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ORIGINAL PAPER

# Effects of temperature and chloride salinity on the functional response of goldfish (*Carassius auratus*)

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**Abstract** Freshwater animals released into temperate urban environments are increasingly subjected to the effects of elevated water temperatures (via climate warming) and salinization (via road salt application). In laboratory experiments, we tested the effects of these stressors on the feeding performance of goldfish (*Carassius auratus*), a globally invasive species frequently released into urban ponds. Using goldfish from a pet supplier, we measured individual functional response (prey consumption rate as a function of prey density) under combinations of two thermal treatments (18 °C and 26 °C) and two chloride treatments (0 ppt and 0.96 ppt). These treatments represent current and projected surface water temperatures and observed mean chloride contamination, respectively, in ponds in the Montreal (Quebec, Canada) region. Feeding rate was consistently higher at the temperature nearest to the known thermal optimum for goldfish (i.e., 26 °C); this supports the environmental matching hypothesis—which predicts that per capita effects, including foraging efficiency, increase as the ambient temperature approaches thermally optimal conditions. Feeding rate was maximum at the combination of 26 °C and 0 ppt. Therefore, the feeding efficiency (and thus the trophic impact) of goldfish varies with combinations of thermal and salinity conditions typical of urban ponds in north temperate regions, with temperature having a larger influence than salinity over this range. A follow-up study testing feeding efficiency at a realistic lower temperature (10 °C; reflecting spring snowmelt conditions) across three levels of salinity (0 ppt, 1 ppt, and 6 ppt) showed that maximum feeding rate increased with salinity. Therefore, we hypothesize that salinity enhances trophic impacts at temperatures below the thermal optimum.

**Keywords** Climate change · Road salt · Invasive species · Feeding efficiency · Impact prediction · Urban ecology

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## Introduction

Urbanization facilitates the success and spread of introduced species, as urban centers are foci for transportation vectors (Borden and Flory 2021; Marchetti et al. 2006; Ricciardi et al. 2017; Santana Marques et al. 2020) and anthropogenic stressors that can select and acclimate individuals for invading other human-altered habitats (Anthropogenic Induced Adaptation to Invade Hypothesis; Briski et al. 2025; Hufbauer et al. 2012). In north-temperate latitudes of North America, salt pollution and warming are the prevailing stressors plaguing urban ponds. In urban regions susceptible to snow and ice, the application of road salt (sodium chloride, NaCl) causes chloride pollution in inland waters, with high inputs in the spring as snow melt and runoff are promoted by urban infrastructure and aesthetics (impervious surfaces) (Dugan et al. 2020). While peak chloride contamination occurs in spring, chloride ions are conservative, and thus long-term application can cause chloride to accumulate and remain present in summer when ponds are simultaneously subjected to heating events (Sutherland et al. 2018). Urban heat island effects amplify the warming of urban ponds, which are typically shallow, lack rooted vegetation, and possess artificial bottom substrate (Brans et al. 2018).

Temperature and salinity are among the most influential environmental variables in aquatic ecosystems, directly affecting fish metabolism, oxygen consumption, survival, growth, and reproduction (Bœuf and Payan 2001). Salinity plays a role in freshwater fish metabolism through the energetic costs of ionic and osmotic regulation for which growth is sacrificed (Altinokand and Grizzle 2001). At salinities near a fish's iso-osmotic point—whereby osmotic equilibrium is established between the individual's body and its surrounding environment—fish spend less energy regulating ions, allowing energy allocation to other tasks such as feeding (Walker et al. 2020).

Similarly, temperature can mediate the performance and distribution of introduced fishes by affecting metabolic rates (Richter et al. 2023). With warming waters, there is (at least initially) an increase in fish metabolic demands, requiring higher ingestion rates and possibly enhancing invader impact (Volkoff and Rønnestad 2020). Temperature shifts toward an invader's thermal optimum are predicted to amplify its per capita effects (e.g., feeding rate) by promoting peak metabolic performance (Environmental Matching Hypothesis; Iacarella et al. 2015; Ricciardi et al. 2013). Conversely, at lower temperatures, fish feeding is expected to decrease due to lower metabolic demands, altering energy balances for the desire and ability to obtain food (Volkoff and Rønnestad 2020).

Efficiency in acquiring limiting resources, notably food, is a determining factor affecting colonization success and the impact of introduced nonnative species (Cuthbert et al. 2019). This efficiency can be compared by quantifying the functional response—the relationship between prey consumption and prey availability (Holling 1959)—across trophically similar species and environmental contexts, using a standardized experimental protocol (e.g., Avlijaš et al. 2022; Cuthbert et al. 2019; Laverty et al. 2017; Mofu et al. 2019). Characteristics of the functional response curve provide information on the consumer's effect on a prey population. A linear (Type I) response is exclusively characteristic of filter-feeding animals (Jeschke et al. 2004). A hyperbolic (Type II) response is considered destabilizing to a prey population owing to a lack of refuge from predation at low prey densities, whereas a sigmoidal (Type III) response is considered stabilizing owing to a reduced predation rate at lower prey densities (Avlijaš et al. 2022; Dick et al. 2013; Oaten and Murdoch 1975). Key parameters of the response are *attack rate* ($a$, the rate of successful prey capture) and *handling time* ($h$, the time spent finding and feeding on prey); the *maximum feeding rate* is estimated as $1/h$ and is the asymptote of the response curve. These parameters allow for comparing responses and their inferred consequences for prey populations; however, in some instances (e.g. a low attack rate coupled with a high handling time), they can result in conflicting inferences. Synthesizing the key parameters in a single metric, the functional response ratio ($\mathrm{FRR} = a/h$), has been shown to have predictive value for invader risk assessment (Cuthbert et al. 2019). Specifically, the FRR can be useful for comparing impacts between species, populations, and contexts—including various abiotic stressors which can mediate the impact of an invader (Ricciardi et al. 2013).

A globally invasive species of emerging concern is the common goldfish (*Carassius auratus*), native to central China but now one of the world's most widely distributed aquatic invasive species. Despite being present in North America for centuries, recent reports of increased spread and local abundance (Boston et al. 2024) raise questions about the factors mediating goldfish invasiveness. Its widespread establishment can be credited to a broad physiological tolerance (e.g. Ford and Beitinger 2005; Schofield et al. 2006), but their local abundance and impacts are expected to be mediated by abiotic variables. Goldfish are commonly released as ornamental fish or as unwanted pets, and therefore are commonly found in urban waterways (Copp et al. 2005), which, in north temperate regions, are subjected to the acute stressors of warming and chloride salinity (from use of road salt).

When the combined effects of temperature and salinity were investigated in goldfish, there was no interaction of temperature and chloride conditions on goldfish thermal tolerance, measured as critical thermal maxima (CTmax); rather, both independently had mediating effects (Claus et al. 2025). However, the negative effects of high salinities (6 ppt) on the onset of agitation behavior were buffered at intermediate temperatures (Claus et al. 2025). In another study, no interaction between these stressors was detected; but growth, food conversion and mean weight increased with salinity (0 vs 6ppt) and temperature (23 °C vs 27 °C) until critical conditions were reached (12 ppt, 31 °C) (Imanpoor et al. 2012).

When investigated independently, salinities of 1–3 ppt (Lawson and Alake 2010; Luz et al. 2008) and temperatures in the range of 25–30 °C (Chen et al. 2019; Nadermann et al. 2019; Pang et al. 2011) stimulate ingestion rates in non-larval life stages. Specific growth rates are generally optimal at temperatures in the range of 25–38 °C (Audige 1921; Imanpoor et al. 2012; Kestemont 1995; Khieokhajonkhet et al. 2023) and salinities ≤ 1ppt (Altinokand and Grizzle 2001; Imanpoor et al. 2012; Lawson and Alake 2010). However, some literature reports optimal salinities of 6ppt and even higher (Küçük, 2013; Luz et al. 2008). The influence of warming and salinity has specifically never been studied in the context of functional response for goldfish.

Using realistic temperature and salinity conditions in the laboratory, we tested the hypothesis that warming and salinization will individually mediate the feeding efficiency of goldfish. Specifically, we predicted that the functional response of goldfish will be higher at 26 °C than at 18 °C, owing to increased metabolic demands at higher water temperatures (Volkoff and Rønnestad 2020). The elevated temperature corresponds with the reported thermal optimum of the species at non-larval life stages (Audige 1921; Ferreira et al. 2014) and thus feeding performance should be enhanced at this temperature, according to the Environmental Matching Hypothesis (Iacarella et al. 2015). Similarly, we predicted that performance should be higher at 0.96 ppt of chloride, near the reported optimal isosmotic concentration (Altinokand and Grizzle 2001; Lawson and Alake 2010; Luz et al. 2008).

## Methods

### Animal provenance and acclimation

We used cultivated (pet store) goldfish as they are the likely source of most urban invasions and thus can be a model species to reveal traits enabling successful establishment in disturbed ecosystems (Copp et al. 2005). Goldfish (n = 61, 90.43 mm ± 7.82 mm) were purchased from a pet supplier in Montreal, QC. The purchased fish were sized-matched using standard length (SL) to the approximate average length of an urban invasive population (caught in October 2022 at Beaver Pond, Montreal, QC, n = 7, 123 mm ± 9.5 mm) and to each other to account for variation in feeding rates (Rall et al. 2012). Clipping of the anal or caudal fin was used to individually identify fish--a method reported to not affect fish fitness (Dietrich and Cunjak 2006; Radcliffe 1950). Goldfish were housed in temperature-controlled chambers. Upon arrival from the supplier, fish were left to acclimate in their transport bags in a chamber at 18 °C for a minimum of 24 h before being placed in their holding aquaria, to allow water and chamber temperatures to equalize and avoid temperature shock (cf. Claus et al. 2025). Fish were housed in 20-gallon (76 L) mesh-covered aquaria (50.8 × 27 × 31.12 cm), with three fish per tank equipped with water filters and air stones following the McGill University animal care protocol (CCAC SOP 519 and AUP 8267). Each tank was stocked with vegetation mimics and coarse gravel substrate for habitat enrichment to encourage natural foraging behaviour (Smith and Gray 2011). The chambers were kept on a 12 h:12 h (L:D) photoperiod to facilitate goldfish diurnal behaviour (Millsopp and Laming 2008; Spieler and Noeske 1984). Water quality variables (pH, ammonia, nitrate, nitrite) were tested weekly; ~ 30% of the water volume was replaced weekly or more frequently when indicated by inadequate water chemistry levels (Claus et al. 2025).

After the 24 h initial holding period, fish were further acclimatized to laboratory conditions (18C) for a minimum of 2.5 weeks before being acclimated to chloride and temperature treatments (Table S1). Individuals were fed a ration of ~ 1% body weight using Nutrafin max sinking protein pellets (9 pellets/fish) on alternating days (Du et al. 2006). After the initial 2.5-week lab acclimation period, the subset of fish (n = 31) intended for the salt treatment were acclimated to 0.96 ppt Cl. Pollution levels caused by road salt application can be measured in the form of chloride concentration (Dugan and Arnott 2022), so we used chloride-specific treatments for the experiments. Tank chloride levels were monitored weekly using a YSI meter and Hach Chloride Test Strips, and these levels were adjusted as necessary for changes due to evaporation. The treatment level of 0.96 ppt was chosen based on summer measurements of specific conductance of Montreal urban ponds converted to chloride values (Lévesque et al. 2020; Wallace and Biastoch 2016). We used the highest recorded conductivity in Montreal ponds (1788 ± 513 µS/cm) to set the treatment threshold, which represents the current maximum possible exposure to chloride ions in a region where there is a known established urban population of goldfish (Beaver Pond Mont-Royal, Montreal, QC; CC, pers. obs.). Once chloride levels were reached, fish were acclimated to the treatment combination for four weeks prior to the functional response trials at 18 °C. Once all trials were completed, a daily increase of 1 °C occurred in the chamber until 26 °C was established, upon which fish were left to acclimatize for four weeks to standardize temperature acclimation time among treatments (Grigaltchik et al. 2012; Sandblom et al. 2014). The same set of foraging trials were conducted at 26 °C on fish that remained at their original chloride treatment. Fish were reused both within and between temperature treatments, but never for the same resource density. This was accounted for in the statistical models (see statistical methods and results).

## Comparative functional response (FR) experiments

Fish were placed as individuals in 10-gallon (37.9L) aquaria (50.8 × 19.05 × 25.4 cm) equipped with an aerator and one plant mimic for habitat enrichment and filled with dechlorinated water and salt to reach housing treatment levels. The lateral sides of each tank were covered with black poster paper to minimize external visual stimuli and control for differences in goldfish consumption caused by shoaling behaviour (Murray et al. 2013; Roy 1992). After a 24-h starvation and acclimation period (Avlijaš et al. 2022; Mofu et al. 2019), each fish was fed a randomized density of commercialized food protein pellets. The same type of food pellets were used for both acclimation and experiments. Pellets did not disintegrate over the 1-h feeding time – as revealed in the control trials. Other studies have found that cyprinids readily consume 1–2 mm pellets and are therefore useful in foraging experiments (Dominguez Almela et al. 2021; Mofu et al. 2019; Oyugi et al. 2012). Pellets were distributed equally across the tanks in 7 replicates of 8 densities (2, 5, 10, 15, 25, 50, 75, and 100 pellets), yielding 56 FR trials per treatment (224 trials in total) (Table S2). Fish were left undisturbed to feed for 1 h (Guo et al. 2017). At the end of the FR trial, individuals were weighed and measured for standard length, returned to their respective holding tanks, and the remaining food items were counted (Mofu et al. 2019; Reid and Ricciardi 2022). A control trial (i.e., with food pellets but no fish predator) was run at each density to confirm no pellet loss because of tank factors. Due to housing limitations, some fish were reused after being permitted to rest for 7 days, but not for trials of the same resource density (Avlijaš et al. 2022; Reid and Ricciardi 2022).

## Maximum feeding rate experiments at low temperature

The results of the previous experiment suggested that salinity has opposing effects on feeding rate at different temperatures. This prompted a follow-up study using new fish from the pet supplier was conducted to test the interaction between a lower water temperature (10 °C) and a range of salinities (0ppt, 1ppt, and 6ppt) on goldfish feeding, modelling realistic conditions of Canadian urban basins during spring melt events (Lévesque et al. 2020; Mayer et al. 1999; Wallace and Biastoch 2016). Fish were acclimated to the experimental temperature (10 °C) for four weeks (Bennett and Beitinger 1997; Nyboer and Chapman 2017; Reid and Ricciardi 2022). Following this, all fish were acclimated to their respective chloride treatment (0ppt, 1ppt, or 6ppt) for one week, prior to the start of experimental trials, to mimic salinity spikes characteristic of typical spring melt events. To initiate the trial, 100 sinking pellets were placed in each tank and goldfish were left to feed undisturbed for 1 h (Guo et al. 2017). Pellets were distributed equally across the tanks. A total of 36 maximum feeding rate (MFR) trials were conducted (12 trials/treatment). After the MFR trial, individuals were weighed and measured for standard length before being placed back in their original holding aquaria, and any remaining pellets in the experimental tanks were counted.

## Statistical analyses

FR data were analyzed using R and R Studio (versions 4.2.2 and 2022.07.2, respectively) along with the *frair* package, following Pritchard et al (2017). A general workflow of model selection, model fitting, and model comparison was applied (Pritchard et al. 2017) using a combination of methods to draw a confident consensus regarding the model (Avlijaš et al. 2022). Model selection is accomplished via three different methods. Firstly, a model is selected using Juliano's method which describes the shape of the response based on polynomial logistic functions. This method provides evidence for Type II or III functional responses with the *frair_test* function of the *frair* package (Pritchard et al. 2017) and was chosen based on the non-replacement experimental design. The second model selection is done by fitting a scaling exponent (q) (such that, in Type II, $q = 0$ and in Type III, $q > 0$) using the *frair_fit* function (Pritchard et al. 2017). Using information criterion (AIC), models fir to Type II and III were compared (Avlijaš et al. 2022). Finally, we visually inspected the plotted curves displaying the relationship between the proportion of prey consumed versus prey provided, where a Type II response is indicated by a decreasing curve and a Type III response by an increase and then subsequently a decline (Avlijaš et al. 2022). When all three methods did not provide a unanimous consensus regarding curve type, the curve was described by the majority determination (Avlijaš et al. 2022).

When the model was chosen, it was then fitted using the *frair_fit* function (Pritchard et al. 2017), which employs nonlinear model estimation optimized by using the maximum likelihood estimation incorporated in the FRAIR package (Pritchard et al. 2017). Type II responses were fit using Roger's random predator equation, and Type III were fit with the Hassel equation (Avlijaš et al. 2022; Hassell 1977; Pritchard et al. 2017; Roger 1972). Here, models were compared using information criteria, AIC.

Lastly, the model is compared among treatment groups. Since FR treatment curves were found to be the same type (see Results), fitted models were compared using *frair_compare* which applies a z-test for likelihood ratio tests (Pritchard et al. 2017). Linear models and linear mixed models with z-scored numeric predictor variables were created using the *lme4* (Bates et al 2014) and *lmerTest* package and REML estimates (Kuznetsova et al. 2017) to test for the effects of treatments and other possible confounds. We used z-score transformed data to unify the scales of variables for comparison and correct for collinearity in the model. Linear Mixed Models (LMM) were used to analyze the effect of prey consumption with respect to temperature treatment, chloride treatment, the interaction of these treatments, and the possible interaction of fish length with the treatments (Table S3) (South et al. 2019). To create the models, random variables were tested for correlation and effect on residual variance. Among the random effects tested (Fig S1.3), fish ID explained the largest proportion of residual variance and was retained in the final models. Multicollinearity was accounted for by testing the correlation among predictor variables mass and length (method = "Pearson"). This method was also used to test for a correlation between fish size and density assigned, to investigate possible bias, following the detection of significance in the models. Models were compared with both AIC and BIC, again using the *stats* package (R Core Team 2022).

All model assumptions and auto-correlations were tested before statistical analysis. Change in fish mass after the duration of the experiments across all treatments was tested for significance by using the Kruskal Wallis test to account for the non-parametric data with the package *rstatix* (Kassambara 2021).

Maximum feeding rate data were analyzed using R and R studio (versions 4.4.0 and 2024.04.24, respectively). Any outliers in the data were detected using the *dplyr* package (Wickham et al. 2023). One outlier was detected, which corresponded to a fish of larger size when compared to the rest of the sample, thus it was excluded from the analysis to avoid skewing data. Data were tested with and without the outlier to determine if its inclusion would have significant impacts. A post-hoc Dunn's test was used to identify which treatment groups significantly differed from others, as it accounts for non-parametric, pairwise, multiple comparisons, using the *dunn.test* package (Dinno 2024).

## Results

### Functional response

Goldfish displayed Type II responses exclusively (Fig. 1), confirmed by all three methods (Table 1;

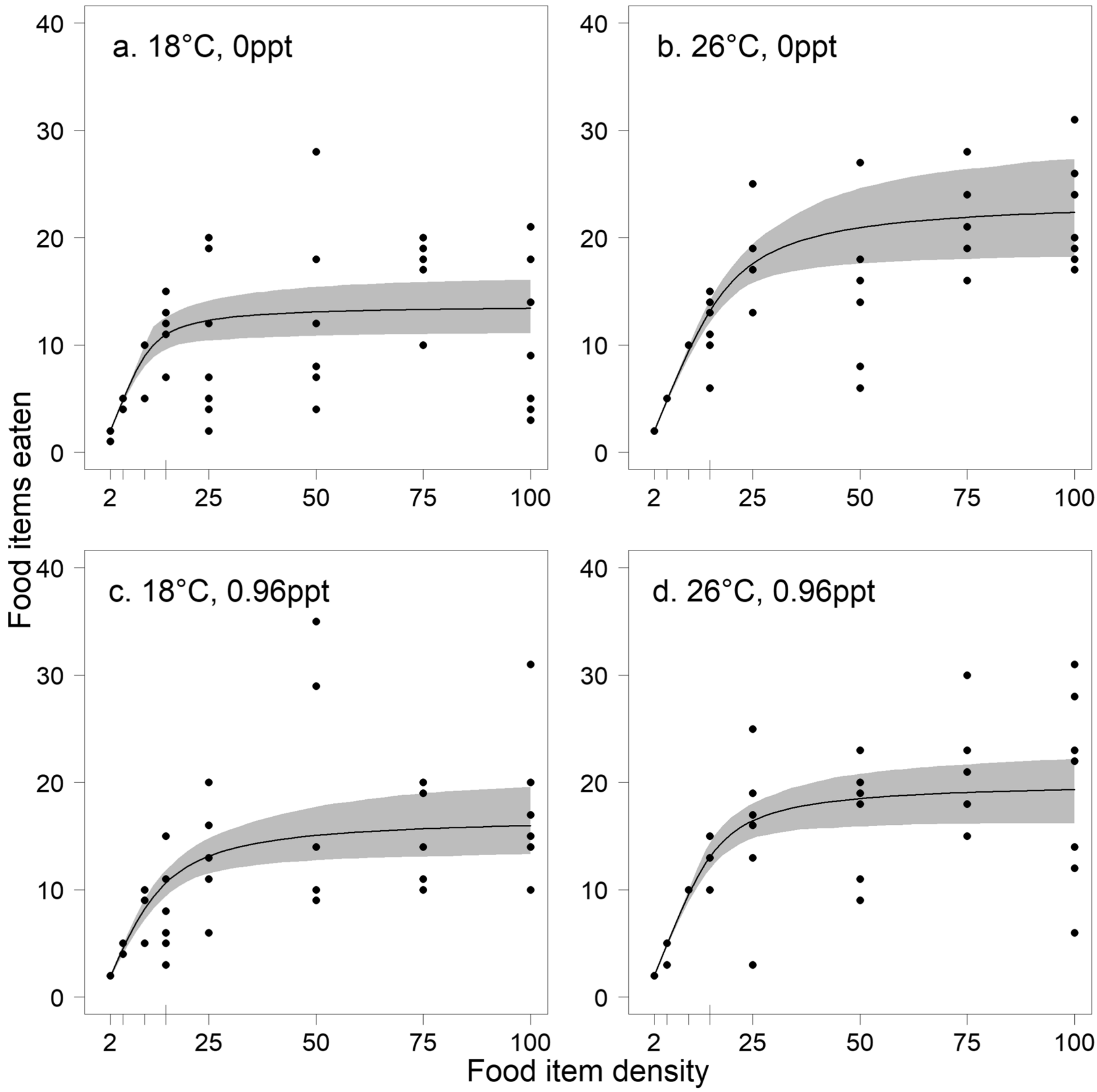

**Fig. 1** The functional response of goldfish under four different treatments. Pet-store goldfish (n = 61) were fed one of 8 known densities using protein fish meal pellets (densities = 2,5,10,15,25,50,75,100), and 7 replicates were conducted at each density (n = 56 trials per treatment, Table S2). Fish were acclimated to the treatment conditions for 4 weeks. The shaded area represents 95% confidence intervals obtained by bootstrapping using the *frair_boot* function (N = 999), the line represents the fitted model, and the circles are the experimental observations

**Table 1** Results of four methods for determining best fit (Type II or III) for the functional response at each treatment. Parameter estimates for each functional response treatment were derived with the *frair_fit* and *frair_compare* functions where *a* = attack rate, *h* = handling time. All models fitted can be found in Table S7 of Supplementary Information. Curves were classified using the Juliano method in which the direction of the 1 st order term (+ or −) indicates type II or III curve respectively. The hypothesis testing method indicates type III if q > 0. Model fitting is done by fitting q = 0 or allowing q to vary. Models are compared with AIC. Visual inspection (Fig. S1) of pellets provided vs. proportion of pellets eaten also allows us to classify the FR curve type. Maximum feeding rate and functional response ratio were calculated with all decimals and rounded here to one decimal

| Treatment | Friar_test | 1 st order term, *p* | q ± SE, *p* | Lowest AIC value | Visual inspection | Fit used | a ± SE, *p* | h ± SE, *p* | Max feeding rate (1/h) | FRR (a/h) |
|---|---|---|---|---|---|---|---|---|---|---|
| 18 °C/0 ppt | Type II | −0.03, 2.2e−16 *** | 0.8 ± NA, NA | Type III | Type II | Type II | 6.5 ± 1.2, 1.438e−08 *** | 0.07 ± 0.003, 2.2e−16 *** | 13.7 | 89.8 |
| 18 °C/0.96 ppt | Type II | −0.03, 2.2e−16 *** | −0.4 ± 0.3, 0.18232 | Type III | Type II | Type II | 3.4 ± 0.5, 5.994e−11 *** | 0.06 ± 0.003, 2.2e−16 *** | 16.9 | 56.9 |
| 26 °C/0 ppt | Type II | −0.03, 2.2e−16 *** | −0.9 ± NA, NA | Type III | Type II | Type II | 4.8 ± 0.6, 1.497e−13 *** | 0.04 ± 0.002, 2.2e−16 *** | 23.6 | 112.7 |
| 26 °C/0.96 ppt | Type II | −0.03, 2.2e−16 *** | 0.2 ± 0.3, 0.52085 | Type II | Type II | Type II | 6 ± 0.9, 1.105e−10 *** | 0.05 ± 0.002, 2.2e−16 *** | 20.1 | 119.2 |

$*p < 0.1$, $**p < 0.01$, $***p < 0.001$; SE, Standard Error

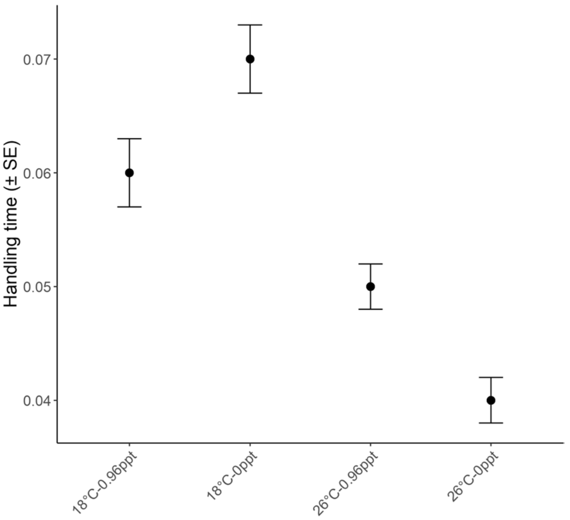

**Fig. 2** Results and standard error (SE) for the pairwise comparisons among handling time for the functional response of pet store goldfish at each treatment. Parameters are compared using the *frair_compare* function, all values are significantly different

Tables S4.1, S4.2, S4.3). Control trials resulted in no pellet loss, indicating that changes in resources were due to predator consumption. According to the functional response ratio (FRR), the per capita effect of goldfish was maximal at the high-temperature/chloride combination (26 °C/0.96ppt) and minimal at the low-temperature/chloride combination (18 °C/0.96ppt) (Table 1, Fig. 2). Generally, the FRR was driven by temperature; whereby fish under 26 °C had higher FRR compared to 18 °C, however, the effects of chloride varied between temperatures (Table 1). With respect to maximum feeding rate, fish showed a higher impact at high temperatures, however, the effect of chloride varied. Fish had a higher MFR at the high temperature/freshwater (26 °C/0ppt) and the lowest at the low temperature/freshwater (18 °C/0ppt) (Table 1). Detailed investigation of model estimates *a* and *h* provided further insight into the variation in FRR and MFR impact results. The model estimates for *a* were significantly different ($p < 0.05$), between 18 °C/0ppt vs 18 °C/0.96ppt and 18 °C/0.96ppt vs 26 °C/0.96ppt (Table S4.4). The model estimates for *h,* were all significantly different ($p < 0.05$) among all treatments (Table S4.4, Fig. 2). Higher temperature consistently corresponded with lower handling time, irrespective of chloride level (18 °C/0ppt > 26 °C/0ppt, 18 °C/0.96ppt > 26 °C/0.96ppt). When temperature treatments were compared across chloride regimes, opposite trends were detected: larger handling time without chloride at 18 °C (18 °C/0ppt > 18 °C/0.96ppt) and larger handling time with chloride at 26 °C (26 °C/0ppt < 26 °C/0.96ppt) (Figs. 1 & 2). When data were bootstrapped and plotted (N = 999), the 95% confidence intervals overlapped for all curves at high density, except for the no-salt treatments at 26 °C and 18 °C (26 °C > 18 °C) (Table S4.3). At low resource densities, consumption was similar across all treatments indicated by the start of the FR curves (Fig. 1).

No significant increase in fish length or mass was detected during the experiment (Fig. S1.3). Fish length (standard length, mm) and mass were correlated (r = 0.91), so only length was used as a measure of body condition in the model as it was the metric used to size-match fish. The number of times an individual fish was reused both within the treatment and among treatments did not explain residual variance in the models and thus was not a random effect impacting consumption, owing to the minimum 7-day resting period (Fig. S1.4). Chloride acclimation was tested for its effect nested among the temperature treatments as fish exposure to chloride was not independent of temperature. The difference in acclimation time to chloride produced by the reuse of fish at 18 °C and then 26 °C did not significantly contribute to residual variance; its impact was accounted for in the chloride variable due to its high correlation (r = 0.90). Individual fish ID did produce significant variation and accounts for variation explained by the housing and experimental tanks and was therefore included in models as a random effect. The results of the LMM reveal that while length affected the proportion of pellets consumed, temperature and chloride, nor their interaction, had a significant impact (Table 2).

## Maximum feeding rate

In the simplified follow up experiment, we looked at maximum feeding rate (correlated to the inverse of handling time). At lower temperatures (10 °C), increased Cl- exposure increases maximum feeding rate up to 6ppt. The MFR study showed that at a lower temperature (10 °C), goldfish feeding did not exclusively increase for salinities at the goldfish iso-osmotic optimum (1ppt). Rather, consumption was enhanced at salinities within (1ppt) and surpassing (6ppt) the goldfish optimum, both of which showed significantly higher feeding than the freshwater treatment (0ppt) (Fig. 3).

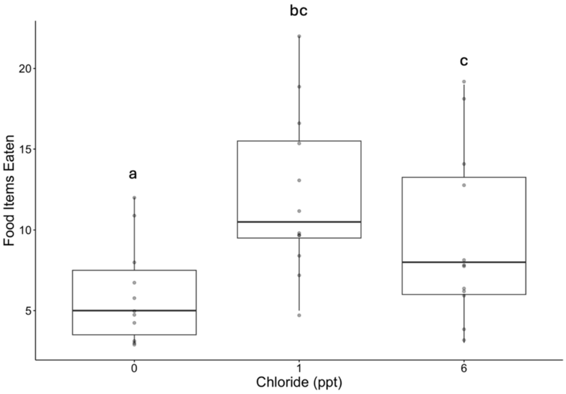

**Fig. 3** Box plot comparing means of the maximum number of pellets eaten during by *Carassius auratus* across three chloride treatments (0ppt, 1ppt, and 6ppt), all held at 10 °C, during the follow-up MFR study. Each treatment was applied to 12 fish, for a total of 36 fish. Standard error bars are shown, alongside raw data for each treatment. An outlier for the data (in 0ppt treatment) was removed prior to plot visualization. Kruskal–Wallis (p = 0.01) and Dunn's (p(0ppt versus 1ppt) = 0.0014; p(0ppt versus 6ppt) = 0.0507) tests indicate significance for comparisons between no-chloride and chloride treatments

**Table 2** Results from the LMM best fit Linear regression models assessing the effects of acclimation treatments (temperature x chloride) on the proportion of pellets eaten. 'Temperature: Chloride' is the interaction between temperature and chloride

| Fixed effects | Estimate | Standard Error | df | t-value | p-value |
|---|---|---|---|---|---|
| (Intercept) | 0.58 | 0.048 | 218 | 12.258 | < 2e−16*** |
| Temperature | 0.094 | 0.067 | 218 | 1.404 | 0.162 |
| Chloride | − 0.0078 | 0.067 | 218 | − 0.117 | 0.907 |
| Temperature: chloride | − 0.022 | 0.095 | 218 | − 0.226 | 0.821 |

## Discussion

### Effect of temperature

Our experimental measurements of the FRR suggest that goldfish will have a greater trophic impact at elevated temperatures near 26 °C. Freshwater temperature groups (18 °C/0ppt vs 26 °C/0ppt) allow for a comparison of the sole effects of warming. As predicted, at 26 °C the FRR and maximum feeding rate were higher and handling time was lower, but there was no difference in attack rate. The heightened performance at temperatures closer to the reported growth optimum of goldfish (i.e. 25–28 °C; Audige 1921; Ferreira et al. 2014) is consistent with the Environmental Matching Hypothesis and with the metabolic theory of ecology (Iacarella et al. 2015; Volkoff and Rønnestad 2020; Walker et al. 2020).

Similar patterns have been reported for other FR studies at elevated and optimal temperatures: fish had higher maximum feeding rates, lower handling times, and lower attack rates, although in this study the difference in attack rate was not significant (Mofu et al. 2019). The inverse relationship between temperature and handling time has been explained in other studies by an increase in metabolic rate that allowed the predator to process more food before complete satiation (Robertson and Hammill 2021). However, traits apart from temperature, such as predator size, can influence the direction of this relationship (Buba et al. 2022), where lower handling times typically correspond with larger predators as larger sizes incur greater metabolic demands in ectotherms (Buba et al. 2022). From our LMM results, individual fish size did influence the amount consumed; however, there was no significant difference in fish size between treatments, indicating that fish size does not explain variation in parameters across temperatures.

The general relationship between temperature and attack rate has been shown to be hump-shaped (unimodal), such that at lower or higher temperatures there is a decline in food search and capture efficiencies (Buba et al. 2022; Englund et al. 2011; Uiterwaal and DeLong 2020). As such, handling time and attack rate can be maximized at different temperatures (Uiterwaal and DeLong 2020). In our case, although 26 °C corresponds with one reported aquaculture growth optimum for goldfish, the optimum for the particular individuals used here may be at an intermediate temperature or towards the high range of their reported optima (Buba et al. 2022), which could explain why there were no significant differences in attack rate along the range of 18–26 °C. In addition, individual goldfish populations (as sold) could have varying physiologies and thus responses to changing conditions. For instance, in another FR study, it was found that goldfish had high attack rates and low handling time (thus higher maximum feeding rate) at 13 °C (Dickey et al. 2022). In our study, we observed the opposite—higher handling time with cooler temperatures (Fig. 2).

### Effect of chloride

When solely comparing the effects of chloride under the high-temperature regime (26 °C: 0ppt vs 0.96ppt), we find support for the Environmental Matching Hypothesis: overall impacts measured via FRR are highest when both variables are at the reported growth optima (26 °C and 0.96ppt). We predicted this to be driven by a reduction in handling time; instead, at 26 °C, handling time significantly increased with salt and no difference in attack rate was noted. The reduced efficiency in consuming and digesting pellets with salt exposure is reflected in the lower maximum feeding rate at the 26 °C/0.96ppt treatment. While it has been reported that goldfish food conversion rate increases with salinity, this occurs at salinities higher than in this study and in fish of smaller size (Altinokand and Grizzle 2001; Luz et al. 2008). Luz et al. (2008) found that goldfish are significantly more efficient at digesting food at salinities up to 2ppt and at 18 °C, which matches well with our finding of a significantly lower handling time and higher MFR at 18 °C/0.96ppt treatment combination; however, FRR is reduced in the salinity treatment (18 °C/0ppt vs 18 °C/0.96ppt), contrary to our second prediction. At low temperatures, we expected to see the highest impact with chloride, which is only observed among the individual FR parameters: higher maximum feeding rate and lower handling time at 18 °C. The overall impact is likely reduced at low temperatures, as the addition of chloride significantly reduced attack rates. Reduced attack rates at low salinity and 18 °C were also observed in another study that examined temperature and salinity effects on the FR of a freshwater amphipod (Cuthbert and Briski 2021).

### Combination of temperature and chloride

Temperature and chloride salinity together influence the outcome: temperature has an overriding effect, but salinity modifies it. Here, we found that feeding efficiency ($1/h$) is higher at 26 °C regardless of salinity treatment, and that the influence of salinity on the feeding rate is reversed at the higher temperature (Fig. 1, 2). The FRR suggests that salinization at realistic chloride concentrations will dampen per capita effects at 18 °C but will amplify them at 26 °C. This has implications for the timing of goldfish release into urban waterbodies. During spring, when runoff increases chloride pollution, the release of cultivated goldfish will have a lower overall trophic impact (FRR) than if they are released during the summer when the inert chloride ions have accumulated. However, if the goldfish are established and persist until the next spring, impacts are likely to increase. Individuals in the follow-up MFR study consumed significantly less than in previous FR studies utilizing higher experimental temperatures within the species optimum (Mofu et al. 2019), whereby increased ingestion rates occurred due to increased metabolic demands and heightened performance (Environmental Matching Hypothesis: Iacarella et al. 2015; Walker et al. 2020). Nadermann et al (2019) found that food intake decreases with temperatures outside of the goldfish's optimal range. Other studies have reported that low temperatures, including 10 °C, induce lethargy and reduce locomotor activity in goldfish, which may prevent fish from capturing food, prolonging their sub-optimal performance (Beitinger et al. 2000; Fry and Hart 1948). Thus, a spike in maximum ingestion at 1 ppt may not have been seen in the follow-up study because of a possible interaction between low temperature and salinity; low temperature may alter goldfish energy allocation that would otherwise allow for optimal performance at salinities near 1 ppt.

The results of the linear mixed model (LMM), whereby only length influenced the proportion of food items consumed, underscore the importance of considering individual variation in per capita effects. Whereas generalized GLM analysis focuses on the interaction of stressors on FR parameters $a$ and $h$, the LMM emphasized that individual fish traits, such as size, can be crucial in determining resource consumption. For example, goldfish are often released into ponds when they outgrow their home aquaria, among other reasons such as illness, aggressive behaviour and rapid reproduction (Gertzen et al. 2008). Therefore, the size structure of an invading population would be useful data for post-establishment risk assessment.

### Functional response caveats

Although we detected Type II curves for all treatments, the experimental design might be biased to produce this relationship, owing to a lack of sufficient complexity and non-mobile prey. Despite using protein pellets to accord with the carnivorous aspect of the goldfish diet, our results can only truly be extrapolated to the detritivore aspect of their omnivorous diet. In another study that conducted FR trials using both frozen chironomid and live *Gammarus pulex* as prey (Guo et al. 2017), the authors found a Type II response for both prey items, but handling time were lower with the live prey. In addition, Guo et al. (2017) found that the per capita effect of goldfish is influenced by body size. The incorporation of body size, along with other data—such as shoaling and foraging behaviours, and local abundance—into predictive models would be more informative. For example, goldfish are often released into ponds when they outgrow their home aquaria, among other reasons such as illness, aggressive behaviour and rapid reproduction (Gertzen et al. 2008). Therefore, the size structure of an invading population would be useful data for post-establishment risk assessment. Furthermore, some FR metrics (e.g. Dickey et al. 2020) incorporate a relative abundance of non-native consumers and trophically analogous natives, thereby integrating classical functional response with a proxy for numerical response. Thus, an important caveat when extrapolating these results – and those of other FR studies – is the consideration of population-level effects, beyond the per capita results shown.

### Implications for risk assessment and management

We tested aquarium-reared individuals of goldfish, as they are the most likely source of invasion into urban ponds through pet release (Copp et al. 2005). In urban environments, resource inputs from runoff can be higher, and chloride pollution and climate warming effects are amplified (Brans et al. 2018; Pagliaro and Knouft 2020). Thus, urban ponds could select for traits that confer goldfish with enhanced invasiveness under rapid environmental change (cf. Hufbauer et al. 2012). If urban ponds act as acclimation hubs, the spread of urbanized goldfish into natural waterbodies could add competitive pressure on native benthic fishes as environmental conditions shift toward those in urban landscapes. The number of individuals that are acclimated and subsequently distributed from urban areas are potentially enormous, given that thousands of goldfish purchased from urban centers are estimated to be released annually (Gertzen et al. 2008). Overall, these results suggest that pet-store goldfish have the potential to promote trophic impacts when released into urban environments, such that the greatest per capita effects of goldfish may occur at water quality conditions near the species' growth optimum, but these impacts vary with combinations of multiple environmental stressors. Finally, urban ponds can facilitate the acclimation of introduced fish species to warming more than native species in natural environments, while also accommodating invaders that are pre-adapted to warmer climates (Correa and Gross 2008; Marchetti et al. 2006).

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## Declarations

**Competing Interests** The authors declare no conflict of interest.

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