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THE INFLUENCE OF RUSTY CRAYFISH AND ZEBRA MUSSEL INVASION ON YELLOW PERCH POPULATION DYNAMICS IN NORTH-CENTRAL MINNESOTA LAKES

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Over the last 50 years, Minnesota Department of Natural Resources standard fisheries survey catch rates of Yellow Perch have declined. Yellow Perch *Perca flavescens* are an important, widespread game fish, are essential prey species for Walleye *Sander vitreus* and other piscivorous fish and rely greatly on benthic resources through many life stages. Aquatic invasive species (AIS) like rusty crayfish *Faxonius rusticus* and zebra mussels *Dreissena polymorpha* have the potential to change water quality, vegetation and prey assemblages in aquatic systems and could cause shifts in energy flow, subsequently altering growth, condition, and maturity of native fish species. In this study, we investigated potential effects of these AIS by sampling 1,783 Yellow Perch from 14 lakes in north central Minnesota. We found that Yellow Perch growth, condition, mortality, and crayfish consumption were not significantly different between groups of lakes with only rusty crayfish present, only zebra mussels present, both AIS present, and neither AIS present. Additionally, variation in these metrics between lakes was not explained well by crayfish consumption. Lake effect and individual variation between populations was more important than the presence or absence of either AIS, indicating that Yellow Perch appear to be adaptive to changing lake conditions resulting from establishment of zebra mussels and/or rusty crayfish.

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Abstract.- Over the last 50 years, Minnesota Department of Natural Resources standard fisheries survey catch rates of Yellow Perch have declined. Yellow Perch *Perca flavescens* are an important, widespread game fish, are essential prey species for Walleye *Sander vitreus* and other piscivorous fish, and rely greatly on benthic resources through many life stages. Aquatic invasive species (AIS) like rusty crayfish *Faxonius rusticus* and zebra mussels *Dreissena polymorpha* have the potential to change water quality, vegetation and prey assemblages in aquatic systems and could cause shifts in energy flow, subsequently altering growth, condition, and maturity of native fish species. In this study, we investigated potential effects of these AIS by sampling 1,783 Yellow Perch from 14 lakes in north-central Minnesota. We found that Yellow Perch growth, condition, and mortality were not significantly different between groups of lakes with only rusty crayfish present, only zebra mussels present, both AIS present, and neither AIS present. Additionally, even though the probability of crayfish presence in stomach contents was different between groups, variation in these metrics among lakes was not explained well by crayfish consumption. Lake effect and individual variation among populations was more important than the presence or absence of either AIS, indicating that Yellow Perch appear to be adaptive to changing lake conditions resulting from establishment of zebra mussels and/or rusty crayfish.

Introduction

Yellow Perch *Perca flavescens* are an important game fish and prey species for top predators like Walleye *Sander vitreus* and Northern Pike *Esox lucius* (Brown et al. 2009; Glade et al. 2023; Sheppard et al. 2015). Larval Yellow Perch are largely pelagic and depend on a diet of zooplankton (Post and McQueen 1998; Whiteside et al. 1985; Wu and Culver 1992). Yellow Perch spend much of their post-larval life in littoral areas, where they primarily consume small fish and invertebrates (Brown et al. 2007; Whiteside et al. 1985) and use benthic structures such as logs and submerged vegetation for shelter and reproduction (Brown et al. 2009). Yellow Perch demonstrate high trophic flexibility and can exhibit broad distributions of benthivory between systems, as opposed to more consistently benthivorous species like the Rock Bass *Ambloplites rupestris* and Pumpkinseed *Lepomis gibbosus* (Vander Zanden and Vadeboncoeur 2002). Even within the same system, Yellow Perch can exhibit individual specialization of habitat use, with a distinction in prey consumption between pelagic and littoral Yellow Perch (Marklund et al. 2019). In large, meso-oceanic lakes (i.e., the Great Lakes System), Yellow Perch can have different feeding behavior and larval survival than smaller lakes due to differences in system function, such as prey availability and predator densities (Fulford et al. 2006). In large lakes, Yellow Perch condition, growth, and diet can even change between different basins (Arco et al. 2015).

Over the last 50 years, Minnesota Department of Natural Resources standard fisheries survey catch rates of Yellow Perch have declined (Bethke and Staples 2015). While Walleye stocking throughout the state increased over the same time period, there is no evidence to suggest increased Walleye abundance has caused the decline in Yellow Perch catch rates (Beck et al. 1996). Some climate-related factors such as winter severity (Farmer et al. 2014), spring storm events (Roseman et al. 1999), ice cover duration (Brandt et al. 2022; Dippold et al. 2020) and increased peak summer and post ice-off temperatures (Brandt et al. 2022) are potential correlates or predictors of Walleye and Yellow Perch recruitment. Environmental degradation due to metal contamination can lead to measurable effects of metabolic capacities, decreased growth rates, and lower condition indices in Yellow Perch (Rajotte and Couture 2002), while degradation due to nutrients and sediment loading can lead to aquatic vegetation loss and decrease landing zones for spawning perch, decreasing recruitment (Arco et al. 2015). The decrease in phosphorous loading to Lake Erie after 1970 is correlated with improved reproduction and larval survival of both Yellow Perch and Walleye (Culver et al. 2009). An increase in water clarity in Lake Shaokatan, Minnesota was associated with a decrease in Yellow Perch mean total length and relative weight, likely because of increased plant growth, improved spawning habitat, higher recruitment rates, and increased intraspecific competition associated with reportedly higher abundance (Skolte et al. 2021).

Invasive species are an ongoing ecological concern for fisheries globally (Gallardo et al. 2016). Rusty crayfish *Faxonius rusticus* are found throughout Minnesota waters and are managed as a regulated aquatic invasive species (AIS) by the Minnesota Department of Natural Resources (MNDNR 2023a). Rusty crayfish are native to the Ohio River Basin but have spread into and past the Great Lakes states through intentional and incidental human introduction for both macrophyte control and bait, and through natural movement through channels and streams (Taylor and Redmer 1996). Minnesota rusty crayfish populations began quickly spreading in the 1990s to inland lakes in Lake and St. Louis County and eventually to north-central counties like Becker, Cass, Itasca, and Beltrami (MNDNR 2023a). Due to greater size and higher feeding rates and metabolisms, rusty crayfish are more aggressive and successful predators than native crayfish (Kuhlmann et al. 2008). The establishment of rusty crayfish populations depends on many factors, such as maximum water depth and drainage (Olden et al. 2011), connectivity between systems (Byron and Wilson 2001), substrate composition (Kershner and Lodge 1995), dissolved calcium concentrations (Edwards et al. 2013), and predator assemblages (Tetzlaff et al. 2010). Once established, however, rusty crayfish are capable of outcompeting native crayfish (Olden et al. 2011), dramatically altering littoral habitats (Wilson et al. 2004), decreasing populations of zoobenthic taxa (McCarthy et al. 2006), influencing benthivory of fish populations (Nilsson et al. 2012), and decoupling littoral and pelagic energy flows in lake food webs (Kreps et al. 2016).

Another species of concern in Minnesota lakes is zebra mussels. Unlike rusty crayfish, whose spread is limited mostly to human introduction or well-connected lake chains (Taylor and Redmer 1996), zebra mussels have many dispersal mechanisms (Benson et al. 2023) and have been documented in almost 600 lakes and river stretches throughout Minnesota (MNDNR 2023b). Zebra mussels are native to Eastern Europe and Western Russia and were introduced into Minnesota via contaminated cargo ship ballast water on Lake Superior in 1989 (MNDNR 2023c). They are managed by the Minnesota Department of Natural Resources as a prohibited invasive species to slow the spread (MNDNR 2023c). Females are very fecund, producing an estimated 960,000 embryos per year in the form of microscopic, free-living larvae called veligers (Keller et al. 2007). Zebra mussels can spread rapidly within a water body due to their planktotrophic larvae that can be carried by currents and wind-driven advection throughout a lake (Johnson and Carlton 1996). New predators of zebra mussels within infested waters have a limited role in suppressing zebra mussel populations (Molloy et al. 1997), contributing to their rapid spread. Zebra mussels are efficient filter feeders that can clear small particles ranging from less than 1 µm (Sprung and Rose 1988) up to 1.2 mm (Horgan and Mills 1997) at rate up to 1 L per zebra mussel per day (Sprung and Rose 1988). Zebra mussels also are particular about which particles they use, and which get excreted as pseudofeces (Baker et al. 1998). Zebra mussel rejection of *Microcystis aeruginosa* promotes algal blooms of this toxic blue-green algae (Vanderploeg et al. 2001), which can result in late post-introduction decreases in water clarity in some systems (Pillsbury et al. 2002). The impact of these invasive mussels is widespread, including decreased Chlorophyll *a* concentration (Qualls et al. 2007), increased water clarity (Barbiero et al. 2009), accelerated extinction rates of native mussel populations (Ricciardi et al. 1998; Schloesser et al. 2006; Stayer and Malcom 2007), undersaturation of dissolved oxygen (Caraco et al. 2000), and fouled water intakes (Connelly et al. 2007). The Walleye population in Mille Lacs Lake, Minnesota has declined, which coincides with a decrease in thermal-optical habitat area caused by warming water temperatures and increased water clarity attributed to the establishment of zebra mussels *Dreissena polymorpha* (Hansen et al. 2019). Such documented changes in Walleye populations may subsequently affect Yellow Perch populations, considering their well-documented predator-prey relationship (Post and Rudstam 1992; Rudstam et al. 1996).

There has been limited documentation of the direct impact rusty crayfish have on Yellow Perch, or of the synergistic impacts of rusty crayfish and zebra mussel presence. Rusty crayfish can forage on zebra mussels (Naddafi and Rudstam 2014) and flourish in the increased food web dependency on littoral energy sources post zebra mussel invasion (Higgins and Vander Zanden 2010; McEachran et al. 2019). This relationship is supported with the increased Smallmouth Bass *Micropterus dolomieu* and crayfish densities in Mille Lacs Lake following zebra mussel introduction (Hansen et al. 2019; Kumar et al. 2016). In a stream experiment, *Faxonius* spp. decreased zebra mussel density by 31% and gastropod densities by 54%, suggesting crayfish can successfully forage on invasive zebra mussels (Perry et al. 2011). Zebra mussels might also change the foraging behavior of crayfish (Beekey et al. 2004). In a laboratory study, the poor vision of crayfish led to decreased consumption of free-swimming and crawling invertebrates that are disguised in zebra mussel clusters, while the tendency of crayfish to burrow between zebra mussel clusters resulted in no significant effect on crayfish foraging success for burrowing invertebrates (Beekey et al. 2004). A mesocosm experiment testing the interactive effects of dreissenid mussels and crayfish density on various crayfish metrics found increased growth only in rusty crayfish, not virile crayfish *Faxonius virilis*, suggesting that invasive crayfish are better able to exploit mussel food resources and that their establishment, spread, and impact could be facilitated by dreissenid mussels (Glon et al. 2017). A recent study looking at the diets of Yellow Perch in two systems with and without rusty crayfish present found that Yellow Perch <100 mm and >200 mm in length had similar consumption rates of crayfish, but that Yellow Perch 100 – 200 mm in length had much higher IRI values for crayfish in the system with rusty crayfish (Kvam 2023). This suggests that rusty crayfish presence affects the diet patterns of Yellow Perch, though sample size is limiting, and further research is required to fully understand the combined effects zebra mussels and rusty crayfish have on fish populations in natural systems. Therefore, the first objective of this study is to test for differences in growth, maximum size, condition, length at maturity, and crayfish consumption of Yellow Perch populations in lakes based on rusty crayfish and zebra mussel invasion status. The second objective is to determine how these population metrics change as crayfish become prevalent in Yellow Perch stomach contents.

Methods

Study Area

The 14 lakes used in this study have been classified into four AIS groups: rusty crayfish and zebra mussels present [RCZM; Cass, Leech (Kabekona Bay), Pike Bay, Woman lakes], only rusty crayfish present (RC; Little Boy, Wabedo, Siseebakwet lakes), only zebra mussels present, (ZM; Bemidji, North Star, Little Winnibigoshish lakes), and neither present (NONE; Blackduck, Grace, Plantagenet, Turtle lakes; Table 1). All are found within north-central Minnesota (Figure 1), with Yellow Perch as an important prey species and all major predators present (Northern Pike, Walleye, and Largemouth Bass *Micropterus nigricans*), providing the opportunity to conduct further research on how invasive species are affecting fish population dynamics. All lakes demonstrate typical morphology and growing seasons of temperate lakes found in the Northern Lakes and Forests Ecoregion of north-central Minnesota (White 2020; Table 1).

Sampling Design

Field data were collected through boat electrofishing from 18 Aug - 9 Sep 2022 during the daytime with one or two dip-netters, and following protocol as described by Reynolds and Dean (2020). The target sample size for each system was 150 Yellow Perch, with 50 fish from each of the three size bins: <100 mm, 100 mm – 200 mm, >200 mm. At each lake, four timed runs and additional targeted runs were completed in different areas of the lake to represent diverse habitat throughout each system (Mrnak 2021). The timed runs ranged from 15-60 minutes to account for catch rates and tank capacity on the boat. All Yellow Perch in the timed runs were collected and catch per unit effort (CPUE) in fish/hour was calculated. Any fish over the targeted sample size of 50 were counted but released. Additional runs were then completed for up to 90 minutes to attempt to fill incomplete bins. Sampled Yellow Perch were then euthanized in an overdose solution of MS222 (>250 mg/kg) and sodium bicarbonate (buffer ratio of 1:2, mass:mass of MS222) for 15 minutes and frozen for later processing, with the leftover solution diluted and disposed of through the sanitary sewer (AVMA 2020). Wet mass (g) and total length (mm) were documented from five fish in each length bin and used to determine conversion factors to account for shrinkage or changes in mass from freezing.

Laboratory Procedures

Frozen Yellow Perch were thawed in cool water baths, then total length was measured to the nearest mm and mass was measured to the nearest 0.01 g. Next, fish were sexed and placed into four categories: immature male, mature male, immature female, and mature female. This was done by dissecting fish and conducting an internal examination of gonadal structures. Sex was determined by the presence of an ovary for females or paired testes for males (Craig 2000). Immature females had a slightly pink ovary and immature males had long and thin testes that were translucent in color (Craig 2000). Mature females had larger, more vascularized ovaries with oocytes present, while mature males were determined to have smooth, white gonads with the presence of milt (Craig 2000). Mature and immature females were the only two categories used in estimation of length at 50% maturity (L50). Next, sagittal otoliths were removed from the inner ear within the skull following procedures outlined in Secor et al. (1992). Otoliths were dried in open vials and stored for later aging and age estimation was completed by a single experienced reader. Otoliths of Yellow Perch ≤ 4 years old were aged using the glycerol method as recommended by Gebremedhin et al. (2019). A whole, clean otolith was immersed in pure glycerol in a petri dish and examined under a 10x stereoscopic microscope using a bright light. Otoliths of Yellow Perch > 4 years old were aged using the crack and burn method as recommended by Christensen (1964). A whole, clean otolith was lightly charred over a candle, and then cracked by applying pressure to the center of the otolith against a flat surface. A drop of oil was then placed over the cracked surface to improve visibility of the annuli. Otoliths were aged for each fish by counting annulus rings. Finally, stomachs were cut open to examine the contents and marked as empty or diet present. In stomachs with diets, presence of crayfish was determined binomially as present or absent (Baker et al. 2013; McQueen and Griffiths 2004).

Data Analysis

All data were analyzed using program R (R Core Team 2023) via RStudio (RStudio Team 2023), where $\alpha = 0.05$. First, total lengths and masses were adjusted with the frozen-wet mass conversion linear regressions, where frozen values (x) were used to predict fresh values (y) for Yellow Perch that were not measured immediately after euthanizing (Figure B1). These length and weight equations were determined for each of the three length bins, as smaller differences in weights and lengths are more impactful for smaller Yellow Perch than large. Frequency of occurrence (%F; Baker et al. 2013) was calculated for all Yellow Perch ≥ 100 mm in each lake by dividing the total number of stomachs with crayfish by the total number of stomachs with a diet. Yellow Perch ≤ 100 mm were not used in this calculation because crayfish consumption does not typically occur until after Yellow Perch exceed 100 mm (Kvam 2023). Mean maximum length (Lmax; VanderBloemen et al. 2020) was calculated by averaging the total lengths of the largest 15 fish caught from each system (Holbrook et al. 2022). Relative condition (Kn) was calculated for Yellow Perch using the formula:

$$Kn = W/W'$$

Where *W* is the weight of an individual fish and *W'* is the length-specific expected weight for a fish as predicted by a weight-length regression equation calculated for all 14 study lakes combined (Le Cren 1951). Mean Kn was then calculated for each lake (Table A1). Female length at 50% maturity (L50; Holbrook et al. 2022) was determined by plotting logistic regression curves of female Yellow Perch maturity (McDonald 2014). Confidence intervals (95%) around mean L50 values were calculated using bootstrapping methods in the boot package (Canty and Ripley 2022), and lakes without enough females sexed were not included in the analysis (Table A2). The sex of some Yellow Perch was undeterminable after the freeze-thaw process, and not included in maturity calculations. A von Bertalanffy growth equation (von Bertalanffy 1938; Taylor 2013) was developed for each lake and used to calculate length at age for ages zero through five (Table A3). Length at age was not developed for Yellow Perch ages 6 and older due to low sample size in some of the study lakes.

Five logistic models were created, including a null model, to predict the probability of crayfish presence in stomach contents by total length of Yellow Perch (Table 2; McDonald 2014). AIS grouping was used as either an additive or interactive effect in the developed models. Akaike information criterion adjusted for small sample size (AIC_c) was used for model selection (Akaike 1974; Hurvich and Tsai 1989; Mazerolle 2023). A generalized linear model with lengths from all four AIS groups combined was used to confirm the consumption of crayfish by Yellow Perch ≥100 mm. Based on the figure and previous studies (Kvam 2023), Yellow Perch do not typically consume crayfish at smaller lengths, and were ultimately left out of the %F calculations to avoid underestimating values.

The four AIS groups were used to group lakes for testing differences in mean values. An analysis of variance (ANOVA) was performed on mean %F, Lmax, length at age, Kn, and female L50 values among groups. Assumptions were checked using a Shapiro-Wilk test ($p > 0.05$) for normality and a Bartlett test ($p > 0.05$) for equal variance, and all data passed except for length at age 4. We compared a Kruskal-Wallis and ANOVA for length at age 4, and there were minimal differences in p-values, so the decision was made to perform a traditional ANOVA on all data for uniformity. Linear regressions were developed to determine relationships between %F of crayfish and all other metrics (Lmax, length at age, Kn, and L50; McDonald 2014).

Results

Crayfish Consumption

Of the 1,783 fish processed, 1,625 Yellow Perch stomachs were analyzed. Some of the stomach contents on small Yellow Perch were indiscernible after the freeze-thaw process, and were excluded. Nine hundred and sixty-three had observable contents, and 545 were from Yellow Perch ≥ 100 mm. The relationship between crayfish presence in stomach contents and total length of Yellow Perch is best explained by an interactive model, where the relationship differs between AIS groups (Table 2; Figure 2). The probability of crayfish presence increases substantially once Yellow Perch exceed 100 mm in total length (Figure 2). Lakes with rusty crayfish or both invasive species have an increased probability of crayfish presence in stomach contents for Yellow Perch > 150 mm (Figure 2). Lakes with zebra mussels have the next greatest probability, and lakes without either AIS have the lowest probability (Figure 2). Mean %F was 23, 40, 61, and 27% for groups NONE, RC, RCZM, and ZM, respectively (SD=27, 12, 14, and 25; Table 3). Differences in mean %F among groups were not significant ($F_{3,10} = 2.6$, P=0.11; Table 4), and variation within groups was very high for lakes with zebra mussels only or neither AIS present (Figure 3). Frequency of occurrence was the highest in Kabekona Bay Lake (74%) and lowest in Blackduck (0%), Grace (0%), and Little Winnibigoshish lakes (0%, Table 5, Figure 3).

Mean Maximum Length

Mean maximum length was 240, 262, 263, and 238 mm for groups NONE, RC, RCZM, and ZM, respectively (SD=28, 32, 25, 4; Table 3). Differences in mean Lmax among groups was not significant ($F_{3,10} = 1.0$, P=0.43; Table 4), and variation within groups was high for all except for lakes with just zebra mussels, which ranged from 236 to 243 mm (Table 5, Figure 4). Lakes without any crayfish consumption (Little Winnibigoshish, Blackduck, and Grace lakes) had some of the the lowest Lmax values (236, 222, and 242 mm, respectively; Table 5). The two lakes with the highest Lmax value were Pike 1691 Bay Lake (292 mm) and Siseebakwet Lake (299 mm), both of which are infested with rusty crayfish (Table 5). They are closely followed, however, by Lake Plantagenet (280 mm), which does not have rusty crayfish (Table 5). Lmax did not have a significant relationship with %F (P = 0.36; Table 6; Figure 5).

Length at Age

Differences in mean length at age among groups were not significant for any ages (Table 4). Although there were no significant differences, some interesting patterns were apparent. Mean length at age was greatest in lakes with zebra mussels for all ages and was consistently low for lakes with rusty crayfish (Table 3; Figure 6). Mean length at age was greater in lakes with both invasive species than in rusty crayfish only lakes for all ages but zero. Length at age had a significant, negative relationship with %F at age-1 (P = 0.045; Figure 7). Interestingly, p-values increased with age, except for ages zero and one (P = 0.07, 0.05, 0.20, 0.34, 0.48, 0.64). Turtle and Little Boy lakes showed the smallest length at age values, compared to Lake Plantaganet, which had some of the greatest lengths at age (Table 5).

Relative Condition

Kn was 1.02, 0.98, 1.02, and 1.00 for groups NONE, RC, RCZM, and ZM, respectively (SD = 0.10, 0.04, 0.04, 0.08; Table 3). Differences in mean Kn among groups were not significant, with no distinguishable patterns among groups ($F_{3,10}$ = 0.3, P = 0.83; Table 4; Figure 8). Relative condition was not related to %F (P = 0.29; Table 6; Figure 9). Blackduck Lake had the highest mean Kn value (1.12), followed closely by Lake Plantagenet (1.10; Table 5). North Star Lake had the lowest mean Kn value (0.91), followed closely by Grace Lake (0.92; Table 5).

Length at 50% Maturity

Due to low sample size, Bemidji, Cass, and Woman lakes were not included in L50 analysis. Mean L50 was 96, 95, 95, and 96 mm for groups NONE, RC, RCZM, and ZM, respectively (SD = 9, 2, 5, 1; Table 3). Differences in mean L50 among groups was not significant ($F_{3,10}$ = 0.1, P = 0.99), though variation within groups was overall low (Figure 10; Table 4). Blackduck Lake had the highest L50 value (105 mm) and Turtle Lake had the lowest (88 mm; Table 5). L50 did not have a significant relationship with %F (P = 0.17; Table 6; Figure 11).

Discussion

The findings of this study suggest that lake effect and variation among populations are more important than the presence or absence of rusty crayfish and zebra mussels in determining Yellow Perch population dynamics, indicating that this species appears to be adaptive to changing lake conditions (Hansen et al. 2020). Increased spatial complexity does not exclusively inhibit feeding by Yellow Perch, which are able to exploit increased prey provided by zebra mussel colonies (Cobb and Watzin 2002), even if their strike success is lower (Mayer et al. 2011a). In Oneida Lake, more zebra mussels led to no change in survival, diet, or numbers of age-0 Yellow Perch and no differences in adult Yellow Perch growth but did result in an increased reliance on benthos and zooplankton of age-3 perch (Mayer et al. 2011b). This is surprising, as zebra mussels can reduce pelagic resources (Higgins and Vander Zanden 2010) and age-0 Yellow Perch are very dependent upon pelagic food sources until they reach lengths exceeding 25-30 mm (Post and McQueen 1998; Wahl et al. 1993; Whiteside et al. 1985; Wu and Culver 1992). There are a few explanations for why this interaction does not result in the decreased survival of age-0 Yellow Perch (Persson et al. 2000; Schael et al. 2011). One study suggests that density-dependent growth is rare during larval stages because larval Yellow Perch tend to feed at maximum levels over a wide range of larval densities (Persson et al. 2000), so it is possible that post-zebra mussel zooplankton densities are still high enough for optimal feeding rates of larval perch. Another study found that Yellow Perch did not typically consume prey in the upper limits of their gape (Schael et al. 2011) so there may be less preferable, but still usable resources to larval perch as smaller, preferable zooplankton sources are depleted. Condition shifts within a system can affect Yellow Perch populations (Skolte et al. 2021), but effects of invasive species on ecological processes and fish populations is variable (Caraco et al. 1997; Barbiero et al. 2009) and cannot necessarily be applied across all unique systems.

Results also revealed that crayfish consumption by Yellow Perch varies greatly between systems and, while it seems to be most probable in lakes with rusty crayfish, percent occurrence neither differs between AIS groupings nor is related to maximum length, length at age, condition, or maturity. The only exception was for length at age 1, where a significant, negative relationship occurred between %F and length at age (P =

0.05). After age 1, the p-value continued to increase, suggesting that any influence crayfish consumption may have on younger perch is lost as fish age. It not surprising that rusty crayfish presence increased probability of occurrence of crayfish, especially for larger fish, and in the presence of zebra mussels. While differences in probability of crayfish consumption was observed, correlations between frequency of occurrence and population dynamics were not. It was theorized that rusty crayfish and zebra mussels would have a synergistic relationship when both are present in lakes, and that this would lead to significant differences in Yellow Perch population dynamics. Rusty crayfish can exploit zebra mussels as a novel food source (Glon et al. 2017; Perry et al. 2011) while also benefitting from the re-allocation of pelagic energy sources to benthic sources (Higgins and Vander Zanden 2010) and increased benthic macroinvertebrate communities (Higgins and Vander Zanden 2010, Ward and Ricciardi 2013). This is supported by experiments documenting rusty crayfish ability to forage within zebra mussel clusters (Beekey et al. 2004) and their improved growth rates in the presence of zebra mussels (Glon et al. 2017). Rusty crayfish are larger and more aggressive than native crayfish and can increase overall crayfish densities when introduced (Kuhlmann 2008). It is possible that any increase in crayfish densities may not increase the overall crayfish consumption of Yellow Perch, a relatively small fish with gape limitations (Schael et al. 2011), since rusty crayfish are more aggressive, exhibit better predator avoidance, and have larger chelae (Garvey et al. 1994; Szela and Perry 2013). The three lakes without any observed crayfish in stomach contents were Blackduck, Grace, and Little Winnibigoshish, and it is possible that poor crayfish densities have resulted in alternative foraging.

Yellow Perch are an important game fish (Brown et al. 2009) and prey species (Glade et al. 2023), but successful management of their populations is likely complicated, and our results indicate that post larval perch may not necessarily benefit from rusty crayfish and zebra mussel control. Trying to reduce AIS numbers can be costly and labor intensive, producing mixed results (Hansen et al 2013; MNDNR 2023d). After intensive trapping efforts of rusty crayfish, researchers in northern Michigan were faced with a threefold increase in pre-harvest densities during removal efforts (Kvistad et al. 2023), while researchers in Wisconsin were rewarded with a 99% population decline over 8 years and no rebound 4 years post-harvest (Hansen et al. 2013). Many efforts have been put towards finding an effective control method for zebra mussels in Minnesota lakes, leading to treatments like Zequanox paired with physical removal (Lund et al. 2017), and copper in the form of EarthTec QZ (Fieldseth and Sweet 2016). Unfortunately, all current treatments of zebra mussels documented by the MN DNR have resulted in the repopulation of adult or juvenile zebra mussels within a few years post-treatment (MNDNR 2023d). While zebra mussel control may be important for other species and for human recreation, Yellow Perch are resilient and may not respond as readily to the introduction or removal efforts of zebra mussels. Fisheries management with direct harvest limits may not be a great option either. Current Yellow Perch harvest rates may not pose long-term negative effects, and environmental factors could be more influential on fish populations (Zhang et al. 2018). Mosel et al. (2015) found that bag limits for Yellow Perch in Wisconsin lakes would need to be reduced from 25 to less than 7 to reduce harvest by more than 25%, and that the minimum length limits were not predicted to improve yield. An indirect way to manage Yellow Perch populations is through management of top-down predators (Hartman and Margraf 2005; Knapp et al. 2020). Lower diversity and abundance of predator populations can lead to high densities of small Yellow Perch and stunted populations (Ridgway and Chapleau 1994). Predation can change the year-class strength of Yellow Perch (Hartmann and Margraf 2005), and so continued selective Walleye and Northern Pike harvest and stocking could be used to change what age-class of Yellow Perch are being predated on (Beck et al. 1996). A decrease in intraspecific competition of medium-sized Yellow Perch could improve growth and condition of remaining Yellow Perch (Skolte et al. 2021). The biggest caveat, however, is that decreasing abundance would only reduce intraspecific competition if prey resources were a limiting factor in Yellow Perch growth (Ridgeway and Chapleau 1994).

Over 1,700 Yellow Perch from 14 different lakes were sampled, and it is unclear whether additional lakes would reveal any significant relationships between Yellow Perch populations and rusty crayfish or zebra mussel invasions across a similar geographic scale. Many researchers have tried to link various climate-, invasive species-, and environmental-related factors to changing Yellow Perch populations, but with very mixed results (Hansen et al. 2022). The results of this study suggest that Yellow Perch populations do not change synchronously across all systems, even with similar environmental inputs and ecological changes. With current available information, Yellow Perch management would be best done on a lake-by-lake basis, though detailed and accurate historical fisheries records and environmental impact assessments are not always available. In order to streamline this management and have meaningful and broadly applicable recommendations, we need to work towards better understanding the environmental, ecological, and anthropogenic factors driving Yellow Perch populations.

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TABLES

Table 1. Summary of 14 study lakes, including aquatic invasive species (AIS) group, Minnesota Department of Natural Resources Division of Waters unique identification number (DOW), county, AIS present, surface area (Area in hectares), and max depth (Max) in meters for the 14 lakes in this study. AIS groups include rusty crayfish *Faxonius rusticus* only (RC), both rusty crayfish and zebra mussels *Dreissena polymorpha* (RCZM), zebra mussels only (ZM), and neither (NONE). Other AIS observed include faucet snail *Bithynia tentaculata* and starry stonewort *Nitellopsis obtusa*.

Lake	AIS Group	DOW	County	AIS present	Area (Ha)	Max (m)
Bemidji	ZM	04013002	Beltrami	Zebra mussels	2,668	23.16
Blackduck	NONE	04006900	Beltrami	Faucet snail	1,097	8.53
Cass	RCZM	04003000	Beltrami	Zebra mussels, rusty crayfish, starry stonewort	6,457	36.58
Grace	NONE	29007100	Hubbard	None	347	12.80
Kabekona Bay	RCZM	11020302	Hubbard	Zebra mussels, rusty crayfish, starry stonewort	382	28.04
Little Boy	RC	11016700	Cass	Zebra mussels, rusty crayfish	587	22.56
North Star	ZM	31065300	Itasca	Zebra mussels	336	27.43
Pike Bay	RCZM	11041500	Cass	Zebra mussels, rusty crayfish	192	28.96
Plantagenet	NONE	29015600	Hubbard	Zebra mussels*	1,024	19.81
Siseebakwet	RC	31055400	Itasca	Rusty crayfish	490	32.00
Turtle	NONE	04015900	Beltrami	Starry stonewort	650	13.72
Wabedo	RC	11017100	Cass	Rusty crayfish	496	28.96
Little Winnibigoshish	ZM	31085000	Itasca	Zebra mussels, faucet snail	405	8.53
Woman	RCZM	11020100	Cass	Zebra mussels, rusty crayfish	2,233	16.46

*An adult zebra mussel was found in Plantagenet in 2023, but it will be grouped as having none since an established population with high densities has not been confirmed.

Table 2. Summary of generalized linear model selection for predictors of the occurrence of crayfish in Yellow Perch stomach contents (Cray_YN) by total length in mm (TL). Effects include aquatic invasive species group (AIS). Model selection results include Akaike information criterion adjusted for small sample size (AIC_c), the change in AIC_c between subsequent models (ΔAIC_c), Akaike weights (w_i), and the number of parameters (K).

Model	AIC_c	ΔAIC_c	w_i	K
Cray_YN ~ TL * AIS	738.08	0	0.99	8
Cray_YN ~ TL + AIS	747.35	9.27	0.01	5
Cray_YN ~ TL	752.73	14.66	0.00	2
Cray_YN ~ AIS	1021.67	283.59	0.00	4
Cray_YN ~ 1	1029.68	291.60	0.00	1

Table 3. Summary of mean and standard deviation (SD) values. Metrics include crayfish frequency of occurrence in stomach contents (%F), maximum length (Lmax), relative condition (Kn), female length at 50% maturity (L50), length at age 0 (LA0), length at age 1 (LA1), length at age 2 (LA2), length at age 3 (LA3), length at age 4 (LA4), and length at age 5 (LA5). AIS groups include no AIS present (NONE), rusty crayfish present (RC), rusty crayfish and zebra mussels present (RCZM), and zebra mussels present (ZM).

	NONE		RC		RCZM		ZM	
Metrics	Mean	SD	Mean	SD	Mean	SD	Mean	SD
%F	23	27	40	12	61	14	27	25
Lmax	240	28	262	32	263	25	238	4
Kn	1.02	0.10	0.98	0.04	1.02	0.04	1.00	0.08
L50	96	9	95	2	95	5	96	1
LA0	53	7	46	5	46	5	54	6
LA1	98	7	91	13	91	6	104	8
LA2	137	17	131	22	132	10	146	16
LA3	168	25	166	28	168	11	180	20
LA4	195	30	197	30	200	11	208	24
LA5	217	34	223	29	228	10	232	28

Table 4. Summary of ANOVA results with aquatic invasive species group (AIS) as an explanatory variable. AIS groups include no AIS present, rusty crayfish present, rusty crayfish and zebra mussels present, and zebra mussels present. Response variables include crayfish frequency of occurrence in stomach contents (%F), maximum length (Lmax), relative condition (Kn), female length at 50% maturity (L50), length at age 0 (LA0), length at age 1 (LA1), length at age 2 (LA2), length at age 3 (LA3), length at age 4 (LA4), and length at age 5 (LA5). Values include degrees of freedom (df) for the numerator and denominator, F-value, and P-value.

Relationship	df numerator	df denominator	F-value	P-value
%F ~ AIS	3	10	2.6	0.11
Lmax ~ AIS	3	10	1.0	0.43
Kn ~ AIS	3	10	0.3	0.83
L50 ~ AIS	3	10	0.1	0.99
LA0 ~ AIS	3	10	1.8	0.21
LA1 ~ AIS	3	10	1.7	0.23
LA2 ~ AIS	3	10	0.5	0.68
LA3 ~ AIS	3	10	0.3	0.85
LA4 ~ AIS	3	10	0.2	0.90
LA5 ~ AIS	3	10	0.2	0.89

Table 5. Summary of crayfish frequency of occurrence in stomach contents of Yellow Perch ≥100 mm (%F), mean relative condition (Kn), mean maximum length (Lmax), mean female length at 50% maturity (L50), length at age 0 (LA0), length at age 1 (LA1), length at age 2 (LA2), length at age 3 (LA3), length at age 4 (LA4), and length at age 5 (LA5), for Lakes Bemidji (BEM), Blackduck (BLA), Cass (CAS), Grace (GRA), Kabekona Bay (KAB), Little Boy (LIT), North Star (NOR), Pike Bay (PIK), Plantagenet (PLA), Siseebakwet (SIS), Turtle (TUR), Wabedo (WAB), Little Winnibigoshish (WIN), and Woman (WOM). L50 was excluded for lakes with small sample sizes of immature Yellow Perch.

Lake ID	%F	Lmax (mm)	L50 (mm)	LA0 (mm)	LA1 (mm)	LA2 (mm)	LA3 (mm)	LA4 (mm)	LA5 (mm)	Kn
BEM	31	235	N/A	48	112	159	195	222	242	1.07
BLA	0	222	105	52	102	144	178	206	229	1.12
CAS	54	250	N/A	40	97	144	183	215	242	1.05
GRA	0	242	96	54	96	131	159	182	201	0.92
KAB	74	273	92	44	84	121	156	189	220	1.05
LIT	52	246	95	44	83	120	155	187	218	1.01
NOR	50	243	97	54	95	129	157	181	200	0.91
PIK	45	292	99	52	93	130	163	194	222	0.96
PLA	48	280	94	43	106	156	197	231	259	1.10
SIS	28	299	93	43	106	157	197	230	257	0.98
TUR	46	218	88	61	90	116	139	161	181	0.95
WAB	41	240	97	52	85	116	145	173	199	0.94
WIN	0	236	96	59	106	149	187	222	254	1.02
WOM	71	237	N/A	46	94	135	171	202	229	1.02

Table 6. Summary of linear regression results, where crayfish frequency of occurrence in Yellow Perch stomach contents (%) as the explantory variable. Response variables include mean values for maximum length (Lmax), relative condition (Kn), female length at 50% maturity (L50), length at age 0 (LA0), length at age 1 (LA1), length at age 2 (LA2), length at age 3 (LA3), length at age 4 (LA4), and length at age 5 (LA5).

Response Variable	R^2	Slope	Intercept	P-value
Lmax	0.07	0.28	240.22	0.36
Kn	$7.0 \cdot 10^{-5}$	$-2.3 \cdot 10^{-5}$	1.01	0.98
L50	0.22	-0.08	98.58	0.17
LA0	0.24	-0.13	54.49	0.07
LA1	0.29	-0.20	104.05	0.05
LA2	0.13	-0.23	144.94	0.20
LA3	0.08	-0.22	178.81	0.34
LA4	0.04	-0.19	206.94	0.48
LA5	0.02	-0.13	230.38	0.64

FIGURES

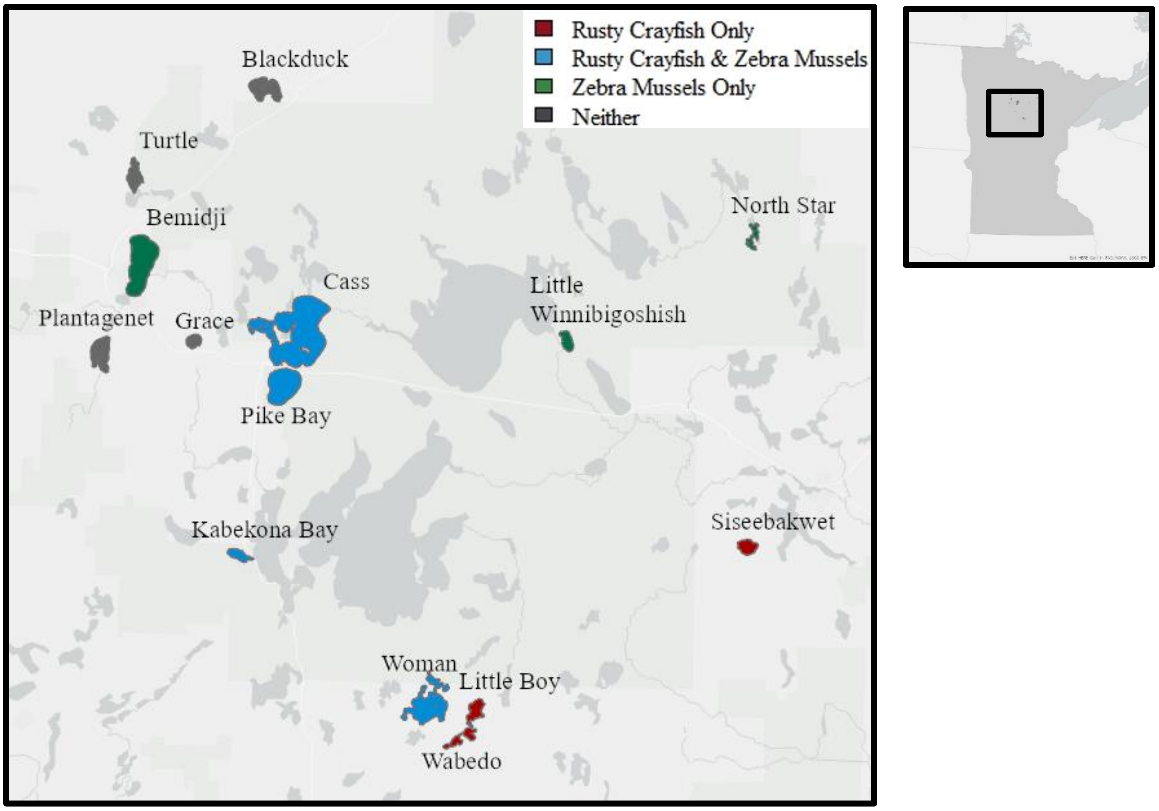

Figure 1. Local map showing the locations of the 14 study lakes where Yellow Perch population dynamics were evaluated between systems with and without rusty crayfish and zebra mussels present. Also shown is a Minnesota reference map of the study area.

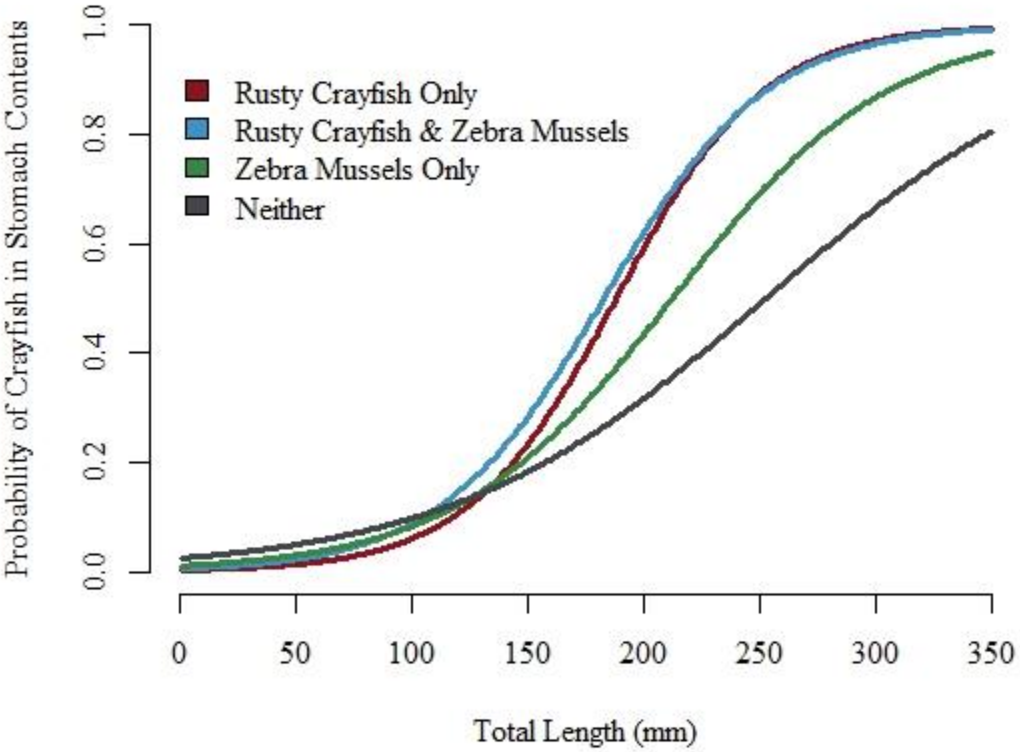

Figure 2. Logistic regression for estimating the probability of crayfish presence in stomach contents versus total length (mm) of Yellow Perch, where slope and intercept varied by aquatic invasive species group. Akaike information criterion adjusted for small sample size (AIC_c) was used to determine the best model based on Akaike differences (ΔAIC_c).

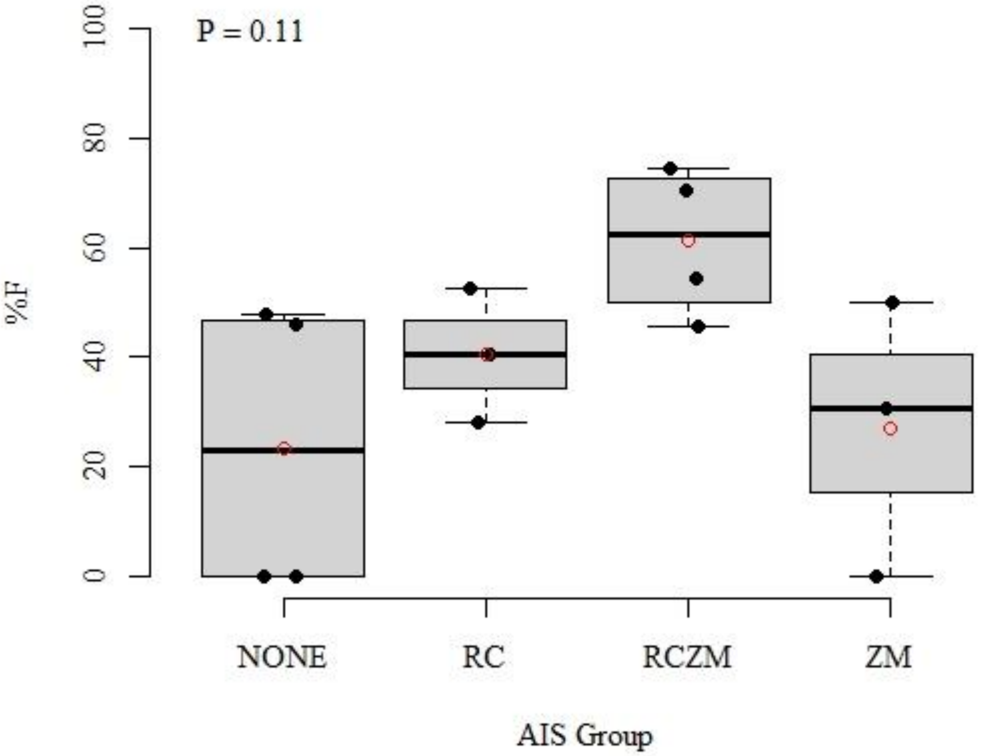

Figure 3. Box and whisker plots of mean frequency of occurrence (%F) of crayfish in the stomach contents of Yellow Perch ≥ 100 mm by aquatic invasive species (AIS) group. AIS groups include no AIS present (NONE), rusty crayfish present (RC), rusty crayfish and zebra mussels present (RCZM), and zebra mussels present (ZM). For each group, the median is shown with a dark horizontal bar, the upper and lower quartiles are represented by the shaded boxes, and means are indicated by open, red circles. The dark circles represent mean %F values calculated for each of the 14 study lakes.

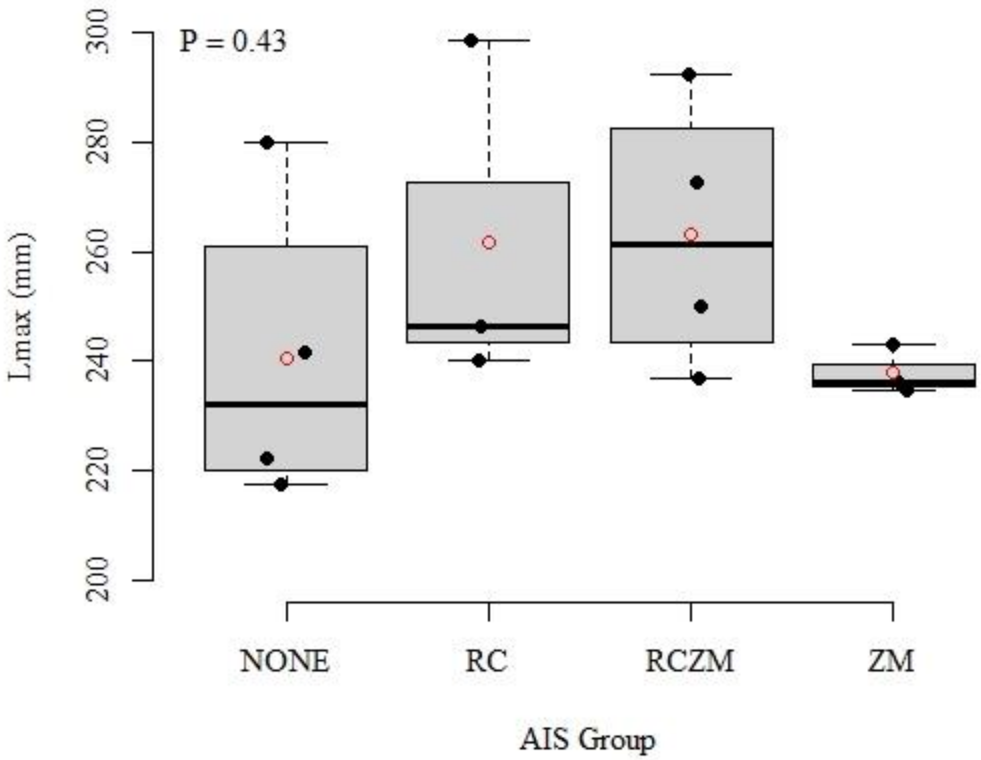

Figure 4. Box and whisker plots of mean maximum length (Lmax) of Yellow Perch by aquatic invasive species (AIS) group. AIS groups include no AIS present (NONE), rusty crayfish present (RC), rusty crayfish and zebra mussels present (RCZM), and zebra mussels present (ZM). Lmax was calculated by averaging the length of the largest 15 Yellow Perch sampled. For each group, the median is shown with a dark horizontal bar, the upper and lower quartiles are represented by the shaded boxes, and means are indicated by open, red circles. The dark circles represent mean Lmax values calculated for each of the 14 study lakes

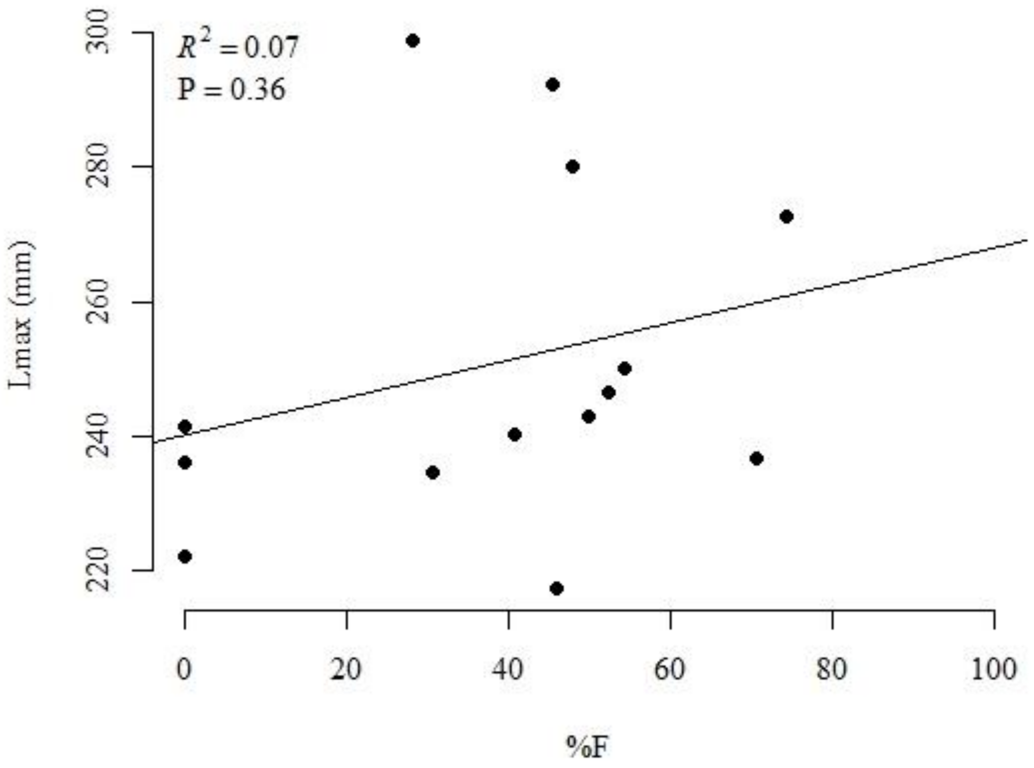

Figure 5. Linear regression between mean maximum length (Lmax) and occurrence of crayfish in the stomach contents of Yellow Perch ≥ 100 mm for all 14 study lakes.

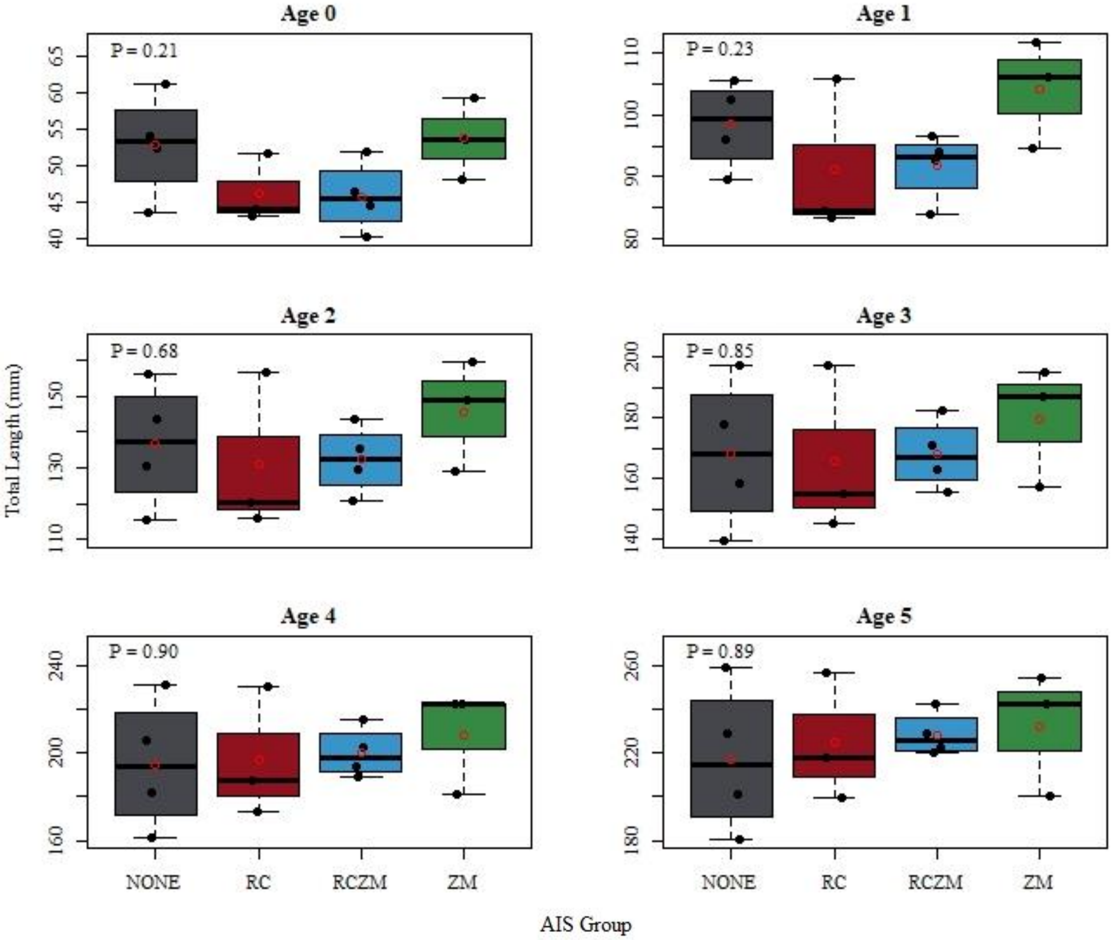

Figure 6. Box and whisker plots of mean length at age (mm) by aquatic invasive species (AIS) group. AIS groups include no AIS present (NONE), rusty crayfish present (RC), rusty crayfish and zebra mussels present (RCZM), and zebra mussels present (ZM). Mean length at age values were calculated for ages zero through five using Von Bertalanffy growth equations developed for each of the 14 study lakes. For each group, the median is shown with a dark horizontal bar, the upper and lower quartiles are represented by the shaded boxes, and means are indicated by open, red circles. The dark circles represent mean length at age values for each of the 14 study lakes.

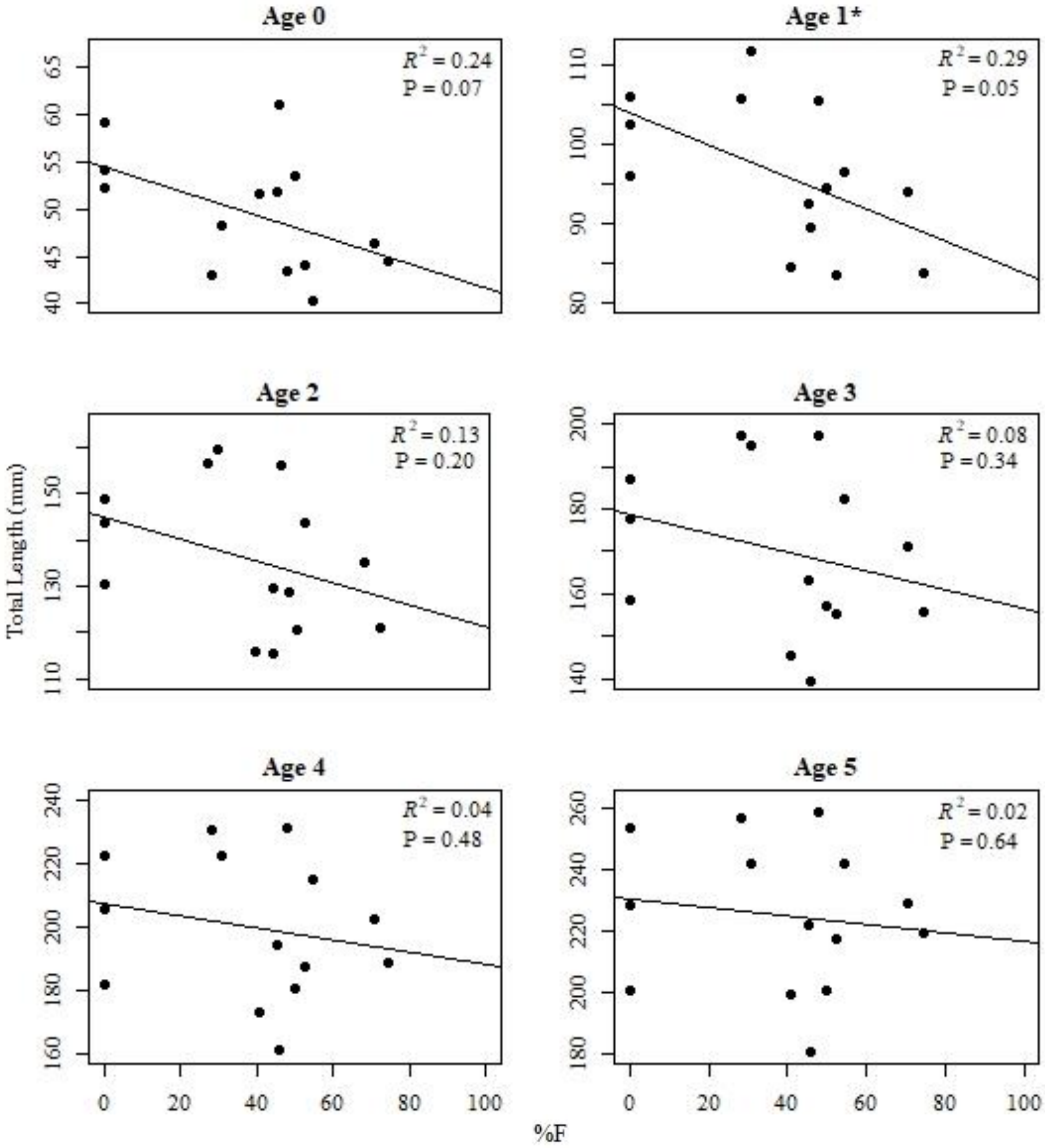

Figure 7. Linear regression plots using total length at age (mm) of Yellow Perch at varying ages regressed against occurrence (%F) of crayfish in the stomach contents of Yellow Perch ≥ 100 mm for all 14 study lakes. The same %F values were used regardless of age.

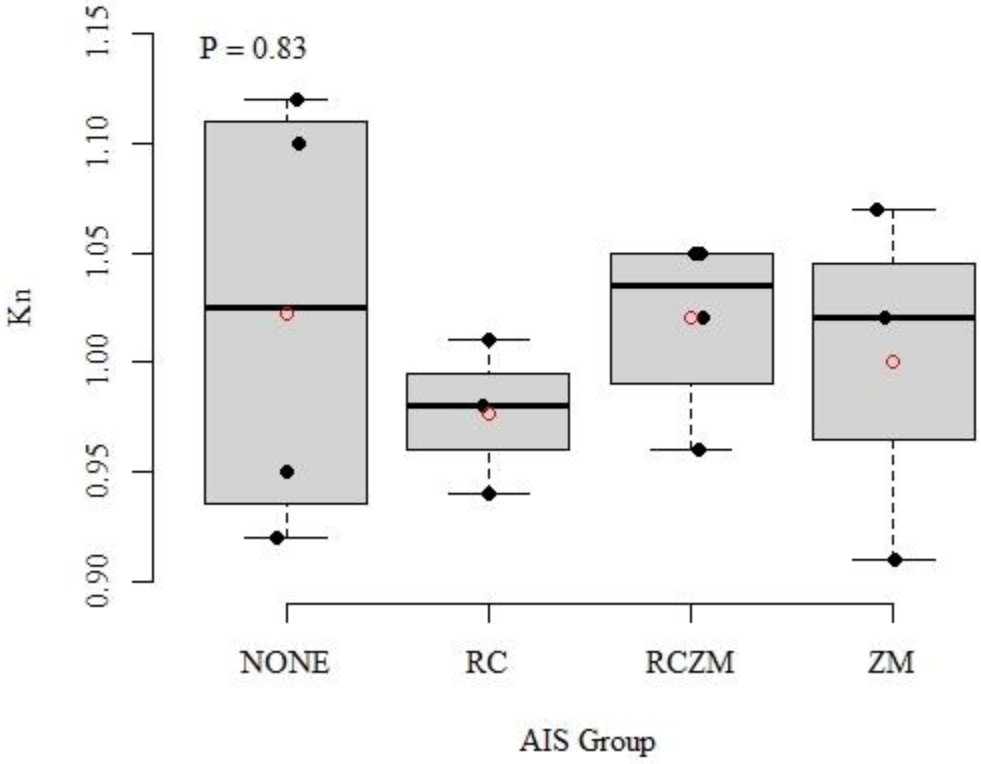

Figure 8. Box and whisker plots of mean relative condition (Kn) of Yellow Perch by aquatic invasive species (AIS) group. AIS groups include no AIS present (NONE), rusty crayfish present (RC), rusty crayfish and zebra mussels present (RCZM), and zebra mussels present (ZM). Kn was calculated for each fish, then averaged for each of the 14 study lakes. For each group, the median is shown with a dark horizontal bar, the upper and lower quartiles are represented by the shaded boxes, and means are indicated by open, red circles. The dark circles represent mean Kn values for each lake.

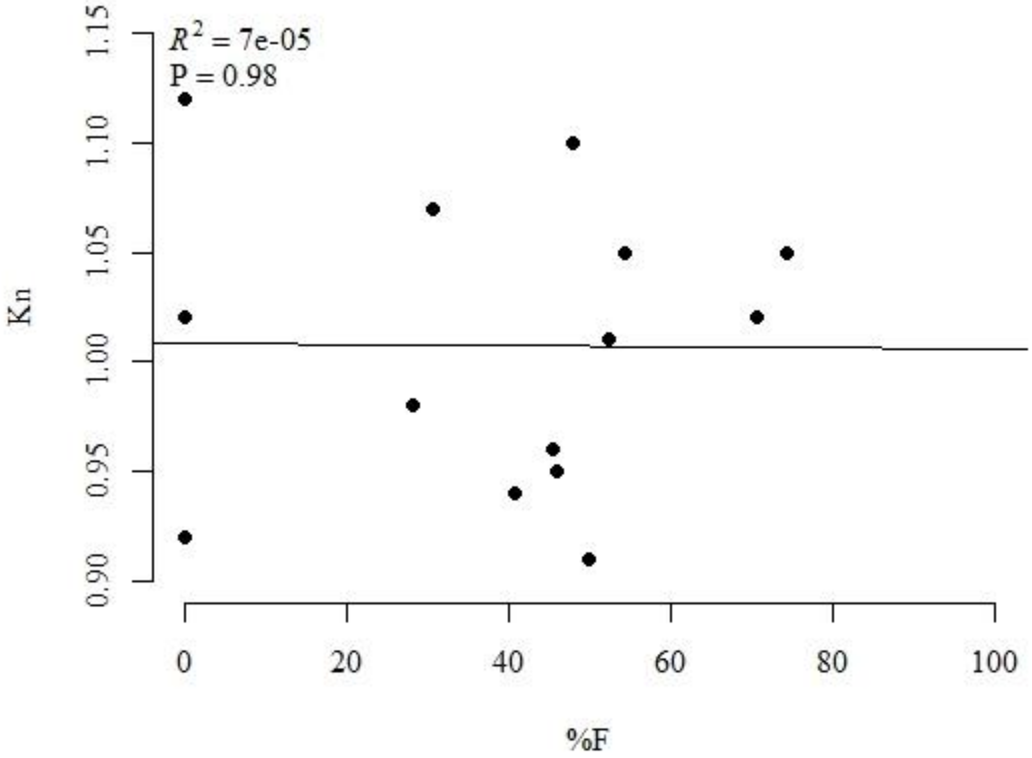

Figure 9. Linear regression between relative condition (Kn) of all sampled Yellow Perch and occurrence of crayfish in the stomach contents of Yellow Perch ≥ 100 mm for all 14 study lakes.

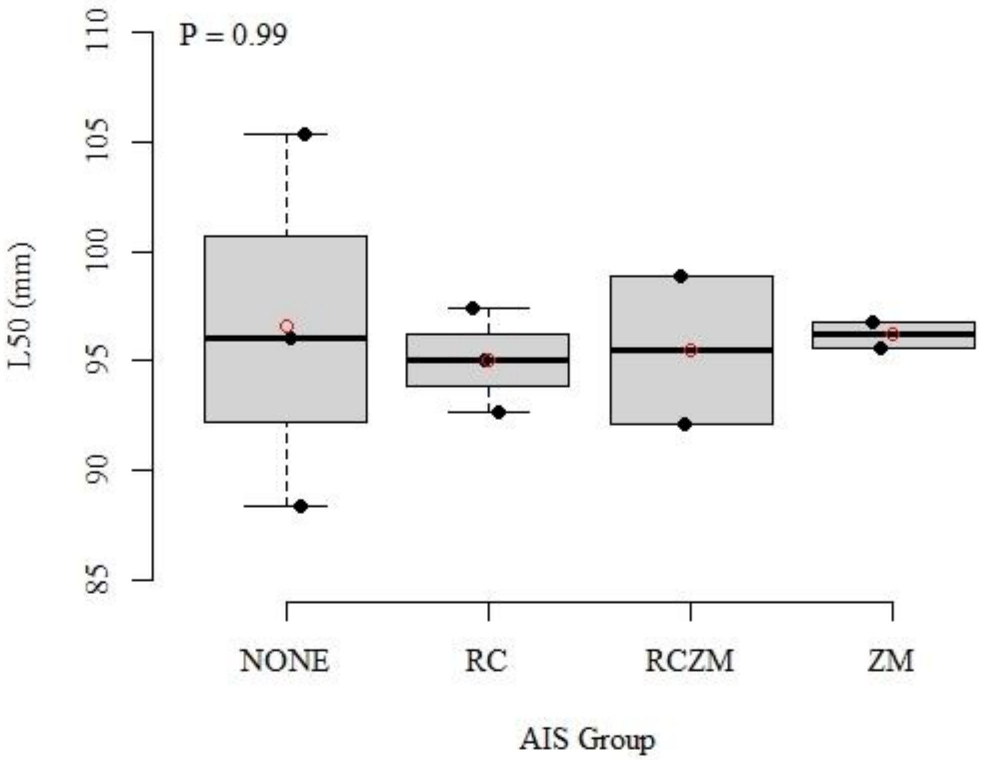

Figure 10. Box and whisker plots of mean female length at 50% maturity (L50) of Yellow Perch by aquatic invasive species (AIS) group. AIS groups include no AIS present (NONE), rusty crayfish present (RC), rusty crayfish and zebra mussels present (RCZM), and zebra mussels present (ZM). L50 was determined using logistic regressions of female Yellow Perch maturation for each system. For each group, the median is shown with a dark horizontal bar, the upper and lower quartiles are represented by the shaded boxes, and means are indicated by open, red circles. The dark circles represent mean L50 values calculated for each of the 14 study lakes.

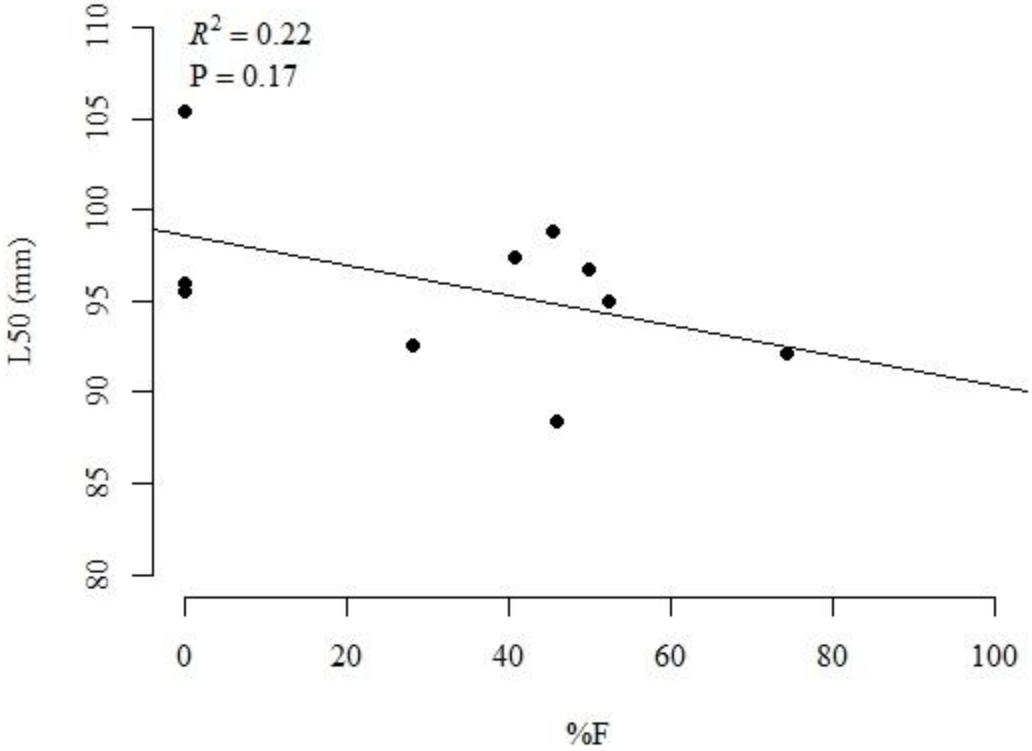

Figure 11. Linear regression between mean female length at 50% maturity (L50, mm) and occurrence of crayfish in the stomach contents of Yellow Perch ≥ 100 mm (%) for all 14 study lakes.

APPENDIX A

Table A1. Mean relative condition (Kn) values for all Yellow Perch in each of the 14 study lakes. Included is standard deviation (SD) and sample size (n).

Lake	Mean Kn	SD	n
Bemidji	1.07	0.11	103
Blackduck	1.12	0.15	115
Cass	1.05	0.11	148
Grace	0.92	0.10	126
Kabekona Bay (Leech Lake)	1.05	0.12	140
Little Boy	1.01	0.8	116
North Star	0.91	0.08	133
Pike Bay	0.96	0.09	144
Plantagenet	1.10	0.08	137
Siseebakwet	0.98	0.08	144
Turtle	0.95	0.11	109
Wabedo	0.94	0.08	129
Little Winnibigoshish	1.02	0.08	115
Woman	1.02	0.08	123

Table A2. Lower confidence levels (LCL), Lengths at 50% maturity (L50), and upper confidence levels (UCL) for female Yellow Perch in each of the 14 study lakes. Lakes without sufficient maturity data are indicated with an N/A (not applicable) in each cell.

Lake	L50	LCL	UCL
Bemidji	N/A	N/A	N/A
Blackduck	105	100	109
Cass	N/A	N/A	N/A
Grace	96	80	101
Kabekona Bay (Leech Lake)	92	83	102
Little Boy	95	90	99
North Star	97	89	103
Pike Bay	99	90	106
Plantagenet	N/A	N/A	N/A
Siseebakwet	93	85	101
Turtle	88	81	97
Wabedo	97	93	101
Little Winnibigoshish	96	92	100
Woman	N/A	N/A	N/A

Table A3. Constants for the von Bertalanffy growth equation, $L(a) = L_\infty (1\text{-}e^{-k(a - t0)})$, where a is age, k is the growth coefficient, t_0 is the theoretical age when size is zero, and L_∞ is asymptotic size.

Lake	L_∞	k	t_0
Bemidji	302.46	0.287	-0.603
Blackduck	335.72	0.194	-0.869
Cass	375.91	0.183	-0.615
Grace	286.09	0.199	-1.048
Kabekona Bay (Leech Lake)	728.61	0.059	-1.063
Little Boy	663.77	0.065	-1.042
North Star	297.36	0.184	-1.078
Pike Bay	509.93	0.092	-1.154
Plantagenet	379.76	0.204	-0.595
Siseebakwet	366.73	0.216	-0.576
Turtle	388.80	0.090	-1.882
Wabedo	652.2	0.056	-1.458
Little Winnibigoshish	564.55	0.097	-1.139
Woman	408.2	0.140	-0.859

APPENDIX B

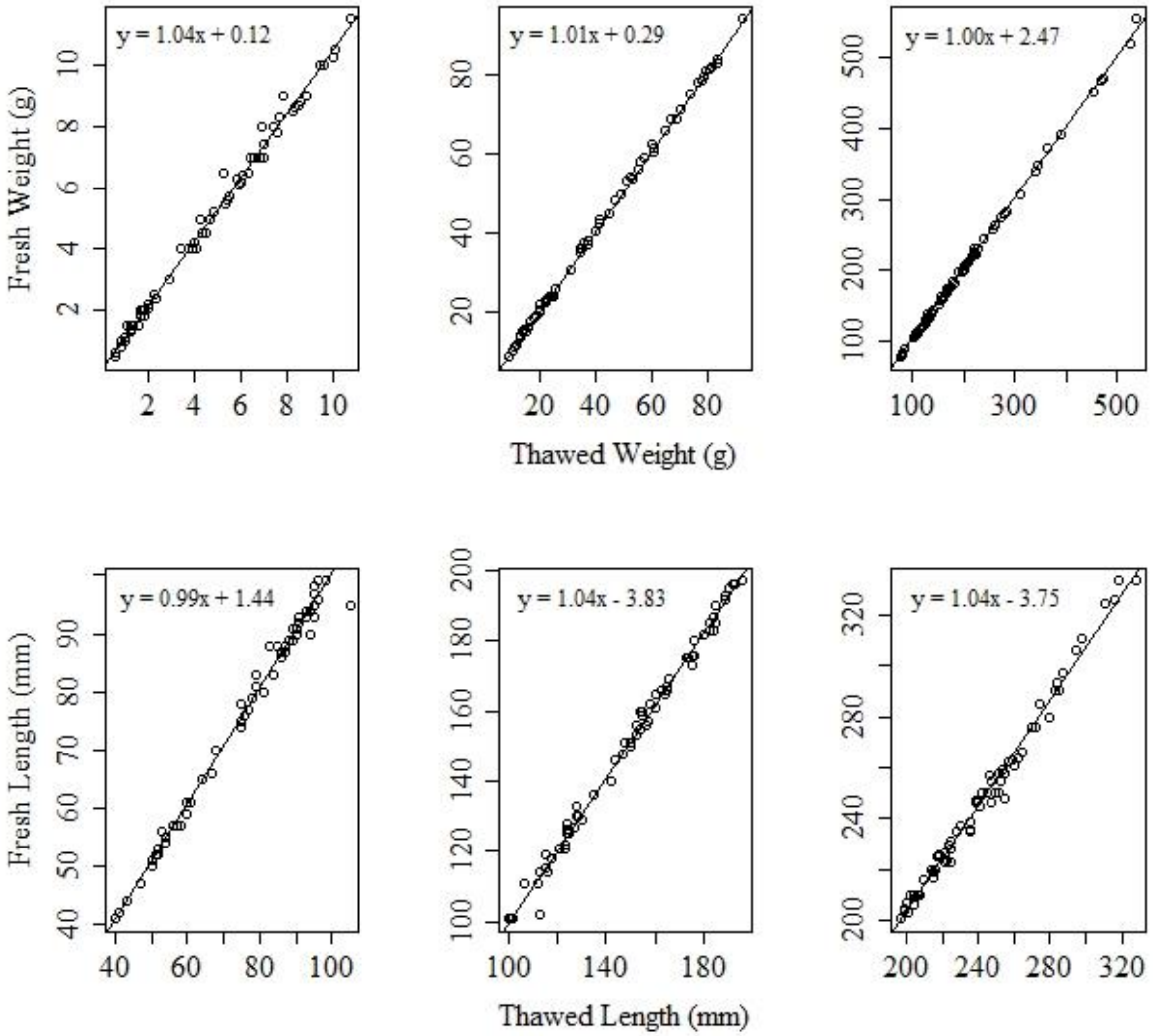

Figure B1. Total length and wet mass conversion regressions for Yellow Perch, developed using 15 fish from each of the 14 study lakes. Fresh lengths were taken prior to freezing, and thawed lengths were taken after freezing and allowing to thaw in cool water. Individual regressions were developed for three different size bins: <100 mm, 100-199 mm, and >200 mm (pictured left to right).

APPENDIX C

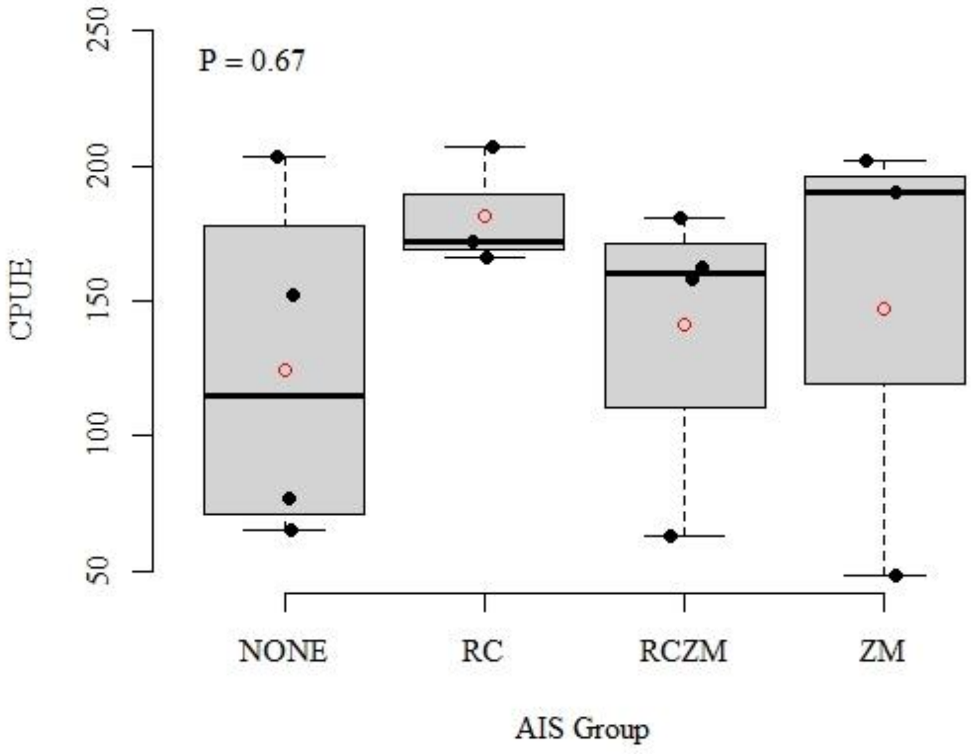

Figure C1. Box and whisker plots of catch per unit effort (CPUE; fish/hr) of Yellow Perch by aquatic invasive species (AIS) group. AIS groups include no AIS present (NONE), rusty crayfish present (RC), rusty crayfish and zebra mussels present (RCZM), and zebra mussels present (ZM). CPUE was determined by counting the number of Yellow Perch caught per hour of boat electrofishing during timed runs with constant power. For each group, the median is shown with a dark horizontal bar, the upper and lower quartiles are represented by the shaded boxes, and means are indicated by open, red circles. The dark circles represent mean CPUE values calculated for each of the 14 study lakes.

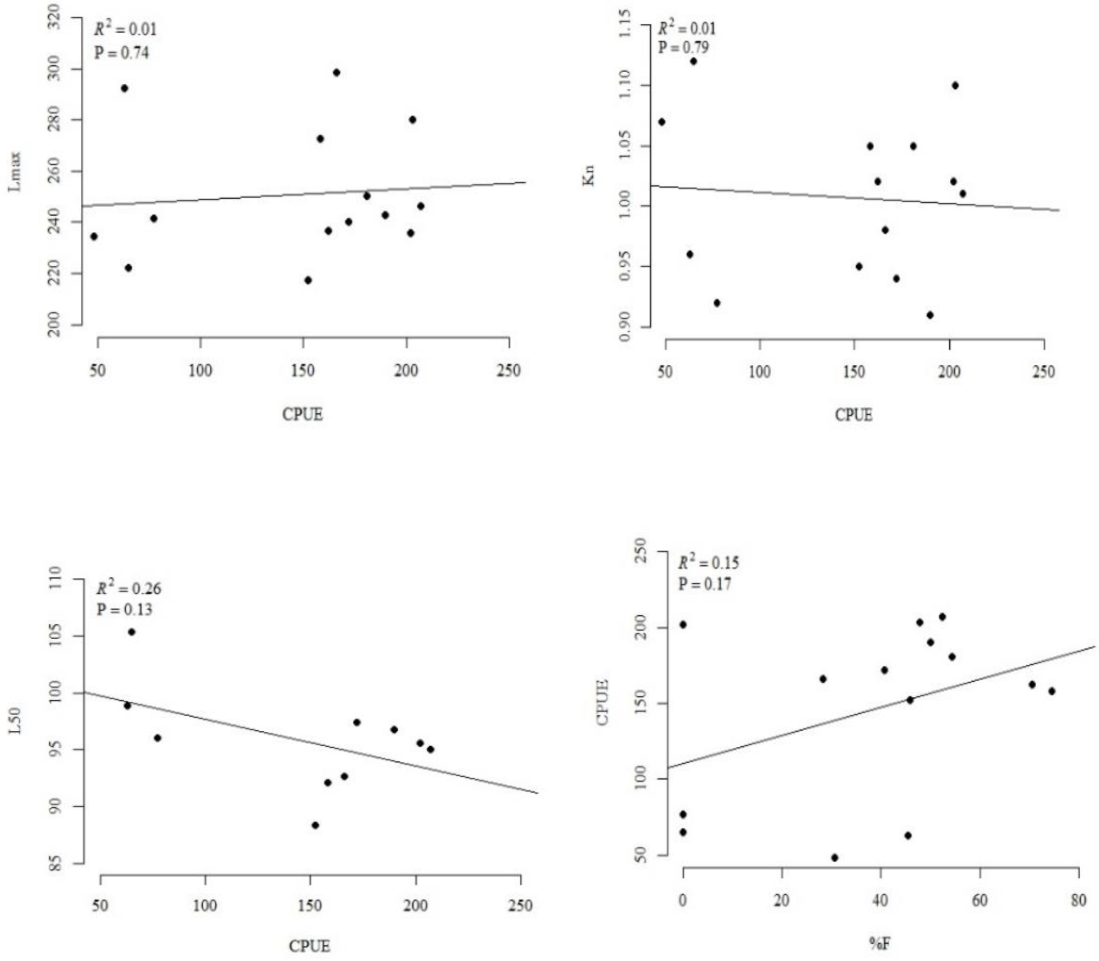

Figure C2. Linear regression between catch per unit effort (fish/hr) and the following Yellow Perch populatioin metrics: mean maximum length (Lmax; mm), relative condition (Kn), female length at 50% maturity (L50; mm) and occurrence of crayfish in the stomach contents of Yellow Perch ≥ 100 mm (%F) for all 14 study lakes.

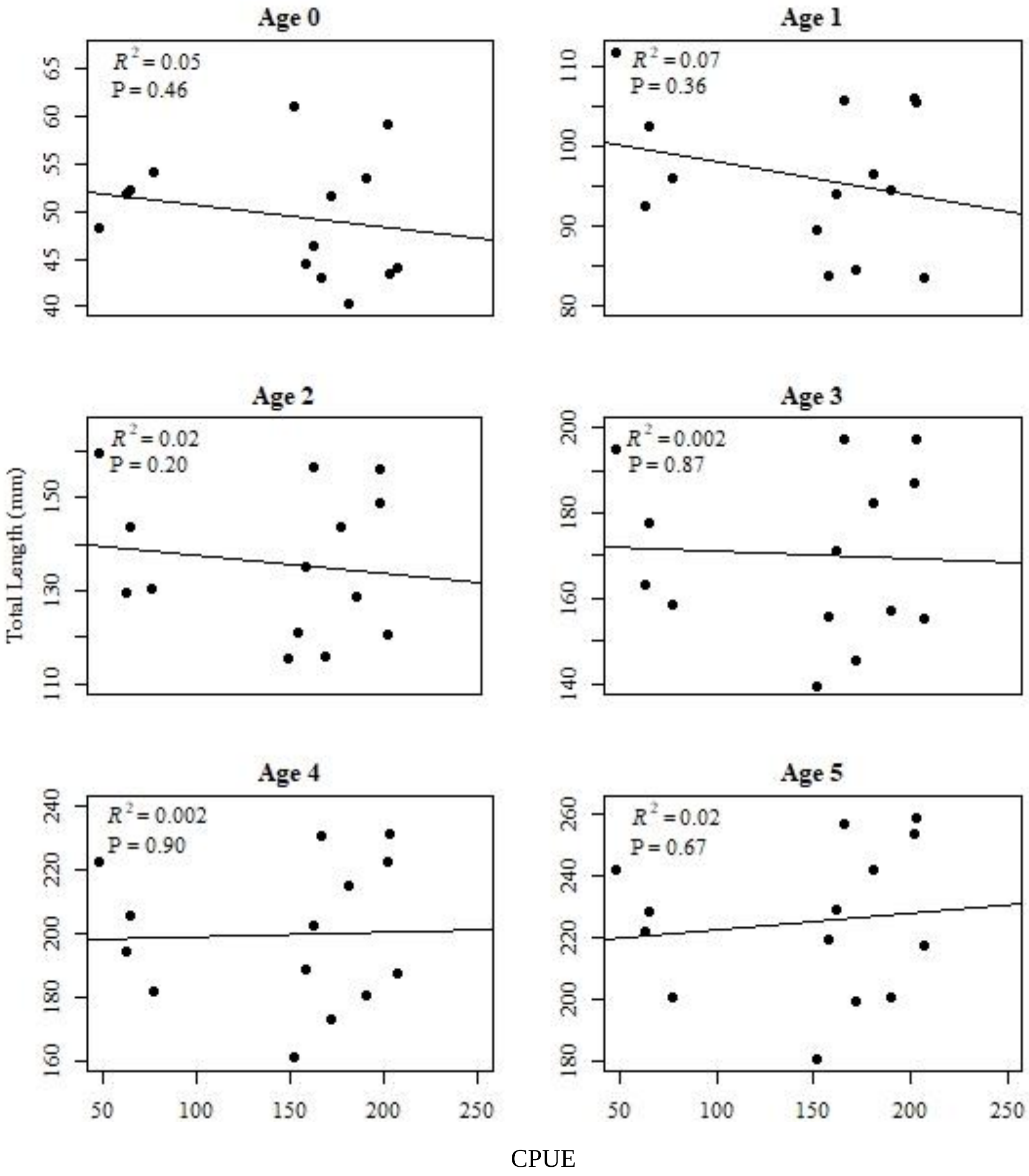

Figure C3. Linear regression plots using total length at age (mm) of Yellow Perch at varying ages regressed against catch per unit effort (CPUE; fish/hr) for all 14 study lakes. The same CPUE values were used regardless of age.