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The effects of acclimation to temperature and chloride salinity on the thermal tolerance of goldfish (*Carassius auratus*)

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Abstract Understanding how nonnative aquatic species respond to changing temperatures and salinities is crucial for risk assessment in an era of rapid global change. Popular ornamental species such as goldfish (*Carassius auratus*) have become widespread and locally abundant, owing to frequent release events and broad environmental tolerance. The critical thermal maximum (CT_{max}) of cultivated goldfish obtained through the pet trade was measured to assess how their thermal tolerance is affected by acclimation to realistic levels of a co-occurring abiotic stressor. Goldfish were exposed to a combination of chloride concentrations (0 ppt, 1 ppt, and 6 ppt; selected based on those measured in urban ponds subjected to road salt pollution) and current and elevated temperatures (18 °C, 21 °C, and 25 °C; selected based on climate projections for the Great Lakes basin). Results revealed a positive response to acclimation temperatures, with those fish exposed to temperatures near the species' growth optimum having the highest CT_{max}, irrespective of chloride treatment. Thermal tolerance further characterized using metrics of agitation and acclimation potential revealed that high chloride levels (6 ppt) cause sub-optimal performance during heat stress, but acclimation to intermediate temperatures buffers these negative effects. Therefore, the effects of multiple potential stressors on thermal tolerance could mediate the invasive success and impact of ornamental goldfish released in urban waterbodies. Goldfish populations presently acclimating to increased warming and salt pollution in urban ponds would likely have a competitive advantage when subsequently introduced to wild ponds that will be altered by these stressors under expanding urbanization in future years.

Keywords Goldfish · Critical thermal maximum · Invasive species · Climate change · Salt pollution

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Introduction

Temperature limits the distribution of species, especially ectotherms, largely by governing their metabolic rates: the speed at which resources are obtained and converted to usable energy (Hutchison 1961). The role of climate warming in mediating the spread and impact of invasive species is a priority research area (Ricciardi et al. 2021). Data on thermal tolerance metrics are needed to inform invasive species risk assessment, as the greatest effect of climate change on species might not be through increasing annual means but rather extreme temperatures (Stachowicz et al. 2002). A co-occurring and potentially

interactive stressor with climate warming in north temperate inland waters is rising salinity (Jeppesen et al. 2020), and both stressors affect fish metabolism, oxygen consumption, survival, growth, and reproduction (Bœuf and Payan 2001). Urban environmental traits (e.g., dark coloration, impervious material, reduced vegetation buffers) amplify warming due to the absorption and re-emission of energy—the urban "heat island effect" (Touchaei and Wang 2015; Wang and Akbari 2016). Urban ponds experience higher mean and maximum summer temperatures with pronounced daily fluctuations (Brans et al. 2018). Wild (rural and semi-rural) ponds and lakes are predicted to experience progressively similar conditions under expanding urbanization.

The direct impact of temperature on physiology and behavior renders data from thermal metrics such as critical thermal maxima and minima (CT_{max} and CT_{min}) essential prerequisites for conservation management of ectotherms under climate change (Teal et al. 2018). CT_{max} measures an organism's lethal upper thermal tolerance and can test how thermal tolerance is affected by acclimation history (Becker and Genoway 1979; Stillman 2003). In CT_{max} experimental trials, fish acclimated to a certain temperature will be subjected to a constant rate of heating until their locomotor activity becomes disorganized with continued exposure (Bennett and Beitinger 1997).

Expansion of road density and associated impervious surfaces increases the demand for road salt application and thus facilitates runoff of chloride contaminants in melting snow during spring thaws. Sodium chloride (NaCl) is the predominant deicing agent used in northeastern North America, causing chloride pollution to increase in parallel with urbanization (Dugan and Arnott 2022; Dugan et al. 2017, 2020). In Canadian urban ponds, chloride levels range from 1 ppt (Montreal, QC; Lévesque et al. 2020; Wallace and Biastoch 2016) to 6 ppt (Col. S. Smith Reservoir, Toronto, Canada; Mayer et al. 1999).

In addition to warming and chloride pollution, a third burgeoning problem for urban ecosystems is invasive species. Quantifying and understanding an invader's response to changing abiotic stressors is critical for predicting colonization success and ecological impact in different environmental contexts (Ricciardi et al. 2021). The pet trade, specifically aquarium species, is a major source of freshwater invaders (Dickey et al. 2023; Evers et al. 2019; Padilla and Williams 2004). This ever-expanding industry is highly unregulated despite the risks it poses to aquatic ecosystems (Padilla and Williams 2004). Online trade has increased the accessibility and distribution of nonnative species, even those whose sale and possession are illegal (Borges et al. 2021). Many pets are intentionally released by owners unaware of responsible disposal methods; a customer Montreal survey revealed that ~ 7% of pet fish owners have reported releasing at least one fish with reasons for disposal being either the pet's aggressive behavior, large size, illness, rapid reproduction, or other (Gertzen et al. 2008). As many as ~ 10,000 fish are estimated to be released by pet owners annually in the upper St Lawrence River centered at Montreal (Gertzen et al. 2008).

Popular ornamental species such as goldfish (*Carassius auratus*), which have become widespread and locally abundant in urban areas (Copp et al. 2005), tend to be successful invaders due to frequent release events (Duggan et al. 2006; Rixon et al. 2005) and broad environmental tolerance. Goldfish tolerate temperatures up to 44.7 °C (Ferreira et al. 2014) and salinities up to 30 ppt (Wang et al. 2023). Reported optimal temperatures for growth are 25–28 °C (Audige 1921; Imanpoor et al. 2012; Kestemont 1995; Khieokhajonkhet et al. 2023). Reported optimal salinity levels are generally 0–1 ppt (Altinokand and Grizzle 2001; Imanpoor et al. 2012; Lawson and Alake 2010), with some studies reporting 6 ppt or higher (Küçük 2013; Luz et al. 2008). Osmoregulation theory suggests that salinities near the iso-osmotic point reduce energy expenditure for ionic regulation, whereas metabolic theory predicts increased metabolism with warming, both of which may optimize growth and reproduction at specific environmental conditions (Walker et al. 2020). Urban waters are warming at a disproportionate rate (Brans et al. 2018; Hester and Bauman 2013) toward summer mean temperatures that align with the growth optimum for goldfish (25–28 °C), a shift that would be expected to increase their per-capita environmental effects (Iacarella et al. 2015).

Studies that have investigated the influence of salinity on fish thermal tolerance have yielded divergent results (Haney and Walsh 2003). In some cases, salinity significantly affected the thermal tolerance, with acclimation to salinities nearing the iso-osmotic optimum (Sardella et al. 2008; Kutty et al. 1980).

Other studies have found that salinity does not impact thermal tolerance (Hines et al. 2019), rather the timing of salinity acclimation can play an important role (Shaughnessy and McCormick 2018). These studies report on anadromous, eurythermal, and euryhaline fishes; in contrast, very few studies focus on freshwater fishes such as goldfish (Lahlou et al. 1969) who often encounter these co-occurring stressors in urban environments.

To evaluate the effects of warming and salinity on the thermal tolerance of goldfish, we tested predictions informed by metabolic theory of ecology and iso-osmotic theory. We predicted that thermal tolerance will be maximal with acclimation to temperatures and salinities nearest the optima reported for goldfish, i.e., 25 °C and 0–1 ppt (Audige 1921; Ferreira et al. 2014; Luz et al. 2008). Reported growth optimums discussed in this study relate to goldfish growth rates reared under these conditions. Furthermore, we predicted that thermal tolerance will be higher when one of the environmental variables (salinity or temperature) is within the species' optimal range.

Methods

Animal provenance and acclimation

Goldfish were purchased from a pet store in Montreal, Quebec. Since no external features allow for identifying sex in goldfish, juveniles (instead of adults) were chosen for CT_{max} trials to control for possible effects of sex on thermal resistance (Hollands 1956) and known salinity tolerance during that life stage (1–10 ppt, > 6 ppt is stressful) (Lawson and Alake 2010; Luz et al. 2008). We used fish with a mass of 15.75 g ± 6.60 and standard length of 7.72 cm ± 0.55, representing juveniles that are age 1 (Lorenzoni et al. 2007).

Goldfish were housed in climate-controlled chambers, following McGill University animal care protocols (SOP519 and AUP 8267). Upon arrival from the pet store, fish were left to acclimate in a chamber at 18 °C for a minimum of 24 h, to allow water and chamber temperatures to equalize and avoid temperature shock. Fish were transferred to 20-gal (50.8 × 27 × 31.12 cm) mesh-covered aquaria, populated with 2 fish per tank and stocked with plant mimics, coarse gravel, air stones, and filters, for water quality and habitat enrichment purposes. Goldfish were fed ~ 0.5% of their body weight daily using commercialized protein pellets (3 Nutrafin sinking pellets/day) (Du et al. 2006) and were kept on a 12 h:12 h (L/D) photoperiod. Following a 2.5-week acclimation period to lab conditions, fish were exposed to a daily change of 1 °C in the growth chamber until the treatment temperature was established.

Experiments were conducted with goldfish acclimated for 3 weeks (Bennett and Beitinger 1997; Nyboer and Chapman 2017; Reid and Ricciardi 2022) to temperatures of 18 °C, 21 °C, and 25 °C, which are within the ranges of the current and forecasted mean maximum summer surface water temperatures of the nearshore Great Lakes (Trumpickas et al. 2009; Trumpickas et al. 2015). An intermediate value of 21 °C was included to allow a more complete exploration of the environmental matching hypothesis by allowing the detection of any deviation from reported optimums. Fish were also acclimated for 3-week acclimation to 0 ppt, 1 ppt, and 6 ppt Cl^- concentrations. These salinity treatments were chosen to reflect the highest chloride levels recorded in Montreal area ponds (Lévesque et al. 2020; Wallace and Biastoch 2016) and near a reported maximum chloride level of an urban waterbody in Toronto, Canada (Col. S. Smith Reservoir) receiving runoff from a multi-way highway (~ 6 ppt) (Mayer et al. 1999). They are also within goldfish iso-osmotic thresholds, not yet stressful for juveniles (Altinokand and Grizzle 2001; Lawson and Alake 2010; Luz et al. 2008). Salinities higher than 6 ppt have been shown to negatively affect growth, food intake and conversion, increase cortisol, and cause muscle dehydration (Luz et al. 2008). The chloride treatments were initiated by dissolving table salt (Windsor Brand, NaCl) in dechlorinated water in increments of 1 ppt per day until a treatment level of either 1 ppt or 6 ppt was reached and timed so that temperature and chloride treatments achieved final levels on the same day; similar salinity increments were conducted by previous studies with no adverse effects (Küçük 2013). Salinity was monitored using a YSI meter, and chloride was recorded using Hach 2,751,340 Chloride Test Strips High Range.

Critical thermal maxima (CT_{max}) experiments

Upper thermal tolerance limits (CT_{max}) of goldfish were tested following established protocols (McDonnell and Chapman 2015; McDonnell et al. 2021; Reid and Ricciardi 2022; Wells et al. 2016). Following a 24-h starvation period, one fish was transferred to a 10-gal tank (50 × 19 × 25 cm), inside an individual isolation box (i.e., a commercial breeding box; 26 × 15 × 16 cm), with opaque divers to prevent fish from seeing the other fish in the second experimental setup. The initial water conditions of the experimental aquaria were the same as the treatment conditions of the fish being tested. The fish was left to acclimate for 30 min in the breeding tank with aeration and an additional 30 min with the heater (a temperature-control unit [JULABO CORIO™ CD heating immersion circulator]), to ensure acclimation to trial condition (Potts et al. 2021; Reid and Ricciardi 2022).

Trials were initiated by increasing water temperature at a fixed rate of 0.3 °C/min (Becker and Genoway 1979). Two trials were run simultaneously and recorded using a camera. The recording was revisited to verify observations post-trial. Exposure to an increase in temperature continued until fish displayed a loss of equilibrium (LOE), denoting the CT_{max} temperature (Becker and Genoway 1979; Bennett and Beitinger 1997; Hutchison 1961). Here, we defined LOE as a non-lethal endpoint marked when a fish fails to maintain dorsal–ventral orientation for a minimum of 3 s (Becker and Genoway 1979; Bennett and Beitinger 1997; Hutchison 1961). At this point, the fish has become so disoriented that it loses the ability to escape conditions that would impact its fitness or result in death (Becker and Genoway 1979; Bennett and Beitinger 1997; Wells et al. 2016).

Another behavior change, agitation, was noted throughout the trial (Kochhann et al. 2021; McDonnell and Chapman 2015). Agitation temperature (T_{ag}) is recorded when a fish searches for a cooler refuge, exhibited as rapid swimming and interpreted as avoidance behavior (Kochhann et al. 2021; McDonnell and Chapman 2015; Wells et al. 2016). In this study, it was defined as the temperature at which the fish begins to quickly swim around the tank for longer than 40 s in an attempt to escape the isolation box. This behavior was determined based on previous pilot trials. Thermal tolerance capabilities are further revealed by measuring the *agitation window* (T_{aw}), the difference between CT_{max}, and the agitation temperature (Wells et al. 2016) and comparing it to the LOE. A large difference between T_{aw} and LOE indicates suboptimal tolerance capacities, such that the fish cannot maintain normal behavior for long periods during heating events (Kochhann et al. 2021), thereby impacting fitness. Here, we refer to optimal thermal tolerance as a heightened ability to withstand thermal stress denoted by higher CT_{max} values and lower T_{ag}.

Temperature and trial length were recorded using JULABO EasyTEMP Professional software. After the display of LOE, temperature increases were halted, and the fish was returned to a recovery tank equipped with 30 ℃ aerated water, which was gradually cooled back to the respective treatment temperature. Following recovery, fish were weighed (g) and measured (standard length, mm). No fish was reused for another CT_{max} trial, and if a death occurred during the trial, the data was discarded. A total of 59 CT_{max} trials were conducted with 5 to 7 replicates performed for each treatment.

From the two behavioral observations (CT_{max}, T_{ag}), additional metrics were derived: thermal agitation window (T_{aw}, the difference between CT_{max} and T_{ag}; Wells et al. 2016), acclimation agitation window (A_{aw}, the difference between T_{ag} and acclimation temperature; McDonnell et al. 2021), and modified thermal safety margin (TSM, the difference between CT_{max} and the acclimation temperature; McDonnell et al. 2021).

Statistical analysis

All data were analyzed and visualized using R and R Studio (version 4.2.2 and 2022.07.2). The effect of acclimation temperatures and chloride on the response variables CT_{max}, T_{ag}, T_{aw}, A_{aw}, and TSM were tested for goldfish using linear mixed models with treatment and condition factor as fixed effects and housing tank as a random effect using the *lme4* package (Bates et al. 2014). The condition factor was calculated using the Fulton factor ($K = mass/length^3$) with a modified equation ($K = [mass/(standard\ length^{0.29})] \times 100$), where the exponent was derived from the regression of log (mass) against log (length) (Richter et al. 2000). Condition factor was included in the models to account for body mass effects on response variables. The confirmation of fixed effects included in the model for each response

variable was supported by AIC and BIC scores using the *stats* package (R Core Team 2022). The random effect of housing tanks was included in each model to account for potential variability among individuals due to housing conditions. Based on the AIC and BIC results, a linear regression including temperature, chloride, and the interaction between temperature and chloride, as a fixed effect was selected for all 5 response variables. Type III ANOVA was used to test for differences in response variables CT_{max}, T_{ag}, T_{aw}, A_{aw}, and TSM using the *car* package (Fox and Weisberg 2019). The effect size was calculated using Eta partial squares. To generate pairwise estimates, post hoc Tukey–Kramer tests were conducted with 95% confidence intervals. All model assumptions were investigated and validated using Levene's test of equal variance, and the Shapiro–Wilk test for normality and plotting residuals using the *car* package. Pairwise comparisons between response variables (CT_{max} and T_{ag}) were made using *t* test. All data was visualized by plotting it using *ggplot2* package (Wickham 2016).

Results

CT_{max} was observed to vary in response to acclimation temperature and chloride independently, but not by the interaction. Goldfish displayed significantly higher CT_{max} values when acclimated to 21 °C and 25 °C (Table 1, Table 2, and Fig. 1). CT_{max} increased with acclimation to increasing temperatures.

Chloride treatment of 1 ppt and 6 ppt also contributed to higher CT_{max}, although to a lesser extent than temperatures 25 °C and 21 °C (Table 1 and Table 2). For chloride, 1 ppt induced the longest time display before LOE, followed by 6 ppt then 0 ppt. Since no interaction was detected, our results do not support the prediction that acclimation to a combination of optimal variables (25 °C/0 or 1 ppt) would exhibit optimal response. Instead, we found that acclimation to optimal temperature (25 °C) and chloride (1 ppt) independently promote heightened response, with temperature having a larger effect. Freshwater conditions (0 ppt) did not significantly promote enhanced thermal response. The effect of temperature was even stronger at 21 °C, below the reported optimum, in comparison to the effects of chloride treatments (1 ppt and 6 ppt) (Table 1).

The thermal agitation temperature (T_{ag}) was influenced by temperature and chloride independently, as well as by their interaction (21 °C/6 ppt) (Table 1 and Table 2). High temperature (25 °C) acclimation resulted in a higher thermal agitation temperature, whereas high chloride treatment (6 ppt) caused a decline; however, the interaction of 21 °C/6 ppt was significant, buffering the effects of high chloride as seen by the higher T_{ag} value at 21 °C/6 ppt than 18 °C/6 ppt or 25 °C/6 ppt (Table 2 and Fig. 1). For each of the nine treatments, there was a significant difference between the temperature at which fish displayed LOE (CT_{max}) and their agitation temperature (Table 3 and Table S2). As such, the thermal agitation window (T_{aw}) follows a similar trend whereby chloride levels of 6 ppt reduced thermal capacities (i.e., higher T_{aw}), but, the response was buffered at intermediate temperatures through a significant interaction at 21 °C/6 ppt causing a smaller T_{aw} (Table 2 and Fig. 1).

However, temperature alone did not influence T_{aw} (Table 1 and Table 2). The acclimation agitation window (A_{aw}) was also influenced in the same manner; negatively affected by 6 ppt chloride and positively by the interaction of 21 °C/6 ppt, with temperature alone having no impact (Table 1 and Fig. 2).

Conversely, the thermal safety margin is influenced by temperature acclimation to 18 °C, and by 6 ppt chloride, but to the latter a small degree (Table 1 and Fig. 3). For all metrics analyzed, the fish condition factor (Fulton's index) did not explain variation in the response variable, as indicated through the AIC and BIC results of the models (Table S1).

Only one fish died during the CT_{max} trials under the treatment of 18 °C/1 ppt.

Discussion

Our experiments indicated the resilience of goldfish to two major stressors encountered in north temperate urban watersheds. Acclimation to high temperature and salinity will increase CT_{max} (Fig. 1), but consideration of other thermal tolerance metrics (T_{ag}, T_{aw}, A_{aw}, TSM) reveals that high salinities have negative effects on thermal tolerance that are buffered at intermediate temperatures (Table 1). These results suggest acute responses to increases in temperature, such as

Table 1 Linear regression models assessing the effects of acclimation treatments (temperature × chloride) on thermal tolerance metrics of *C. auratus*

Fixed effects	Estimate	Standard error	df	*t* value	*p* value
Critical thermal maximum (CT_{max})					
(Intercept)	35.66	0.34	48	105.52	< 2e − 16***
21 °C	2.02	0.43	48	4.68	1.34e − 05***
25 °C	4.39	0.44	48	9.91	3.40e − 13***
1 ppt	1.08	0.44	48	2.44	0.019*
6 ppt	0.94	0.44	48	2.12	0.039*
21 °C:1 ppt	0.18	0.60	48	0.31	0.76
25 °C:1 ppt	− 0.89	0.63	48	− 1.43	0.16
21 °C:6 ppt	− 0.77	0.60	48	− 1.29	0.20
25 °C:6 ppt	− 0.59	0.61	48	− 0.96	0.34
Agitation temperature (T_{ag})					
(Intercept)	30.05	0.89	45	33.83	< 2e − 16***
21 °C	1.44	1.16	45	1.24	0.22
25 °C	5.21	1.16	45	4.48	5.01e − 05***
1 ppt	1.83	1.20	45	1.52	0.14
6 ppt	− 7.60	1.16	45	− 6.54	4.97e − 08***
21 °C:1 ppt	0.36	1.67	45	0.22	0.83
25 °C:1 ppt	− 2.39	1.67	45	− 1.43	0.16
21 °C:6 ppt	5.86	1.60	45	3.65	0.00068***
25 °C:6 ppt	1.70	1.60	45	1.06	0.30
Thermal agitation window (T_{aw})					
(Intercept)	5.61	0.95	45	5.91	4.24e − 07***
21 °C	0.65	1.24	45	0.52	0.61
25 °C	− 0.83	1.24	45	− 0.67	0.51
1 ppt	− 1.08	1.29	45	− 0.84	0.40
6 ppt	8.54	1.24	45	6.87	1.61e − 08***
21 °C:1 ppt	− 0.033	1.79	45	− 0.018	0.99
25 °C:1 ppt	1.83	1.79	45	1.03	0.31
21 °C:6 ppt	− 6.70	1.72	45	− 3.90	0.00031***
25 °C:6 ppt	− 2.28	1.72	45	− 1.33	0.19
Acclimation agitation window (A_{aw})					
(Intercept)	12.05	0.89	45	13.56	< 2e − 16***
21 °C	− 2.56	1.16	45	− 2.20	0.033*
25 °C	− 1.79	1.16	45	− 1.54	0.13
1 ppt	1.83	1.20	45	1.52	0.13
6 ppt	− 7.60	1.16	45	− 6.54	4.97e − 08***
21 °C:1 ppt	0.36	1.67	45	0.22	0.83
25 °C:1 ppt	− 2.39	1.67	45	− 1.43	0.15
21 °C:6 ppt	5.86	1.60	45	3.65	0.00068***
25 °C:6 ppt	1.70	1.60	45	1.06	0.30
Thermal safety margin (TSM)					
(Intercept)	17.66	0.31	45	56.51	< 2e − 16***
21 °C	− 1.92	0.41	45	− 4.68	2.63e − 05***
25 °C	− 2.61	0.41	45	− 6.39	8.23e − 08***
1 ppt	0.74	0.42	45	1.76	0.086
6 ppt	0.94	0.41	45	2.29	0.027*
21 °C:1 ppt	0.33	0.59	45	0.56	0.58

Table 1 (continued)

Fixed effects	Estimate	Standard error	df	*t* value	*p* value
25 °C:1 ppt	−0.56	0.59	45	−0.95	0.35
21 °C:6 ppt	−0.84	0.56	45	−1.49	0.14
25 °C:6 ppt	−0.59	0.56	45	−1.04	0.31

Asterisks denote significant *p* values (* < 0.05; ** < 0.01; *** < 0.001)

Table 2 Results of a type III ANOVA examining the effects of acclimation treatments (temperature × chloride) on the thermal tolerance metrics of *C. auratus*. Effect size was calculated using Eta partial squares. Models used were based in the best fit AIC criteria

Factor	χ^2	df	*p* value	Effect size
Critical thermal maximum (CT_{max})				
(Intercept)	11,135.06	1	< 2e − 16***	1.00
Acclimation temperature	100.66	2	< 2e − 16***	0.94
Acclimation chloride	6.68	2	0.036*	0.51
Interaction (temperature*chloride)	6.30	4	0.178	0.50
Agitation temperature (T_{ag})				
(Intercept)	1144.37	1	2.2e − 16***	0.98
Acclimation temperature	23.00	2	1.015e − 05***	0.98
Acclimation chloride	82.47	2	< 2.2e − 16***	0.98
Interaction (temperature*chloride)	20.83	4	0.00034***	0.98
Agitation window (T_{aw})				
(Intercept)	34.93	1	3.42e − 09***	0.61
Acclimation temperature	1.70	2	0.43	0.61
Acclimation chloride	79.76	2	< 2.2e − 16***	0.61
Interaction (temperature*chloride)	22.35	4	0.00017***	0.61
Acclimation agitation window (AAW)				
(Intercept)	183.98	1	< 2.2e − 16***	0.89
Acclimation temperature	4.95	2	0.084	0.89
Acclimation chloride	82.47	2	< 2.2e − 16***	0.89
Interaction (temperature*chloride)	20.83	4	0.00034***	0.89
Thermal safety margin (TSM)				
(Intercept)	3192.93	1	< 2.2e − 16***	1.00
Acclimation temperature	42.21	2	6.83e − 10***	1.00
Acclimation chloride	5.57	2	0.062	1.00
Interaction (temperature*chloride)	6.42	4	0.17	1.00

Asterisks denote significant *p* values (* < 0.05; ** < 0.01; *** < 0.001)

in the form of extreme heat events that are expected to increase in frequency and intensity in aquatic ecosystems (Woolway et al. 2021).

CT_{max} experiments highlighted the broad thermal capabilities of goldfish, which were able to withstand temperatures up to 40.04 °C before displaying LOE. This is consistent with published upper thermal tolerances of goldfish acclimated to a similar temperature (Ferreira et al. 2014; Ford and Beitinger 2005; Khieokhajonkhet et al. 2023; Yanar et al. 2019). Here, as in other studies, there is a uniformly positive trend between thermal acclimation and CT_{max}, which holds across a broad range of body masses, 2.45–16.47 g (Khieokhajonkhet et al. 2023; Yanar et al. 2019). Salinity tolerance has been found to vary with goldfish life stage (and thus body size), with tolerance of younger fish reduced (max tolerance of 6 ppt: Imanpoor et al. 2012) compared with older life stages (max tolerance of 20 ppt; Küçük 2013). In this study, we did not find an effect of size (mass and length amalgamated via Fulton's condition factor) on CT_{max} (Table S2), contrary to

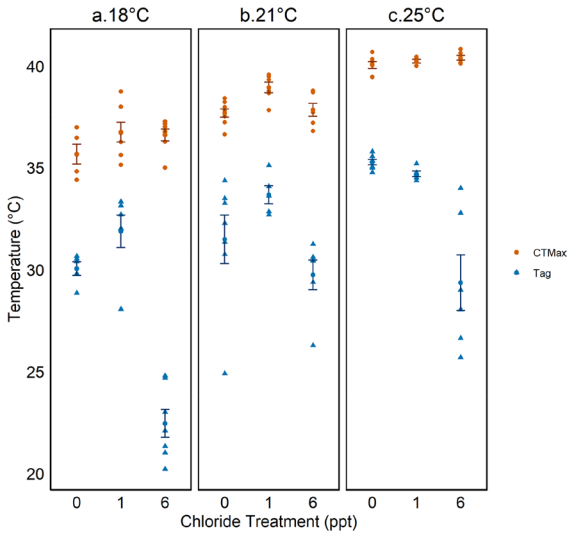

Fig. 1 Mean values of critical thermal maximum (CT_{max}; ± SE) and thermal agitation temperature (T_{ag}; ± SE) of goldfish (*Carassius auratus*) acclimated to 9 individual treatments, grouped here by the three acclimation temperatures, **a** 18 °C, **b** 21 °C, and **c** 25 °C, plotted by their chloride level ($n = 57$ for T_{ag} and $n = 54$ for CT_{max}). Fish were acclimated to treatments for 3 weeks before trials. For the CT_{max} results, post hoc Tukey Kramer test (95% CI) reveals significant differences between the temperature groups and chloride groups, but not between chloride levels within the temperature groups. The differences between CT_{max} and T_{ag} for each treatment were all statistically significant (*t* test). The distance between CT_{max} and T_{ag} represents the thermal acclimation window (T_{aw})

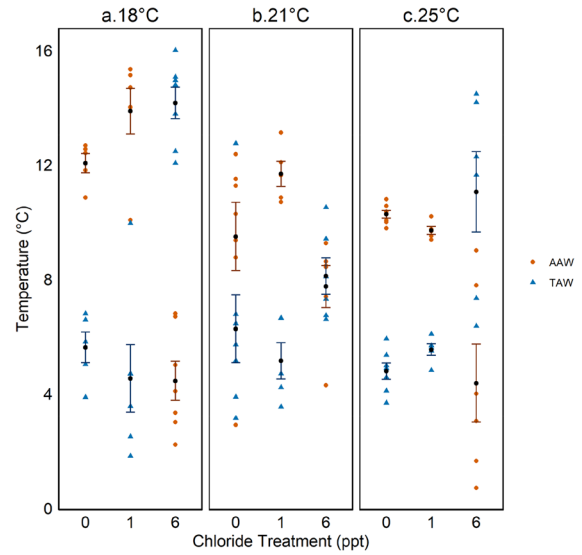

Fig. 2 Mean values of thermal agitation window and thermal acclimation window (± SE) of goldfish (*Carassius auratus*) acclimated to 9 individual treatments, grouped here by the three acclimation temperatures, **a** 18 °C, **b** 21 °C, and **c** 25 °C, and plotted by their chloride level ($n = 57$). Fish were acclimated to treatments for 3 weeks before trials

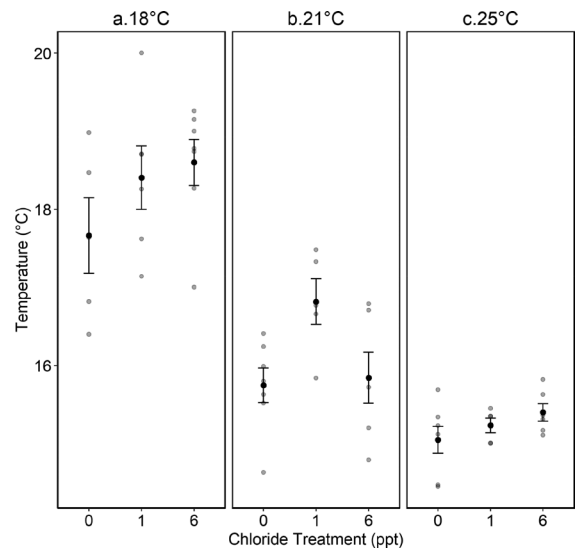

Fig. 3 Thermal safety margin (TSM; ± SE) of goldfish (*Carassius auratus*) acclimated to the 9 possible treatments, grouped here by the three acclimation temperatures, **a** 18 °C, **b** 21 °C, and **c** 25 °C, plotted by their chloride level ($n = 57$). Fish were acclimated to treatments for 3 weeks before trials

what was reported for other species (Recsetar et al. 2012). We investigated the effects of chloride on the tolerance of a single stage (juveniles), whereas comparisons with other life stages would have allowed an assessment of ontogenetic patterns.

We had predicted an enhanced capacity for goldfish to respond to acute thermal stress when acclimated to multiple conditions within the presumed optimum range. Contrary to our prediction, there was no interaction detected for the 25 °C/1 ppt or 25 °C/0 ppt treatments (Table 2). Instead, we found that acclimation at the reported growth optimal temperature of 25 °C yielded the highest CT_{max} results (40.40 °C) irrespective of chloride exposure, followed by acclimation at 21 °C (Table 1). The optimal salinity level of 1 ppt contributed to a heightened CT_{max} response, as did the salinity treatment of 6 ppt, but this was not the case for 0 ppt (Table 1). The lack of thermal enhancement (i.e., higher CT_{max}, lower T_{ag}) in freshwater (0 ppt)

Table 3 Summary of mean CT_{max} ($n=54$) and T_{ag} ($n=57$) values for each of the 9 treatments. The mean is followed by the standard error for each metric (SE)

Treatment	CT_{max}	T_{ag}
18 °C/0 ppt	35.66, 0.48	30.05, 0.33
18 °C /1 ppt	36.74, 0.48	31.87, 0.74
18 °C /6 ppt	36.60, 0.29	22.45, 0.68
21 °C /0 ppt	37.68, 0.20	31.48, 1.12
21 °C /1 ppt	38.94, 0.27	33.67, 0.40
21 °C /6 ppt	37.84, 0.33	29.74, 0.73
25 °C /0 ppt	40.05, 0.17	35.26, 0.13
25 °C /1 ppt	40.23, 0.08	34.69, 0.12
25 °C /6 ppt	40.40, 0.11	29.36, 1.36

suggests that the salinity optimum for thermal tolerance capacity is within the reported 1–6 ppt range (Küçük 2013; Luz et al. 2008).

Acclimation to temperatures of < 21 °C and salinities of 1–6 ppt likely reduce the energy needed for metabolism and osmoregulation, allowing for an enhanced response to acute heat stress, as indicated by a high CT_{max} that was not significantly different from the 0 and 1 ppt conditions—contrary to expectations. While this study assumed a growth optimum for salinity near 1 ppt, there is much inconsistency in the literature concerning reported tolerance and performance across life stages and fish size, whereby the reported optimum is much higher in some cases (Imanpoor et al. 2012; Küçük 2013), which perhaps explains why we detected positive effects at 6 ppt.

It was also predicted that acclimation to either one of the variables at an optimal range would heighten thermal tolerance when the other variable was non-stressful. While there was support for this claim at the 25 °C treatments, enhanced thermal capabilities (higher CT_{max}) were not consistent at the 1 ppt or 0 ppt treatment across all temperatures. These results might reflect a potential trade-off in energy allocation for goldfish, whereby the cost of metabolic regulation is more reduced than that of osmoregulation near the optimal temperature. Across these treatment levels, temperature appears to be a primary driver, whereas chloride is secondary, in mediating the physiological capabilities of goldfish (Walker et al. 2020).

Conversely, acclimation temperature alone played no influence on the thermal agitation window; instead, salinities of 6 ppt accelerated the onset agitation behavior (i.e., lower T_{ag}) in comparison to the other reference groups, creating a larger thermal window (Fig. 1). However, acclimation to 25 °C affected the agitation temperature itself. During acute heat stress episodes, the conditioned avoidance response of goldfish is sensitive to acute temperature changes (cf. Hoyland et al. 1979), with heightened avoidance behavior (i.e., higher T_{ag}) occurring in 25 °C acclimated fish (Table 2). While exposure to 6 ppt prolongs the onset of LOE, possibly through a reduction in iso-osmotic regulation cost, salinity-associated behavioral changes might be at play by reducing T_{ag} and thus increasing T_{aw}. A study by Lawson and Alake (2010) found that non-stressful salinities (4–10 ppt) are associated with a weaker threat response via increases in erratic movement. Their results help explain our finding that, although acclimation to temperatures (21–25 °C) allows goldfish to withstand greater heat stress, acclimation to salinity 6 ppt increases avoidance behavior, as indicated by a lower T_{ag} value, and thereby causes sub-optimal performance under heat stress conditions (Table 1). At a sub-optimal temperature of 21 °C, the onset of avoidance behavior is delayed by comparison. Reynolds and Casterlin (1979) found an "activity well" (a decline in activity) in goldfish with acclimation to a temperature near their final preferendum (28 °C). We hypothesize that, when combined with another stressor, this activity well shifts, owing to a trade-off in energy allocation of metabolism and osmoregulation. The high chloride level also impedes the ability of goldfish to acclimate to temperature changes, as indicated by the acclimation agitation window; however, there is an overlap between when the fish begin to agitate and their acclimation window at the 6 ppt treatment and the intermediate temperature of 21 °C.

Some studies suggest that thermal optima for aquatic ectotherms are overestimated in the absence of consideration of metabolic demands and energy acquisition (Buba et al. 2022; Delong et al. 2018; Uiterwaal and DeLong 2020). In contrast to a presumed monotonic relationship between temperature and metabolic rate, fish might instead perform optimally at an intermediate temperature in a unimodal response (Delong et al. 2018; Uiterwaal and DeLong 2020). In our study, the interaction of temperature and chloride could cause a trade-off in energy costs (cf. Walker et al. 2020), changing performance at the reported optimum variables.

For other stenohaline fishes, stress response was strengthened with chronic exposure to high salinities strengthened, but was weakened with temperature increases; presumably, high salinities reduce the baseline concentration of cortisol, which in turn facilitates stress reactivity when exposed to additional stressors (Walker et al. 2020).

Implications for goldfish invasion risk

The realistic treatment scenarios used here add insight into the role of urban ponds in acclimating goldfish to anthropogenic stressors. We propose that chronic exposure to high temperatures and salt pollution in urban ponds confers a competitive advantage to goldfish as they subsequently invade wild (rural and semi-rural) lentic ecosystems that will likely become increasingly urbanized in the future. This is analogous to the scenario in which populations adapted to human-altered habitats in their native range perform well when invading similar human-altered habitats in a novel range ('Anthropogenically Induced Adaptation to Invade' hypothesis; Hufbauer et al. 2012).

The capacity for goldfish to acclimate to urban stressors is compromised by a narrow acclimation window at 6 ppt salinities, diluting their potential to tolerate stress from heat waves or general warming trends. The early onset of agitation behavior that generally occurs at 6 ppt can also hinder goldfish establishment or post-establishment success, as a consequence of fish replacing routine adaptive behavior (such as foraging, shelter refuge, and feeding) with thermal avoidance behavior (Wells et al. 2016). Given that this redirection of energy could result in reduced competitiveness if natives are more tolerant to chloride, multi-stressor experiments should be conducted on various resident species commonly found in habitats invaded by goldfish.

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Author contribution CC, MH, and AR contributed to the study's conception and design. Experimental protocols were developed by CC and MH. Data collection and analysis were conducted by CC. The manuscript was written by CC, and all authors contributed to subsequent editing and have approved the final manuscript.

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Data availability Data collected in this study are available as electronic supplementary material.

Declarations

Ethics approval All procedures involving animals complied with the McGill University Animal Care Committee (AUP #MCGL-8267).

Competing interests The authors declare no competing interests.

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