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ORIGINAL PAPER

Effects of substrate and elevated temperature on the growth and feeding efficiency of an invasive cyprinid fish, Tench (*Tinca tinca*)

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Abstract Research has linked ecologically-damaging invasive animals to a suite of traits including rapid rates of growth and exploitation of food resources, but such traits can vary substantively across habitats. In this study, the growth rate and functional response of tench (*Tinca tinca*), a benthivorous Eurasian fish invading the Great Lakes–St. Lawrence River basin, were measured when exposed to treatment combinations of two physical habitat variables: substrate (rocks versus sand) and temperature (18 vs 26 °C, the latter being within the range of maximum mean summer nearshore temperatures projected for the lower Great Lakes under climate warming). In spite of their reported preference for fine-sediment habitat, tench did not exhibit impaired rates of consumption, or growth, on rocks compared to sand. Although tench require vegetated fine-sediment habitat for spawning, their efficient foraging on coarse substrate suggests that behavioural plasticity contributes to their ability to rapidly colonize large heterogeneous waterbodies. Furthermore, tench functional response shifted from a stabilizing Type III to a de-stabilizing Type II as temperature increased from 18 to 26 °C. Climate warming could thus erode the ability of prey to exploit refugia against tench predation, possibly resulting in significant local declines in prey populations and enhanced competition for food resources with native benthivorous fishes. Our results provide insight into the influence of physical habitat conditions on the foraging efficiency of this global aquatic invader. Experimental comparisons of invader performance under different environmental contexts offer a valuable tool for informing risk assessment.

Keywords Biological invasion · Climate change · Context dependence · Freshwater Fish · Functional response · Growth rate · Sediment size

Introduction

Invasions by non-native species can have substantial ecological impacts on biodiversity and food webs, particularly in insular ecosystems such as islands and inland waters (Dextrase and Mandrak 2006; Ricciardi et al. 2011, 2013; Blackburn et al. 2019). However,

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impacts can vary greatly across habitats and over time, owing to the influence of local environmental variables (e.g., Kestrup and Ricciardi 2009; Barrios-O'Neill et al. 2015; Mofu et al. 2019; Iacarella et al. 2015). These context dependencies pose a major challenge for risk assessment and require carefully designed experiments to relate invader impact to specific biotic and abiotic conditions.

A burgeoning global contributor to context-dependent variation in invader impact is climate warming (Ricciardi et al. 2021). Temperature change can alter predator–prey interactions in aquatic systems (Watz et al. 2014; South et al. 2017, 2018; Mofu et al. 2019; Khosa et al. 2020) and exerts a strong influence on the stability of populations and food webs (Fussmann et al. 2014; Daugaard et al. 2019). Evidence from a meta-analysis suggests that the community-level impacts of freshwater invaders are higher when ambient water temperature more closely matches their physiological optimum (Iacarella et al. 2015). Similarly, a more recent meta-analysis found unimodal effects of temperature on the relationship between per capita feeding rate and resource density (i.e., the consumer's functional response), further suggesting that foraging efficiency under various temperature regimes depends on the position of ambient temperature relative to the consumer's optimum (Uiterwaal and DeLong 2020). Feeding rate is a valuable indicator of potential impact, as high-impact invaders tend to consume resources at greater rates than trophically-similar native species and less disruptive invaders (Ricciardi et al. 2013; Dick et al. 2014, 2017).

An emerging invasion threat in the Great Lakes Basin

The need for expeditious risk assessment that accounts for context dependencies is highlighted by the recent spread of a Eurasian freshwater fish, the tench (*Tinca tinca*), through the St. Lawrence River towards the Great Lakes (Avlijaš et al. 2018). After expanding throughout the river, the tench was finally detected in Lake Ontario in October 2018, when a single specimen (465 mm fork length, 1.4 kg mass) was captured in Bay of Quinte (A. Mathers, Ontario MNRF, personal communication). Despite the global invasion history of the species, tench impacts have been assessed in only a few studies and these were often confounded by its co-occurrence with other introduced fishes (Avlijaš et al. 2018). Reported impacts include high predation pressure on invertebrate prey (Brönmark 1994; Beklioglu and Moss 1998; Neveu 2001) and reduced abundances of native fishes through resource competition (Giles et al. 1990; Kennedy and Fitzmaurice, 1970). In Canada, ongoing population expansion and spread of tench in the Great Lakes-St Lawrence River basin has raised management concerns for native benthivorous fishes in both Quebec (MFFP 2020) and Ontario (OFAH/OMNRF Invading Species Awareness Program 2021). Concerns are most notable for redhorse species (Catostomidae: *Moxostoma* spp.), including taxa that are identified by Canadian legislation as 'species at risk' (Species at Risk Act 2002), as these overlap with tench in their habitat use and dietary preference for benthic invertebrates (Mongeau 1992; Coker et al. 2001). The sparseness of past impact studies, compounded by the uncertainty surrounding how environmental context mediates impact, hinders the application of invasion history as a guide to prioritize tench for management and thus could delay interventions during a critical early invasion stage in the Great Lakes.

Tench per capita effects, such as their maximum feeding rate, can be expected to vary spatially in large heterogeneous systems. For example, tench are generally reported in habitats dominated by fine sediments such as sand (Rowe et al. 2008), and their preference for fine sediments over rocks is suggested by experimental evidence (Perrow et al. 1996; Rendón et al. 2003; Gallardo et al. 2006). Therefore, it seems reasonable to expect that the species is better adapted to foraging on sand than on rocks, although no previous study has examined substrate as a mediating factor in their trophic impacts (reviewed by Avlijaš et al. 2018). Studies conducted on other fishes and aquatic invertebrates have found that complex habitat structure—such as that created by interstices among coarse sediments—increases predator-free space and thus reduces predation efficiency, an effect most pronounced at low prey densities (Hildrew and Townsend 1977; Alexander et al. 2012; Toscano and Griffen 2013; Barrios-O'Neill et al. 2015; Barrios-O'Neill et al. 2016). If tench are indeed adapted to foraging on fine sediments, their consumptive impacts and energy acquisition should vary between habitats with contrasting substrates.

In this study, we assessed the effects of environmental context on tench growth and foraging efficiency in two sets of experiments. One set of experiments tested the prediction that tench body mass is reduced when fish are feeding for an extended period amongst rocky substrate compared to sand. A second set of experiments compared the functional response of tench exposed to two different substrates (rocks, sand) and two temperatures (18 °C, 26 °C), and tested the prediction that feeding rates are higher at an increased temperature within the upper limit of the preferred thermal range of the species (20–26 °C; Penáz et al. 1989), regardless of substrate type. Functional response experiments allow for the estimation and comparison of different parameters affecting consumer foraging efficiency: attack rate (the rate of successful search and capture of prey) and handling time (time spent subduing, eating, and digesting the prey). Generally, at high prey densities, consumption is limited by handling time, with maximum feeding rate being the inverse of handling time; whereas at low prey densities consumption may be limited by the predator's ability to locate and capture prey (Holling 1959, 1965). The shape of the functional response relationship indicates whether prey have a density-dependent refuge from predation (i.e., a sigmoidal, or Type III, response) or, alternatively, if the invader is able to deplete prey at low densities (a hyperbolic, or Type II, response) and thus drive the prey population to local extinction (Oaten and Murdoch 1975). Therefore, a comparison of functional responses of invaders under different environmental contexts, such as temperature and substrate, can yield valuable insight into their trophic impacts (Dick et al. 2014, 2017; South et al. 2017; Mofu et al. 2019).

Methods

Growth experiment—study design and data analysis

Fifteen adult tench (290–351 mm total length, 332–646 g mass) were captured using fyke nets and beach seines in littoral areas of the St. Lawrence River near Sorel, QC, between July 12 and July 20, 2018. Within a few hours of capture, the fish were transported to an outdoor mesocosm array located at McGill University's Gault Nature Reserve at Mont Saint Hilaire, QC. Each mesocosm was a closed system consisting of a plastic 1000 L tub filled with conditioned municipal tap water sourced from the Richelieu River. A pump continuously circulated 6800 L of water per hour from the bottom of the tub into a 140 L filtration container suspended above the mesocosm. The filter consisted of three layers of material: (1) a coarse sponge, (2) fine filter floss, and (3) a biological filter supported on a substrate of plastic bio-balls and lava rock. Filtered water returned to the mesocosm under the force of gravity, continuously disturbing the surface of the water and thus re-oxygenating it. Each mesocosm was shaded from direct sunlight by two layers of a UV-reflecting polyethylene sheet, one attached directly on top of the mesocosm tub and a second layer installed overhead (see Figure S3, Supplementary Information).

Prior to the start of the experiment, fish were acclimated individually for 25 days in the mesocosms with no added substrate and were fed commercial sinking pellets. Following introduction of fish to the mesocosms, water quality was monitored daily and partial water changes (20%) were done until the biological filter developed sufficiently to transform all ammonia and nitrites into nitrates. Subsequently, ammonia, nitrites, and nitrates were tested weekly, and nitrate levels were reduced with partial water changes when necessary. A digital logger affixed to the bottom of the mesocosm recorded temperature at 15 min intervals for the duration of the experiment.

The experiment consisted of three substrate treatments with five replicates. In the first treatment, rinsed commercial sand (~0.5 mm grain size) was added to one third of the mesocosms (~5 cm depth). The second treatment had cleaned commercial river rocks (2–4 cm grain size) as substrate (~8 cm depth). The interstices created by the clumped river rocks were sufficiently large to provide refuge for the invertebrate prey used in the experiment. The final third of the mesocosms was left without any added substrate. We assigned treatments to the mesocosms in the array using an interspersed design. Total length and weight of each fish was measured at the start of the experiment (August 14, 2018) and at the end of the experiment 58 days later (October 11, 2018).

During the experiment, mesocosms were stocked weekly with live invertebrates consisting of amphipods, isopods, dragonfly nymphs, mayfly nymphs, and pulmonate (planorbid and physid) snails captured in the St. Lawrence River at Pointe-des-Cascades, QC. The invertebrates were divided into 15 equal portions with the same number and size of individuals for each species, before being distributed to the mesocosms. The quantity of invertebrates collected was deemed unlikely to meet the nutritional requirements of tench, so live prey were supplemented with sinking commercial pellets (7 g per fish) added to the mesocosms three times per week. The pellets promptly sank to the bottom of the mesocosms, the fish therefore had to search and feed on the pellets in the substrate rather than suspended in the water column.

Changes in fish mass between the start and end of the experiment were compared using a one-way ANOVA with three groups. Potential biases introduced by differences in temperature between mesocosms and initial fish size were assessed using linear regressions that tested the effect of these variables on changes in fish mass, in addition to testing differences between the groups by ANCOVA using initial fish mass as a covariate. All statistical analyses were done using R version 3.6.2.

Functional response experiments—study design

For the second set of experiments, 13 juvenile tench (< 200 mm) were collected using multiple gears (fyke nets, seining, boat electrofishing, backpack electrofishing) from three locations (Melocheville, Lac Saint Pierre, and Sorel) in the St. Lawrence River, QC, between May 22 and June 16, 2018. Fish were transported to the lab and placed in aquaria equipped with filters and conditioned, nutrient-cycled tap water, within a temperature-controlled chamber maintained at 18 °C. Physid snails (~ 7 mm in length) were also collected from the St. Lawrence River (at Pointe-des-Cascades, QC) to be used as live prey.

Fish were acclimated to lab conditions for 5 weeks prior to starting the experiment in three aquarium tanks with 2–3 fish per tank. Each holding tank had a mix of sand, aquarium gravel, and rocks (2–4 cm grain size), so each fish would be accustomed to feeding over a variety of substrates similar to those at the field sites where fish were collected. The chamber was set to a 12:12 dark/light cycle, and red bulbs were used because experimental evidence shows that red spectrum light reduces stress and increases locomotor activity for this nocturnal species (Owen et al. 2010), which actively seeks low-light conditions among dense vegetation during the day (Gallardo et al. 2006). Furthermore, all sides of experimental and holding tanks were covered with black mesh to create shade. Fish in the holding tanks were fed ad libitum, with 0.6 g of sinking commercial pellets per fish three times per week.

Prior to running trials, each fish was placed in an experimental tank with either rocks or sand as substrate and allowed to acclimate for 24 h in the 12:12 dark/light cycle, during which it was left unfed to standardize hunger levels. Each fish was then presented with one of six densities of live physid snails (2, 4, 8, 16, 32, 64 individuals) and allowed to feed for 3 h under red light. All treatments were conducted in triplicate at each density, as is standard in functional response experiments with fish (e.g. Alexander et al. 2014; Guo et al. 2017; Laverty et al. 2017; Dickey et al. 2021). Controls tested the survival of snails in experimental tanks with no fish. The experiment was concluded by returning the fish to its holding tank and counting how many snails had been consumed. Our experimental fish ranged between 135 and 199 mm total length (mean 164 mm), and 20–68 g mass (mean 38 g); we allowed for this breadth in size range because capturing sufficient numbers of tench under 200 mm in length in riverine habitats proved to be challenging, despite applying multiple sampling gears (seining, fyke nets, backpack electrofishing) and substantial effort (two consecutive weeks of daily sampling). To avoid introducing bias due to fish size, we reused the same group of fish in all four treatments, with the exception of one fish (163 mm length) that died while being acclimated for 26 °C trials and was used only in the 18 °C trials. Additionally, to obtain three replicates of six densities, it was necessary to reuse fish for different density trials within substrate/temperature treatments. Each fish was reused at most once and had at least 7 rest days in the holding tank between trials, during which it was fed pellets three times a week; the same fish was never reused in replicates of the same density treatment. Once all trials were completed at 18 °C, the fish were placed in their holding tanks and temperature was increased in the chamber at the rate of 1 °C per day until it reached 26 °C. Fish were allowed to acclimate to the temperature for 5 weeks. The experiment was repeated exactly as before, with the addition of a 7th density (90 snails) to obtain an asymptote in the functional response curve that would allow model fitting. Trials for the two substrate treatments were conducted simultaneously at each temperature.

Prey mobility was compared between temperatures in the presence of fish cue by placing physid snails of the same size and source as used in the experiment, into 10L glass tanks, with no substrate, and lined with a 0.5 mm grid. Each tank was filled with water obtained from the tench holding aquaria, which was expected to trigger predator-avoidance behavior (Covich et al. 1994). Time (seconds) spent moving and distance traveled (number of 0.5 mm squares) were measured for individual snails at each temperature in 10 replicates. Differences between movements under the two temperature treatments were compared using a Mann–Whitney-Wilcoxon test.

Functional response experiments—data analysis

Functional response data were analyzed in R version 3.6.2, following Pritchard et al. (2017). Given that there is no consensus on the best method to determine curve type, we tested whether a Type II or Type III curve was a better fit for each treatment by combining information from four commonly used tests: (1) the frair_test, a function based on the Juliano method, which fits logistic functions to proportional consumption data and uses forward selection to determine whether the curve best fits either a Type II or Type III response, based on the sign and significance of first-order and second-order terms; (2) the hypothesis-testing method, in which a generalized form of the functional response model is fitted with a scaling exponent q ($q=0$ indicates a Type II response, whereas $q>0$ indicates a Type III response); (3) using an information criterion, AICc, to compare models fitted to Type II and Type III equations; and (4) visual inspection of plotted curves of the proportion of prey consumed versus prey density provided (Fig. 2). We examined evidence from all four methods to determine whether each functional response curve constructed from our data is best described as a Type II or a Type III. When there was consensus across all four methods, we considered the curve to be a typical Type II or III. As empirically constructed curves occupy a continuum of responses between classical Type II and Type III models, determinations from the four methods are not always unanimous; under such circumstances we considered the curve to be best described by the type indicated by the majority determination, but we qualified it as a 'weak' Type II or Type III relationship.

Next, we fitted the appropriate model using the Frair package in R to estimate and compare attack rate a (for Type II responses only, as attack rate is not constant in Type III responses) and handling time h (for all responses). As prey were not replaced during each experiment, the models with Type II curves were fitted using the Rogers random predator equation solved with the 'lambertW' function (Pritchard et al. 2017). Type III models were fitted with the Hassel equation or using the Flex model available in Frair when the former could not be fitted (that is, when the Hessian was not invertible). As it is not possible to compare parameter estimates for models fitted with different response curves, we also used the Flex model option in Frair to compare Type II and Type III models (Pritchard et al. 2017). We plotted the bootstrapped values (N = 999) for each treatment and compared them visually to observe differences in overlap between functional response curves at low prey abundances.

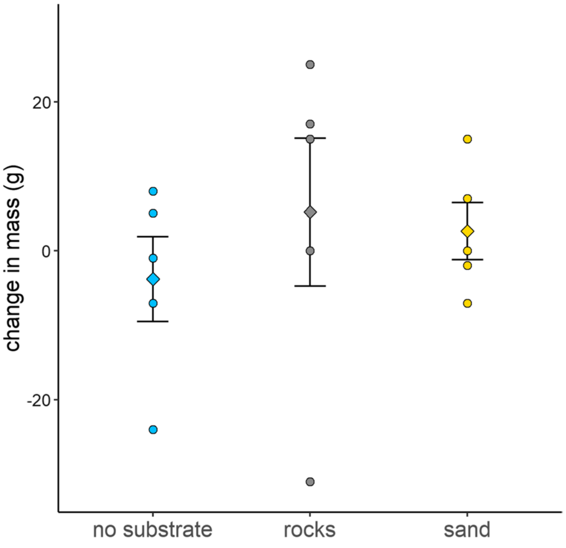

Fig. 1 Change in mass of fish after the two-month experiment across three treatments: no substrate, rocks, sand. There is no significant difference between the groups. Circles = observations; diamonds and bars = mean and standard error

Results

Growth experiments

There was no mortality during either treatment. Tench growth was not significantly affected by substrate [F(2,12) = 0.44, $P = 0.65$; Fig. 1 and Table S3 in Supplementary Information], although there was a tendency for greater growth on the rock treatment when the low outlier was removed (ANOVA, F(2,11) = 3.19, $P = 0.08$; Figure S4 and Table S3). Changes in the mass of the fish were not correlated with minor differences in temperature between mesocosms, nor with initial fish length (Table S2; Figures S1 and S2). Initial fish mass was a non-significant covariate (ANCOVA, F(2,11) = 0.61, P = 0.56; Table S3). The residuals of the ANOVA conformed to assumptions of normality and heteroscedasticity (Table S3).

Functional response experiments

Temperature had a significant effect on functional response. Our examination of evidence from all four methods indicates that the best fitted responses were Type III at 18 °C and Type II at 26 °C. At 26 °C the Juliano method and visual inspection indicated a Type II response, whereas the hypothesis-testing and AICc methods did not differentiate between the two curve types to a level that met statistical significance. For the rocky substrate treatment at 18 °C, all four tests agreed on a Type III response. For the sand treatment at 18 °C, the Juliano method suggested a Type II response, whereas the other three methods found significant evidence a Type III; we therefore classified it as a weak Type III (Table 1 and Fig. 2; additional details are provided in Table S4). Control trials resulted in no prey loss, suggesting that all prey losses observed in the treatments were attributable to fish consumption. The estimates for handling time (h) and attack rate (a) were obtained, where possible (Table 2), by fitting flex models for treatments at 18 °C, rather than Type III models—which were problematic to estimate and fit, owing to large variance in the data. Parameters for treatments at 26 °C were fitted using Type II models.

The model estimates for h differed significantly only between responses on different substrates at 26 °C (Table 3) with tench on rocky substrate having a lower h and, therefore, a higher maximum feeding rate than those on sand. Attack rate was also marginally lower on rocks than on sandy substrates at 26 °C ($P = 0.056$). When data were bootstrapped (N = 999) and plotted, the 95% confidence intervals overlapped for all curves at high densities (Fig. 3; values reported in Table S6, Supplementary Information). However, at low prey densities, consumption was reduced on rocky substrate at 18 °C compared to 26 °C (Fig. 3B), whereas no difference in consumption on sand was detected between temperatures. At 18 °C, consumption was lower on rocky substrate compared to sand (Fig. 3C). Additionally, variance between bootstrapped estimates of h was larger at 18 °C than 26 °C (Fig. 4),

Consumption was not affected by holding tank ($P = 0.39$; see linear model results in Table S7, Supplementary Information). As expected (Byström et al. 2006; Toscano and Griffen 2013), consumption was affected by fish length ($P = 0.007$), which we held

Table 1 Results of four methods for determining best fit (Type II or Type III) for the functional response curve at each treatment

Substrate	Temp (°C)	1st order term, P	$q \pm$ SE, P	Lowest AICc value	Visual inspection
Sand	18	$-0.03, 1.3 \times 10^{-8}$*	1.22 ± 0.44, 0.005*	Type III*	Type III
Sand	26	$-0.03, 2.2 \times 10^{-16}$*	0.40 ± 0.39, 0.30	Type II	Type II
Rocks	18	0.1, 0.02*	1.34 ± 0.66, 0.04*	Type III*	Type III
Rocks	26	$-0.018, 2.1 \times 10^{-9}$*	0.03 ± 0.30, 0.92	Type II	Type II

The Juliano method classifies curves as Type II or Type III if the first order term is negative or positive, respectively. Hypothesis testing classifies curves as Type III if q is > 0, models fitted with q = 0 and where q is allowed to vary are compared with AICc (all AICc scores are provided in Table S4 of Supplementary Information). Asterisks indicate significant results, and we report Standard Error (SE). A visual inspection of the relationship between prey provided and the proportion of prey eaten allows us to classify the relationship based on the slope of the curve (Fig. 2)

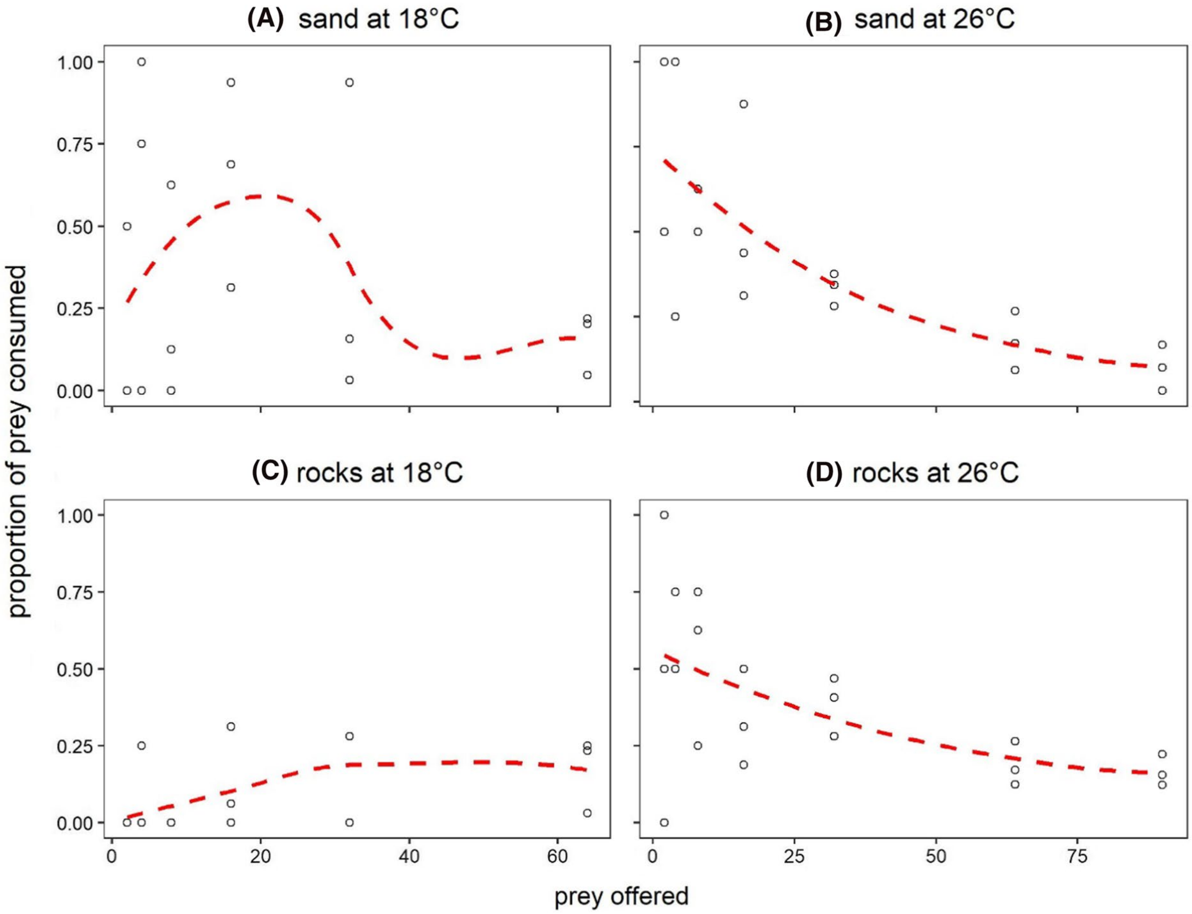

Fig. 2 Relationship between proportion of prey consumed and prey provided for Sand treatments at 18 °C (**A**) and 26 °C (**B**), and Rock treatments at 18 °C (**C**) and 26 °C (**D**). The hatched line is a smooth curve fitted by loess using the geom_smooth function from the ggplot package in R. Curves with continuous declining slopes indicate a Type II response, and curves that show an initial increase and then a decline indicate a Type III response

Table 2 Parameter estimates for each Functional Response treatment (± standard error, SE) derived with the frair_fit function. Other model results (all models fitted with flex fits, models with outliers removed) can be found in Table S5 of Supplementary Information

Substrate	Temp (°C)	Fit used	a ± SE, *P*	h ± SE, *P*	Max feeding rate (1/h)
Sand	18	flex	n/a	$0.27 \pm 0.03, < 2 \times 10^{-16}$	4.06
Sand	18	Type II	$0.30 \pm 0.062, 1 \times 10^{-6}$	$0.17 \pm 0.03, 7 \times 10^{-8}$	5.78
Sand	26	Type II	$0.58 \pm 0.14, 2 \times 10^{-5}$	$0.25 \pm 0.03, 2 \times 10^{-16}$	4.05
Rocks	18	flex	n/a	$0.21 \pm 0.08, 0.006$	4.68
Rocks	26	Type II	$0.29 \pm 0.06, 3 \times 10^{-6}$	$0.16 \pm 0.02, 1 \times 10^{-10}$	6.11

Table 3 Parameter comparisons (a = attack rate, h = handling time) between functional response curves using frair_compare

Treatments compared	a ± SE, *P*	h ± SE, *P*	Fit used
Rocks 18–Sand 18 °C	n/a	− 0.03 ± 0.082, 0.70	Flex
Rocks 26–Sand 26 °C	0.29 ± 0.15, 0.056	0.083 ± 0.038, 0.0284*	Type II
Rocks 18–Rocks 26 °C	n/a	− 0.074 ± 0.16, 0.65	Flex
Sand 18–Sand 26 °C	n/a	− 0.026 ± 0.04, 0.55	Flex
Sand 18–Sand 26 °C	− 0.28 ± 0.15, 0.06	− 0.074 ± 0.04, 0.08	Type II

Note that it is not possible to estimate a single attack rate for curves that do not follow a Type II shape since, by definition, attack rate changes between prey densities

* indicate significant results, and we report Standard Error (SE)

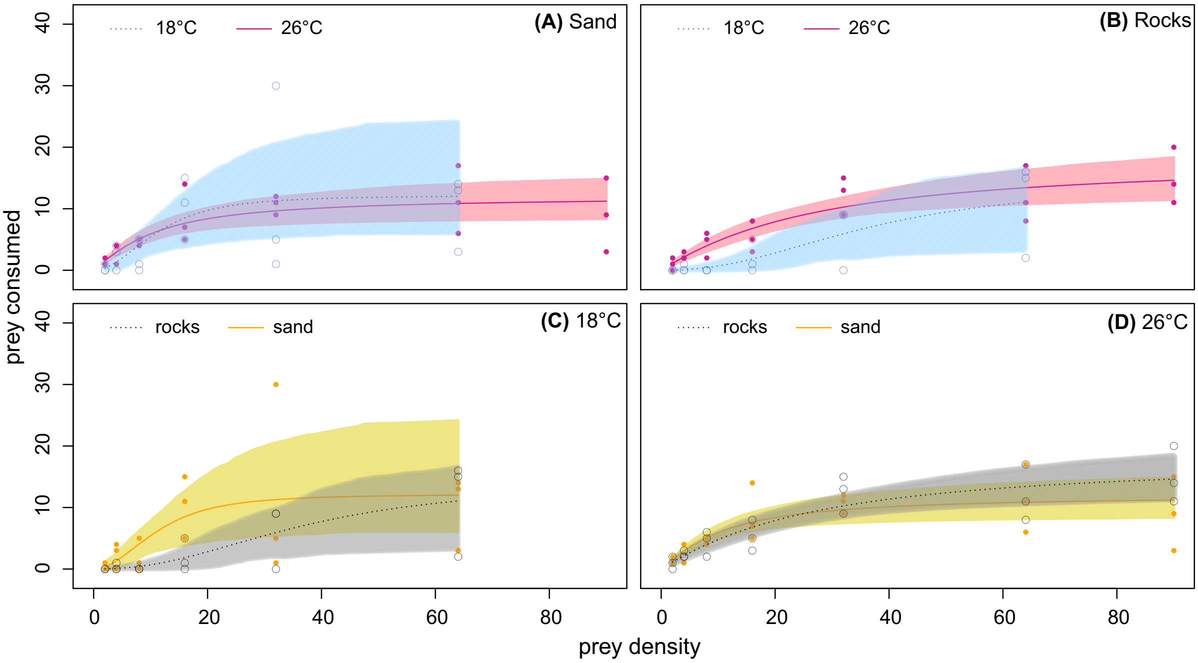

Fig. 3 Functional responses of tench on physid snails. Top graphs compare the functional responses at 18 °C (blue shading, dotted line, open circles) and 26 °C (red shading, solid line, solid circles) over sand (**A**) and rocks (**B**). The bottom graphs compare the response on sand (yellow shading, solid orange line, orange circles) and rocky substrate (gray shading, dotted line, open circles) at 18 °C (**C**) and 26 °C (**D**). Shaded area represents 95% confidence intervals obtained by bootstrapping using the frair_boot function (N = 1999), the line represents the fitted model, and the circles are the experimental observations

constant across treatments by using the same individuals at both temperatures and sediment types. No significant increase in fish length was detected during the duration of the experiments, and fish size was not correlated with prey density assigned, which might have otherwise biased results (Fig. 2; Table S7).

Prey movement data was not normally distributed, but variances were not significantly different (Shapiro test *P*-value = 0.02 for time and 0.03 for distance; Bartlett test *P*-value = 0.38 for time and 0.91 for distance). Experiments measuring prey movements indicated that snails travel significantly larger distances (*P* = 0.02) and for longer periods of time (*P* = 0.04), at 18 °C compared to 26 °C (Fig. 5).

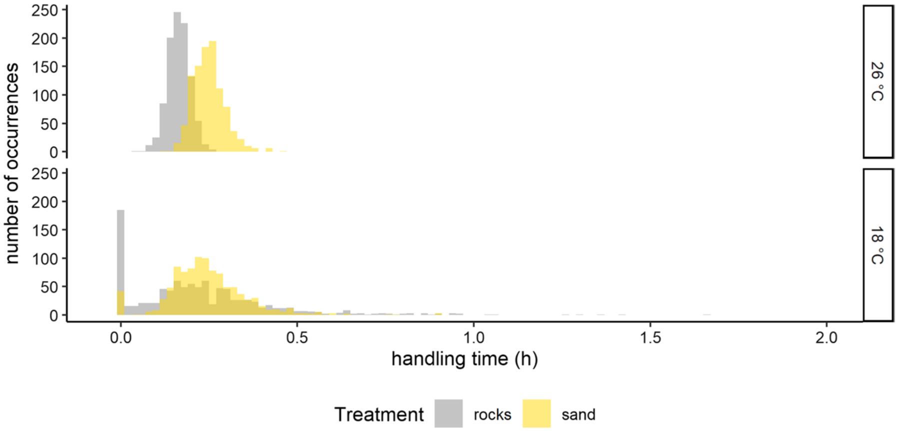

Fig. 4 Variation in bootstrapped estimates of handling time for functional responses of tench at 18 °C (bottom), 26 °C (top), over rocks (gray) and over sand (yellow)

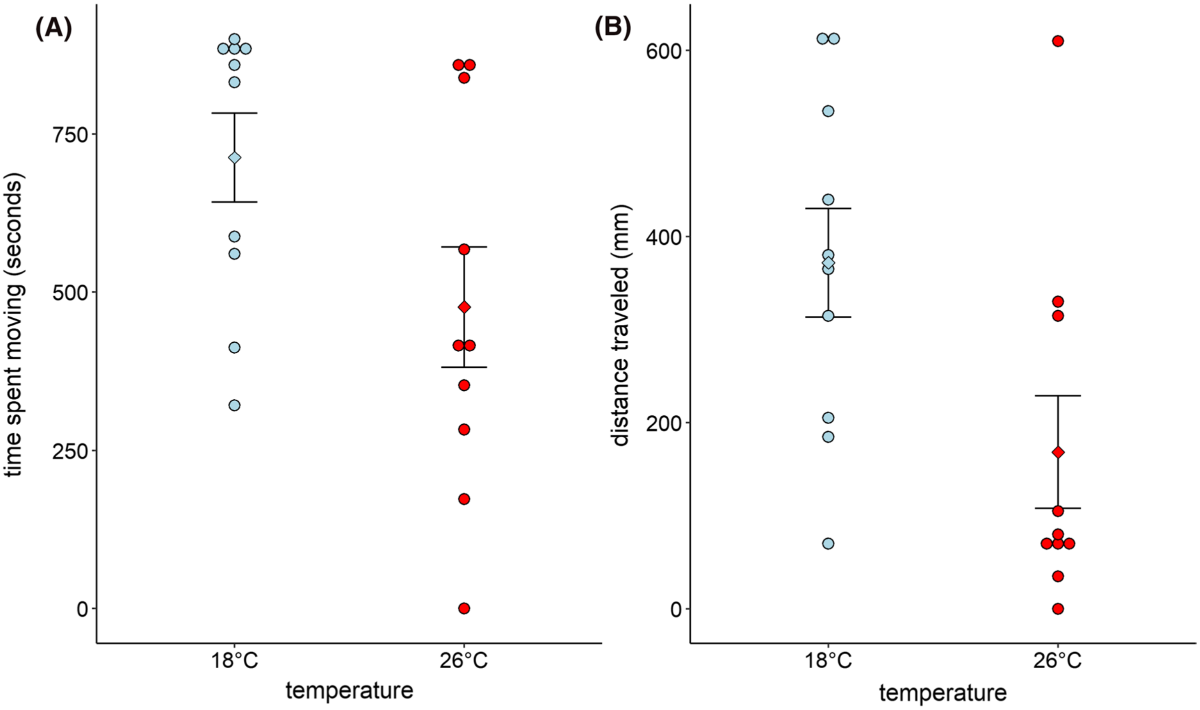

Fig. 5 Differences between snail movement at 18 °C and 26 °C in terms of (**A**) time spent moving (Wilcox test, $P=0.04$) and (**B**) distance traveled (Wilcox test, $P=0.02$). Circles = observations; diamonds and bars = mean and standard error

Discussion

Effect of substrate on feeding and growth

Contrary to the reported preference of tench for fine sediments (Perrow et al. 1996; Rendón et al. 2003; Gallardo et al. 2006; Rowe et al. 2008), its survival, growth, and foraging ability were not impaired on rocky substrate compared to sand. All mesocosms were exposed to the same environmental conditions including temperature (Figures S1 and S2). Over the two-month trials, tench were able to locate and consume sufficient food on rocky substrate such that their increase in mass was not significantly different from the sand treatment; in fact, there was a tendency of higher growth in the rocky mesocosms (Fig. 1). The functional response experiments corroborated this finding: at 26 °C, tench exposed to rocky substrate had a significantly higher maximum feeding rate, although attack rate was higher on sand. When temperature was lowered to 18 °C, the difference in handling time between substrates became negligible and there was still no apparent advantage of feeding on sand compared to rocks. Furthermore, if tench are indeed better adapted to feeding on soft substrate, we might expect to observe a shift in the functional response curve from Type III on rocks to Type II on sand, especially assuming that small snails can use interstitial spaces among rocks as refugia at low prey densities. Such effects have been observed elsewhere: for example, a field study found a lower abundance of physid snails on soft vegetated habitat versus rocky habitat in the presence of a molluscivorous fish (Hansen et al. 2013). In our study, at 18 °C and low prey densities (2–16 snails), tench predation was higher on sand than on rocks, yet the difference at low prey densities was not sufficiently large to shift the functional response curve to Type II (Fig. 3C). Similarly, at 26 °C, despite significant differences in attack rate and handling time between sand and rocks, the consumption on both substrate types resulted in total prey depletion (Type II). The lack of a shift in functional response between substrate treatments indicates that either (1) tench are effective at capturing snails regardless of how snails use substrate as a refuge (e.g. interstitial retreat or burial in sand, both such behaviours were observed when quantifying uneaten snails at the end of the trials), or (2) other predator-avoidance behaviours of this prey species (e.g. emergence from the water) are of greater importance. In either case, such predator-avoidance behaviours are not artifacts of laboratory conditions, but are well-documented strategies of physid snails (Alexander and Covich 1991a, b; Covich et al. 1994; Dewitt et al. 1999; McCarthy and Fisher 2000). However, the second explanation seems unsatisfactory given the results of other mesocosm experiments finding that physid snails *Physella gyrina* did not move to the surface to escape fish predation when provided with physical cover under which snails could hide (Turner 1996; Turner et al. 1999). We conclude that depletion of prey by tench is not likely to be substantially higher on soft substrates compared to rocky ones.

The observed association of tench with soft sediments in the field might be largely attributable to its phytophilic spawning and use of macrophyte beds for juvenile refuge (Wright and Giles 1991; Vriese et al. 1994; Perrow et al. 1996; Wolter 2001). Soft substrate itself might offer additional refuge for tench from piscivores. In aquaria and mesocosms with sand, alarmed individuals will dive to the bottom to stir up a cloud of sediment, perhaps to obscure themselves for predator avoidance (S. Avlijaš, pers. obs.). However, while tench might be captured at higher densities on soft substrates for the aforementioned reasons, our results suggest that this species can exert intensive predation pressure in rocky habitats, especially at elevated temperatures at which the predator–prey interaction becomes destabilizing. An additional consideration is that tench have dispersed through large swathes of rocky habitat in Lake Champlain, Richelieu River, and St. Lawrence River. Contrary to some descriptions of tench as a non-migratory species (Moyle 2002), a recent study of tench movement in the St. Lawrence region documented extensive dispersal activity with individual fish traveling as far as 250 km (Morissette et al. 2021). The ability of tench to feed on rocky substrates, combined with its relatively deep body shape and capacity to grow beyond the gape-size limitation of most piscivorous fishes in the Great Lakes–St. Lawrence River basin (Gaeta et al. 2018), could have facilitated its rapid spread through sections of the St. Lawrence River devoid of soft vegetated habitat. Government factsheets, technical reports, and online databases that discuss tench invariably emphasize its association with fine sediments (Table S8, Supplementary Information). Although tench are abundant in wetlands, unnuanced assumptions about this invader's habitat preferences and ability to thrive in other environments can undermine risk assessment.

Our experiments exclusively used sand (0.05 mm grain size) rather than mud or silt, because without rooted vegetation the fish would easily and frequently suspend finer sediments and thus create a confounding effect of turbidity in our treatments. Significant differences may exist between feeding efficiency on mud/silt versus rocks, or across a broader range of grain sizes, and should be explored in future experiments. Finally, given that tench are often associated with aquatic vegetation and their mouth position is terminal (rather than subterminal), they might feed substantively on epiphytic invertebrates in addition to benthic prey; hence, it would be useful to test a treatment involving macrophytes and epiphytic invertebrates in the experimental arena.

Effect of temperature

A potential confounding factor of our temperature trials is that they were not completely randomized but rather were run in two consecutive series—that is, at 18 °C and 26 °C, respectively. As explained in the Methods, this was a consequence of re-using the same group of fish to ensure proper size (weight) matching and allow a suitable length of time for acclimation to the higher temperature. Functional response experiments with fish have shown that maximum feeding rate is dependent on individual body size (Toscano and Griffen 2013; Schröder et al. 2016). Similarly, our study found that fish weight is correlated with prey consumption rate (Table S7). Although it seems plausible that the feeding performance of the fish could be altered after an intervening time period between the two series of temperature trials, owing perhaps to enhanced learning or adaptive behaviour, we view this as unlikely because (1) we used a prey taxon that is common in the environment from which the fish were collected and is a known dietary component; (2) the fish had several weeks to acclimate to experimental conditions (tanks, substrate, light regime) prior to the onset of the first series of experiments; and (3) in the intervening period, the fish were maintained in the same temperature chamber in which the only environmental change was temperature increase during acclimation. Therefore, the differences in functional response between 26 and 18 °C are more likely attributable to the 8 °C shift in temperature than any other factor.

Tench have a broad thermal tolerance encompassing near freezing temperatures (Penáz et al. 1989) and a critical maximum (CTmax) of 37.8 ± 0.3 °C (S. Avlijaš, unpubl. data; see Supplementary Information), but its preferred temperature range is much narrower (20–26 °C; Penáz et al. 1989). Temperature drove a destabilizing shift in functional response from Type III at 18 to Type II at 26 °C on both rocky and sandy substrates. The loss of the low-density refuge reflects a combination of increased predator efficiency and reduced predator avoidance. In the presence of predator cue, snail movement activity was enhanced at 18 °C compared to 26 °C, and it is possible that increased mobility at the lower temperature improved their success in locating refugia during the 3 h experiment. However, when temperatures decline well below their preferred range, tench might reduce their energetic investment in searching for prey to the point where they cease feeding entirely over winter (Kennedy and Fitzmaurice 1970; Guijarro et al. 2003). Although we did not observe a significant difference in handling time between temperature treatments, variance was higher at 18 °C. At 26 °C, bootstrapped values of handling time follow a normal distribution between 0 and 1; whereas at 18 °C, there was great dispersion consisting of many low values (high maximum feeding rate) and many values larger than 1 (a maximum feeding rate of less than 1 snail per hour; Fig. 4). We speculate that tench feed less frequently at lower temperatures such that hunger levels might be insufficiently standardized by a pre-trial starvation time of 24 h (a common protocol for functional response experiments with fish; Alexander et al. 2014; Barrios O'Neill et al. 2016; South et al. 2018; Mofu et al. 2019; Khosa et al. 2020). If, at low temperatures, tench habitually feed every few days, some individuals already might not have fed for a day or more prior to being placed in acclimation without food and, consequently, can have a higher energy demand resulting in very low handling times. Conversely, fish that fed just prior to the 24 h starvation period could be less inclined to feed during our trial. Lower temperatures are expected to reduce fish activities in general. For example, a telemetry study conducted from January to June in Ireland, though limited to a single individual, showed a positive correlation between temperature and tench movement (Donnelly et al. 1998). This is consistent with increased activity that we observed incidentally while caring for fish in holding tanks as the temperature was ramped up from 18 to 26 °C, and warrants being explored under controlled experimental conditions.

At sites where introduced consumers exhibit Type II responses, the resulting pressure on prey communities could exacerbate competitive impacts on trophically similar consumers. In aquatic environments, shifts in functional response type under changing temperature have been previously reported in a marine fish (South et al. 2018), a marine crustacean (Taylor et al. 2003), and freshwater ciliates (Daugaard et al. 2019). Other studies that examined the influence of temperature on functional responses of fishes (Watz et al. 2014; South et al. 2017; Mofu et al. 2019; Khosa et al. 2020), benthic stream invertebrates (Archer et al. 2019), estuarine mysids (Wasserman et al. 2018), and freshwater copepods (Cuthbert et al. 2019), did not detect shifts in response type, but did observe changes in attack rate, handling time, or both, as a function of temperature. Shifts in functional response type with increasing temperature are typically detected when prey have access to predator-free space. More often than not, functional response experiments are conducted with no consideration of habitat complexity (but see Wasserman et al. 2016; South et al. 2017), thereby forcing a Type II response (Alexander et al. 2012). Conducting functional response experiments in bare arenas can thus pre-empt ecologically-relevant behaviour, even when the variable of interest is temperature rather than substrate complexity.

Given the extent to which functional responses can differ across prey items (Ranta et al. 1984; Guo et al. 2017), future experiments should examine temperature-dependent functional responses of tench to a variety of prey. Gastropods are a major component of tench diets (Brönmark 1994; Gonzalez et al. 2000). Physid snails, in particular, are common in the stomach contents of tench and other benthivorous fishes collected from the St. Lawrence River, Richelieu River, and Lake Champlain (S. Avlijaš, unpubl. data). In these same waterbodies, gastropods are often dominant, in frequency and volume, in stomachs of yellow perch (*Perca flavescens*), white sucker (*Catostomus commersonii*), copper redhorse (*Moxostoma hubbsi*), pumpkinseed (*Lepomis gibbosus*), and American eel (*Anguilla rostrata*), among other species (Latour et al. 1980; Boisclair and Leggett 1989; Mongeau et al. 1992; Watzin et al. 2008; A. Ricciardi, unpubl. data). Therefore, physid snails are appropriate prey for assessing trophic and competitive impacts of tench. However, it would also be useful to test prey that (unlike physids) do not exhibit a negative response to temperature increase, so as to resolve whether the response shift is due to changes in prey escape or predator efficiency. We recognize that more informative assessments of how predator–prey relationships are affected by temperature and habitat complexity would require testing the relative performance of both predator and prey under different habitat conditions (Öhlund et al. 2015).

Our results are consistent with findings of recent meta-analyses of the relationship between functional response and temperature, which show that per capita effects decline as environmental conditions move farther from its the physiological optimum (Englund et al. 2011; Rall et al. 2012; Uiterwaal and DeLong 2020). One study found that the effect of temperature was stronger on attack rate than on handling time, although effects on both parameters were significant (Englund et al. 2011). A more general meta-analysis (Uiterwaal and DeLong 2020) reported that the temperature at which attack rate is optimized is different from that for handling time. Similarly, our results indicate that handling time and attack rate are not affected by temperature equally: differences in handling time between temperatures were not significant, whereas temperature had such a disparate effect on attack rate that it resulted in two different response types. Additional experiments should test predation at more finely resolved temperature increments to identify the optimum for tench foraging efficiency.

In habitats where tench are likely to establish in Lake Ontario, such as nearshore areas and embayments, 26 °C is representative of maximum summer temperatures measured during the past decade (Murphy et al. 2012; Leisti et al. 2015; Gertzen et al. 2016). With climate warming, the number of days of extreme temperatures is expected to increase (Trumpickas et al. 2009). Given that increased temperature alters the relationship between tench and its prey, climate warming may exacerbate tench impacts on some invertebrate populations and, thus, intensify their competitive interactions with native fishes that have overlapping diets.

Conclusions

To the extent that small-scale experiments can accurately scale up to clarify species interactions in the field, the findings of this study have implications for risk assessment and management of a globally successful invader. Elevated temperature can alter the functional response of tench, resulting in increased per capita consumption of low-density prey that could destabilize prey populations. Consequently, we hypothesize that climate warming will intensify tench predation on gastropods, thus driving indirect effects on food webs (e.g. trophic cascades) and exacerbating competition with native benthivorous fishes. These considerations emphasize the need to assess the potential impacts of emerging aquatic invaders under projected climate change scenarios. Further, our results suggest that tench survival, growth, and feeding efficiency are not impaired on the putatively suboptimal environment provided by rocky substrates, and thus can partly explain this species' ability to spread rapidly through heterogeneous systems. Given that habitat plasticity is a characteristic of successful invaders (Vázquez 2006), the capacity of tench to grow and forage well in diverse habitat conditions adds to evidence that it poses a high invasion risk in North American inland waters (Avlijaš et al. 2018).

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Author contributions SA, NEM, and AR designed the study. SA conducted the experiments, analyzed the data, and drafted the manuscript. All authors commented and approved the final version of the manuscript.

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Data availability The data that support the findings of this study are openly available in OSF at osf.io/uam49, https://doi.org/10.17605/OSF.IO/UAM49.

Declarations

Conflict of interest The authors declare that they have no conflict of interest.

Ethical approval All experiments have been approved by McGill University Animal Care Committee (AUP #2014–7560).

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