampa population declined from 18°C to 28°C and growth declined at temperatures above 25°C. This population comes from an aquaculture facility where the maximum temperature reached is 26°C, so the decline in growth at higher temperatures is logical. However, it is harder to explain the decrease in feeding rate with temperatures, which suggests that the peak feeding rate is at 18°C or lower. The relationship between temperature and feeding rate appeared to change with latitude. High-latitude populations like the Prussian carp and Lac des Battures experienced a positive relationship between temperature and feeding rate, indicating a peak feeding rate at 28°C or higher, the Cootes Paradise population demonstrated no significant change in feeding rate, and the Tampa population experienced a negative relationship between feeding rate and temperature.

Overall mean feeding rate also declined with increasing latitude. The exception to this was the Tampa population, which had an intermediate feeding rate. Growth rate at a restricted ration increased with increasing latitude, with the exception of a very elevated growth rate in the Pennsylvania population. Goldfish at high latitudes appear to require less energy but are able to grow faster, implying they have a higher growth efficiency. This implies that they require a smaller amount of energy to support metabolic activities, leaving more energy available for growth. If this is true, we might expect to see that fish from higher latitudes have a lower standard metabolic rate. This relationship was observed in freshwater walleye populations: higher metabolic rate and feeding rates were found in low latitude populations (Galarowicz and Wahl, 2003). The opposite trend was found in several marine fish species (Arnott et al., 2006; Gardiner et al., 2010).

Finally, the Environmental Matching Hypothesis proposes that the per capita effects of an invader decline as habitat conditions move further from its physiological (growth) optimum (Iacarella et al., 2015). If temperature is the limiting abiotic constraint, we would expect the per capita effect, reflected by foraging efficiency, to be correlated with the optimal growth temperature. This is not apparent in our results. However, Iacarella et al. (2015) noted that the optimal growth temperature is often considered to be overestimated when measured in the lab. The optimal growth temperature is dependent on the ration (Jobling, 1993), and in the lab fish are fed *ad libitum*; in the wild, food is more limited and so the optimum is expected to be lower.

We used a more restricted feeding regime and indeed found that the highest growth rates occurred at much lower temperatures than what was previously reported in the literature. However, maximum feeding rate is, by definition, measured under conditions of unrestricted food availability. If a fish can consume only 1% of its body weight in prey in a day and we assume a Type II functional response (Holling, 1965), then the maximum feeding rate would likely rise with temperature until it reached the maximum possible feeding rate of a 1% ration. This would create an asymptote in feeding rate across a range of temperatures instead of a single peak. This asymptote at lower densities can be observed in previous studies of the effect of temperature on functional response (Iacarella et al., 2015; Oyugi et al., 2012). The maximum trophic impact would then occur wherever the optimal growth temperature and the asymptote coincided. For example, for the Prussian carp population, the average mass of the fish was approximately 15g. The average mass of the bloodworms was 0.003g. At this mass, 50 worms comprise 1% of their weight in food, so the maximum trophic impact for this population might occur somewhere near 22°C, as feeding rate rises to an asymptote and growth rate is still high. As the ration of available food increases, the optimal growth temperature would increase and the asymptote in the maximum feeding rate curve would narrow, so the temperature at which maximum impact occurred would increase. The optimum growth temperature observed when rations are provided *ad libitum* would therefore represent the highest temperature at which maximum impact occurs for that population.

4. Implications and caveats

Overall, goldfish populations seem to follow countergradient variation in growth and a latitudinal pattern in which mean feeding rate declined with increasing latitude. The high-latitude Prussian carp population appeared to fit within the latitudinal patterns observed in the goldfish populations.

There were no differences found between Prussian carp and goldfish that cannot be explained by the latitudinal provenance of their respective populations. The Prussian carp population did not deviate from the growth and feeding patterns observed in the goldfish populations. However, to test differences between the species, sympatric populations need to be compared. In this case, since Prussian carp appear to be a new introduction to North America and have a limited distribution thus far, it would be easier to compare populations across a latitudinal gradient in Europe, where they have a longer invasion history and are more likely to have acclimated or adapted to the local climate.

Both the Prussian carp population and most of the goldfish populations appear to have adjusted to the temperature and seasonality of the area from which they were collected, which is perhaps surprising given that some of these populations have very recent introduction histories. Prussian carp were discovered in Alberta in 2006, although it is not clear when they were introduced. Lac des Battures was created in the 1990s, so the goldfish population became established at some point within the past ~25 years; their presence was confirmed as early as 2005 (Élise Bélanger, Nature-Action Québec, personal communication). The Cootes Paradise population was established in the 1960s (Whillans, 1979), and the Pennsylvania goldfish breeding farm began operations in 1923. Blackwater Creek Koi Farms in Central Florida closed its doors to outside fish in 2002. It is possible that the source populations for these species had a similar evolutionary climate history; but it seems likely that all these populations have, to some extent, adjusted their growth and feeding patterns to their respective environments. We do not know whether these changes are genetic or phenotypic, although the short time period for some populations (the Prussian carp and Lac des Battures populations, in particular) suggests a strong phenotypic component.

One of the caveats to these experiments was that the average mass of the larger size class for the Tampa population was much lower than the average mass of the other populations, although there was overlap between the Lac des Battures, Cootes Paradise Marsh and Tampa populations. This could mean that the effects of population and mass are partially confounded. A GAM of the effect of mass and temperature on specific growth rate for all fish of both size classes from Tampa indicated that the effect of mass on growth was negative. If the growth of larger fish from this population was measured, it is likely that their growth rate would be lower and the countergradient variation in growth rate would be more pronounced. In the multivariate model of growth and feeding rate, Tampa fish consumed an intermediate amount of prey compared to the other populations. The amount of food consumed was found to increase with size. From the literature we know that while the amount of food consumed increases with size, the relative amount of food eaten (consumption/mass) decreases with increasing mass (Cuenco et al., 1985). Therefore, if larger Tampa fish were tested, we might expect them to consume less after adjusting for mass. However, initial linear additive models with growth rate or feeding rate as response variables and with temperature, mass, and population as covariates, found that the variance inflation factor was very low for all three variables in both models, indicating that mass and population have a low correlation.

Another caveat for these experiments was the use of pet store populations to characterize growth and feeding rate patterns in southern climates. Since these populations likely experience some conditions that are different from wild populations, they may not be truly representative of how goldfish respond to climate. For example, the Pennsylvania population may have an unusually high growth rate because high growth rates have been artificially selected for over the years. However, in discussion with aquaculture farms and pet store vendors we confirmed that these populations experience ambient temperatures year-round, which means they must respond to the same constraints of growing season length and extreme temperatures. It is also important to characterize these farmed populations because they represent potential source populations for introductions around North America. Goldfish from warm climates like Tampa are regularly shipped to pet stores and wholesalers in cold climates, and pet release continues to be a main source of goldfish introductions (Gertzen et al., 2008; Maceda-Veiga et al., 2013). Although these goldfish from warm climates may be poorly adapted to conditions in higher latitudes at present, as the climate warms they could have an advantage over native species that are still adapted to short growing seasons and cold temperatures.

Finally, while we made the assumption that the variation between latitudes would be larger than the variation within latitudes, stronger inferences could be made if there was replication of populations within a latitudinal band. Unfortunately, time constraints and logistics did not allow for this replication to occur in this study. Similar countergradient patterns in growth rate have been documented in other freshwater fishes along a latitudinal gradient in studies that also lacked replication between populations. Nonetheless, multi-population comparisons of thermal metrics should be done across contrasting latitudes. However, for Prussian carp, the invasion history in North America is so recent that different populations in Alberta and Saskatchewan may not be independent; a study of European populations would be necessary to examine latitudinal differences.

General conclusions

Goldfish and Prussian carp populations exhibit latitudinal patterns in growth and feeding rate, despite recent invasion histories in some populations. The results demonstrate that goldfish are a flexible species able to rapidly adapt or acclimate to temperature and seasonality within a short period of time after introduction. Prussian carp also have a broad tolerance to a range of conditions and seem to have adjusted to the local climate in Alberta; without knowing the source of this introduction, we cannot determine the extent to which they had to adjust their growth and feeding. Countergradient variation in growth rate indicates that seasonality is an important constraint on the life history of juvenile goldfish, although high growth rates at cooler temperatures in high-latitude populations indicate that the range of temperatures experienced in the growing season is also important.

Future research should examine to what extent the patterns seen in these experiments are genetic or environmental. A useful direction of study would be to examine the rate of adaptation and acclimation to changing temperature and growing season length in goldfish, to have a better idea of how flexible their response to climate change might be. As Prussian carp continue to spread south from Saskatchewan and Alberta, there is also an ideal opportunity to observe how the species responds to warmer climates. A reciprocal transplant and common garden experiment that included Prussian carp populations along a gradient from the invasion front to the original discovery site could help determine whether local adaptation is occurring at each site and how quickly this adaptation is occurring relative to time since invasion (cf. Colautti and Barrett, 2013).

The results of this study do not appear to support the Environmental Matching Hypothesis (Iacarella et al. 2015). However, an important factor that was not considered in the hypothesis (when temperature is the abiotic constraint) was the effect of food availability on the relationship of growth and feeding rate to temperature. Future experiments could examine whether manipulating prey density as well as temperature affects the temperature at which maximum trophic impact would occur. Daily feeding rate could be measured during the period of the growth experiment by collecting uneaten food each day. As primary productivity levels change with climate change, food availability could play an important role alongside temperature in governing the variation in impact of non-native species (Lehman, 2002; O'Beirne et al., 2017).

The rapid adaptation or acclimation by goldfish and Prussian carp indicate that disturbances caused by ongoing climate change could provide an opportunity for both species to thrive due to reduced competition from more vulnerable native species that are not able to adapt as quickly. Both species are currently increasing their abundance (and presumably impacts) on ecosystems in North America. It is crucial to continue monitoring these populations to better understand how to prevent and mitigate their impacts under climate change.

References

Abramenko, M.I., 2000. Goldfish *Carassius auratus gibelio* (Bloch) occur in the Russian area of the Black Sea. Dokl. Biol. Sci. 374, 502–505.

Akaike, H., 1987. Factor analysis and AIC. Psychometrika 52, 317–332. https://doi.org/10.1007/BF02294359

Alabaster, J.S., Lloyd, R.S., 2013. Water quality criteria for freshwater fish. Elsevier.

Allan, J.D., McIntyre, P.B., Smith, S.D.P., Halpern, B.S., Boyer, G.L., Buchsbaum, A., Burton, G.A., Campbell, L.M., Chadderton, W.L., Ciborowski, J.J.H., Doran, P.J., Eder, T., Infante, D.M., Johnson, L.B., Joseph, C.A., Marino, A.L., Prusevich, A., Read, J.G., Rose, J.B., Rutherford, E.S., Sowa, S.P., Steinman, A.D., 2012. Joint analysis of stressors and ecosystem services to enhance restoration effectiveness. PNAS 201213841. https://doi.org/10.1073/pnas.1213841110

Almeida, D., Ribeiro, F., Leunda, P.M., Vilizzi, L., Copp, G.H., 2013. Effectiveness of FISK, an invasiveness screening tool for non-native freshwater fishes, to perform risk identification assessments in the Iberian Peninsula. Risk Anal 33, 1404–1413. https://doi.org/10.1111/risa.12050

Altinok, I., Grizzle, J.M., 2001. Effects of brackish water on growth, feed conversion and energy absorption efficiency by juvenile euryhaline and freshwater stenohaline fishes. J. Fish Biol. 59, 1142–1152. https://doi.org/10.1111/j.1095-8649.2001.tb00181.x

Apalikova, O.V., Eliseikina, M.G., Kovalev, M.Yu., Brykov, V.A., 2008. Collation of data on the ploidy levels and mitochondrial DNA phylogenetic lineages in the silver crucian carp *Carassius auratus gibelio* from Far Eastern and Central Asian populations. Russ. J Genet. 44, 873–880. https://doi.org/10.1134/S1022795408070168

Árnason, T., Björnsson, B., Steinarsson, A., Oddgeirsson, M., 2009. Effects of temperature and body weight on growth rate and feed conversion ratio in turbot (*Scophthalmus maximus*). Aquaculture 295, 218–225. https://doi.org/10.1016/j.aquaculture.2009.07.004

Arnott, S.A., Chiba, S., Conover, D.O., 2006. Evolution of intrinsic growth rate: metabolic costs drive trade-offs between growth and swimming performance in *Menidia menidia*. Evolution 60, 1269–1278. https://doi.org/10.1111/j.0014-3820.2006.tb01204.x

Audige, M.P., 1921. Sur la croissance des poissons maintenus en milieu de temperature constante. Compte rendu des séances de la Societe de Biologie, *172*, 287-289.

Balashov, D.A., Recoubratsky, A.V., Duma, L.N., Ivanekha, E.V., Duma, V.V., 2017. Fertility of triploid hybrids of Prussian carp (*Carassius gibelio*) with common carp (*Cyprinus carpio* L.). Russ. J. Dev. Biol. 48, 347–353. https://doi.org/10.1134/S1062360417050034

Balik, İ., Özkök, R., Çubuk, H., Uysal, R., 2004. Investigation of some biological characteristics of the silver crucian carp, *Carassius gibelio* (Bloch 1782) population in Lake Eğirdir. Turk. J. Zool. 28, 19–28.

Balon, E.K., 2004. About the oldest domesticates among fishes. J. Fish. Biol. 65, 1–27. https://doi.org/10.1111/j.0022-1112.2004.00563.x

Banarescu, P., 1964. Pisces—Osteichthyes (Pesti ganoizi si ososi) [Pisces—Osteichthyes (ganoid and teleost fish)]. Vol. XIII. Fauna Republicii Populare Romine. Bucuresti: Acad. Rep. Pop. Romine.

Bastlová, D., Květ, J., 2002. Differences in dry weight partitioning and flowering phenology between native and non-native plants of purple loosestrife (*Lythrum salicaria* L.). Flora 197, 332–340. https://doi.org/10.1078/0367-2530-00049

Battle, H.I., 1940. The embryology and larval development of the goldfish (*Carassius auratus* L.) from Lake Erie. Ohio J. Sci. 40, 82-93.

Beatty, S.J., Allen, M.G., Whitty, J.M., Lymbery, A.J., Keleher, J.J., Tweedley, J.R., Ebner, B.C., Morgan, D.L., 2017. First evidence of spawning migration by goldfish (*Carassius auratus*); implications for control of a globally invasive species. Ecol. Freshw. Fish 26, 444–455. https://doi.org/10.1111/eff.12288

Becker, G.C., 1983. Fishes of Wisconsin. University of Wisconsin press 1052.

Billerbeck, J.M., Schultz, E.T., Conover, D.O., 2000. Adaptive variation in energy acquisition and allocation among latitudinal populations of the Atlantic silverside. Oecologia 122, 210–219. https://doi.org/10.1007/PL00008848

Brett, J.R., 1944. Some lethal temperature relations of Algonquin Park fishes. Publ. Ont. Fish. Res. Lab, Univ. Toronto Series 63, 1–49.

Busst, G.M.A., Britton, J.R., 2015. Quantifying the growth consequences for crucian carp *Carassius carassius* of competition from non-native fishes. Ecol. Freshw. Fish 24, 489–492. https://doi.org/10.1111/eff.12155

Busst, G.M.A., Britton, J.R., 2017. Comparative trophic impacts of two globally invasive cyprinid fishes reveal species-specific invasion consequences for a threatened native fish. Freshw. Biol. 62, 1587–1595. https://doi.org/10.1111/fwb.12970

Cocking, A.W., 1959. The effects of high temperatures on roach (*Rutilus rutilus*) : II. The effects of temperature increasing at a known constant rate. J. Exp. Biol. 36, 217–226.

Colautti, R.I., Barrett, S.C.H., 2013. Rapid adaptation to climate facilitates range expansion of an invasive plant. Science 342, 364–366. https://doi.org/10.1126/science.1242121

Connelly, N.A., O'Neill, C.R., Knuth, B.A., Brown, T.L., 2007. Economic impacts of zebra mussels on drinking water treatment and electric power generation facilities. Environ. Manage. 40, 105–112. https://doi.org/10.1007/s00267-006-0296-5

Conover, D.O., 1990. The relation between capacity for growth and length of growing season: evidence for and implications of countergradient variation. Trans. Am. Fish. Soc. 119, 416–430.

Conover, D.O., Present, T.M.C., 1990. Countergradient variation in growth rate: compensation for length of the growing season among Atlantic silversides from different latitudes. Oecologia 83, 316–324.

Copp, G.H., Vilizzi, L., Mumford, J., Fenwick, G.V., Godard, M.J., Gozlan, R.E., 2009. Calibration of FISK, an invasiveness screening tool for nonnative freshwater fishes. Risk Analysis 29, 457–467. https://doi.org/10.1111/j.1539-6924.2008.01159.x

Copp, G.H., Sayer, C.D., 2020. Demonstrating the practical impact of publications in Aquatic Conservation – The case of crucian carp *Carassius carassius* in the East of England. Aquat. Conserv. 30, 1753–1757. https://doi.org/10.1002/aqc.3353

Craggs, S. 2016, January 7. Discarded goldfish are taking over Hamilton's harbour. CBC News. Available from https://www.cbc.ca/news/canada/hamilton/headlines/discarded-goldfish-are-taking-over-hamilton-s-harbour-1.3394203 [accessed 14 January 2019].

Crivelli, A.J., 1995. Are fish introductions a threat to endemic freshwater fishes in the northern Mediterranean region? Biol. Conserv. 2, 311–319.

Cuenco, M.L., Stickney, R.R., Grant, W.E., 1985. Fish bioenergetics and growth in aquaculture ponds: I. Individual fish model development. Ecol. Modell. 27, 169–190. https://doi.org/10.1016/0304-3800(85)90001-8

Daghigh Roohi, J., Sattari, M., Nezamabadi, H., Ghorbanpour, N., 2014. Occurrence and intensity of parasites in Prussian carp, *Carassius gibelio* from Anzali wetland, southwest Caspian Sea. Iran. J. Fish. Sci. 13, 276–288.

Davydov, O.N., Kurovskaya, L.Y., Temnikhanov, Y.D., Neborachek, S.I., 2012. Parasites of some invasive fishes of the fresh water. Hydrobiol. J. 48, 72–84.

De Kay, J.E., Seward, W.H., 1842. Zoology of New York; or, The New York Fauna; comprising detailed descriptions of all the animals hitherto observed within the state of New York, with brief notices of those occasionally found near its borders, and accompanied by appropriate illustrations. W. & A. White & J. Visscher :, Albany : https://doi.org/10.5962/bhl.title.2079

Deacon, J.E., Hubbs, C., Zahuranec, B.J., 1964. Some effects of introduced fishes on the native fish fauna of southern Nevada. Copeia 1964, 384–388. https://doi.org/10.2307/1441031

Docherty, C., Ruppert, J., Rudolfsen, T., Hamann, A., Poesch, M., 2017. Assessing the spread and potential impact of Prussian Carp *Carassius gibelio* (Bloch, 1782) to freshwater fishes in western North America. BioInvasions Rec. 6, 291–296. https://doi.org/10.3391/bir.2017.6.3.15

Du, Z.-Y., Liu, Y.-J., Tian, L.-X., He, J.-G., Cao, J.-M., Liang, G.-Y., 2006. The influence of feeding rate on growth, feed efficiency and body composition of juvenile grass carp (*Ctenopharyngodon idella*). Aquacult. Int. 14, 247–257. https://doi.org/10.1007/s10499-005-9029-7

Dudgeon, D., Arthington, A.H., Gessner, M.O., Kawabata, Z.-I., Knowler, D.J., Lévêque, C., Naiman, R.J., Prieur-Richard, A.-H., Soto, D., Stiassny, M.L.J., Sullivan, C.A., 2006.

Freshwater biodiversity: importance, threats, status and conservation challenges. Biol. Rev. 81, 163–182. https://doi.org/10.1017/S1464793105006950

Elger, M., Hentschel, H., 1981. The glomerulus of a stenohaline fresh-water teleost, *Carassius auratus gibelio*, adapted to saline water. Cell Tissue Res. 220, 73–85. https://doi.org/10.1007/BF00209967

Elgin, E., Tunna, H., Jackson, L., 2014. First confirmed records of Prussian carp, *Carassius gibelio* (Bloch, 1782) in open waters of North America. BioInvasions Rec. 3, 275–282. https://doi.org/10.3391/bir.2014.3.4.09

Elliott, J.M., 1975. The growth rate of brown trout (*Salmo trutta* L.) fed on maximum rations. J. Anim. Ecol. 44, 805–821. https://doi.org/10.2307/3720

Elliott, J.M., 1976. The energetics of feeding, metabolism and growth of brown trout (*Salmo trutta* L.) in relation to body weight, water temperature and ration size. J. Anim. Ecol. 45, 923–948. https://doi.org/10.2307/3590

El-Shamy, F.M., 1978. Dynamics of feeding and growth of bluegill (*Lepomis macrochirus*) in Lake Wingra and Lake Mendota, Wisconsin. Hydrobiologia 60, 113–124. https://doi.org/10.1007/BF00163176

Emery, L., 1985. Review of fish species introduced into the Great Lakes, 1819-1974 (Technical Report No. 45). Great Lakes Fisheries Commission.

Englund, G., Öhlund, G., Hein, C.L., Diehl, S., 2011. Temperature dependence of the functional response. Ecol. Lett. 14, 914–921. https://doi.org/10.1111/j.1461-0248.2011.01661.x

Erfmeier, A., Bruelheide, H., 2005. Invasive and native *Rhododendron ponticum* populations: is there evidence for genotypic differences in germination and growth? Ecography 28, 417–428. https://doi.org/10.1111/j.0906-7590.2005.03967.x

Evangelista, C., Cucherousset, J., Lecerf, A., 2019. Contrasting ecological impacts of geographically close invasive populations. Oecologia 189, 529–536. https://doi.org/10.1007/s00442-018-04333-5

Fagernes, C.E., Stensløkken, K.-O., Røhr, Å.K., Berenbrink, M., Ellefsen, S., Nilsson, G.E., 2017. Extreme anoxia tolerance in crucian carp and goldfish through neofunctionalization of duplicated genes creating a new ethanol-producing pyruvate decarboxylase pathway. Scientific Reports. https://doi.org/10.1038/s41598-017-07385-4

Faillace, C.A., Lorusso, N.S., Duffy, S., 2017. Overlooking the smallest matter: viruses impact biological invasions. Ecol. Lett. 20, 524–538. https://doi.org/10.1111/ele.12742

Fletcher, A.S., 1998. A parasite-host checklist for Monogenea from freshwater fishes in Australia, with comments on biodiversity. Syst. Parasitol. 41, 159–168. https://doi.org/10.1023/A:1006039101265

Ford, T., Beitinger, T.L., 2005. Temperature tolerance in the goldfish, *Carassius auratus*. J. Therm. Biol. 30, 147–152. https://doi.org/10.1016/j.jtherbio.2004.09.004

Froese, R., 2006. Cube law, condition factor and weight–length relationships: history, meta-analysis and recommendations. J. Appl. Ichthyol. 22, 241–253. https://doi.org/10.1111/j.1439-0426.2006.00805.x

Fry, F. E. J. 1947. Effects of the environment on animal activity. Publ. Ontario Fish. Res. Lab. 55,1-62.

Galarowicz, T.L., Wahl, D.H., 2003. Differences in growth, consumption, and metabolism among walleyes from different latitudes. Trans. Am. Fish. Soc. 132, 425–437. https://doi.org/10.1577/1548-8659(2003)132<0425:DIGCAM>2.0.CO;2

Gallardo, B., Clavero, M., Sánchez, M.I., Vilà, M., 2016. Global ecological impacts of invasive species in aquatic ecosystems. Glob. Chang. Biol. 22, 151–163. https://doi.org/10.1111/gcb.13004

Gardiner, N.M., Munday, P.L., Nilsson, G.E., 2010. Counter-gradient variation in respiratory performance of coral reef fishes at elevated temperatures. PLoS One 5, e13299. https://doi.org/10.1371/journal.pone.0013299

Gertzen, E., Familiar, O., Leung, B., 2008. Quantifying invasion pathways: fish introductions from the aquarium trade. Can. J. Fish. Aquat. Sci. 65, 1265–1273. https://doi.org/10.1139/F08-056

Gilchrist, G.W., 1995. Specialists and generalists in changing environments. I. Fitness landscapes of thermal sensitivity. Am. Nat. 146, 252–270. https://doi.org/10.1086/285797

Gillet, C., Billard, R., Breton, B., 1977. Effets de la température sur le taux de gonadotropine plasmatique et la spermatogenèse du poisson rouge *Carassius auratus*. Can. J. Zool. 55, 242–245. https://doi.org/10.1139/z77-028

Golovanov, V.K., 2013. Ecophysiological patterns of distribution and behavior of freshwater fish in thermal gradients. J. Ichthyol. 53, 252–280. https://doi.org/10.1134/S0032945213030016

Gonzalez, A., Lambert, A., Ricciardi, A., 2008. When does ecosystem engineering cause invasion and species replacement? Oikos 117, 1247–1257. https://doi.org/10.1111/j.0030-1299.2008.16419.x

Guo, Z., Sheath, D., Trigo, F.A., Britton, J.R., 2017. Comparative functional responses of native and high-impacting invasive fishes: impact predictions for native prey populations. Ecol. Freshw. Fish 26, 533–540. https://doi.org/10.1111/eff.12297

Halas, D., Lovejoy, N., Mandrak, N., 2018. Undetected diversity of goldfish (*Carassius* spp.) in North America. Aquat. Invasions 13, 211–219. https://doi.org/10.3391/ai.2018.13.2.03

Hänfling, B., Bolton, P., Harley, M., Carvalho, G.R., 2005. A molecular approach to detect hybridisation between crucian carp (*Carassius carassius*) and non-indigenous carp species (*Carassius* spp. and *Cyprinus carpio*). Freshw. Biol. 50, 403–417. https://doi.org/10.1111/j.1365-2427.2004.01330.x

Havens, K.E., Beaver, J.R., 2013. Zooplankton to phytoplankton biomass ratios in shallow Florida lakes: an evaluation of seasonality and hypotheses about factors controlling variability. Hydrobiologia 703, 177-187.

Haynes, G.D., Gongora, J., Gilligan, D.M., Grewe, P., Moran, C., Nicholas, F.W., 2012. Cryptic hybridization and introgression between invasive cyprinid species *Cyprinus carpio* and *Carassius auratus* in Australia: implications for invasive species management. Anim. Conserv. 15, 83–94. https://doi.org/10.1111/j.1469-1795.2011.00490.x

Hedrick, R.P., Waltzek, T.B., McDowell, T.S., 2006. Susceptibility of Koi Carp, Common Carp, Goldfish, and Goldfish × Common Carp Hybrids to Cyprinid Herpesvirus-2 and Herpesvirus-3. J. Aquat. Anim. Health 18, 26–34. https://doi.org/10.1577/H05-028.1

Hellmann, J.J., Byers, J.E., Bierwagen, B.G., Dukes, J.S., 2008. Five potential consequences of climate change for invasive species. Conserv. Biol. 22, 534–543. https://doi.org/10.1111/j.1523-1739.2008.00951.x

Henderson, P.A., Bird, D.J., 2010. Fish and macro-crustacean communities and their dynamics in the Severn Estuary. Mar. Pollut. Bull. The Severn Estuary and Bristol Channel: A 25 year critical review 61, 100–114. https://doi.org/10.1016/j.marpolbul.2009.12.017

Hessenauer, J.-M., Wills, T., 2016. Status of the fisheries in Michigan waters of Lake Erie and Lake St. Clair, 2016. Lake St. Clair Fisheries Research Station.

Holčík, J., Žitňan, R., 1978. On the expansion and origin of *Carassius auratus* in Czechoslovakia. Folia Zool. 27, 279–288.

Holling, C.S., 1965. The functional response of predators to prey density and its role in mimicry and population regulation. Mem. Ent. Soc. Can. 97, 5–60. https://doi.org/10.4039/entm9745fv

Iacarella, J.C., Dick, J.T.A., Alexander, M.E., Ricciardi, A., 2015. Ecological impacts of invasive alien species along temperature gradients: testing the role of environmental matching. Ecol. Appl. 25, 706–716. https://doi.org/10.1890/14-0545.1

Jang, M.-H., Kim, J.-G., Park, S.-B., Jeong, K.-S., Cho, G.-I., Joo, G.-J., 2002. The current status of the distribution of introduced fish in large river systems of South Korea. Int. Rev. Hydrobiol. 87, 319–328. https://doi.org/10.1002/1522-2632(200205)87:2/3<319::AID-IROH319>3.0.CO;2-N

Jawad, L., Al-Faisal, A., Al-Mukhtar, M., 2012. Presence of the non-indigenous fish species, gibel carp, *Carassius gibelio* (Family: Cyprinidae) in Basrah province freshwater systems, Iraq. Water Res. Manage. 2, 41–44.

Jeffries, D.L., Copp, G.H., Maes, G.E., Handley, L.L., Sayer, C.D., Hänfling, B., 2017. Genetic evidence challenges the native status of a threatened freshwater fish (*Carassius carassius*) in England. Ecol. Evol. 7, 2871–2882. https://doi.org/10.1002/ece3.2831

Jiang, F.-F., Wang, Z.-W., Zhou, L., Jiang, L., Zhang, X.-J., Apalikova, O.V., Brykov, V.A., Gui, J.-F., 2013. High male incidence and evolutionary implications of triploid form in northeast Asia *Carassius auratus* complex. Mol. Phylogenet. Evol. 66, 350–359. https://doi.org/10.1016/j.ympev.2012.10.006

Jobling, M., 1993. Bioenergetics: feed intake and energy partitioning, in: Rankin, J.C., Jensen, F.B. (Eds.), Fish Ecophysiology, Chapman & Hall Fish and Fisheries Series. Springer Netherlands, Dordrecht, pp. 1–44. https://doi.org/10.1007/978-94-011-2304-4_1

Kalous, L., Bohlen, J., Rylková, K., Petrtýl, M., 2012. Hidden diversity within the Prussian carp and designation of a neotype for *Carassius gibelio* (Teleostei: Cyprinidae). Ichthyol. Explor. Freshw. 21, 11–18.

Kalous, L., Rylková, K., Bohlen, J., Šanda, R., Petrtýl, M., 2013. New mtDNA data reveal a wide distribution of the Japanese ginbuna *Carassius langsdorfii* in Europe. J. Fish Biol. 82, 703–707. https://doi.org/10.1111/j.1095-8649.2012.03492.x

Kessel, N.V., Dorenbosch, M., Boer, M.R.M.D., Leuven, R.S.E.W., Velde, G.V.D., 2011. Competition for shelter between four invasive gobiids and two native benthic fish species. Curr. Zool. 57, 844–851. https://doi.org/10.1093/czoolo/57.6.844

Kestemont, P., 1995. Influence of feed supply, temperature and body size on the growth of goldfish *Carassius auratus* larvae. Aquaculture 136, 341–349. https://doi.org/10.1016/0044-8486(95)00060-7

Khosravi, M., Abdoli, A., Ahmadzadeh, F., Saberi-Pirooz, R., Rylková, K., Kiabi, B.H., 2020. Toward a preliminary assessment of the diversity and origin of Cyprinid fish genus *Carassius* in Iran. J. Appl. Ichthyol. 36, 422–430. https://doi.org/10.1111/jai.14039

Kırankaya, Ş., 2013. Life-history traits of the invasive population of Prussian carp, *Carassius gibelio* (Actinopterigi: Cypriniformes: Cyprinidae), from Gelingüllü Reservoir, Yozgat, Turkey. Acta Ichthyol. Piscat. 43, 31–40. https://doi.org/10.3750/AIP2013.43.1.05

Kottelat, M., Freyhof, J., 2007. Handbook of European freshwater fishes. Kottelat, Cornol and Freyhof, Berlin.

Küçük, S., 2013. The effects of salinity on growth of goldfish, *Carassius auratus* and crucian carp, *Carassius carassius*. Afr. J. Biotechnol. 12. https://doi.org/10.4314/ajb.v12i16.

Lantry, B.F., Stewart, D.J., 1993. Ecological energetics of rainbow smelt in the Laurentian Great Lakes: An interlake comparison. Trans. Am. Fish. Soc. 122, 951–976. https://doi.org/10.1577/1548-8659(1993)122<0951:EEORSI>2.3.CO;2

Latorre, D., Masó, G., Hinckley, A., Verdiell-Cubedo, D., Tarkan, A.S., Vila-Gispert, A., Copp, G.H., Cucherousset, J., da Silva, E., Fernández-Delgado, C., García-Berthou, E., Miranda, R., Oliva-Paterna, F.J., Ruiz-Navarro, A., Serrano, J.M., Almeida, D., 2018. Inter-population variability in growth and reproduction of invasive bleak *Alburnus alburnus* (Linnaeus, 1758) across the Iberian Peninsula. Mar. Freshwater Res. 69, 1326. https://doi.org/10.1071/MF17092

Lehman, J.T., 2002. Mixing patterns and plankton biomass of the St. Lawrence Great Lakes under climate change scenarios. J. Great Lakes Res. 28, 583–596. https://doi.org/10.1016/S0380-1330(02)70607-2

Lewisch, E., Soliman, H., Schmidt, P., El-Matbouli, M., 2015. Morphological and molecular characterization of *Thelohanellus hoffmanni* sp. nov. (Myxozoa) infecting goldfish *Carassius auratus auratus*. Dis. Aquat. Org. 115. https://doi.org/10.3354/dao02870

Liasko, R., Koulish, A., Pogrebniak, A., Papiggioti, O., Taranenko, L., Leonardos, I., 2011. Influence of environmental parameters on growth pattern and population structure of *Carassius auratus gibelio* in Eastern Ukraine. Hydrobiologia 658, 317–328. https://doi.org/10.1007/s10750-010-0502-6

Liebenberg, M. 2020, July 22. Prussian carp continues invasion of river system in Saskatchewan. Prairie Post. Available from https://www.prairiepost.com/saskatchewan/prussian-carp-continues-invasion-of-river-system-in-saskatchewan/article_ad049846-cc43-11ea-a671-cf9ffbcb815e.html [accessed 23 September 2020].

Liu, W., Maung-Douglass, K., Strong, D.R., Pennings, S.C., Zhang, Y., 2016. Geographical variation in vegetative growth and sexual reproduction of the invasive *Spartina alterniflora* in China. J. Ecol. 104, 173–181. https://doi.org/10.1111/1365-2745.12487

Liu, X.-L., Li, X.-Y., Jiang, F.-F., Wang, Z.-W., Li, Z., Zhang, X.-J., Zhou, L., Gui, J.-F., 2017. Numerous mitochondrial DNA haplotypes reveal multiple independent polyploidy origins of hexaploids in *Carassius* species complex. Ecol. Evol. 7, 10604–10615. https://doi.org/10.1002/ece3.3462

Lorenzoni, M., Corboli, M., Ghetti, L., Pedicillo, G., Carosi, A., 2007. Growth and reproduction of the goldfish *Carassius auratus*: a case study from Italy, in: Gherardi, F. (Ed.), Biological Invaders in inland waters: profiles, distribution, and threats, invading nature - Springer series in invasion ecology. Springer Netherlands, Dordrecht, pp. 259–273. https://doi.org/10.1007/978-1-4020-6029-8_13

Ludyanskiy, M.L., McDonald, D., MacNeill, D., 1993. Impact of the zebra mussel, a bivalve I invader: *Dreissena polymorpha* is rapidly colonizing hard surfaces throughout waterways of the United States and Canada. Bioscience 43, 533–544. https://doi.org/10.2307/1311948

Luo, J., Gao, Y., Ma, W., Bi, X. -Y., Wang, S. -Y., Wang, J., Wang, Y. -Q., Chai, J., Du, R., Wu, S. -F., Meyer, A., Zan, R. -G., Xiao, H., Murphy, R.W., Zhang, Y. -P., 2014. Tempo and mode of recurrent polyploidization in the *Carassius auratus* species complex

(Cypriniformes, Cyprinidae). Heredity (Edinb.) 112, 415–427. https://doi.org/10.1038/hdy.2013.121

Luo, J., Zhang, Y.-P., Zhu, C.-L., Xiao, W.-H., Huang, S.-Y., 1999. Genetic diversity in crucian carp (*Carassius auratus*). Biochem. Genet. 37, 267–279. https://doi.org/10.1023/A:1018751008848

Lusková, V., 2004. Changes of ploidy and sexuality status of '*Carassius auratus*' populations in the drainage area of the River Dyje (Czech Republic). Ecohydrol. Hydrobiol. 4, 165–171.

Lusková, V., Lusk, S., Halačka, K., Vetešník, L., 2010. *Carassius auratus gibelio*—The most successful invasive fish in waters of the Czech Republic. Russ. J. Biol. Invasions 1, 176–180. https://doi.org/10.1134/S2075111710030069

Maceda-Veiga, A., Escribano-Alacid, J., de Sostoa, A., García-Berthou, E., 2013. The aquarium trade as a potential source of fish introductions in southwestern Europe. Biol. Invasions 15, 2707–2716. https://doi.org/10.1007/s10530-013-0485-0

Mada, Y., Hiroshima U., Umino, T., Arai, K., 2001. Genetic evidence of gynogenetic reproduction and clonal nature of triploid and tetraploid cyprinid fish *Carassius langsdorfii* collected from the Kami-dokanbori moat in the Imperial Palace [Japan]. Nippon Suisan Gakkai Shi 67, 217-221.

Magalhães, A.L.B., 2006. First record of lernaeosis in a native fish species from a natural environment in Minas Gerais state, Brazil. Pan American Journal of Aquatic Sciences 1, 8–10.

Magalhães, A.L.B., Jacobi, C.M., 2013. Asian aquarium fishes in a Neotropical biodiversity hotspot: impeding establishment, spread and impacts. Biol. Invasions. 15, 2157–2163. https://doi.org/10.1007/s10530-013-0443-x

Martínez-Aquino, A., Aguirre-Macedo, L., 2019. Metacercariae of *Haplorchis pumilio* (Looss, 1896) in *Carassius auratus* (Linnaeus, 1758) from Mérida City, Yucatán, Mexico: a co-introduced parasite. Bioinvasions Rec. 8, 712–728. https://doi.org/10.3391/bir.2019.8.3.29

Martinho, F., Leitão, R., Viegas, I., Dolbeth, M., Neto, J.M., Cabral, H.N., Pardal, M.A., 2007. The influence of an extreme drought event in the fish community of a southern Europe temperate estuary. Est. Coast. Shelf Sci. 75, 537–546. https://doi.org/10.1016/j.ecss.2007.05.040

Matras, M., Stachnik, M., Borzym, E., Maj-Paluch, J., Reichert, M., 2019. Potential vector species of carp edema virus (CEV). J. Fish Dis. 42, 959–964. https://doi.org/10.1111/jfd.13000

Mcneil, D.G., Closs, G.P., 2007. Behavioural responses of a south-east Australian floodplain fish community to gradual hypoxia. Freshw. Biol. 52, 412–420. https://doi.org/10.1111/j.1365-2427.2006.01705.x

Modde, T., Scalet, C.G., 1985. Latitudinal growth effects on predator-prey interactions between largemouth bass and bluegills in ponds. N. Am. J. Fish. Man. 5, 227–232. https://doi.org/10.1577/1548-8659(1985)5<227:LGEOPI>2.0.CO;2

Monello, R.J., Wright, R.G., 2001. Predation by goldfish (*Carassius auratus*) on eggs and larvae of the eastern long-toed salamander (*Ambystoma macrodactylum columbianum*). J. Herpetol. 35, 350–353. https://doi.org/10.2307/1566132

Mugiya, Y., Tanaka, S., 1992. Otolith development, increment formation, and an uncoupling of otolith to somatic growth rates in larval and juvenile goldfish. Nippom Suisan Gakkai Shi. 58, 845–851. https://doi.org/10.2331/suisan.58.845

Murai, T., Andrews, J.W., 1977. Effects of salinity on the eggs and fry of the golden shiner and goldfish. Prog. Fish-Cult. 39, 121–122. https://doi.org/10.1577/1548-8659(1977)39[121:EOSOTE]2.0.CO;2

Nakamura, K., 1995. Physiological characteristics of goldfish endurability in air. Fish. Sci. 61, 455–457. https://doi.org/10.2331/fishsci.61.455

Nalepa, T.F., Schloesser, D.W., 1992. Zebra Mussels biology, impacts, and control. CRC Press.

Nelson, D.O., Prosser, C.L., 1979. Effect of preoptic lesions on behavioral thermoregulation of green sunfish, *Lepomis cyanellus*, and of goldfish, *Carassius auratus*. J. Comp. Physiol. 129, 193–197. https://doi.org/10.1007/BF00657653

Nico, L., Schofield, P., Larson, J., Makled, T., Fusaro, A., 2018. *Carassius auratus* (Linnaeus, 1758): U.S. Geological Survey, Nonindigenous Aquatic Species Database, Gainesville, FL [WWW Document]. URL http://nas.er.usgs.gov/queries/FactSheet.asp?speciesID=508 (accessed 12.12.18).

Nico, L.G., Fuller, P.L., 1999. Spatial and temporal patterns of nonindigenous fish introductions in the United States. Fisheries 24, 16–27. https://doi.org/10.1577/1548-8446(1999)024<0016:SATPON>2.0.CO;2

O'Beirne, M.D., Werne, J.P., Hecky, R.E., Johnson, T.C., Katsev, S., Reavie, E.D., 2017. Anthropogenic climate change has altered primary productivity in Lake Superior. Nat. Commun. 8, 15713. https://doi.org/10.1038/ncomms15713

Oyugi, D.O., Cucherousset, J., Baker, D.J., Britton, J.R., 2012. Effects of temperature on the foraging and growth rate of juvenile common carp, *Cyprinus carpio*. J. Therm. Biol. 37, 89–94. https://doi.org/10.1016/j.jtherbio.2011.11.005

Pagnucco, K.S., Maynard, G.A., Fera, S.A., Yan, N.D., Nalepa, T.F., Ricciardi, A., 2015. The future of species invasions in the Great Lakes-St. Lawrence River basin. J. Great Lakes Res., The Great Lakes Futures Project: Using Scenario Analysis to Develop a Sustainable Socio-ecologic Vision for the Great Lakes-St. Lawrence River Basin 41, 96–107. https://doi.org/10.1016/j.jglr.2014.11.004

Paschos, I., Nathanailides, C., Tsoumani, M., Perdikaris, C., Gouva, E., Leonardos, I., 2004. Intra and inter-specific mating options for gynogenetic reproduction of *Carassius gibelio* (Bloch, 1783) in Lake Pamvotis (NW Greece). Belg. J. Zool. 134, 55-60.

Paulovits, G., Tatrai, I., Matyas, K., Korponai, J., Kovats, N., 1988. Role of Prussian carp (*Carassius auratus gibelio* Bloch) in the nutrient cycle of the Kis-Balaton Reservoir. Int. Rev. Hydrobiol. 83, 467–470.

Petering, R.W., Johnson, D.L., 1991. Distribution of fish larvae among artificial vegetation in a diked Lake Erie wetland. Wetlands 11, 123–138. https://doi.org/10.1007/BF03160844

Power, M., McKinley, R.S., 1997. Latitudinal variation in lake sturgeon size as related to the thermal opportunity for growth. Trans. Am. Fish. Soc. 126, 549–558. https://doi.org/10.1577/1548-8659(1997)126<0549:LVILSS>2.3.CO;2

Prentis, P.J., Wilson, J.R.U., Dormontt, E.E., Richardson, D.M., Lowe, A.J., 2008. Adaptive evolution in invasive species. Trends Plant Sci. 13, 288–294. https://doi.org/10.1016/j.tplants.2008.03.004

Rahel, F.J., Olden, J.D., 2008. Assessing the effects of climate change on aquatic invasive species. Conserv. Biol. 22, 521–533. https://doi.org/10.1111/j.1523-1739.2008.00950.x

Reutter, J.M., Herdendorf, C.E., 1975. Thermal discharge from a nuclear power plant: predicted effects on Lake Erie Fish. Ohio J. Sci. 76, 39-45.

Reynolds, W.W., Casterlin, M.E., Matthey, J.K., Millington, S.T., Ostrowski, A.C., 1978. Diel patterns of preferred temperature and locomotor activity in the goldfish *Carassius auratus*. Comp. Biochem. Physiol. A Mol. Integr. Physiol. 59, 225–227. https://doi.org/10.1016/0300-9629(78)90211-6

Ribeiro, F., Rylková, K., Moreno-Valcárcel, R., Carrapato, C., Kalous, L., 2015. Prussian carp *Carassius gibelio*: a silent invader arriving to the Iberian Peninsula. Aquat. Ecol. 49, 99–104. https://doi.org/10.1007/s10452-015-9508-5

Ricciardi, A., 2006. Patterns of invasion in the Laurentian Great Lakes in relation to changes in vector activity. Divers. Distrib. 12, 425–433. https://doi.org/10.1111/j.1366-9516.2006.00262.x

Ricciardi, A., 2007. Are modern biological invasions an unprecedented form of global change? Conserv. Biol. 21, 329–336. https://doi.org/10.1111/j.1523-1739.2006.00615.x

Ricciardi, A., Hoopes, M., Marchetti, M., Lockwood, J., 2013. Progress toward understanding the ecological impacts of nonnative species. Ecol. Monogr. 83, 263–282. https://doi.org/10.1890/13-0183.1

Ricciardi, A., Neves, R.J., Rasmussen, J.B., 1998. Impending extinctions of North American freshwater mussels (Unionoida) following the zebra mussel (*Dreissena polymorpha*) invasion. J. Anim. Ecol. 67, 613–619. https://doi.org/10.1046/j.1365-2656.1998.00220.x

Richardson, M.J., Whoriskey, F.G., 1992. Factors influencing the production of turbidity by goldfish (*Carassius auratus*). Can. J. Zool. 70, 1585–1589. https://doi.org/10.1139/z92-218

Richardson, M.J., Whoriskey, F.G., Roy, L.H., 1995. Turbidity generation and biological impacts of an exotic fish *Carassius auratus*, introduced into shallow seasonally anoxic ponds. J. Fish Biol. 47, 576–585. https://doi.org/10.1111/j.1095-8649.1995.tb01924.x

Rodde, C., Vandeputte, M., Allal, F., Besson, M., Clota, F., Vergnet, A., Benzie, J.A.H., de Verdal, H., 2020. Population, temperature and feeding rate effects on individual feed efficiency in European sea bass (*Dicentrarchus labrax*). Front. Mar. Sci. 7. https://doi.org/10.3389/fmars.2020.578976

Rogozin, D.Y., Pulyayevskaya, M.V., Zuev, I.V., Makhutova, O.N., Degermendzhi, A.G., 2011. Growth, diet and fatty acid composition of gibel carp *Carassius gibelio* in Lake Shira, a brackish water body in southern Siberia. J. Sib. Fed. Univ. Biol. 4, 86–103.

Roy, A.W., Johansen, P.H., 1970. The temperature selection of small hypophysectomized goldfish (*Carassius auratus* L.). Can. J. Zool. 48, 323–326. https://doi.org/10.1139/z70-052

Roy, L.H., 1992. Intra- and interspecific food competition between a native amphibian, (*Notophthalmus v. viridescens*) and an exotic fish, (*Carassius auratus*). MSc. thesis, McGill University, Montreal.

Ruppert, J.L.W., Docherty, C., Neufeld, K., Hamilton, K., MacPherson, L., Poesch, M.S., 2017. Native freshwater species get out of the way: Prussian carp (*Carassius gibelio*) impacts both fish and benthic invertebrate communities in North America. R. Soc. Open Sci. 4, 170400. https://doi.org/10.1098/rsos.170400

Rybczyk, A., 2006. Selected aspects of biological characteristics of the Prussian carp (*Carassius auratus gibelio* Bloch, 1783)- food, feeding, and condition. Acta Sci. Pol. Piscaria 5, 69-82.

Rylková, K., Kalous, L., Bohlen, J., Lamatsch, D.K., Petrtýl, M., 2013. Phylogeny and biogeographic history of the cyprinid fish genus *Carassius* (Teleostei: Cyprinidae) with focus on natural and anthropogenic arrivals in Europe. Aquaculture 380–383, 13–20. https://doi.org/10.1016/j.aquaculture.2012.11.027

Rylková, K., Kalous, L., Šlechtová, V., Bohlen, J., 2010. Many branches, one root: First evidence for a monophyly of the morphologically highly diverse goldfish (*Carassius auratus*). Aquaculture 302, 36–41. https://doi.org/10.1016/j.aquaculture.2010.02.003

Rypel, A.L., 2012. Meta-analysis of growth rates for a circumpolar fish, the northern pike (*Esox lucius*), with emphasis on effects of continent, climate and latitude. Ecol. Freshw. Fish 21, 521–532. https://doi.org/10.1111/j.1600-0633.2012.00570.x

Saat, T., Veersalu, A., 1996. The rate of early development in perch *Perca fluviatilis* L. and ruffe *Gymnocephalus cernuus* (L.) at different temperatures. Ann. Zool. Fenn. 33, 693–698.

Şaşı, H., 2008. The length and weight relations of some reproduction characteristics of Prussian carp, *Carassius gibelio* (Bloch, 1782) in the south Aegean region (Aydın-Turkey). Turkish J. Fish. Aquat. Sci. 8, 87–92.

Saulic, M., Stojicevic, D., Matkovic, A., Bozic, D., Vrbnicanin, S., 2013. Population variability of weedy sunflower as invasive. Presented at the 4th ESENIAS Workshop: International Workshop on IAS in Agricultural and Non-Agricultural Areas in ESENIAS Region, Çanakkale, Turkey, 16-17 December 2013., Çanakkale Onsekiz Mart University, p. 7.

Sayer, C.D., Emson, D., Patmore, I.R., Greaves, H.M., West, W.P., Payne, J., Davies, G.D., Tarkan, A.S., Wiseman, G., Cooper, B., Grapes, T., Cooper, G., Copp, G.H., 2020. Recovery of the crucian carp *Carassius carassius* (L.): Approach and early results of an

English conservation project. Mar. Freshw. Ecosyst., 1–14. https://doi.org/10.1002/aqc.3422

Schofield, P.J., Brown, M.E., Fuller, P.L., 2006. Salinity tolerance of goldfish *Carassius auratus* L., a non-native fish in the United States. Florida Scientist; Orlando 69, 258–268.

Scott, W.B., Crossman, E.J., 1973. Freshwater fishes of Canada. Ottawa : Bull. Fish. Res. Board Can.

Sezaki, K., Watabe, S., Tsukamoto, K., Hashimoto, K., 1991. Effects of increase in ploidy status on respiratory function of ginbuna, *Carassius auratus langsdorfi* (Cyprinidae). Comp. Biochem. Physiol. A: Mol. Integr. Physiol. 99, 123–127. https://doi.org/10.1016/0300-9629(91)90246-9

Shimizu, Y., Oshiro, T., Sakaizumi, M., 1993. Electrophoretic studies of diploid, triploid, and tetraploid forms of the Japanese silver crucian carp, *Carassius auratus langsdorfii*. Jpn. J. Ichthyol. 40, 65–75. https://doi.org/10.11369/jji1950.40.65

Specziár, A., 2002. An in situ estimate of food consumption of five cyprinid species in Lake Balaton. J. Fish Biol. 60, 1237–1251. https://doi.org/10.1111/j.1095-8649.2002.tb01717.x

Specziár, A., Tölg, L., Bíró, P., 1997. Feeding strategy and growth of cyprinids in the littoral zone of Lake Balaton. J. Fish Biol. 51, 1109–1124. https://doi.org/10.1111/j.1095-8649.1997.tb01130.x

Strain, E.M.A., Johnson, C.R., 2013. The effects of an invasive habitat modifier on the biotic interactions between two native herbivorous species and benthic habitat in a subtidal rocky reef ecosystem. Biol. Invasions. 15, 1391–1405. https://doi.org/10.1007/s10530-012-0378-7

Strayer, D.L., Dudgeon, D., 2010. Freshwater biodiversity conservation: recent progress and future challenges. J. North Am. Benthol. Soc. 29, 344–358. https://doi.org/10.1899/08-171.1

Strecker, A.L., Arnott, S.E., Yan, N.D., Girard, R., 2006. Variation in the response of crustacean zooplankton species richness and composition to the invasive predator *Bythotrephes longimanus*. Can. J. Fish. Aquat. Sci. 63, 2126–2136. https://doi.org/10.1139/f06-105

Suzuki, N., Kanzaki, K., 1974. Respiratory responses to hypoxic conditions in crucian carp living in different habitats. Nippon Suisan Gakkai Shi. 40, 57–62. https://doi.org/10.2331/suisan.40.57

Takada, M., Tachihara, K., Kon, T., Yamamoto, G., Iguchi, K., Miya, M., Nishida, M., 2010. Biogeography and evolution of the *Carassius auratus*-complex in East Asia. BMC Evol. Biol. 10, 7. https://doi.org/10.1186/1471-2148-10-7

Tarkan, A.S., Gaygusuz, Ö., Gaygusuz, Ç.G., Saç, G., Copp, G.H., 2012. Circumstantial evidence of gibel carp, *Carassius gibelio*, reproductive competition exerted on native fish species in a mesotrophic reservoir. Fish. Manag. Ecol. 19, 167–177. https://doi.org/10.1111/j.1365-2400.2011.00839.x

Tropical Fish Farming in Florida [WWW Document], 2021. Florida Tropical Fish Farms Association. URL https://www.ftffa.com/content/fish_farming_in_fl.php (accessed 1.18.21).

Trumpickas, J., Shuter, B.J., Minns, C.K., 2009. Forecasting impacts of climate change on Great Lakes surface water temperatures. J. Great Lakes Res. 35, 454–463. https://doi.org/10.1016/j.jglr.2009.04.005

Tweedley, J.R., Hallett, C.S., Beatty, S.J., 2017. Baseline survey of the fish fauna of a highly eutrophic estuary and evidence for its colonisation by goldfish (*Carassius auratus*). Int. Aquat. Res. 9, 259–270. https://doi.org/10.1007/s40071-017-0174-1

Urban, M.C., 2007. The growth–predation risk trade-off under a growing gape-limited predation threat. Ecology 88, 2587–2597. https://doi.org/10.1890/06-1946.1

Vasile, O., 2019. Is *Carassius gibelio* (Pisces, Cyprinidae) a native or non-native species in Romania? Scientific Annals of the Danube Delta Institute 24, 77–84. https://doi.org/10.7427/DDI.24.08

Veer, G. van der, Nentwig, W., 2015. Environmental and economic impact assessment of alien and invasive fish species in Europe using the generic impact scoring system. Ecol. Freshw. Fish 24, 646–656. https://doi.org/10.1111/eff.12181

Vetesník, L., Halacka, K., Simková, A., 2013. The effect of ploidy and temporal changes in the biochemical profile of gibel carp (*Carassius gibelio*): a cyprinid fish species with dual reproductive strategies. Fish Physiol. Biochem. 39, 171–80. http://dx.doi.org.proxy3.library.mcgill.ca/10.1007/s10695-012-9688-z

Villeneuve, F., Copp, G.H., Fox, M.G., Stakėnas, S., 2005. Interpopulation variation in growth and life-history traits of the introduced sunfish, pumpkinseed *Lepomis gibbosus*, in southern England. J. Appl. Ichthyol. 21, 275–281. https://doi.org/10.1111/j.1439-0426.2005.00679.x

Wang, L., He, J., Liang, L., Zheng, X., Jia, P., Shi, X., Lan, W., Xie, J., Liu, H., Xu, P., 2012. Mass mortality caused by Cyprinid Herpesvirus 2 (CyHV-2) in Prussian carp (*Carassius gibelio*) in China. Bull. Eur. Ass. Fish Pathol. 35.

Weatherley, A.H., 1970. Effects of superabundant oxygen on thermal tolerance of goldfish. Biol. Bull. 139, 229–238. https://doi.org/10.2307/1540139

Weber, M.J., Brown, M.L., Wahl, D.H., Shoup, D.E., 2015. Metabolic theory explains latitudinal variation in common carp populations and predicts responses to climate change. Ecosphere 6. https://doi.org/10.1890/ES14-00435.1

Whillans, T.H., 1979. Historic transformations of fish communities in three Great Lakes bays. J. Great Lakes Res. 5, 195–215. https://doi.org/10.1016/S0380-1330(79)72146-0

White, C.R., Alton, L.A., Frappell, P.B., 2012. Metabolic cold adaptation in fishes occurs at the level of whole animal, mitochondria and enzyme. Proc. Royal Soc. B 279, 1740–1747. https://doi.org/10.1098/rspb.2011.2060

Winandy, L., Denoël, M., 2013. Introduced goldfish affect amphibians through inhibition of sexual behaviour in risky habitats: an experimental approach. PLoS One 8, e82736. https://doi.org/10.1371/journal.pone.0082736

Woodward, G., Perkins, D., Brown, L., 2010. Climate change and freshwater ecosystems: Impacts across multiple levels of organization. Philos. Trans. R. Soc. Lond. B Biol. Sci. 365, 2093–2106. https://doi.org/10.1098/rstb.2010.0055

Wouters, J., Janson, S., Lusková, V., Olsén, K.H., 2012. Molecular identification of hybrids of the invasive gibel carp *Carassius auratus gibelio* and crucian carp *Carassius carassius* in Swedish waters. J. Fish Biol. 80, 2595–2604. https://doi.org/10.1111/j.1095-8649.2012.03312.x

Xiao, J., Zou, T., Chen, Y., Chen, L., Liu, S., Tao, M., Zhang, C., Zhao, R., Zhou, Y., Long, Y., You, C., Yan, J., Liu, Y., 2011. Coexistence of diploid, triploid and tetraploid crucian carp (*Carassius auratus*) in natural waters. BMC Genet. 12, 20. https://doi.org/10.1186/1471-2156-12-20

Yalcin Ozdilek, S., Jones, R.I., 2014. The diet composition and trophic position of introduced Prussian carp *Carassius gibelio* (Bloch, 1782) and native fish species in a Turkish river. Turk. J. Fish. Aquat. Sci. 14. https://doi.org/10.4194/1303-2712-v14_3_19

Yamahira, K., Conover, D.O., 2002. Intra- vs. interspecific latitudinal variation in growth: adaptation to temperature or seasonality? Ecology 83, 1252–1262. https://doi.org/10.1890/0012-9658(2002)083[1252:IVILVI]2.0.CO;2

Yao, Z., Zhang, X., Lai, Q., Zhou, K., Gao, P., 2020. Acute exposure to key aquaculture environmental stressors impaired the aerobic metabolism of *Carassius auratus gibelio*. Biology 9, 27. https://doi.org/10.3390/biology9020027

Zou, J., Rogers, W.E., Siemann, E., 2007. Differences in morphological and physiological traits between native and invasive populations of *Sapium sebiferum*. Funct. Ecol. 21, 721–730. https://doi.org/10.1111/j.1365-2435.2007.01298.x

Appendix

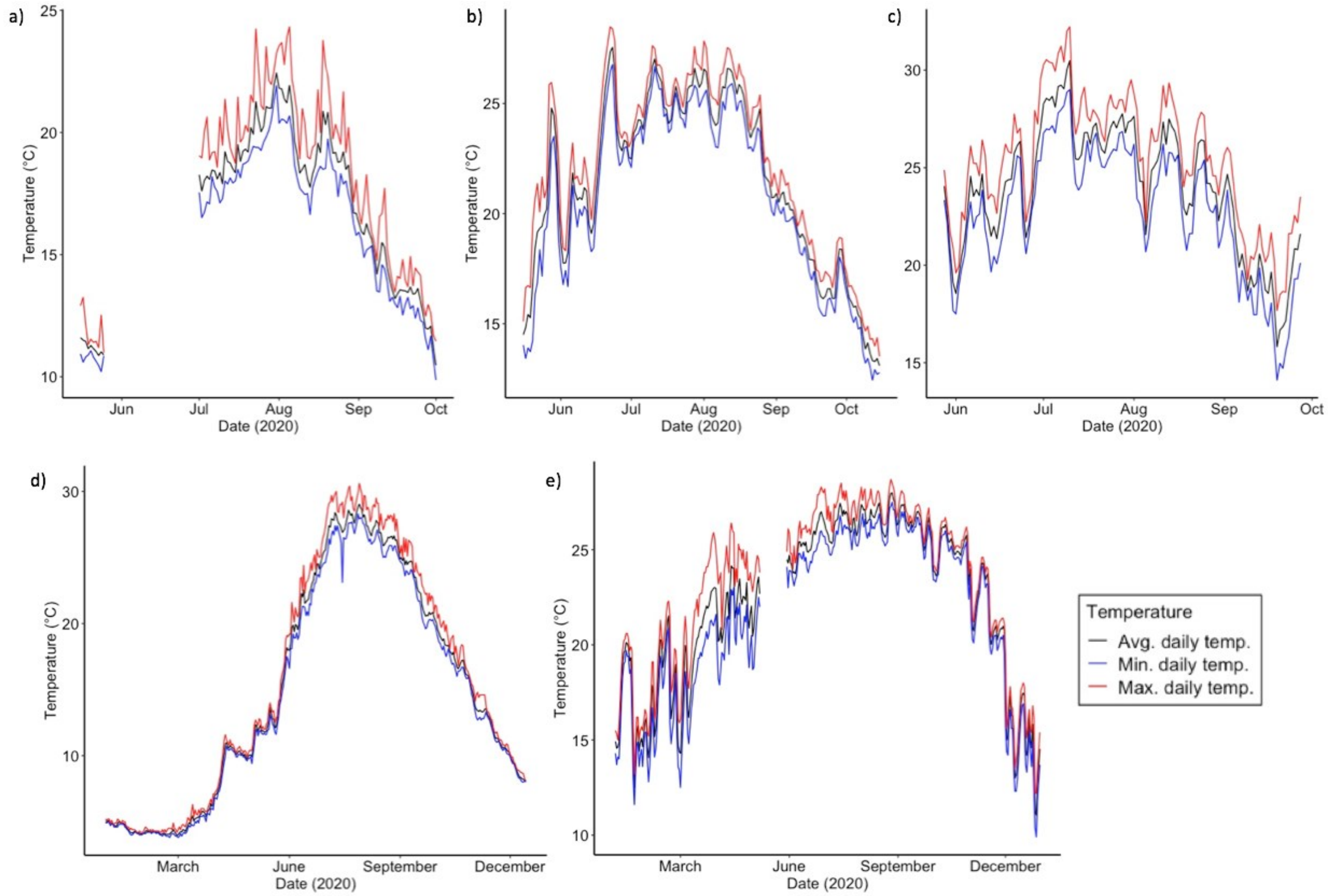

Figure A1. Temperature profiles for a) Blood Indian Creek Reservoir, b) Lac des Battures, c) Cootes Paradise Marsh, d) Juniata River entering Raystown Lake near Mercersburg, PA e) Cypress Creek in Orlando, FL