

**Exploring the effect of predator experience on Yellow Perch (*Perca flavescens*)
behaviour and predator recognition.**

A thesis presented to

The Faculty of Graduate Studies

of

Lakehead University

by

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In partial fulfillment of the requirements

for the degree of

Master of Science in Biology

January 17th, 2020

Abstract

Recreational and commercial fisheries are important resources that can be vulnerable to disruption by invasive species, particularly the introduction of top predators into water systems that have not previously supported them. How prey fish species assess and respond to predation significantly influences their vulnerability to this disruption. In this experiment, 12 groups of 8 Yellow Perch (*Perca flavescens*) from four lakes with different exposures to piscivorous predators were placed into enclosures to observe and record their behaviour around a food source and use of their environment, as well as how the presence of a predator within the enclosure might affect this behaviour. In the first trial, perch started in the half of the enclosure opposite a food source and upon removal of a central barrier, were allowed access to a suspended porous container filled with food. After this a second trial was conducted but with a Northern Pike (*Esox lucius*) present in the half of the enclosure with food to determine how the perch behavior changed from the first trial. In response to the presence of a predator, predator-experienced Yellow Perch consistently and significantly increased schooling and cover use while decreasing foraging behaviour at the food source while in contrast, predator-naive Yellow Perch did not significantly alter their behaviour. These trends in behaviour were consistent across two rounds of sampling (summer and fall). This study demonstrates that previous predator experience significantly affects Yellow Perch foraging and exploration behaviour in the presence of a predator, highlighting that populations without previous predator experience might be more susceptible to the detrimental effects of invasion by top predators.

Keywords: anti-predator response, experimental enclosure, exploration, fisheries management, foraging, invasive species, prey naivety, schooling, top predator

Lay Summary

Faculty and students in the Department of Biology are bound together by a common interest in explaining the diversity of life, the fit between form and function, and the distribution and abundance of organisms. This study has shown major differences in the exploration and foraging behaviour of Yellow Perch, attributed to their experience with top predators. In the presence of a predator, predator-experienced Yellow Perch reduced foraging and exploration behaviour while increasing schooling behaviour, whereas predator-naïve Yellow Perch showed almost no changes in behaviour to the introduction of a predator. These results highlight that the ability of a prey fish species to assess and respond to new predators (e.g., through species invasions) is not equal among populations, and that a population's history with top predators is a significant factor in a population's vulnerability to disruption by invasive top predators like Northern Pike. These findings have important management implications, indicating that prey fish population in currently predator-free lakes have a higher risk of local extinction than lakes with native predators.

Acknowledgements

I would like to offer immense thanks to my advisor Dr. Michael Rennie as well as the members of my committee (Dr. Douglas Morris, Dr. Constance O'Connor, and external examiner Dr. Beren Robinson).

Thank you to everyone at the International Institute for Sustainable Development Experimental Lakes Area (IISD-ELA) with special thanks to Chandra Rodgers, Lauren Hayhurst, Lee Hrenchuk, Stefano Strapazzon and the IISD-ELA operations staff.

My thanks to the CEE lab, Lakehead University and both the Department of Biology and the Department of Graduate Studies, the Ontario Ministry of Natural Resources as well as Jon Kereliuk.

This project would not have been possible without funding from the Canada Research Chair program, NSERC, the Canadian Foundation for Innovation and the generous support of the IISD-Experimental Lakes Area.

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Introduction

Predation is a selective mechanism that has been shown to significantly influence the behaviour, fitness, and life history of prey species (Lima & Dill 1990; Wisenden 2000, Rennie *et al.* 2010). This selective pressure can operate through direct mortality or by how the perceived risk of predation influences decision making of prey fish (Lima & Dill 1990). In the presence of predation, prey species must balance their risk of predation with their typical behaviour such as foraging or mating (Sih 1988). This balance is often characterized as a threat-sensitive trade-off between activities that increase fitness but may come with increased exposure and risk, versus behaviours that reduce risk but sacrifice time and energy that could be spent on other behaviours (Lima & Dill 1990; Wisenden 2000; Mirza & Chivers 2001b). Activities like foraging, mating and resource defence are behaviours that increase fitness while also increasing exposure to predation while activities like hiding, increased cover utilization reduce this risk but reduce energy intake as well (Lima & Bednekoff 1999).

Thus, for prey species to maximize fitness, it is important that they can accurately assess predation threats and respond appropriately according to the level of threat present (Mirza & Chivers 2001a; Mirza & Chivers 2001b). Failure to recognize threats or respond to them can result in increased mortality while being overly cautious might needlessly sacrifice opportunities to forage or reproduce (Hirsch & Bolles 1980; Mirza *et al.* 2003).

The ability of fish to accurately assess predation risk is different among species and different among populations within a species (Giles & Huntingford 1984; Smith 1999; Brown 2003). For some species of fish, predator identification or anti-predator

behaviours such as hiding come innately, and are possibly inherited, as demonstrated in experiments with hatchery-reared Steelhead Trout (*Oncorhynchus mykiss*) that responded to odour from their historically common predator Dolly Varden (*Salvelinus malma*) despite isolation from these predators for 15 generations (Chivers & Smith 1994; Scheurer *et al.* 2007).

Often though, the ability of prey fish to recognize threats is through releaser-induced recognition learning, when stimulus of a threat is paired with a chemical compound called an alarm cue, contained within the skin of certain prey fish that is released when the skin is damaged such as through predation (Suboski 1990; Chivers & Smith 1998). Many prey fish species, such as Yellow Perch, respond to conspecific alarm cue without needing experience with predators and thus can be conditioned with alarm cue to recognize different stimuli as threats (Mirza *et al.* 2003). This recognition can occur as rapidly as demonstrated by Fathead Minnows (*Pimephales promelas*) and European minnows (*Phoxinus phoxinus*) being conditioned to a novel predator after a single pairing of visual or chemical cues with conspecific alarm cue (Mathis & Smith 1993; Chivers & Smith 1994). Recognition from a single instance of pairing has been demonstrated to last for months as in the case of Fathead Minnows that retained recognition of the paired stimuli that lasted for at least 69 days (Chivers & Smith 1994). The Fathead Minnows in this experiment were conditioned to either a Goldfish or a Northern Pike and the minnow response was specific to the identity of the fish it had been conditioned to (e.g. minnows conditioned to Northern Pike did not respond to stimuli from Goldfish and vice versa; Chivers & Smith 1994). Other experiments however, demonstrated that prey fish could respond more generally to a potential predator. Fathead

Minnows responded with anti-predator behaviour to a novel species that was closely related to a predator they had been conditioned to recognize as a threat with the intensity of their response influenced by how closely the new predators features matched those of a familiar predator or how phylogenetically related that predator was to a threat that the minnows had been conditioned to (Ferrari *et al.* 2007).

In many of these cases, releaser-induced learning requires continual reinforcement through the pairing of visual and/or chemical cues from predators with alarm cues from conspecifics (Magurran 1990; Suboski 1990; Smith 1999; Brown 2003). The necessity for continual reinforcement could be adaptive allowing for prey responses to conspecific alarm cues or predators to change as prey fish grow, potentially changing habit and diet preference and subsequently altering their risk to predators (Wisenden 2000; Hawkings *et al.* 2008). Indeed, prey fish under greater predation pressure in the wild show a greater plasticity and modification of their anti-predator responses than populations under less predation pressure (Giles & Huntingford 1984; Magurran 1986; Magurran 1990). Similarly, the requirement for continual reinforcement in predator recognition also suggest that these behaviours are costly; i.e., the loss of the behaviour in the absence of predators suggests that behaviours that facilitate predator avoidance are maladaptive in the absence of predators.

If identification and response of predators requires continual reinforcement for many prey fish species and if anti-predator behaviours are closely linked to trade-offs in other selective forces such as growth and fecundity, then such anti-predators might be lost in the absence of predation risk (Réale *et al.* 2010; Sih & Giudice 2012). Without the tradeoff of increased mortality, prey fish that spend more time with behaviours that

increase fitness (e.g., foraging, mating, resource defence) might have greater success than prey fish displaying cautious behaviour (Sih & Giudice 2012; Castanheira *et al.* 2013). Over many generations, a population in the absence of predation might develop significant behavioural differences in their foraging and exploratory aggressiveness compared to a population under pressure from predation (Sih & Giudice 2012; Castanheira *et al.* 2013). This may in turn increase the susceptibility of these populations to invasive top predators when compared to a population more familiar with predation (Lima & Dill 1990). For example, at the IISD-Experimental Lakes Area (IISD-ELA), Northern Pike were experimentally introduced into three lakes as part of whole lake manipulation experiments in the 1980s and early 1990's (Findlay *et al.* 1994; Elser *et al.* 1998; Elser *et al.* 2000). Subsequent sampling of these lakes in 2012 showed extirpations of many prey fish species from these lakes, including Yellow Perch (*Perca flavescens*) which otherwise commonly coexist with Northern Pike in other lakes in the region (Nicholson *et al.* 2015).

These observations led me to explore whether there is an interaction between previous predator experience and the presence of a predator that might help explain the extirpations of prey fish observed at the IISD-ELA following predator introductions. I designed an experiment that would allow me to evaluate the behaviour of groups of prey fish from different predator exposure histories under the presence or absence of predators. To achieve this, I replicated experimental enclosures with groups of 8 Yellow Perch with different predator exposure histories and evaluated their behaviour in the presence of a food attractant both in the absence and presence of a Northern Pike

predator. Changes in behaviour due to the presence of a predator were then compared between perch from lakes with different predator exposure histories.

Yellow Perch were used as my model prey fish for several reasons. First, they were one of several species that underwent extirpation from lakes at the IISD-ELA following predator (Northern Pike) introductions (Nicholson *et al.* 2015). However, more so than other species that were extirpated from Northern Pike introductions, they are broadly distributed at the IISD-ELA and throughout North America, existing in lakes both with and without Northern Pike present (Beamish *et al.* 1976). Second, they are ecologically important, occupying a key mid-trophic position in aquatic communities connecting primary consumers to predators, where they graze plankton and as act as prey for larger piscivorous predators such as Walleye (*Sander vitreus*), Northern Pike, and Lake Trout (*Salvelinus namaycush*), many of which are popular trophy fish (Brown *et al.* 2009; Nicholson *et al.* 2015). Third, Yellow Perch themselves are important in both commercial and recreational fisheries where they are among the top five species caught by anglers (Fisheries and Oceans survey of recreational fishing in Canada 2015; NOAA Landings Database). Given their broad geographic distribution, recreational value, economic importance and their potential sensitivity to predator introductions, Yellow Perch were deemed broadly relevant to understanding prey fish vulnerabilities to predator introductions.

With the concept of risk-reward trade-offs in mind, I expected there to be significant differences in how Yellow Perch with different predator exposure histories would respond to the presence of a predator. Specifically, that predator-naïve Yellow Perch (i.e., prey fish without predator experience to shape their behaviour) would be less sensitive to

predation risk (i.e., less likely to alter their behaviour in the presence of a predator) than prey fish that are predator-experienced. I believed this would manifest as predator naïve fish not significantly altering their use of cover, schooling behaviour, and foraging between trials lacking a predator to trials with a predator. I believed this would contrast with predator-experienced perch that would significantly reduce foraging time, and increased schooling and cover use between the two trials. Further, I expected that predator-naïve Yellow Perch would show behaviours that would facilitate increased foraging (e.g., more time in open areas) than predator-experienced fish, even in the absence of predators reflecting an overall tendency away from more cautious behaviours in novel environments (Réale *et al.* 2010; Sih & Giudice 2012; Castanheira *et al.* 2013).

Materials and Methods

Experimental Design:

To evaluate the potential interaction between previous predator experience and the presence of a predator on Yellow Perch exploration and foraging behaviour, Yellow Perch were collected from two lakes with top piscivorous predators and two lakes lacking top predators (Figure 1). These perch were placed in experimental enclosures which were designed to allow me to manipulate cover, food supply, and predation presence (Figure A1, A2). During experimentation, two of these enclosures were assembled along the shore of these lakes and 8 Yellow Perch were placed into each enclosure. The behaviour of the 8 Yellow Perch in each group was filmed for 20 minutes in two different experimental trials. The first trial examined Yellow Perch behaviour without a predator in the enclosure, while the second trial tested these same perch with a Northern Pike present

in half the enclosure, thus allowing me to compare if and how the groups of Yellow Perch changed their behaviour in response to the presence of Northern Pike.

To evaluate repeatability in the Yellow Perch behaviour observed over time (i.e., to ensure there were no potential seasonal changes in perch behaviour from the start to the end of the experiment), a second round of experiments was initiated in September (two weeks following the conclusion of the first round of testing). Tests were conducted on the first two lakes examined (one with and one without Northern Pike).

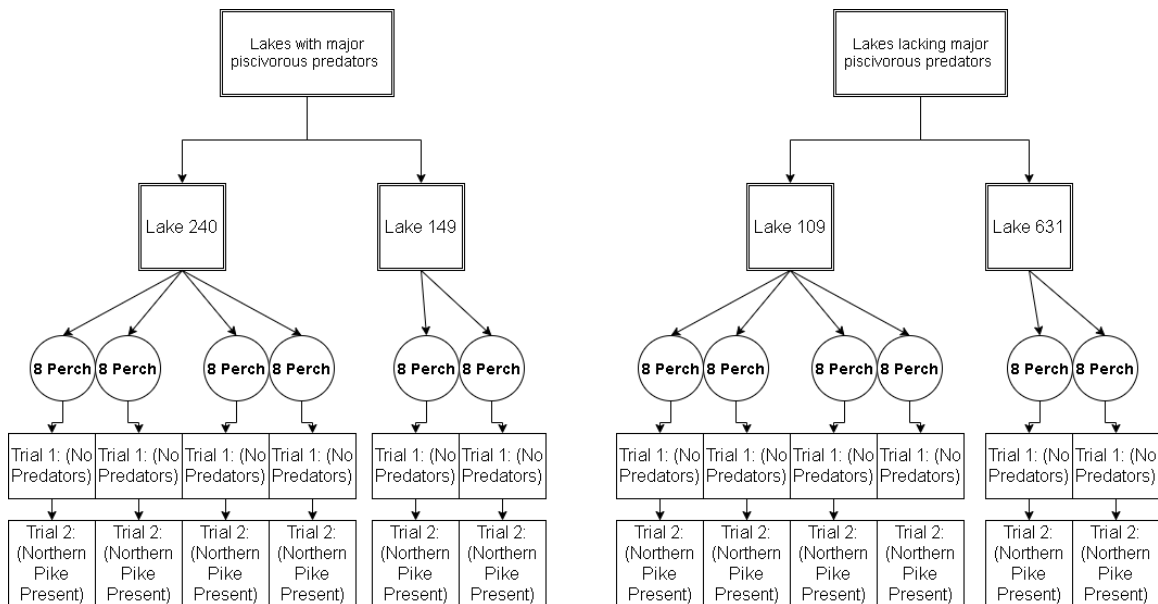


Figure 1: Diagram of experimental design featuring two different lakes per history of piscivorous predation. Note two lakes were replicated a second time to confirm consistent results. Two experimental enclosure tubs are used per testing period with the same 8 Yellow perch in each tub being used in both the first and second trials.

Collection and Location:

All fish used in the experiment were collected from freshwater lakes in the International Institute for Sustainable Development Experimental Lakes Area (IISD-ELA), Ontario, Canada, in the fall of 2016. A total of 192 Yellow Perch were collected from Lakes 240, 109, 149, and 631, in the early afternoon using a beach seine and short set gill nets (<10 minutes; 25.4 mm stretched mesh size).

96 Yellow Perch were collected from each of lakes 240 and 149 which contained top piscivorous predators, and a similar number of Yellow Perch were collected from lakes 109 and 631 which lack top piscivorous predators. Yellow Perch used in the experiment had an average fork length (measured from the tip of nose to the fork of the tail) of 87 ± 3.4 mm (with a range between 83 mm to 92 mm). Five Northern Pike were collected from each of Lake 240 and 149 through angling and trap nets. Northern Pike used in the experiment had an average fork length of 474 ± 21.7 mm and were between (433 to 503 mm).

Species composition and morphology of study lakes are listed in Table 1 and Table 2 respectively. All fish were collected under an Ontario Ministry of Natural Resources Licence to Collect Fish for Scientific Purposes (Licence No. 1082446, Issuer Account No. 1690010) and Lakehead AUP # 1465331.

Table 1: Species composition of lakes used in the experiment (The “X” indicates species presence). Data are based on previous sampling (Beamish *et al.* 1976; Rennie unpublished data).

Fish Species	Lake 240	Lake 149	Lake 631	Lake 109
Yellow Perch (<i>Perca flavescens</i>)	X	X	X	X
Northern Pike (<i>Esoc lucius</i>)	X	X		
White Sucker (<i>Catostomus commersonii</i>)	X	X	X	X
Lake herring (<i>Coregonus artedi</i>)	X			
Pearl dace (<i>Margariscus margarita</i>)	X		X	X
Slimy sculpin (<i>Cottus cognatus</i>)	X			
Emerald shiner (<i>Notropis atherinoides</i>)		X		
Fathead Minnow (<i>Pimephales promelas</i>)		X	X	X
Blacknose shiner (<i>Notropis heterolepis</i>)			X	X
Johnny Darter (<i>Etheostoma nigrum</i>)			X	
Trout-perch (<i>Percopsis omiscomaycus</i>)			X	

Table 2: Physical characteristics of Yellow Perch lakes used in the experiment.

IISD-ELA Lake #	Area (Hectares)	Maximum Depth (Meters)
Lake 240	44	13
Lake 149	27	4
Lake 631	39	8
Lake 109	16	10

Temporary Housing:

At each lake, 16 of the captured Yellow Perch were placed into enclosures before experimentation and allowed to acclimate for at least 24 hours. Several additional Yellow Perch were retained in an inner liner from a fish pen (see below) which was a mesh bag (1 x 1 x 1 m with 4 mm holes) that was submerged and suspended in the lake to provide replacements in the event of non-experimental mortality and/or provide food for captive Northern Pike used during experiments.

Before experimentation, Northern Pike were kept in partially submerged fish pens (0.91 m x 1.52 m x 0.91m) composed of a mesh bag with 4mm holes, inside a galvanized steel wire cage with 5 mm square holes and a 1 mm thick wire (Figure A3). The mesh bag kept Northern Pike in the pen and prevented contact with the wire walls that could potentially damage the fish, while the wire cage keeps other fish out of the pen. The pen was placed in a shaded area if possible or was covered with tarpaulins when shade wasn't present. Northern Pike were fed a diet of 1 to 2 live Yellow Perch per Northern Pike every 3-4 days. The use of live fish was necessary to ensure they eat as Northern Pike have been observed to ignore even recently dead prey (B. Allan, unpublished data). This

feed rate is similar to other studies involving Northern Pike (Chivers 1994) and previous work has shown Northern Pike in captivity have survived for at least 3 months on a diet of 1 to 2 live fish (between 40-100 mm) every 4 to 5 days (B. Allan, unpublished data). In previous work at the ELA, up to 6 Northern Pike have been housed in pens for 24 hours, and up to 4 days in trap nets, with no evidence of injury among individuals (M. Rennie, personal communication).

All the housed fish were monitored regularly for unhealthy characteristics as described by Lakehead University SOP#: A-30-BAF.

Transport:

As some of the lakes in the experiment lacked top predators, Northern Pike were transported from other lakes to the experiment sites set up on the shore of Yellow Perch source lakes. To do this, Northern Pike were transported in either a PVC pipe that was filled with fresh lake water and capped to form a water tight seal (Elser *et al.* 2000) or for shorter distances, pike were carried in large rectangular coolers filled with fresh lake water. All-Terrain-Vehicles or trucks were used to transport Northern Pike to more distant research sites. The duration of transport was less than an hour in every case. Similar transport techniques have been used in previous studies to transport Northern Pike with minor mortality reported during transport (Elser *et al.* 2000). Using this method, I observed no Northern Pike mortality during the current study.

Experimental Enclosures:

Experimental enclosures were designed to evaluate Yellow Perch behaviour in a large environment simulating the nearshore region of a lake where cover, food supply,

and predation presence could be controlled and standardized (Figure A1, A2). Two replicate enclosures were used at each lake location. Each enclosure was large enough to contain and protect both the group of 8 prey fish as well as a single medium-sized top predator while also being easy to clean between lakes and open enough to allow video recordings of fish behaviour. Due to the distance and remoteness of the research lakes, portability of the enclosures was also crucial in the design, permitting easy assembly and disassembly.

The enclosures were constructed from large circular black tubs 178 cm in diameter and 48cm deep. A water pump powered by a 12-volt battery was used to provide both enclosures with fresh lake water at a rate of 750 litres per hour, allowing for complete turnover of the water in enclosures water every 6 hours. Small holes were drilled into the top few inches of each tub to allow for drainage and prevent overfilling.

Enclosures were equipped with a moveable barrier to limit movement of fish and divide the enclosure into two halves. One half of the enclosure contained all 8 Yellow Perch at the start of the experiment, while the other half contained either a food attractant or a food attractant plus a Northern Pike (see details below). A small weighted permeable food container with frozen bloodworms was suspended in the centre of the farthest point in the mesocosm from the gate (Figure A4). A second sectioning of the mesocosm was made, perpendicular to the moving barrier, into areas with or without cover. Thus, the determination of cover use on either side of the barrier was possible (e.g. cover and an open region was available on both the side with food or food plus Northern Pike and the side with no food that was inaccessible by Northern Pike).

The central barrier bisecting the enclosures was composed of a chicken wire panel held by a fitted wooden frame. The hexagonal gaps in this chicken wire were large enough to allow the passage of the Yellow Perch in this experiment but prevented the passage of Northern Pike of the size used in this experiment. Built into each centre barrier was a set of metal tracks and a pulley system that was used to raise and lower a mesh screen gate slotted into tracks; this screen controlled the access of Yellow Perch to the other half of the enclosure (e.g., the side with the food attractant, or the food attractant and the Northern Pike). The long ropes of the pulley system could be used to operate a gate from a few meters away from the enclosure, limiting the disturbance to the fish in the enclosure from the researcher in the experiment.

To create open areas and areas simulating natural cover, rubber mats which held rows of upright bamboo rods (simulating native horsetail *Equisetum spp.*) were placed down along each half of the enclosures (Figure A5, A6). These rubber mats were weighed down with coils of woven nylon line with a lead core. The spacing between the bamboo rods allowed for Northern Pike to enter them at specific angles, but severely limited their turning and maneuverability, making it more difficult to catch perch occupying these areas of cover.

To protect the contents of the enclosures from outside wildlife when enclosures are unattended, a perimeter fence and a wire roof were created and attached to the enclosure tubs. Six PVC pipe sections were secured to wooden wedges which were glued at equidistant points around the outside of the enclosure tubs. Wooden posts with holes drilled through the tops were inserted into these PVC pipe holsters allowing wooden wall frames with chicken wire panels to be secured between the posts with snap ties. The

bottoms of these frames were then secured with zip ties to drilled holes along the top of the curved lip of the tubs. The roofs of the enclosures were each made from two long wooden bars, each with attached flexible piping forming a “D” shape covered with wire. The wooden bars were held up by the centre frame while the piping and wire rested on the tops of the wooden poles around the perimeter to fully cover the top of the enclosure.

To record the behaviour of the fish in the enclosure, two remotely activated video recorders were mounted atop the middle of the central wooden frame, underneath the wire roof, facing down at each half of the enclosure (Figure A7). To help provide better contrast for tracking fish movements from video recordings, white and blue non-toxic aquarium gravel was spread over the bottoms of the enclosures.

At each lake, two replicate enclosures were used for experimentation. Enclosures were assembled on the shore beside the perch lakes with shaded spots. In areas with lacking natural shade, tarps were placed over the enclosures to provide shade. After experiments at a lake were concluded, the enclosures were disassembled and transported to the main base camp for cleaning. To prevent movement of organisms between lakes, all equipment moved between research sites was cleaned by rinsing with a hose and then left out to sun dry for four days following recommendations from Ontario Federation of Anglers and Hunters (<http://www.invadingspecies.com/clean-boats-clean-tournaments-2/>).

Experimental trial 1 (observation of Yellow Perch behaviour without predator in enclosure):

Eight Yellow Perch were removed from the submerged mesh holding bag in the lake and placed into one half of each enclosure. Fish were allowed to acclimate for 24 hours. Two hours before the experiment began, any tarps covering the enclosures were removed to allow for sufficient light levels inside the enclosure to permit video to be clearly recorded. Using remote video recorders, the Yellow Perch in the enclosures were monitored to ensure all eight perch in each enclosure were alive and behaving normally. The suspended food source was then added into the half of the enclosure without Yellow Perch, centered in-between areas with and without cover. 10 minutes after the introduction of the food source, the video recorders were activated and the mesh gate of the centre barrier was lifted by the pulley system from a distance, allowing Yellow Perch access into the half of the enclosure containing the food source. The Yellow Perch were filmed for 20 minutes after opening the gate to measure fish behaviour. At the end of 20 minutes of video recording, Yellow Perch in each enclosure were gently herded back into their starting halves of the enclosures using a bubble wand; a bubbler that was attached to a battery-operated air pump secured to a long wooden pole that could reach inside the enclosures from the top once the roof of the enclosure was removed. Once perch were all back on the non-food half of the enclosure (i.e. back where they started), the mesh screen gate was lowered into the closed position to prevent further movement across the centre barrier and to prepare for the second trial of the experiment. The food source in the plastic container was removed from the enclosure and emptied while one Northern Pike was added into the half of the enclosure previously containing the food source.

Experiment trial 2 (observation of Yellow Perch behaviour with predator in enclosure):

The second experimental trial was conducted 24 hours after the first trial, giving all fish (both predator and prey) in the experimental enclosure 24 hours to acclimate, but kept separate by the screen barrier. The same Yellow Perch from the first trial were also used in the second trial. The experimental method of trial 2 was the same as trial 1 except that a Northern Pike was present on the side of the enclosure that would contained the food attractant. As in the first trial, the food container was added into the enclosure 10 minutes prior to experimentation. After 10 minutes, the centre gate was lifted and all fish were filmed for 20 minutes. At the conclusion of 20 minutes of filming, all Yellow Perch were dip netted out of the enclosures, counted, and placed in a separate tub of water where they were euthanized with an aqueous tricane methanesulfonate (TMS) overdose followed by cervical dislocation. Northern Pike were then dip netted out of enclosures and, if this was their first use in the experiment, they were returned to their partially submerged fish pens in the lake to await transport to another research site for their second use in the experiment, otherwise they were euthanized in the same manner as the perch with an aqueous TMS overdose followed by cervical dislocation. These euthanizations followed guidelines set out in Lakehead University SOP#: A-34-BAF. To reduce the number of fish needed in the experiment, Northern Pike were first used in the enclosures along the shore of their source lake and then used again in enclosures along the shore of lakes that lacked piscivorous predators before they were ultimately euthanized.

Scoring of Yellow Perch Behaviour:

Behavioral measurements were quantified from the recorded video of the enclosures to be able to compare the different populations of Yellow Perch. At the start of each 20 minute segment of film, the starting positions of all 8 Perch were marked on a screenshot of the video and numbered from 1 to 8. Each individual perch was then tracked for these 20 minutes as it moved through the enclosure. During this time, the following Yellow Perch behaviours were recorded: Time spent in open areas (lacking cover), number of approaches to and the time spent at the suspended food source, time spent schooling with another perch, and the number of times a fish successfully schooled with another fish. The **time in open areas** of the enclosure was measured as the count (in seconds) each Yellow Perch had <50% of its body length in an area that lacked cover.

Approaches to the food source were defined as the count of each unique instance a Yellow Perch came within a half a body length of the suspended food source and stayed at the food source least 3 seconds. **Time spent at the food source** was defined as the sum of the number of seconds that a Yellow Perch spent within half a body length of the suspended food source during approaches to the food source that lasted at least 3 seconds.

Schooling attempts were defined as the count of the number of times a Yellow Perch spent at least 3 seconds within two body lengths of at least one other Yellow Perch.

Finally, **schooling time** was defined as the sum of the number of seconds that a Yellow Perch spent within two body lengths of at least one other Yellow Perch during schooling attempts that were at least 3 seconds long.

The average total time or average total instances of each of these behaviours was calculated for each experimental tub (which was my experimental unit of replication) to

use in analysis. These variables allowed me to quantify the exploration and foraging behaviour of Yellow Perch both before and after pike were introduced into the enclosure.

Statistical Analysis:

To re-emphasise, my hypothesis was that there would be a significant interaction for the majority of behaviours evaluated between the history of experience of Yellow Perch with Northern Pike (i.e., Yellow Perch from lakes with or without Northern Pike) and the presence or absence of Northern Pike, indicating a distinct difference in behaviour to predator exposure depending on the history of predator experience for prey. To evaluate these interactions, I used the statistical program R (version 3.5.1, R Core Team, 2018) and the lme4 package to perform linear mixed-effects modelling on each of the Yellow Perch response behaviours recorded. To evaluate the significance of the interaction between predator history and predator presence (and where relevant, main effects of either predator history or predator presence separately), comparisons were made among nested models of varying complexity using log-likelihood ratio tests. For each variable analyzed, the significance of the interaction term was first determined as the log-likelihood ratio test comparing the full model (Equation 1) with a similar model lacking the interaction term between history and pike presence (Equation 2):

$$\mathbf{Eq\ 1)}\ y = \textit{history} + \textit{presence} + \textit{history*presence} + I|\textit{lake} + I|\textit{tub} + \varepsilon$$

$$\mathbf{Eq\ 2)}\ y = \textit{history} + \textit{presence} + I|\textit{lake} + I|\textit{tub} + \varepsilon$$

Where y is the response variable (behaviour) of interest, *history* is the fixed effect of predator experience history of the Yellow Perch (e.g., from a lake with Northern Pike or a lake lacking predators), *presence* is the fixed effect of presence or absence of a

Northern Pike in the enclosure, and *history*presence* is the interaction between these two fixed effects. The *lake* under investigation and the *tub* (enclosure) being observed were included as random effects in the models, and ε is the error term in the model.

If the comparison between the complex model (Equation 1) and the simple model (Equation 2), resulted in a *p*-value below a critical α of 0.05, I interpreted it as evidence of a significant interaction between predator history and pike presence for the behavioural variable under analysis.

A non-significant interaction term prompted the investigation of the main fixed effects in the model. To evaluate the effect of predator presence, I used log-likelihood ratio tests as above comparing Equation 2 to Equation 3, and to evaluate the effect of predator history, comparisons were made between Equation 2 and Equation 4:

$$\mathbf{Eq\ 3)}\ y = \mathit{history} + I|\mathit{lake} + I|\mathit{tub} + \varepsilon$$

$$\mathbf{Eq\ 4)}\ y = \mathit{presence} + I|\mathit{lake} + I|\mathit{tub} + \varepsilon$$

To determine how seasonality might have affected the result between the 1st and 2nd rounds of sampling conducted in the summer and fall at Lake 240 (contains Northern Pike) and Lake 109 (No Northern Pike) I ran log-likelihood ratio tests comparing complex model (Equation 5) to a simpler model (Equation 6)

$$\mathbf{Eq\ 5)}\ y = \mathit{sampling\ round} + \mathit{presence} + I|\mathit{tub} + \varepsilon$$

$$\mathbf{Eq\ 6)}\ y = \mathit{presence} + I|\mathit{tub} + \varepsilon$$

These terms in these equations are the same as before but with the addition of the sampling round as a fixed effect representing whether a population was sampled at the beginning or end of the experiment.

Results

Pike presence in the trials resulted in greater changes in predator-experienced Yellow Perch behaviour than in predator-naïve Yellow Perch. The model comparison analyses indicated that the interaction between predator history and pike presence in the trials was significant for all 5 behavioural variables recorded (Table 3).

Table 3: Results of Log-likelihood Ratio Tests comparing fixed-effect interaction term between Yellow Perch history with predators and pike presence for Mixed-Effect models. In the model, perch history with predators and pike presence in the trial are fixed effects, while the source lake for the population and testing tub are random effects.

Variable being analyzed	$X^2_{(7,6)}$	<i>p</i> -value
Time spent in open areas lacking cover	4.3939	0.0361
Time spent schooling with another perch	22.1276	<0.0001
Number of schooling attempts	41.5667	<0.0001
Time spent at the food source	8.5799	0.0034
Number of approaches to the food source	15.7861	0.0001

Perch that were predator-experienced significantly decreased the time spent in open areas compared to predator-naïve perch when pike were present, which showed similar times spent in open areas regardless of the presence of predators (Figure 2). The time spent schooling with conspecifics increased in the presence of predators for predator-experienced perch compared to predator-naïve perch, which showed consistent rates of schooling regardless of pike presence (Figure 3). Similarly the number of

different schooling attempts also increased for predator-experienced Yellow Perch in the presence of pike compared to predator-naïve perch, which was not different in the presence or absence of pike (Figure 4). Finally, the time spent at the suspended food source (Figure 5) and the number of approaches to that food source (Figure 6) were lower for predator-experienced perch in the presence of pike compared to predator-naïve perch, which showed no significant differences in the presence of pike.

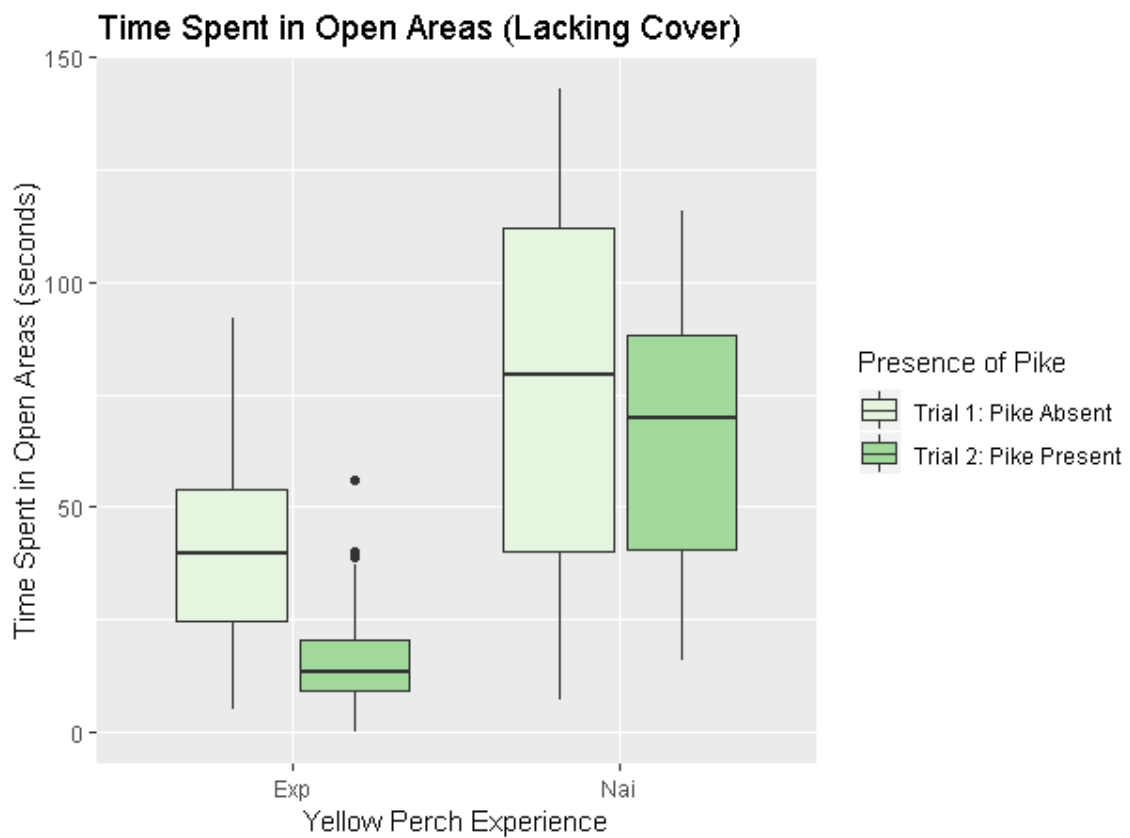


Figure 2: Box plot of the time Yellow Perch spent in open areas lacking cover in the 20 minute recordings. The graph divided by Yellow Perch history of experience with predators (Exp = Experienced with predators, Nai = Naïve to predators) and by whether a pike was present in the experimental trial (light = absent, dark = present).

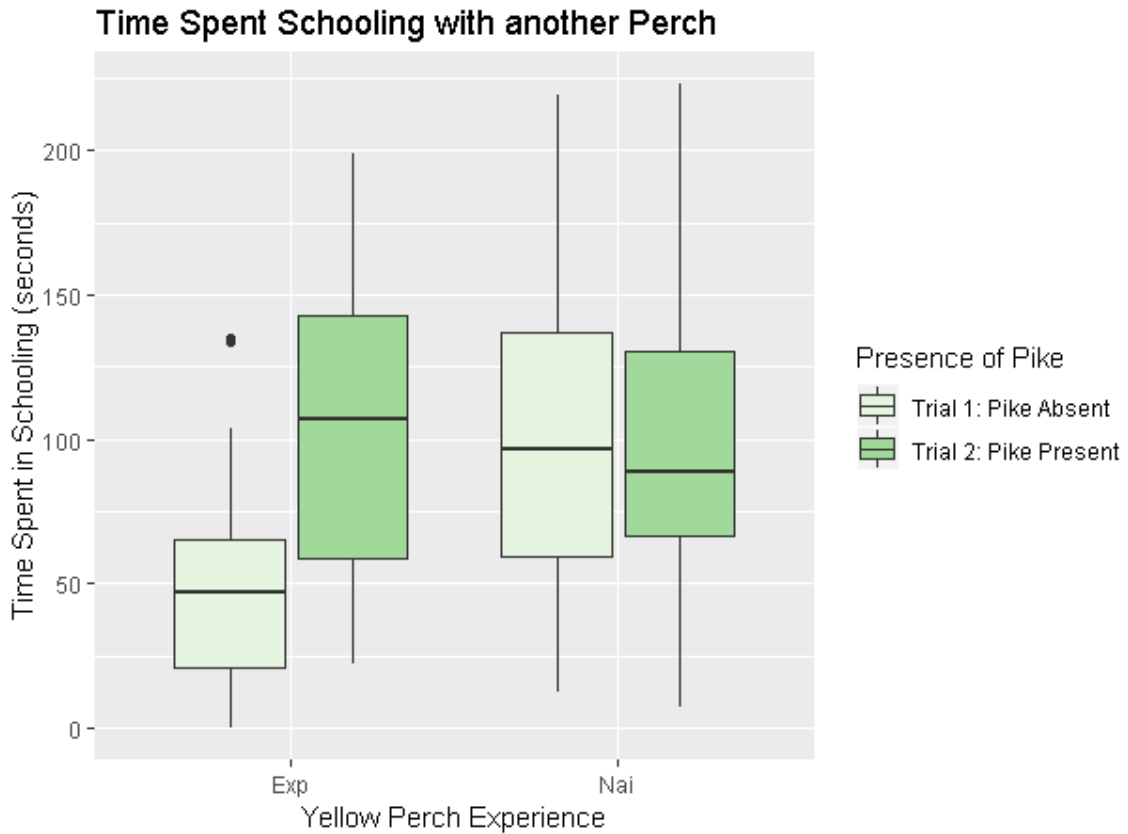


Figure 3: Box plot of the time Yellow Perch spent schooling with a least one other perch in the 20 minute recordings. The graph divided by Yellow Perch history of experience with predators (Exp = Experienced with predators, Nai = Naïve to predators) and by whether a pike was present in the experimental trial (light = absent, dark= present).

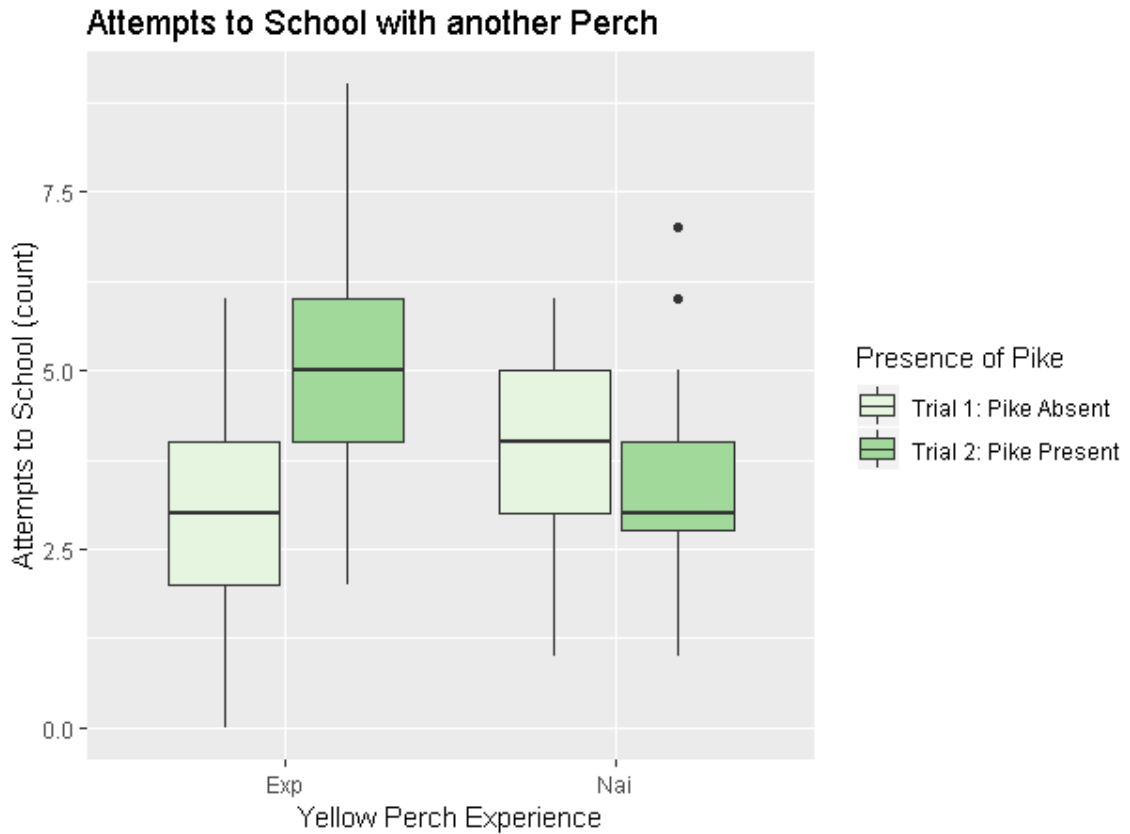


Figure 4: Box plot of the number of different attempts to school made by Yellow Perch in the 20 minute recordings. The graph divided by Yellow Perch history of experience with predators (Exp = Experienced with predators, Nai = Naïve to predators) and by whether a pike was present in the experimental trial (light = absent, dark = present).

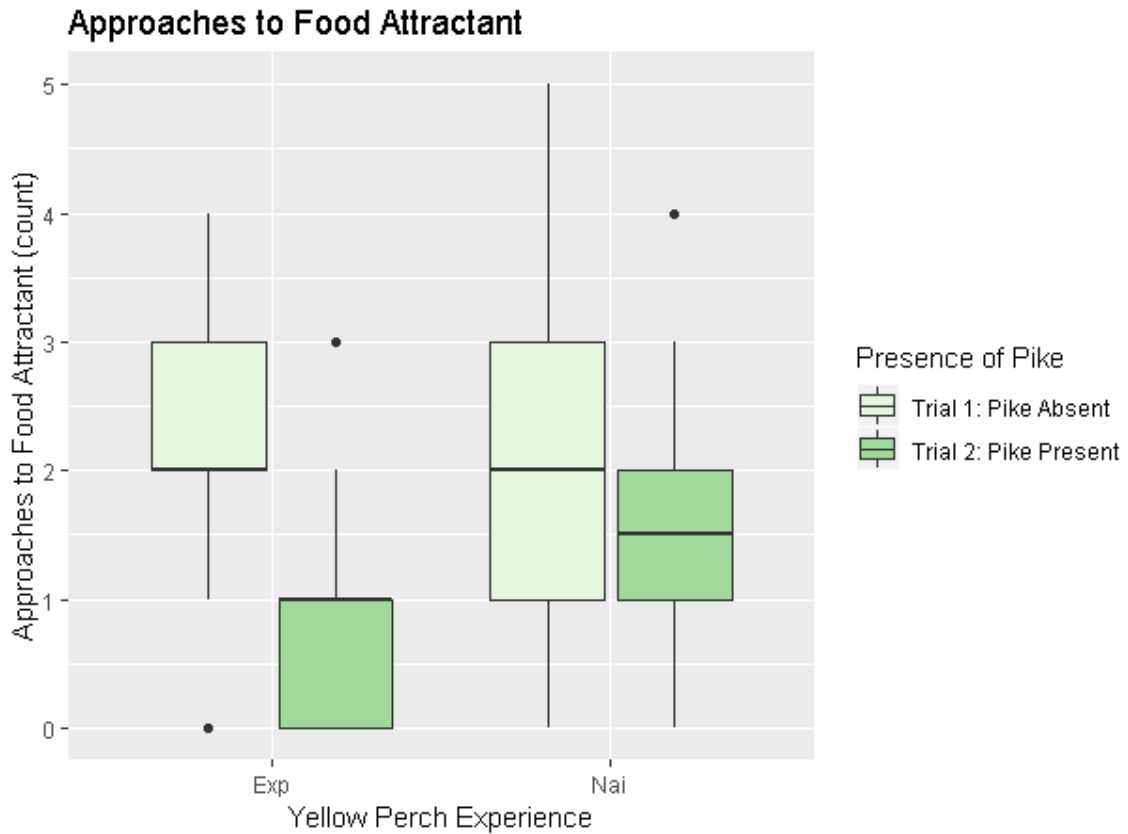


Figure 5: Box plot of the number of different approaches within half a body length to the food attractant made by Yellow Perch in the 20 minute recordings. The graph divided by Yellow Perch history of experience with predators (Exp = Experienced with predators, Nai = Naïve to predators) and by whether a pike was present in the experimental trial (light = absent, dark = present).

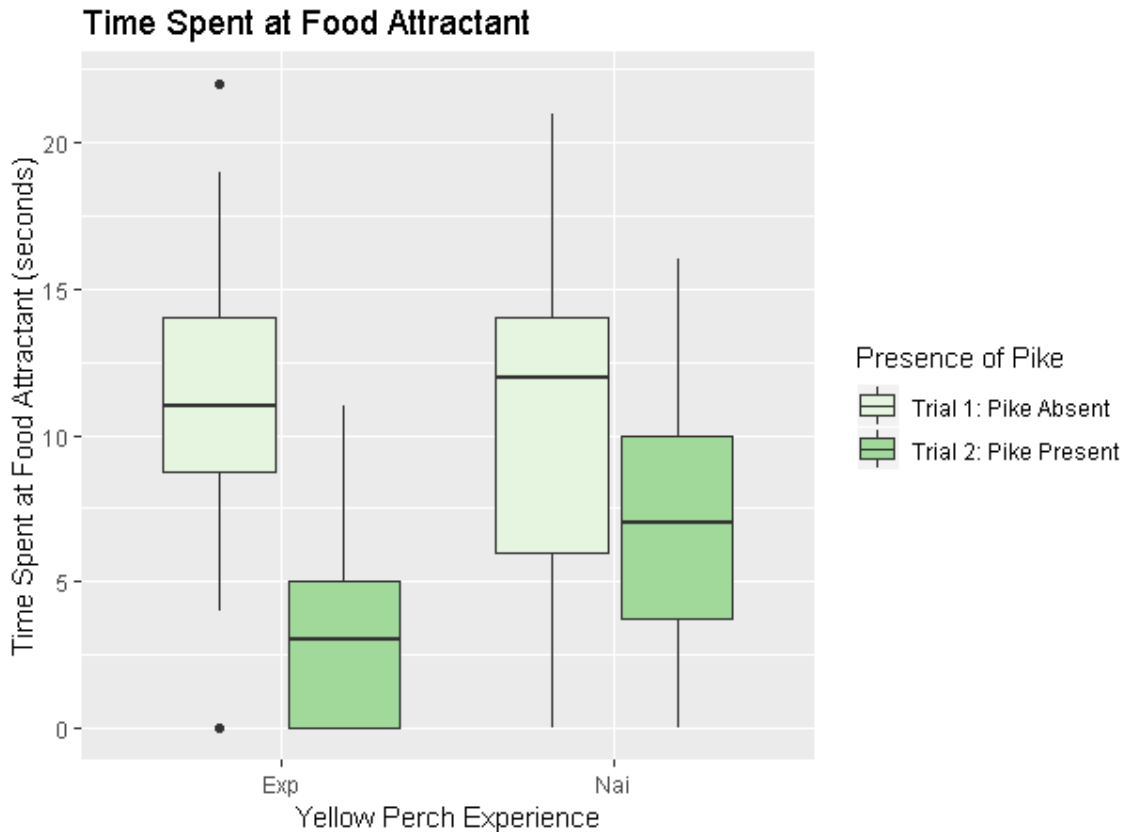


Figure 6: Box plot of the time Yellow Perch spent within half a body length of the food attractant in the 20 minute recordings. The graph divided by Yellow Perch history of experience with predators (Exp = Experienced with predators, Nai = Naïve to predators) and by whether a pike was present in the experimental trial (light = absent, dark = present).

The consistency of the sampling rounds (summer vs fall) for Lake 240 (contains Northern Pike) and Lake 109 (No Northern Pike) were statistically the same for nearly all beavhours (i.e. conducting the experiment in the summer versus September did not alter the consistency of the results; Table 4). The only behaviour observed to differ significantly between summer and fall trials was the number of approaches to the food source in Lake 109, with fewer approaches in the fall versus the summer (Table 4, Figure

10). Importantly, the overall the trend in behavioural changes for these populations in response to Northern Pike presence was still the same between sampling rounds; i.e., the predator-experienced fish always responded to the presence with a change in behaviour whereas predator-naïve fish showed almost no significant response to the presence of a predator (Figures 7-11).

Table 4: Results of Log-likelihood Ratio Tests comparing fixed-effect of sampling round on the data. In the model the sampling round and pike presence in the trial are fixed effects, while the testing tub is a random effect.

Variable being analyzed	Lake 240 Results	Lake 109 Results
Time spent in open areas lacking cover	$X^2_{(5,4)} = 1.7378$ $p\text{-value} = 0.1874$	$X^2_{(5,4)} = 0.2618$ $p\text{-value} = 0.6089$
Time spent schooling with another perch	$X^2_{(5,4)} = 6.7935$ $p\text{-value} = 0.091$	$X^2_{(5,4)} = 0.8008$ $p\text{-value} = 0.3709$
Number of schooling attempts	$X^2_{(5,4)} = 0.0266$ $p\text{-value} = 0.8702$	$X^2_{(5,4)} = 1.9437$ $p\text{-value} = 0.1633$
Number of approaches to the food source	$X^2_{(5,4)} = 0.1414$ $p\text{-value} = 0.7069$	$X^2_{(5,4)} = 6.2944$ $p\text{-value} = 0.0121$
Time spent at the food source	$X^2_{(5,4)} = 0.0324$ $p\text{-value} = 0.8571$	$X^2_{(5,4)} = 0.9053$ $p\text{-value} = 0.3413$

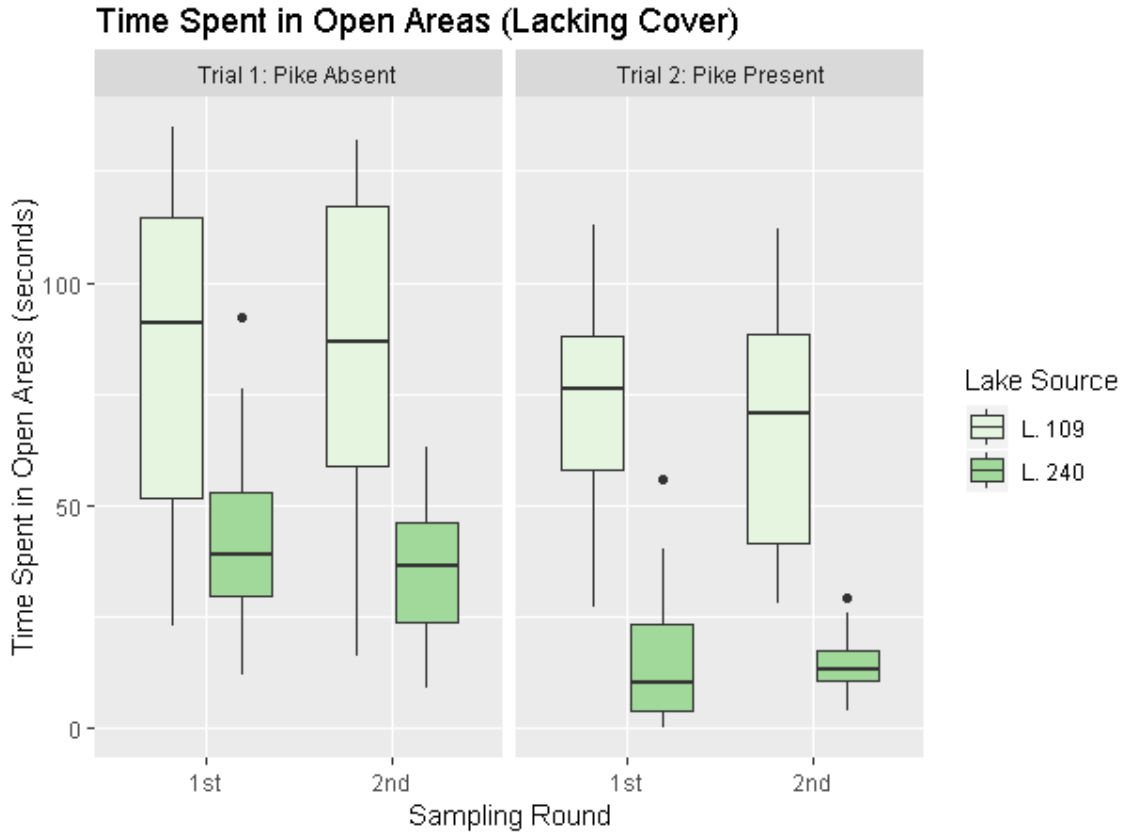


Figure 7: Box plot of the time Yellow Perch spent in open areas lacking cover comparing the 1st and 2nd sampling rounds. The graph divided by timing of the sampling round (1st = Beginning of the experiment, 2nd = End of experiment) and the source lake the Yellow Perch are from (light = Lake 109 [Pike absent], dark = Lake 240 [Pike present]).

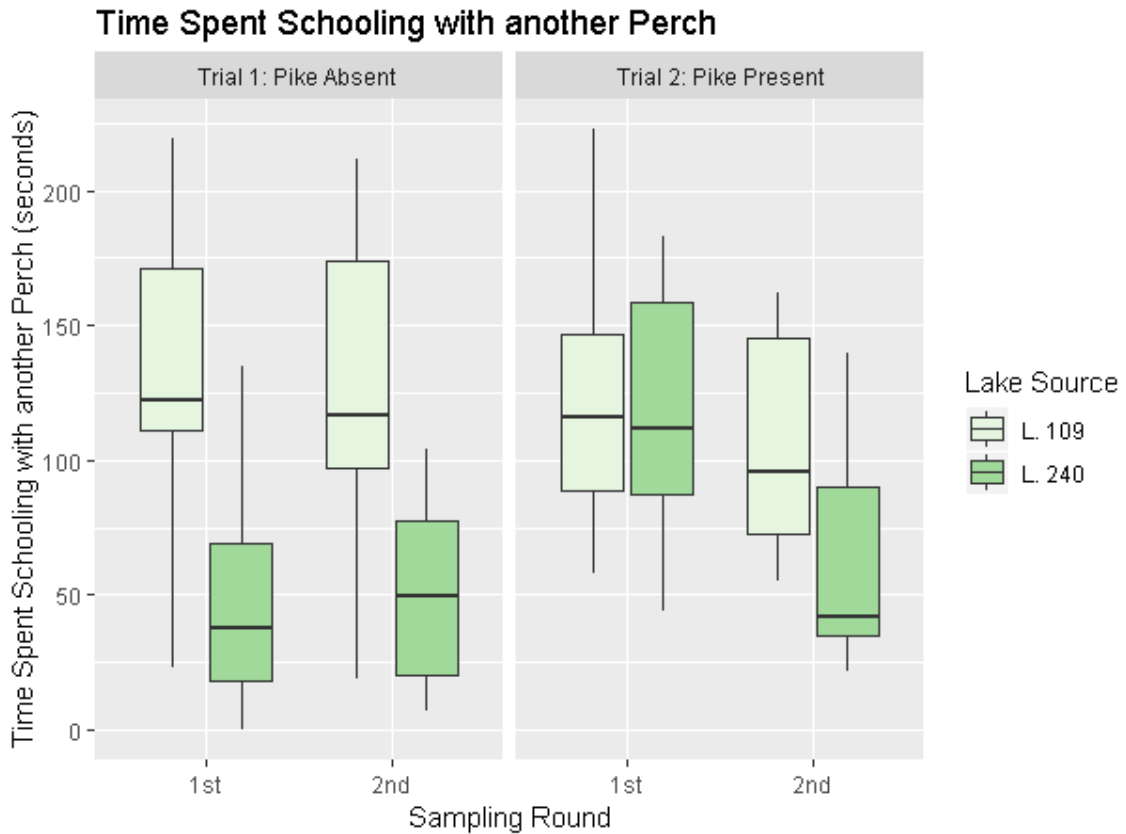


Figure 8: Box plot of the time Yellow Perch schooling with a conspecific comparing the 1st and 2nd sampling rounds. The graph divided by timing of the sampling round (1st = Beginning of the experiment, 2nd = End of experiment) and the source lake the Yellow Perch are from (light = Lake 109 [Pike absent], dark = Lake 240 [Pike present]).

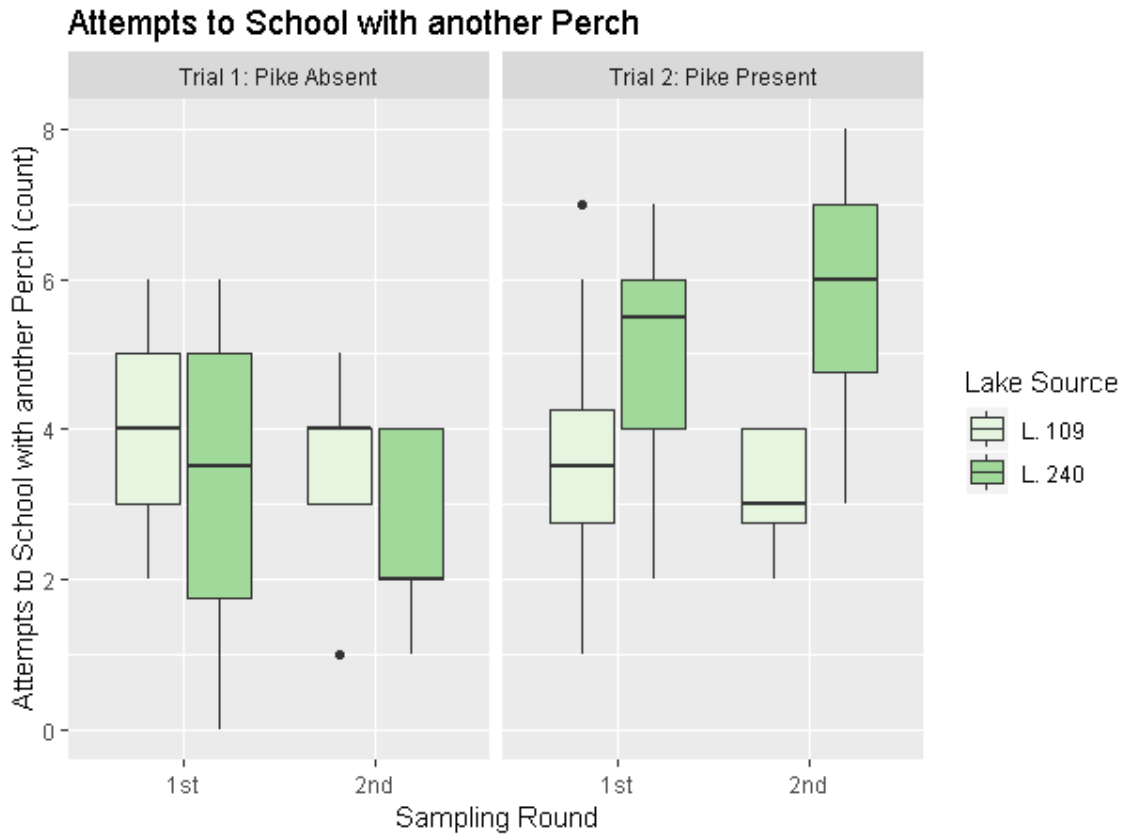


Figure 9: Box plot of the attempts to school with a conspecific made by Yellow Perch comparing the 1st and 2nd sampling rounds. The graph divided by timing of the sampling round (1st = Beginning of the experiment, 2nd = End of experiment) and the source lake the Yellow Perch are from (light = Lake 109 [Pike absent], dark = Lake 240 [Pike present]).

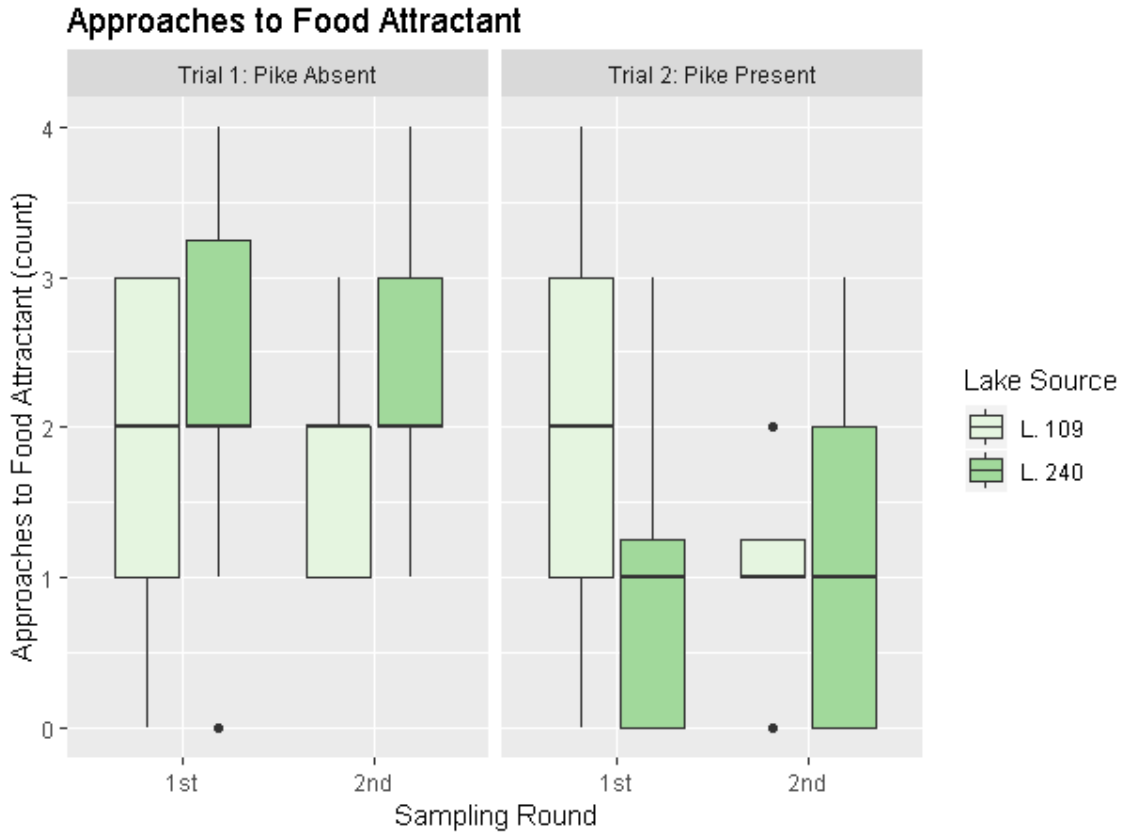


Figure 10: Box of the number of different approaches within half a body length to the food attractant made by Yellow Perch comparing the 1st and 2nd sampling rounds. The graph divided by timing of the sampling round (1st = Beginning of the experiment, 2nd = End of experiment) and the source lake the Yellow Perch are from (light = Lake 109 [Pike absent], dark = Lake 240 [Pike present]).

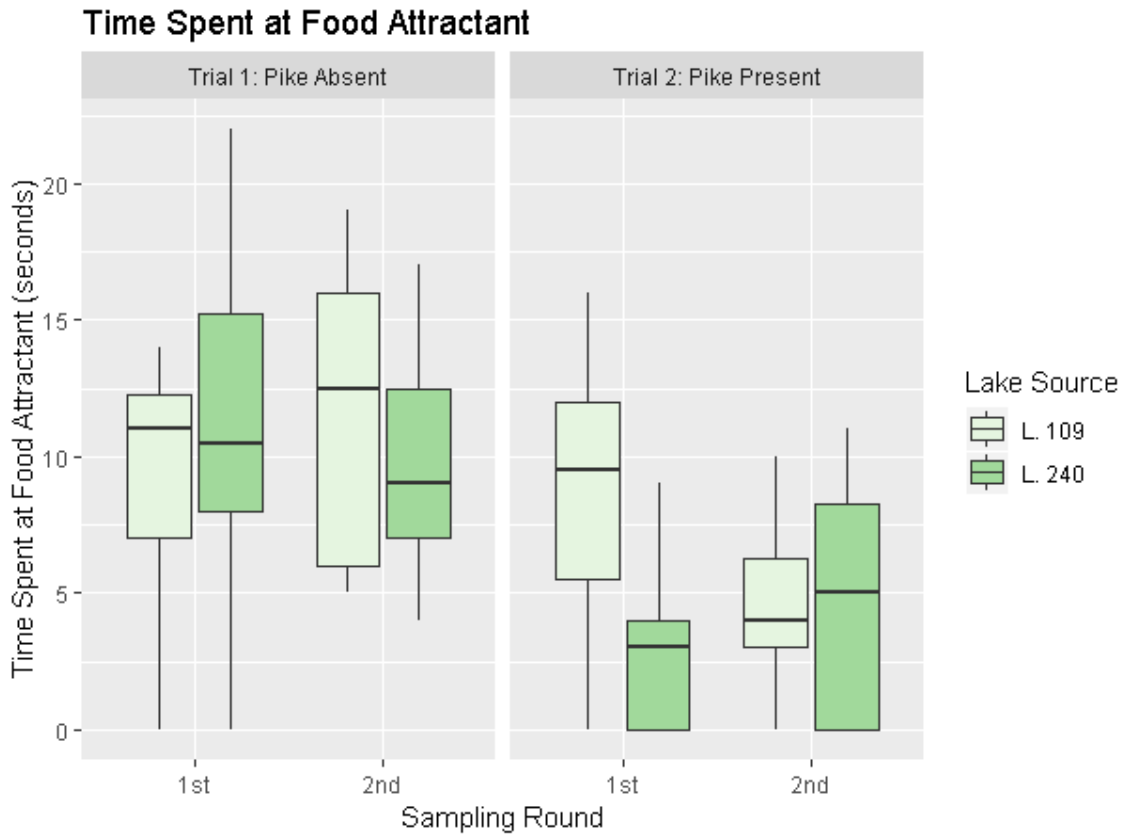


Figure 11: Box plot of the time Yellow Perch spent within half a body length of the food attractant comparing the 1st and 2nd sampling rounds. The graph divided by timing of the sampling round (1st = Beginning of the experiment, 2nd = End of experiment) and the source lake the Yellow Perch are from (light = Lake 109 [Pike absent], dark = Lake 240 [Pike present]).

Discussion

I found evidence of significant differences in how predator presence modifies prey behaviour for fish with different histories of piscivorous predator exposure for the five behavioural variables I measured. These differences manifested as significant behavioral changes, in response to the presence of the Northern Pike, that were observed in the predator-experienced Yellow Perch which were not mirrored in the predator-naïve perch. These differences included significant reductions of the time predator-experienced Yellow Perch spent in open areas that lacked cover and decreases in foraging behaviour with a reduction in the number of approaches to the food attractant and the time spent at that food attractant. By comparison, predator-naïve Yellow Perch did not significantly alter these activities and the behaviour of these fish was similar when the Northern Pike was both absent and present from the enclosure. In addition, inexperienced Yellow Perch did not alter for schooling behaviour in the presence of a predator while in predator-experienced perch responded to Northern Pike presence by increasing schooling attempts and schooling with conspecifics for longer periods of time.

Based on literature findings regarding the role of predator experience in sensitivity to novel predators (Patten 1997; Mirza & Chivers 2000; Zhao *et al.* 2006), my prediction was that there would be differences in how Yellow Perch responded to the presence of a predator based on predator experience such that predator-naïve Yellow Perch would be less sensitive to exposure to a novel predator than experienced Yellow Perch. The results of this experiment generally support my hypothesis; in all variables measured, there was no clear difference in predator-naïve Yellow Perch, while predator-experienced Yellow Perch always responded.

Unlike my predictions, predator-experienced Yellow Perch did not consistently demonstrate more risk-averse behaviour in the absence of predators that would reflect a more cautious approach to exploring novel environments. I thought that exploratory behaviour in predator-experienced Yellow Perch would be generally lower than in predator-naïve populations with the expectation that experienced fish would be more risk averse while naïve fish might be more active (Sih & Giudice 2012; Castanheira *et al.* 2013). Instead differences between these Yellow Perch with different histories of predation exposure only appeared to manifest in the presence of Northern Pike. Interestingly however, comparisons of the use of open areas and time spent schooling when evaluating seal consistency among behaviours do seem to support this hypothesis- fish from Lake 109 (predator-naïve) consistently used open areas more and schooled more frequently than predator-experienced fish from Lake 240. As I only had the capacity to examine two lakes of each predator exposure history (experienced versus naïve), these findings suggest that perhaps base-level behaviours in the absence of a predator may be more subtle such that additional populations would need to be included in order to definitively test this hypothesis of different basal levels of exploratory and foraging behaviour.

Another unexpected result was the comparatively high time spent schooling for predator-naïve fish which occurred even in the absence of predators. This behaviour may be driven by increases in foraging efficiency that can occur as a group, due in part to increases in the discovery of food patches (and the ability to cue in on conspecifics who find patches of prey), particularly when food is heterogeneously distributed, as opposed the defensive advantages typically associated with this behaviour such as increased

vigilance for predators (Partridge 1982; Eklov 1992). As one fish in a school cues in on a food or prey patch, the close proximity to other individuals allows the group to cue in on the foraging opportunity (Eklov 1992).

Assuming that these behavioural response indeed reflect differences in foraging and mating opportunities for Yellow Perch, a possible avenue for future research might be to investigate if these observed behavioural differences between predator-naïve versus predator-experienced perch might result in differential growth and size. In Yellow Perch, greater predator densities have been observed to result in smaller populations of faster growing fish which reach larger sizes than perch from lakes lacking major piscivorous predators (Brown 2009; Rennie *et al.* 2010). However, increased growth rates in the presence of, top predators are also likely a function of reduced prey densities due to increased predator mortality, resulting in reduced competition for resources (Buskirk & Yurewicz 1998). Teasing apart the impacts of density-dependence versus foraging efficiency in natural environments (with predators present) is difficult if not impossible to disentangle. Potential differences in growth rates between predator-experienced and predator-naïve prey fish could be evaluated with a common garden' experiment, where fish are grown under similar conditions. In such an experiment, I would predict more rapid growth rates in predator-naïve vs predator experienced Yellow Perch as a result of higher predicted foraging in predator-naïve populations (Rodd & Reznik 1997; Réale *et al.* 2010; Sih & Giudice 2012; Castanheira *et al.* 2013; Bassar *et al.* 2015). However, the results of this experiment suggest that these differences might only be manifested if a perceived threat of predation were included as part of the experiment, as behavioural

differences between populations with different histories of predator exposure and experience were only clearly manifest while in the presence of a predator.

This experiment evaluated predation threat as represented by Northern Pike, but the generalization of these findings to other predator species is not known. It may therefore also be of interest to change the species used as the predator in study and run this experiment again. The predator-experienced Yellow Perch in this experiment were familiar with Northern Pike but it might be informative to learn how Yellow Perch use this experience to respond to a novel predator or other large fish and how these prey fish generalize risk (Ferrari *et al.* 2007).

As I have demonstrated in this study, there does appear to be significant difference in how Yellow Perch respond to predation based on their previous experience with predators. This would suggest that these predator-naïve Yellow Perch would be at greater risk of predation mortality under a scenario of predator introductions or range expansion. Yellow Perch however, are a species that contain alarm cue pheromones in their epidermis cells, that are released when damaged, which should allow them to acquire recognition of predators rapidly after the population starter (Mathis & Smith 1993; Chivers & Smith 1994; Mirza & Chivers 2001). As such, the extirpation of Yellow Perch from lakes at the IISD-ELA following Northern Pike introductions is potentially surprising (Findlay *et al.* 1994; reviewed in Nicholson *et al.* 2015). In theory, once Yellow Perch began experiencing predation mortality from Northern Pike, the pairing of conspecific alarm cue with visual cues from the Northern Pike would allow them to acquire recognition of this predator. In Lake 221 of the Experimental Lakes area the Yellow Perch population disappeared 20 years after the introduction of Northern Pike

into the lake and 12 years after pike harvest from the lakes had stopped (Nicholson *et al.* 2015). Perhaps a factor in this event could have been that the capacity for Yellow Perch anti-predator responses were muted or limited, indicating some sort of constraints in modification and plasticity of their behaviour possibly due to having lacked a history of predation pressure to drive selection for anti-predator abilities (Giles & Huntingford 1984; Magurran 1986; Magurran 1990). The predator-naïve perch in this experiment demonstrated more risky behaviour than the predator experience perch in the presence of Northern Pike. This failure to appropriately respond to a threat of predation could help to explain why prey fish communities suffered such extreme declines in these lakes while in other nearby lakes Northern Pike and many of these prey species coexist in equilibrium (Nicholson *et al.* 2015).

There are many documented cases where invasions by top predators has resulted in major trophic cascades affecting the food webs of lakes by changing community structure (Debatas *et al.* 2003; Byström *et al.* 2007; Ricciardi and MacIsaac 2011). In a subarctic lake in Sweden, a Northern Pike invasion resulted in significant change in the community composition with Northern Pike replacing Arctic Char (*Salvelinus alpinus*) as the top predator and eliminating it from the lake as well as significantly reducing the numbers of the once abundant Ninespined Stickleback (*Pungitius pungitius*; Byström *et al.* 2007). As Northern Pike altered the community structure of this ecosystem, they also supplemented their diets with macroinvertebrates allowing them adapt to conditions of low prey availability compare with native Arctic char who the Pike both consumed and competed with (Byström *et al.* 2007). Invertebrate feeding in Northern Pike monoculture lakes is well documented (Venturelli & Tonn 2006). This adaptability to a range of

conditions of prey availability by Northern Pike may also help to explain the severity that their introductions have on novel environments (Haught & von Hippel 2011, Nicholson *et al.* 2015).

This study highlights that the anti-predator response of prey species differs between populations. In Yellow Perch, this anti-predator response is significantly modified by experience with predators and a history of inter-specific piscivorous predation. When top predators are introduced into lakes where they have historically been absent, large impacts to prey fish communities have been observed including extirpations (Byström *et al.* 2007; Haught & von Hippel 2011; Nicholson *et al.* 2015). As the climate warms, it can also facilitate range expansion of species resulting in new species overlaps and dispersals, some of which may lead to the introduction of top predators into lakes that do not currently support predators (Sharma *et al.* 2009). As these changes occur, it is important that we identify areas and populations that may be particularly vulnerable and in need of management to reduce the likelihood and impact of predator introductions. My study demonstrates that separate populations of a prey species, despite existing closely within the same region, have significantly different responses and vulnerabilities to predation. Fisheries managers should look at the historical presence of top predators as an indicator of vulnerability to top predator introductions and should be cautious making any assumptions based on stable community assemblages that may exist close by.

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Appendix A



Figure A1: Image of one of the experimental enclosures used in the experiment (before water was added showing the gravel used to provide contrast for visual recordings and the bamboo cover plates on either side of the central gate and barrier to provide cover for Yellow Perch.



Figure A2: Image of one of the experimental enclosures filled with water. The perimeter fence of the enclosure was composed of 8 wooden panels zip-tied to support posts and the lip of the tub. The roof (not shown) was made from two half-moon shaped panels that rested on top of the support posts. Remotely activated video recorders are attached to the centre wooden frame that supports the moveable mesh gate that is used to restrict movement between the halves of the enclosure.



Figure A3: Image of submerged fish pens (0.91 m x 1.52 m x 0.91m) composed of a mesh bag with 4mm holes surrounded by a galvanized steel cage with 5 mm square holes and a 1 mm thick wire, used for temporary housing of fish used in the experiments.



Figure A4: Image of a Yellow Perch (pictured at the top of the container lid) inspecting the bloodworm food attractant used in the experiments and contained in a weighted suspended porous container.



Figure A5: Image of one of the floor plates with bamboo rods used in the enclosures to provide cover for the Yellow Perch, simulating native *Equisetum spp.* Spaces between the bamboo are large enough for a pike to swim through though maneuvering is difficult providing an advantage to the smaller Yellow Perch in this area.



Figure A6: Image of Yellow Perch utilizing bamboo cover inside the experimental enclosures. Yellow Perch can be seen swimming on the upper right side of the image.



Figure A7: Image of the remotely activated video recorders that were mounted on a bracket above the centre of the enclosure. Each camera viewed one half of the enclosure. Images from the enclosure were processed and the data intergrated for each enclosure and trial of the experiment.