Comparison of multi-piscivore foraging success on native and invasive prey fish under variable light intensities

A THESIS
SUBMITTED TO THE FACULTY OF
UNIVERSITY OF MINNESOTA
BY

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IN PARTIAL FULFILLMENT OF THE REQUIREMENTS
FOR THE DEGREE OF
MASTER OF SCIENCE

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May 2020

Acknowledgements

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Chapter 1

A brief background on predator-prey interactions

Ecological community structure is often heavily impacted by invasions from nonnative species (Ricciardi & MacIssac 2000) in various ways including altered energy pathways (Johnson et al. 2005), species compositions (Karatayev et al. 2002, Stiers et al. 2011), and habitat and landscape modifications (Crooks 2002). Changes in species diversity caused by invasive species are driven by competition with the nonnative species for food (Bergstrom & Mensinger 2009) and shelter (Dubs & Corkum 1996), while native species also face similar or greater amounts of predation pressure once displaced to a less preferred habitat since predators are naïve to the new prey (Sih et al. 2010). This imbalance continues until the predators recognize the new prey resource, which can take years (Lockwood et al. 2013). However, it's unclear if this is purely based on predator behavior or if prey avoidance abilities differ between invasive and native prey. Predator-prey interactions are a vital piece of information that help predict and understand changes observed in community structure (Carpenter et al. 1985) and through observing specific interactions between species, we can better understand food web dynamics and invasion biology.

Round Goby Invasion

The Laurentian Great Lakes watershed has experienced more than 182 aquatic nonnative introductions (Ricciardi 2006) which includes invasive species (causing ecological, economical, or human health harm) and introduced species (nonnatives that were introduced for ecological or economical value; Lockwood et al. 2013). The Round Goby *Neogobius melanostomus* invaded the Laurentian Great Lakes in 1990 (Jude et al.

1992) and first appeared in the Duluth-Superior Harbor in 1998 (Leino & Mensinger 2016). Round gobies have been known to compete with many native benthic fishes including Mottled and Slimy Sculpins (*Cottus bairdii* and *C. cognatus*, respectively; Janssen & Jude 2001, Bergstrom et al. 2009), and Common Logperch *Percina caprodes* (Bergstrom et al. 2009, Balshine et al. 2005) which includes competition for habitat, shelter, and food (Janssen & Jude 2001, Balshine et al. 2005, Bergstrom et al. 2009). Along with competing native fish for common prey such as macroinvertebrates, Round Gobies also utilize *Dreissenid* mussels which provides a source of energy native prey cannot access (Ghedotti et al. 1995) although *Dreissenid* mussels are not a preferred prey item (Coulter et al. 2011).

When competing for shelter, Round Gobies are more aggressive and successful when compared to Mottled Sculpin (Dubs & Corkum 1996). This displacement from shelters, along with general displacement from preferred rocky habitats *in situ* should increase consumption of native prey due to less cover to hide in. After the lag phase where predation does not occur or occurs in very reduced amounts, the Round Goby has been integrated into predator diets (Johnson et al. 2005, Crane & Einhouse 2016) and have become the dominant prey item for Smallmouth Bass (Johnson et al. 2005, Crane & Einhouse 2016), Burbot (Johnson et al. 2005, Jacobs et al. 2010), and Lake Trout (Dietrich et al. 2006, Rush et al. 2012). High predation on Round Goby is likely driven by high densities in the great lakes with densities greater than 100 individuals m^{-2} (Chotkowski & Marsden 1999), but the efficiency of native predators to capture invasive compared to native prey has not been observed.

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Background on predator-prey interactions

Sequential binary decisions that occur during a predator-prey interaction may include location, pursuit, attack and capture (O'Brien 1979). Location is defined as predator orientation towards the prey (O'Brien 1979) and following successful location outside of the predator's attack range, will pursue prey or immediately attack. Attack probabilities are correlated with distance, prey size and density, relative speeds of the predator and prey, predator satiation level, and habitat (Gill & Hart 1998, Gill 2003, Turesson et al. 2006, Curio 2012) while capture and retention success are often influenced by prey avoidance behaviors (Godin 1997, Lundvall et al. 1999) and habitat complexity (Scharf et al. 2006, DeBoom & Wahl 2013). Predators have two main strategies when hunting prey: pursuing or ambushing prey. However, the two strategies are not mutually exclusive because Largemouth Bass *Micropterus salmoides* utilize both strategies depending on plant density (Savino & Stein 1982). In open water and less densely vegetated areas, Largemouth Bass are characterized as pursuit predators but switch to ambush predators when in dense vegetation (Savino & Stein 1982). Pursuit predators search for food and actively chase and attack the prey (O'Brien 1979). If the first attack is unsuccessful or the prey fled prior to attack, pursuit predators will continue to pursue until the prey is either captured or lost. Conversely, ambush predators remain still, hiding in structure (weed beds, rocky outcrops, woody debris, etc.) until prey are located and wait until the opportune moment to attack prey (Savino & Stein 1989), although if the prey flees before a predator strike is initiated predator pursuit will not occur.

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During each stage of an interaction, a variety of sensory systems are used including the visual, mechanosensory (composed of inner ear and lateral line), olfactory, and gustatory systems. A brief description of each system is detailed below.

Vision

Vision is the primary sensory system used for locating prey during the day, and sometimes at night, by a large majority of fishes. Some fishes specialize in feeding during low-light conditions such as Lake Trout (Vogel & Beauchamp 1999, Keyler et al. 2015, 2019), Walleye (Vandenbyllaardt et al. 1991), Sauger (Ali & Anctil 1977), and Burbot (Probst & Eckmann 2009) while others are most successful in high-light environments such as largemouth bass (Howick & O'Brien 1983), Atlantic Salmon (Hansen et al. 1992), and Northern Pike (Skov et al. 2002). Within a predator-prey interaction, vision is used to locate prey and initiate strikes by Muskellunge when light is present (New et al. 2001). Locating prey using vision shows predator tendencies towards prey in the anterior visual field (Job & Bellwood 1996, New et al. 2001). However, once located fish with ablated lateral lines attack at significantly reduced distances and at reduced angular deviations compared to control fish (New et al. 2001), suggesting vision is primarily used in location and less so at every other stage during an interaction.

Mechanoreception

Mechanoreception, comprised of the inner ear and lateral line, is mostly used during the pursuit and capture stages (New et al. 2001). The range of the lateral line has been previously estimated to range from one to two body lengths (Braun et al. 2002),

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although other behavioral and sensory physiology trials have shown the range to be under a body length (New et al. 2001, Palmer et al. 2005, Richmond et al. 2004). However, blinded fish are equally as successful compared to controls suggesting all of the critical information regarding prey is still acquired via only the lateral line (New et al. 2001). Similarly, nocturnal fish primarily utilize the lateral line for prey detection like the Mottled Sculpin finding planktonic prey (Janssen et al. 1995, Janssen 1996, Janssen 1997). When pursuing prey, the lateral line is the primary sensory system tracking prey and when ablated, frequencies of attacks and captures greatly diminish (Pohlmann et al. 2004). Even in the presence of light, some predators like Largemouth Bass and Green Sunfish, which were trained to feed from a tube, select for attacking water pressure changes (established via jets) rather than visually-presented prey (Janssen & Corcoran 1993) which suggests lateral line stimuli can override visual input while directing strikes.

Chemoreception

Chemoreception, comprised of the olfactory and gustatory systems, can be used to detect the presence of prey in an area but lack the specificity for precise location or directional cues (Kasumyan 2004). This is due to constant water perturbations from predator and prey movements, currents, and wind action which dissipate chemical cues rapidly. In behavioral trials, blinded predators with abated lateral lines were very ineffective in capturing prey, suggesting olfaction and/or gustation could not provide all of the critical information needed to locate prey, let alone capture them (Liang et al. 1998, New et al. 2001). Similarly, gustation was thought to be used during prey pursuit

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but trials with the European Catfish show gustation has little effect during pursuit. Rather, gustation is necessary for finding stationary food (Brown 1982, Pohlmann et al. 2001). Thus, chemoreception likely plays a very minor role in capturing moving prey.

Use of Multiple Predators and Prey

Behavioral trials on predator-prey interactions often focus on an ecologically important relationship between one predator and prey species' interactions and rarely factor in multiple species (Webb 1984, Rahel & Stein 1988, Savino & Stein 1989). Of the studies that have used multiple predators, only one has used more than one predator species at a time (Rahel & Stein 1988) which provides the ability to compare inter- and intraspecific differences in prey capture success. Rahel & Stein (1988) found the use of multi-species predator trials important as prey behavior was drastically different between the two predators alone, but when the predators were combined the prey behavior was mainly driven by one predator species, with slight changes in behavior to avoid the other predator. Thus, the use of multiple predator species is underutilized and should be a focus of future studies.

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Chapter 2

Comparison of multi-piscivore foraging success on native and invasive prey fish under variable light intensities

Abstract

The majority of fish predator-prey studies have focused on interactions using a single predator. We explored the complexity of foraging at different times of the day by examining the interactions of paired native predators (Burbot *Lota lota* or Smallmouth Bass *Micropterus dolomieu*) with either native (Mottled Sculpin *Cottus bairdii*) or invasive (Round Goby *Neogobius melanostomus*) benthic prey (n=20). The study allowed the comparison of a pursuit (Smallmouth Bass) and ambush (Burbot) predator. Trials were performed under natural relevant lighting conditions with downwelling light intensity and emission spectrum matched to the irradiance at 10 m depth found in the St. Louis River estuary during summer at night, civil twilight, sunrise, and midmorning. Smallmouth Bass were more active than burbot and initiated 1,510 reactions that resulted in the successful capture of 61 Round Goby and 103 Mottled Sculpin (10.9% success rate overall) whereas Burbot initiated 475 reactions resulting in 24 successful retentions including 9 Round Goby and 15 Mottled Sculpin (5.0% success rate overall). The percentage of successful retentions was greater for Smallmouth Bass at 10.9% compared to only 5.0% for Burbot. Reaction probabilities to each prey differed significantly which resulted in a two-fold increase in attacks on Mottled Sculpin compared to Round Gobies within the same time period. Reaction distances for both predator species did not differ in regard to prey species, but Smallmouth Bass reacted farther than Burbot (max. reaction distances of 159 and 98 cm, respectively). Greater success of native predators on native

prey likely cause predators to expend more energy capturing invasive prey and cause higher mortality on native prey populations due to greater predator success.

Introduction

Predator-prey interactions often determine aquatic community structure (Carpenter et al., 1985) with a multitude of factors affecting interactions, outcomes, and effects (Higham et al., 2015). These include the sensory abilities of the predator and prey (Liem 1978, Lundvall et al. 1999, Beauchamp et al. 1999) and the effects of environmental variables on these sensory systems (Utne-Palm 2002, Lönnstedt et al. 2013, Santos-Pata et al. 2018). Previous studies on predator-prey interactions have focused primarily on interspecific interactions of a single visually mediated predator and one prey species (O'Brien 1979, Nielsen 1980, Vogel & Beauchamp 1999, Mazur & Beauchamp 2003, Jönsson et al. 2013, Hansen et al. 2013, Keyler et al. 2015, 2019). However, predators often attack a variety of prey species and face both inter- and intraspecific competition for prey resources. Few predator-prey experiments have used multiple predator species (Webb 1984, Savino & Stein 1989) or more than one predator in a trial (Sweka & Hartman 2003), and none used multiple predator species simultaneously in trials observing individual predator-prey interactions.

Environmental conditions such as light, temperature, turbidity, and turbulence combined with biological factors such as sensory systems, satiation, motivation, locomotor ability, and crypsis all factor into the predator/prey aquascape (Ward et al. 2006). For fishes that rely on vision for attack or escape, an important environmental

factor is light intensity. In oligotrophic freshwater environments, downwelling light is primarily composed of blue-green wavelengths (500-550 nm) that become red shifted as primary production increases (Jerome et al. 1983). In visually limited environments, such as at depth and/or during the night, fishes use their mechanosensory lateral line for detection of prey and predators until sufficient light is available to mediate visual interactions. Thus, throughout predator-prey interactions, vision and mechanoreception can be used to varying degrees. For example, muskellunge (*Esox masquinongy*) rely primarily on vision to detect prey in daylight conditions, however strike initiation is based on a combination of lateral line and visual input, and only the lateral line is used in the final moments to capture prey (New et al. 2001).

Sequential binary decisions that may occur during a predator-prey interaction include location, pursuit, attack and capture (O'Brien 1979). Location is defined as predator orientation towards the prey (O'Brien 1979). Following successful location outside of the predator's attack range, mobile predators will pursue prey or immediately attack. Conversely, ambush predators wait until prey are within striking distance which some have also defined as pursuit (O'Brien 1979). Attack probabilities are correlated with distance, prey size and density, relative speeds of the predator and prey, predator satiation level, and habitat (Gill & Hart 1998, Gill 2003, Turesson et al. 2006, Curio 2012). Capture and retention success are often influenced by prey avoidance behaviors (Godin 1997, Lundvall et al. 1999) and habitat complexity (Scharf et al. 2006, DeBoom & Wahl 2013). Reaction distance, which is the distance between predator and prey at the time of initial predator orientation is a common metric describing a predator's effective

search distance (Howick & O'Brien 1983, Miner & Stein 1996, Vogel & Beauchamp 1999) and is used in predictive models examining foraging success and responses to environmental changes (i.e. increased turbidity; Vogel & Beauchamp 1999).

The Round Goby *Neogobius melanostomus* invaded the Laurentian Great Lakes in 1990 (Jude et al. 1992) and has negatively impacted native species. Round Gobies displace and outcompete native benthic fishes including Mottled and Slimy Sculpins *Cottus bairdii* and *C. cognatus*, respectively (Janssen & Jude 2001, Bergstrom et al. 2009) and Common Logperch *Percina caprodes* (Balshine et al. 2005, Bergstrom et al. 2009). Several reasons have been hypothesized to account for this dominance including the Round Goby's aggressive behavior (Dubs & Corkum 1996), generalized diet (Janssen & Jude 2001), and prolific reproduction (MacInnis & Corkum 2000), while native predatory fishes have adjusted to increased Round Goby populations by incorporating them into their diets (Johnson et al. 2005, Crane & Einhouse 2016). However, the ability of the Round Goby to avoid native piscivore predation has not been studied.

Native piscivores that feed on Round Goby include visual predators such as Smallmouth Bass *Micropterus dolomieu* (Johnson et al. 2005, Crane & Einhouse 2016), Lake Trout *Salvelinus namaycush* (Jacobs et al. 2010), Walleye *Sander vitreus* (Johnson et al. 2005, Reyjol et al. 2010), Sauger *Sander canadensis* (Reyol et al. 2010), and Yellow Perch *Perca flavescens* (Johnson et al. 2005, Reyol et al. 2010). Burbot *Lota lota* also feeds on the Round Goby (Johnson et al. 2005, Hensler et al. 2008, Jacobs et al.

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2010), but primarily relies on mechanoreception and tactile gustation to locate prey (Brown 1982).

The range overlap of the Mottled Sculpin and Round Goby provides an opportunity to compare how native and invasive species are currently impacted by native predators. Additionally, the use of visual and non-visual predators allows for the comparison of different strategies in capturing the invasive and native prey. Studies of invasive species have focused on their impacts on native species occupying similar niches and if native predators have integrated the invasive species into their diet (Mills et al. 1993, MacIssac 1999). Competition with invasive species often causes native prey declines, leading to subtle declines in predators until either native prey populations rebound or native predators begin predating upon invasive prey (Lockwood et al. 2013). Predator success in capturing different prey species is well studied (Webb & Skadsen 1980, Webb 1984, Savino & Stein 1989), but no literature exists about contrasting piscivore success in capturing similar native and invasive prey. We hypothesize that predatory responses to our prey, the native Mottled Sculpin and invasive Round Goby, will be similar given their cryptic coloration and benthic habitat. However, we expect Round Goby to be more difficult to capture than Mottled Sculpin based on the displacement of sculpin in areas invaded by Round Goby. Our objectives were to 1) generate reaction distance models for adult Smallmouth Bass and Burbot to benthic prey and 2) determine how capture efficiencies of native piscivores differ between Mottled Sculpin and Round Goby at each stage of the predator-prey interaction. We conducted

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controlled experiments in laboratory foraging arenas under varying light conditions to pursue those objectives.

Methods

Fish collections and care.—Round Gobies were collected via baited minnow traps and trawling in the Duluth-Superior Harbor, and Mottled Sculpin were captured via backpack electroshocking from St. Louis River tributaries. Smallmouth Bass were collected via angling in the St. Louis River and Burbot were collected via ice fishing the Duluth-Superior Harbor and electrofishing in Shagawa and Harriet Lakes in Ely, MN. All fishes were collected between May 15th to October 18th, 2018 and January 16th to August 20th, 2019 in water at depths ≤ 10 m. Smallmouth Bass (n = 18) and Burbot (n = 16) ranged from 290-425 mm and 285-490 mm total length (T_L). Sub-samples of Round Goby ranged from 60-74 mm (n=60) and Mottled Sculpin ranged from 64-78mm (n=60) T_L. Fishes were transported in coolers filled with pondwater solution (deionized (DI) water, 0.6% NaCl, 0.7% KCl, and 1.7% $CaCl_2 \cdot 2H_2O$) and 0.5% API Stress Coat Plus (Mars Fishcare Inc., Chalfront, PA) that were equipped with battery-operated air pumps for water circulation. When needed, ice sealed in plastic bags was added to maintain water temperatures within ± 1.5°C of the water temperature at the collection site. Fish were separated by species into 568 L holding tanks and maintained at 16 °C under a 14h:10h day:night light cycle. Recirculated water was biologically, mechanically, and chemically filtered and water quality was tested daily for the first week after fish introductions and twice weekly thereafter. All fishes were fed three times per week with Burbot and

Smallmouth Bass given live minnows while round Gobies and Mottled Sculpin were fed

California Blackworms *Lumbriculus variegatus*.

Experimental setup

The foraging arena consisted of a 1900 L (2.3 m × 1.0 m × 0.7 m) fiberglass tank

with water depth maintained at 0.5 m, with the sides lined with black cloth to reduce light

reflection, and rounded inserts placed in the corners to minimize corner effects. Three

Plexiglas viewing windows in the side of the tank provided lateral camera placement.

Substrate consisted of tan-brown pea gravel (KolorScape[TM], Atlanta, GA) up to 2.5 cm in

depth. Eight light engines were mounted 1.2 m above the water surface and contained

LED lights with a peak wavelength of 510 nm (cyan color; Cree XLamp XR Series,

Durham, NC) with irradiance adjusted by an external controller. For lower light

intensities, light diffusing cones (Savage Universal Corp., Chandler, AZ) were suspended

below the light engines to reduce point-source intensity. For greater light intensities

(sunrise and midmorning), diffusing cones were removed to reach required intensities.

Three 850 nm peak wavelength infrared LED lights (CMVision, Houston, TX) provided

illumination during dark and low-light conditions. Trials were monitored with charged

coupled device (CCD) infrared sensitive (Vantage model LBC7081, Lorex Technology,

Markham, ON) cameras with three mounted above the tank and three mounted flush to

the plexiglass viewing port. Videos were saved to a DVR (ECO2 series, LH130, Lorex

Technologies, Markham, ON) and analyzed offline.

Light intensity calculations

The light intensities for the experimental tank were adjusted to mimic the downwelling irradiance at a depth of 10 meters for the following times: night (without astral light contribution), civil twilight with the sun -6° and -4° below the horizon, sunrise, and midmorning (solar elevation of 46° in August at 10:30 am in Duluth, MN). Measured lake surface irradiances assumed a summer day with 25% cloud cover to represent the average cloud cover in Duluth, MN (NOAA Duluth Office Report, 2018). Tank surface irradiances were calculated using the Beer-Lambert equation (Hutchinson, 1957):

Eq 1. $I_x = I_0 e^{-kx}$

where I_0 is the August 17th surface irradiance, x is the depth, k is the attenuation coefficient (0.7 for Duluth-Superior Harbor), and I_x is the is the irradiance (light intensity) at depth.

Five different irradiances representing night (8.45×10^8 photons m^{-2} s^{-1}), civil twilight at -6 and -4 degrees below the horizon (5.27×10^{10} and 6.32×10^{12} photons m^{-2} s^{-1}, respectively), sunrise (8.78×10^{13} photons m^{-2} s^{-1}), and midmorning (8.94×10^{15} photons m^{-2} s^{-1}) were tested. Civil twilight and sunrise irradiances were based on Kishida (1989; 34.3853° N, 132.4553° E), while midmorning irradiance were converted from values for a summer morning at 10:30 am with 25% cloud cover (Fahnenstiel et al. 1984; 47.2855° N, -90.6879° W). All values were converted to photons m^{-2} s^{-1} (Thimijan & Heins, 1983; Harrington et al. 2015) for biological applicability (Johnsen 2014), and tank surface irradiances were measured using an International Light Technologies ILT1700 Research

Radiometer with a SED033/F/HMR/W broadband silicon detector (Peabody, MA). Trials were run during the corresponding periods of the day (i.e. dark, CT-6, Midmorning, CT-4, dark) to reduce differences based on circadian rhythms. The experiments were performed in a walk-in cold room with two layers of 1 mm black fabric atop one layer of 1 mm black plastic on the outside and 0.5 mm aluminum foil on the inside of the door. Night trials were conducted with all internal cold room and external laboratory lights turned off with dark adapted human observers unable to detect any light following 30 minutes of dark adaptation.

Experimental trials

Foraging trials were conducted from June 15th, 2018 to November 9th, 2018 and June 14th, 2019 to September 18th, 2019. A crossed design with two predatory fish per trial was used with two Smallmouth Bass or Burbot, or one Smallmouth Bass and one Burbot. Three trials were run per predator treatment for both prey species at all light intensities (except for Burbot at the highest intensities due to inactivity) resulting in 78 trials. Food was withheld for all fishes at least 24 hours prior to a trial. Each trial consisted of two predators and twenty prey with all fishes acclimated for at least one hour in their respective sections of the arena. Each section of the arena was separated by an opaque plexiglass divider creating 0.77 m × 1.0 m and 1.53 m × 1.0 m sections for predators and prey respectively. At the onset of each trial, the divider was lifted and predators were allowed to forage for two hours, upon which predators were removed and the number of remaining prey were counted. Surviving prey were maintained in separate

tanks for at least 24 hours between trials and used in a maximum of six trials. Predators were not tested again for at least 24 hours to allow for prey digestion and the maximum number of trials for predators was five for smallmouth and seven for Burbot. Similar sized predators were used to reduce size effects. The prey species and light intensity was randomly assigned for each predator pair.

Analysis

Video was recorded at 20 fps with 720 by 480-pixel resolution and analyzed frame by frame beginning with the frame immediately prior to predator orientation using ImageJ (NIH, v. 1.52a). A 20 × 20 cm plexiglass square was placed on the bottom of the tank for image calibration. To minimize wall effects, the limited number of reactions (7%) to prey fleeing against or remaining immobile on the wall were excluded from analysis. A predator-prey interaction was defined as a predator detecting a moving or immobile prey, or a moving prey that was not detected within the predator's detection radius.

Foraging success

Foraging success was calculated as the probability of the predator locating, attacking, capturing, and retaining prey (O'Brien 1979, Richmond et al. 2004, Keyler et al. 2015, 2019). Location, hereafter reaction, was defined as the predator orienting to a single moving prey (O'Brien 1979). Due to the difficulty of determining when predators may have reacted to or passed immobile prey, reaction success was not calculated for

immobile prey. However, immobile prey that elicited reactions were factored into the attack, capture, and retention percentages.

The predator reaction distance was defined as the distance from the dorsal midpoint of the predator's eyes to the dorsal midpoint of the prey body at the time of orientation. The reaction angle was defined as the angle between the line generated for the reaction distance and the line along the predator's longitudinal axis with the anterior of the head being 0°. The probability of a predator reaction to a prey was calculated as the number of reactions to moving prey divided by the total number of prey moving within the predator's detection radius for each light intensity. The detection radius was calculated as the average of the peak reaction distance for each predator from each trial (n=6) at each light intensity.

An attack was defined as a rapid burst of speed by the predator towards the prey (Sweka & Hartman 2003) that included the predator opening its mouth during the terminal phase of the attack (O'Brien 1979). Attacks resulted in either a capture or an escape and the probability of attack was calculated as the number of attacks divided by the total number of reactions.

A capture was defined as the prey contained in the predator's mouth (O'Brien 1979) and resulted in either a retention or an escape. Capture probabilities were calculated as the number of prey contained divided by the total number of attacks.

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Retentions were defined as prey ingestion (Richmond et al. 2004) and were categorized as either successful or unsuccessful. Retention probability was calculated as the number of prey ingested divided by the total number of captures.

Models

Average peak reaction distances were collected by taking the maximum reaction distance for each predator species used in a trial and averaging those distances. Reaction distances were averaged for Round Goby and Mottled Sculpin trials from same- and crossed-predator trials. An analysis of covariance (ANCOVA) was used to test for differences between same- and crossed-predator trial peak reaction distances at each light intensity. A Michaelis-Menten function (O'Neill et al. 1989) was used to estimate the relationship between light intensity and reaction distance for smallmouth to both benthic prey species. The equation was as follows:

Eq 2: $R_d = R_{max} * l * (\alpha + l)^{-1}$

where R_d is the estimated reaction distance in cm, α is the half-saturation constant, and R_{max} is the reaction distance at a given light intensity (l). R_{max} and α were estimated using a non-linear regression in SigmaPlot 14.0 (Systat Software Inc., San Jose, California). Similar models have been used to estimate the reaction distances of Yellow Perch (*Perca flavescens*, Richmond et al. 2004) and Lake Trout (*Salvelinus namaycush*, Holbrook et al. 2013, Keyler et al. 2015, 2019). Next, a parabolic function on log_{10} transformed light intensities was used to estimate the relationship between light intensity and reaction distance for smallmouth with the following equation:

Eq 3. $R_d = a + (b * l) + (c * l^2)$

where the estimated reaction distance (R_d) is calculated from log of light intensity ($\log_{10}l$) and the 3 constants (a, b, and c). Parameters were calculated using a non-linear regression in SigmaPlot. The parabolic function was used to test the relationship between light intensity and reaction distance for Burbot due to a greatly reduced reaction distance at high light intensities.

Statistical Analysis

All statistical analyses were performed in SigmaPlot on normally distributed data with the averages and standard error shown. A One-way Analysis of Variance (ANOVA) was used to test for frequency differences in total reactions per trial between prey as well as the effect of irradiance on predator reaction distance. Next, a Chi-square test was used to test the effect of same- vs crossed-predator effects on reactions to prey. Finally, to determine the differences of predator success at each interaction stage, a two-tailed Fischer's exact test was used. All tests were analyzed with an alpha of 0.05 to indicate significance.

Results

There were a total of 1,985 predator orientations to prey with Smallmouth Bass accounting for three times more orientations than Burbot. However, the prey distribution was relatively similar with Smallmouth orienting 53% to Round Goby (799 Round Goby/711 Mottled Sculpin) and 54% of Burbot reactions were to the invasive species

(256 Round Goby and 219 Mottled Sculpin). There was no significant difference in frequency of reactions between prey species (χ^2=0.14, df=1, P=0.7) for either predator. Smallmouth Bass attacked 630 times (326 Round Goby, 304 Mottled Sculpin) with 26% retained (n= 164; 61 Round Goby, 103 Mottled Sculpin). while Burbot displayed a 20% retention (N=118; 9 Round Goby, 15 Mottled Sculpin),

Predator Behavior

Smallmouth Bass were continually in motion throughout the experiments with fish alternating between swimming and gliding during the dark and civil twilight trials before switching to continuous swimming at higher irradiances. Smallmouth Bass averaged swimming (defined as continuous caudal fin movement) for 36 ± 3.5 minutes in the dark, 77 ± 4.7 and 78 ± 5.3 minutes for CT-6 and CT-4, respectively, 107 ± 7.8 at sunrise and 91 ± 9.2 min during midmorning trials. The number of reactions was significantly reduced at midmorning (31 ± 4.6 reactions) compared to dark (53 ± 6.5), CT-6 (48 ± 8.3), CT-4 (56 ± 5.3), and sunrise (54 ± 9.7);(One way ANOVA: $F_{4, 56}$=3.21, P=0.019).

Burbot rarely moved in the dark except when reacting to prey (11 ± 1.8 min swimming). At CT-6 and CT-4, Burbot swimming increased (87 ± 6.8 and 72 ± 11.3 mins respectively) before they became relatively inactive at sunrise (4 ± 5.3 mins). The number of reactions were relatively low at dark and sunrise (6 ± 2.3 and 2 ± 4.5 reactions, respectively and increased significantly at CT-6 and CT-4 (44 ± 5.2 and 33 ± 7.3 reactions, respectively; One-way ANOVA $F_{3, 45}$=5.71, P=0.002)

During Smallmouth Bass-Burbot trials, Smallmouth Bass behavior remained similar to intraspecific trials. However, Burbot increased swimming and the number of reactions and attacks at all light intensities (excluding midmorning which were omitted). Burbot swam for 32 ± 5.2 min and reacted 9 ± 2.3 times at dark, increasing to 101 ± 9.1 mins and 49 ± 3.1 reactions at CT-6 and 89 ± 12.6 mins and 35 ± 4.5 reactions at CT-4, and then decreasing back to 8 ± 4.5 mins swimming and 3 ± 2.5 reactions at sunrise. Interspecific interactions occurred occasionally with both predators reacting to the same prey 13% of the time (of 732 interactions); however, no aggression was observed between Smallmouth Bass and Burbot. Interspecific trials significantly increased the number of reactions that individual Burbot had to prey [201 in Smallmouth Bass-Burbot trials, 137 per Burbot in Burbot-only trials; Chi Square test: $\chi^2 = 14.63$, df=1, $P = 0.0001$], but Smallmouth Bass showed no significant difference in total reactions [531 per Smallmouth Bass (single) compared to 439.5 per Smallmouth Bass (double); Chi Square test: $\chi^2 = 2.12$, df=1, $P = 0.15$].

Smallmouth Bass

During the dark trials, the maximum reactive distance for Smallmouth Bass was 55 cm, with the majority of the reactions (>90%) taking place within 45 cm of the fish with an average reaction distance of 14.2 ± 2.5 cm (Fig. 1). As light intensity increased, the maximum reaction distance increased to 159 cm during sunrise trials (36.1 ± 3.2 cm), but most reactions (>70%) remained within 45 cm until midmorning, where although the

maximum reactive distance decreased to 114 cm, the average reaction distance increased to 44.0 ± 6.41 cm (Fig. 1).

No significant difference was found for Smallmouth Bass reactive distance between paired Smallmouth Bass and Smallmouth Bass-Burbot trials (ANCOVA: $F_{1,59}=0.223$, $P=0.639$), and therefore the data was pooled (n=60). Approximately half the trials had peak reaction distances (33 of 60) to moving prey, with the remaining reactions to immobile prey. Peak reaction distances varied by light intensity with all reactions in the dark and sunrise trials occurring to moving prey whereas at midmorning, only one reaction was to moving prey. CT-4 and CT-6 only had 2 and 6 of the 12 reactions to moving prey, respectively. The peak reactive distances (n=12 at each light intensity) for Smallmouth Bass across light intensities was significantly greater at CT-4 (100.0 ± 5.3 cm), sunrise (108.2 ± 7.0 cm), and midmorning (84.1 ± 6.0 cm; Fig. 2) than dark (40.1 ± 2.7 cm) and CT-6 (67.5 ± 6.5 cm); (One-way ANOVA: $F_{1,118}=15.141$, $P<0.001$). The Michaelis-Menten model used light intensity (in photons m^{-2} s^{-1}; x-axis) to estimate the variance in Smallmouth Bass peak reaction distance (cm; y-axis) with parameter estimates ($R^2=0.71$, Fig. 2a) of $R_{max}=101.5060$ (t=35.00, $P<0.0001$) and $\alpha=1.33 \times 10^9$ (t=4.72, $P<0.0001$), with both parameters being significant to the model fit. Alternatively, the parabolic function with the same y-axis but a $\log_{10}$-scaled x-axis returned a fit of $R^2=0.90$ (Fig. 2b) with the following parameters: $a=-434.33$, $b=78.13$, and $c=-2.85$ with a significant interaction between the variables ($F_{3,5}=35.21$, $P<0.01$).

The reaction angles of Smallmouth Bass to both prey were similar but varied with light intensity. Most reactions were $\pm 60°$ to the anterior portion of the head (defined as 0°) at all light intensities (78%, 91%, 83%, 86%, and 49% for dark, CT-6, CT-4, sunrise, and midmorning respectively). In the dark, 97% of all reactions were $\pm 90°$ to the anterior portion of the head and as light intensity increased, more reactions ranged posteriorly occurred laterally up to $\pm 120°$ (99%, 99%, 96%, 91% for CT-6, CT-4, sunrise, and midmorning respectively). Most successful captures occurred when predators reacted within $\pm 60°$ anterior of the head (72% of all captures) whereas $\pm 90°$ and $\pm 120°$ only added 16% and 4%, respectively.

Smallmouth Bass consumed 61 Round Goby and 103 Mottled Sculpin, which resulted in only a 10.8% success rate following initial orientation (Table 1). Smallmouth Bass detection probabilities to moving prey differed in the dark with Round Gobies eliciting significantly more reactions (Fischer's Exact: $P<0.001$); however, both prey had an equal likelihood of eliciting a Smallmouth Bass reaction at sunrise (Fischer's Exact: $P= 0.80$). Smallmouth at CT-6, CT-4, and midmorning trials had significantly greater likelihoods of reacting to moving Mottled Sculpin (Fischer's Exact: $P<0.001$ for CT-6, CT-4, and Midmorning). In Smallmouth Bass-only trials, the two Smallmouth Bass reacted to the same prey 17% of the time (of 979 interactions). There was no significant difference in the likelihood of attack for either species except at CT-4 when Smallmouth Bass were more likely to attack Mottled Sculpin (Fischer's Exact: $P<0.05$). Smallmouth Bass had significantly greater capture probabilities for Mottled Sculpin at every light level except CT-6 (Fischer's Exact: Dark: $P<0.05$; CT-6: $P=0.80$; CT-4: $P<0.05$; Sunrise:

$P<0.01$; Midmorning: $P<0.001$). Retention probabilities were the same except at sunrise where a significantly greater number of Round Goby were retained compared to Mottled Sculpin (Fischer's Exact: $P<0.05$).

Burbot

The maximum reactive distance for Burbot during dark trials was 12 cm, with the majority of reactions within 10 cm (>95% of interactions, reaction distance 5.6 ± 1.4 cm; Fig. 3). As light intensity increased, the maximum reaction distance increased to 98 cm at CT-4 (18.0 ± 3.59 cm) before decreasing to less than 20 cm at sunrise (9.7 ± 2.71 cm).

The maximum reaction distances for Burbot in Burbot-only and Burbot-Smallmouth Bass trials were not significantly different, so the data was combined (N=48 measurements; ANCOVA: $F_{1, 47}=0.004$, $P=0.95$). Parameter value estimates for the model ($R^2=0.88$, Fig. 4) were as follows: a=-824.6265, b=152.3739, and c=-6.6288 with a significant interaction between the variables($F_{3,4}=32.43$, $P<0.01$), although no parameter was significant by itself (a: t=-4.75, $P=0.13$; b: t=4.90, $P=0.13$; c: t= -4.88, $P=0.13$). The peak reactive distance of Burbot was significantly greater at CT-6 (43.2 ± 1.6 cm) and CT-4 (44.8 ± 1.46) that dark (8.7 ± 0.4 cm) and sunrise 8.7 ± 1.0 cm One-way ANOVA: $F_{3,47}=67.0$, $P<0.001$) ; Fig. 2). Burbot primarily reacted to moving prey (87.5%) with all reactions in the dark to moving prey, 67.7 % at CT-6, and 91% at CT-4 and sunrise

The reaction angles of Burbot to both prey were similar and did not vary between light or dark trials. Most reactions were $\pm 60°$ to the anterior portion of the head at dark,

CT-6, and CT-4 (79%, 71%, 66%, respectively) but at sunrise most reactions were posterior to ± 90° (63%). Unlike Smallmouth Bass, as light intensity increased lateral reactions were not observed as frequently with only 13% of all reactions occurring at angles > ± 90°. Most successful captures (86%) at CT-6 occurred when predators reacted within ± 60° anterior of the head compared to only 20% at CT-4. Instead, most successful captures at CT-4 (70%) occurred from ± 60-90°. Comparatively, successful captures and dark and sunrise did not correspond to any certain area.

Burbot orientations to prey resulted in a 5% retention rate [N=24: 9 Round Goby, 15 Mottled Sculpin; Table 1]. Few intraspecific interactions occurred, with both Burbot reacting to the same prey less than 2% of the interactions. Similar to Smallmouth Bass, the largest difference in success between prey species occurred when reacting to moving prey. Furthermore, Burbot reacted significantly more to Round Goby than Mottled Sculpin within each light intensity (Fischer's Exact: Dark: $P<0.001$; CT-6: $P<0.001$; CT-4: $P<0.001$; Sunrise: $P<0.05$; Table 1). The likelihood of a Burbot attack only differed at CT-4 and sunrise which showed a significant selection for Mottled Sculpin (Fischer's Exact: $P<0.001$ and $P<0.05$, respectively), and there were no significant differences between capture or retention efficiencies of Burbot between prey.

Discussion

Environmental conditions often dictate the frequency and effectiveness of predatory foraging events. Reaction distances for each predator did not vary between prey species, but the probability of reacting to prey was significantly different between

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prey species and light intensities. Peak mean reaction distances of both predators followed parabolic functions with maximum reaction distances of 159 cm and 98 cm for Smallmouth Bass and Burbot, respectively. Attack probabilities varied for Burbot at CT-4 and sunrise while Smallmouth Bass capture probabilities were significantly different at every light intensity except CT-6. Overall, differences in probability of location/detection paired with differences in capture probabilities for Smallmouth Bass led to significantly more Mottled Sculpin consumed than round Gobies. This means that both predators consume native and invasive prey but are more successful when attacking the native species.

Limitations of estimating reaction distance

The experiments were able to examine predator-prey interactions over a wide range of light levels in a moderately sized tank under natural relevant downwelling light. However, the study has several limitations that need to be acknowledged. To ensure observation, fish need to be limited to confined areas, where corners and walls may influence behavior and predator-prey outcomes. While three-dimensional refuge was not provided, benthic species can also use crypsis or partially bury into the substrate to avoid detection. With free swimming prey, it was easier to determine when predators detected and pursued prey but with immobile prey, it was difficult to discern if prey were detected unless close range attacks were initiated. Additionally, the investigator is limited to determining when the predator visibly reacted and/or pursued a prey and not when sensory detection first occurred.

Previous studies have defined reaction of predators to prey as an orientation toward prey which allowed for a dichotomous answer, reaction or no reaction (O'Brien 1979, Richmond et al. 2004, Keyler et al. 2015, 2019). Due to the difficulty of not knowing when predators swam by immobile prey and did not orient, we only calculated reactions to moving prey. Previous studies measuring reaction distance across light intensities have found saturation curves similar to the Michaelis-Menten function (Richmond et al. 2004, Keyler et al. 2015, 2019) However, our findings show a parabolic function provided a better model. This provides an interesting comparison to the Nurminen & Horppila (2006) feeding study which also used a parabolic model but in response to diminishing light intensities in the face of increasing turbidity. However, many factors can influence predator reaction distances which include but are not limited to light inhibition (Vogel & Beauchamp 1999), predator and prey behaviors (Webb 1982, 1984), and turbulence (Pekcan-Hekim et al. 2013).

Both Burbot and Smallmouth Bass use visual and mechanosensory systems to mediate predation. In the absence of light, the lateral line is the main sensory system mediating predator-prey reactions and the dark trials allow the range of this system to be determined (Coombs et al. 1992, Palmer et al. 2005, Schwalbe et al. 2012). Reactions during light trials that occur past the reaction range of the lateral line are vision based; however, strikes inside this distance could be initiated via the lateral line or vision. The range of the lateral line has been previously estimated to range from one to two body lengths (Braun et al. 2002), although other behavioral and sensory physiology trials have

shown the range to be under a body length (New et al. 2001, Palmer et al. 2005, Richmond et al. 2004).

Effect of light on predation success

Smallmouth Bass reaction distances increased non-linearly with increasing light intensity as previously observed for visual predators, including Lake Trout (Vogel and Beauchamp 1999, Keyler et al. 2015, 2019), Yellow Perch *Perca flavescens* (Richmond et al. 2004), Bluegill *Lepomis macrochirus* (Vinyard & O'Brien 1976), and White Crappie *Pomoxis annularis* (O'Brien et al. 1986). However, Smallmouth Bass reacted to prey throughout all trials despite being considered to only be active after sunrise and before sunset (Demers et al., 1996). Biotelemetry tracking indicated elevated activity levels during the day (estimated 0800-1600 in 24-hour periods during June to October; dependent on day length) suggesting feeding would only occur during our midmorning light intensities (Demers et al., 1996). However, at the midmorning light intensity Smallmouth Bass swam less than at sunrise and the peak reaction distance decreased, indicating Smallmouth Bass do not react as far to prey at increasing light intensities after sunrise. Interestingly, the number of attacks did not differ across light intensities, suggesting the correlation between activity level and feeding behavior may not be as strong as previously thought.

When modeling the peak reaction distance of Smallmouth Bass, the Michaelis-Menten function suffered clear process error owing to the lack of fit (Fig. 2). Instead of plateauing as previously seen in studies (Vogel & Beauchamp 1999, Richmond et al.

2004, Keyler et al. 2015, 2019), peak reaction distances decreased in response to higher light levels at midmorning likely due to either retinal overstimulation or behavioral adaptations. Reaction distances either plateau or decrease as light intensity increases because retinal image sizes and apparent contrast decrease at farther distances (Aksnes & Utne 1997). Since cryptic prey already have low apparent contrast which decreases with distance, paired with reduced prey movements at high light, Smallmouth Bass are unable to locate prey at farther distances. *In situ*, behavioral responses of Smallmouth Bass to high light do not show movement to deeper offshore areas during the day (Bevelhimer 1995) to seek optical refuge but rather seek shelter in woody debris (Crook & Robertson 1999, Fore et al. 2007). The parabolic function, which fit well ($R^2=0.90$) and also predicts the reduction of the visual sensitivity at higher light intensities was a better model. However, the parabola does predict a high-light environment where the reaction distance would only use mechanoreception, so future studies should include even greater light intensities to better understand to what degree very high light intensities impact reaction distance.

The maximum reaction distance from dark trials divided by predator size provides an estimate for the lateral line detection radius. Smallmouth Bass had a mechanosensory detection radius of 11.2% of their T_L ($\bar{x} = 352$ mm T_L; 40 cm range in dark). Mechanoreception is primarily used in light-limited environments, with juvenile Smallmouth Bass (T_L $\bar{x} = 99$ mm) found to react up to 10.1% of their T_L on horsefly larva in high-turbidity conditions (40 Nephelometric Turbidity Units; Sweka & Hartman 2003) which is similar to our detection radiuses. In toadfish with chronically implanted

electrodes, the detection range of the lateral line to prey was determined to be 40% of the body length (Palmer et al. 2005). These reaction distances show a relatively limited range of the lateral line for successful prey detections.

Burbot foraging has been observed throughout the day and night (Harrison et al. 2013) but high light intensities inhibit feeding (Kavaliers 1980, Fischer 2004). However, Burbot had a relatively limited reaction distance in the dark at only 3.2% of their body length ($\bar{x}$ = 380 mm T_L, 12 cm maximum reaction distance;) with limited numbers of attacks in dark trials (34 reactions in dark compared to 259 and 198 at CT-6 and CT-4 respectively). Burbot were more successful at prey detection at civil twilight light intensities than the dark, which suggests Burbot rely more on vision for feeding than previously thought. This is also supported via reaction angles in which the bulk of reactions occur anterior to the head, suggesting vision plays a significant role.

The observed diel bank migrations (DBM) of Burbot at night are hypothesized to be driven by increased foraging success at very low light, increasing bioenergetic gains (feed in warm waters, digest in cool waters), and predator avoidance (Harrison et al. 2013). Surprisingly, there were low numbers of attacks and little swimming in dark trials suggesting Burbot DBMs are not driven by foraging success in darkness and that at least some light is required for feeding, such as contributions from astral sources in the field. As the seasonal length of night increases and with cyclical variation likely based on lunar phases, adult Burbot enter shallower waters (up to 5 m). These DBMs are ultimately driven by length of day (and thus inversely length of night) and temperature (Cott et al.

2015). DBMs indicate that peak Burbot activity in the shallows occurs between our dark and CT-6 trials (Cott et al. 2015), but foraging success was greatest for Burbot at CT-6 and CT-4. This suggests that Burbot DBMs may be driven by the need to balance downwelling light intensities that increase prey detection against high light levels that inhibit visual foraging. The light intensities at CT-6 and CT-4 may produce optical foraging environments for Burbot; however, these conditions last on average for only 5 minutes at dawn before getting exponentially brighter as it approaches sunrise. However, by regulating depth with increasing light intensities, Burbot may extend time for optimal foraging. The transition between diurnal and nocturnal species at dawn often results in increased prey and thus crepuscular hunting may be an adaptation to greater predation success.

Predator competition

Smallmouth Bass did not appear to be affected by Burbot in combined predator trials since the capture success remained the same between con- and heterospecific trials, but Smallmouth Bass did compete within conspecific trials. Smallmouth Bass were less successful in capturing benthic prey in the presence of conspecifics compared to heterospecific competitors, similar to findings reported in Winemiller & Taylor (1987). Studies focusing on interspecific competition between Smallmouth Bass and other piscivores (Walleye: Johnson & Hale 1977, Wuellner et al. 2011; Largemouth Bass: Winemiller & Taylor 1987; Rock Bass: George & Hadley 1979) have shown Smallmouth Bass have greater prey capture success compared to competitors. Our results show that

Burbot presence had no effect on Smallmouth Bass capture efficiencies but whereas the previous studies above had similar overall consumption between predator species, Burbot did not consume nearly as many prey as Smallmouth Bass. Unlike a conspecific Smallmouth Bass, Burbot did not elicit as many prey movements which initiated competition between conspecific Smallmouth Bass.

Interspecific competition studies between Burbot and other piscivores (Stone Loach: Fischer 2000; Lake Trout: Jacobs et al. 2010; Arctic Charr: Knudsen et al. 2010) all found no significant differences in predator success. Interestingly, Burbot did not have a significant impact on Smallmouth Bass foraging success but the presence of Smallmouth Bass did significantly increase the frequency of Burbot reactions to prey. This resulted in a slight increase in prey captures, but Burbot had low overall amounts of prey consumption. The increase in Burbot reactions could be caused by prey fleeing more frequently from the actively moving Smallmouth Bass which increases the probability of visual or mechanosensory detection by Burbot.

Prey-based differences

Smallmouth Bass reaction distances did not significantly differ between prey species within light levels, but the probability of Smallmouth Bass reactions were significantly higher for Mottled Sculpin except in dark and sunrise trials. In Webb (1984), Smallmouth Bass were more successful attacking prey when prey remained immobile rather than when prey were fleeing. Predator reactions were consistent with this pattern but could also be rooted in the prey's escape behavior. Examination of prey

behavior could reveal differences that effect the probability of detection by predators which led to greater capture success on Mottled Sculpin than round Gobies at all light intensities.

Like Smallmouth Bass, Burbot reaction distances did not significantly differ between prey species but the reaction probabilities of Burbot to round Gobies was significantly greater than Mottled Sculpin across all light intensities. Burbot are known to heavily rely on external receptors (olfactory, gustatory or mechanosensory) to locate benthic prey (Brown 1982, Hinkens and Cochran 1988). While olfaction can provide long range indication of prey presence, in small tank studies with a large number of predator and prey movements constantly disturbing the water, it is unlikely to provide directional cues (Kasumyan 2004). The only other significant difference between prey species for Burbot was the number of attacks at higher light intensities. Although Burbot reacted more to Gobies, the probability of attack was significantly greater on Mottled Sculpin at CT-4 and sunrise, which may be driven by prey behaviors.

Ecological impact on native predators

Mottled and slimy sculpin populations and other benthic species have declined in many areas where round Gobies have invaded due to invasives outcompeting native species for food and shelter (Dubs and Corkum 1996, Janssen and Jude 2001, Harris et al. 2018, Volkel 2019). Many native predators including Smallmouth Bass and Burbot have altered their diets to incorporate the more abundant Round Goby (Steinhart et al. 2004, Crane & Einhouse 2016, Johnson et al. 2005, Hensler et al. 2008). In Lake Erie, Burbot

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and Smallmouth Bass derived as much as 75% of their diet from round Gobies (Johnson et al. 2005). However, the dietary switch to round Gobies has had contrasting results on growth for Smallmouth Bass and Burbot.

Smallmouth Bass growth rates have increased when consuming primarily round Gobies in Lake Erie (Ohio Department of Natural Resources 2003, New York State Department of Environmental Conservation 2003, Steinhart et al. 2004, Crane & Einhouse 2016), even though round Gobies are a less energy-dense prey compared to native species (i.e. sculpins; Johnson et al. 2005). Based on our reduced capture efficiencies of Smallmouth Bass predating on round Gobies, more energy would be required to catch similar amounts of round Gobies compared to sculpins. However, the large abundance of round Gobies in these areas, reaching in excess of 100 individuals per m^2 in some locations (Chotkowski & Marsden 1999) likely increases the capture efficiencies resulting in increased length-at-age Smallmouth Bass.

Burbot growth rates have varied when incorporating round Gobies into their diet, with some reports of increased mean length-at age (Ohio Department of Natural Resources 2003, New York State Department of Environmental Conservation 2003, Steinhart et al. 2004) while others have reported decreased weight-at-length and lower mean lengths of Burbot feeding in goby-infested areas in Lake Michigan and Lake Huron (Hensler et al. 2008). We observed similar Burbot capture efficiencies between prey species, which suggests Burbot do not expend more energy attacking round Gobies over sculpins. However, with similar efficiencies and amount of prey consumed Burbot should

lose weight based on round Gobies being a less dense prey item (Johnson et al. 2005),

explaining at least part of the decreased weight observed by Hensler et al. (2008). Like

Smallmouth Bass, the increased weight by Lake Erie Burbot are likely explained by

round Gobies in high abundance, increasing overall success during predation events.

Summary

Taken together, our findings show that differences in the probability of reacting to

and capturing a prey may drive greater Mottled Sculpin consumption over the invasive

Round Goby. Vision plays a larger role in Smallmouth Bass locating prey which can

react to prey 140 cm away while Burbot, a primarily low light forager, can react to prey

100 cm away but often only reacts to prey within one body length. High Mottled Sculpin

consumption compared to Round Goby raises concerns for population stability, along

with the closely related slimy sculpin. Since prey behaviors heavily determine the success

of predator captures, analyzing prey escape behaviors will help understand at what point

during the predator interactions a certain behavior increases or decreases the likelihood of

a predator capture. Our predator success data, when combined with nutritional values of

the prey (Johnson et al. 2005), may also be used in future bioenergetics models to better

understand the energy required to capture certain prey, and the net benefits that are

derived from using a given prey source.

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Table 1. Probability of occurrence at each stage of a predator interaction. Probability of reaction was calculated from the number of moving prey. Probability of attack was calculated from the total number of reactions (moving and still prey), with captures and retentions calculated from the total success of the prior stage. In the parentheses is the total sample size, followed by the significance from Fischer's exact test. Significance values correspond to * < 0.05, ** < 0.01, *** <0.001.

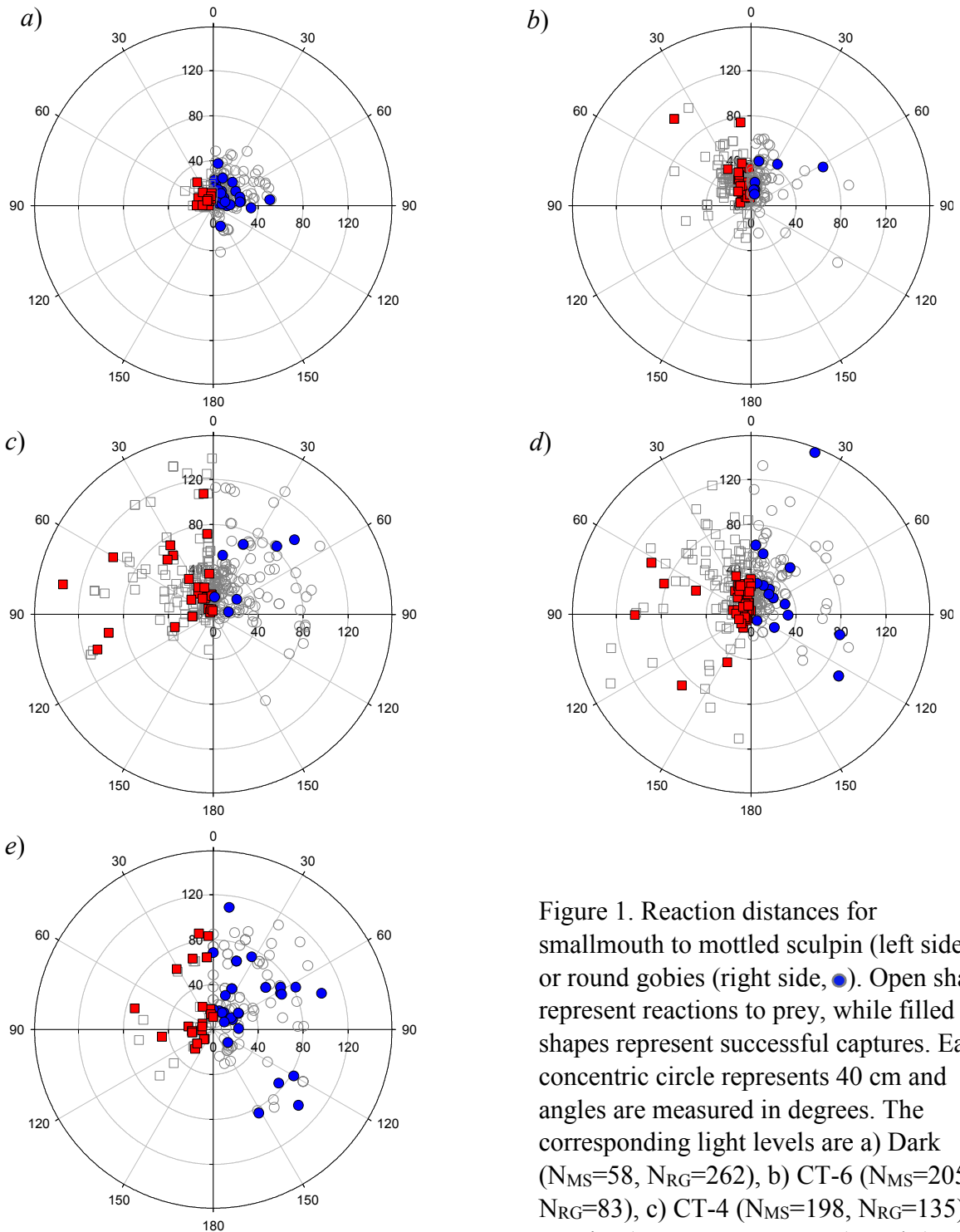| Light Level	Predator	Prey	$P_{reaction}$			P_{attack}			$P_{capture}$			$P_{retention}$		
Dark	BB	RG	0.36	(43)	***	0.40	(15)	—	0.50	(6)	—	0.33	(3)	—
		MS	0.09	(157)		0.24	(17)		0.50	(4)		1.00	(2)	
	SMB	RG	0.37	(691)	***	0.40	(301)	—	0.23	(120)	*	0.52	(27)	—
		MS	0.22	(263)		0.49	(68)		0.42	(33)		0.79	(14)	
CT-6	BB	RG	0.52	(197)	***	0.25	(109)	—	0.37	(27)	—	0.50	(10)	—
		MS	0.23	(634)		0.24	(152)		0.22	(37)		0.88	(8)	
	SMB	RG	0.45	(159)	***	0.26	(84)	—	0.32	(22)	—	0.71	(7)	—
		MS	0.72	(253)		0.38	(202)		0.37	(76)		0.82	(28)	
CT-4	BB	RG	0.26	(389)	***	0.14	(112)	***	0.31	(16)	—	0.40	(5)	—
		MS	0.14	(291)		0.45	(44)		0.25	(20)		0.80	(5)	
	SMB	RG	0.58	(185)	***	0.25	(136)	*	0.21	(34)	*	0.86	(7)	—
		MS	0.89	(176)		0.37	(199)		0.42	(73)		0.55	(31)	
Sunrise	BB	RG	0.27	(51)	*	0.20	(20)	*	0.50	(4)	—	0.50	(2)	—
		MS	0.09	(47)		0.67	(6)		0.50	(4)		1.00	(2)	
	SMB	RG	0.76	(142)	—	0.37	(147)	—	0.28	(54)	**	1.00	(15)	*
		MS	0.74	(186)		0.45	(181)		0.51	(82)		0.76	(42)	
Midmorning	BB		—			—			-			-		
			—			—			-			-		
	SMB	RG	0.55	(161)	***	0.74	(131)	—	0.30	(97)	***	0.72	(29)	—
		MS	0.90	(63)		0.68	(57)		0.64	(39)		0.80	(25)	

Figure 1. Reaction distances for smallmouth to mottled sculpin (left side, ■) or round gobies (right side, ●). Open shapes represent reactions to prey, while filled shapes represent successful captures. Each concentric circle represents 40 cm and angles are measured in degrees. The corresponding light levels are a) Dark (N_{MS}=58, N_{RG}=262), b) CT-6 (N_{MS}=205, N_{RG}=83), c) CT-4 (N_{MS}=198, N_{RG}=135), d) Sunrise (N_{MS}=180, N_{RG}=146), and e) Midmorning (N_{MS}=56, N_{RG}=130).
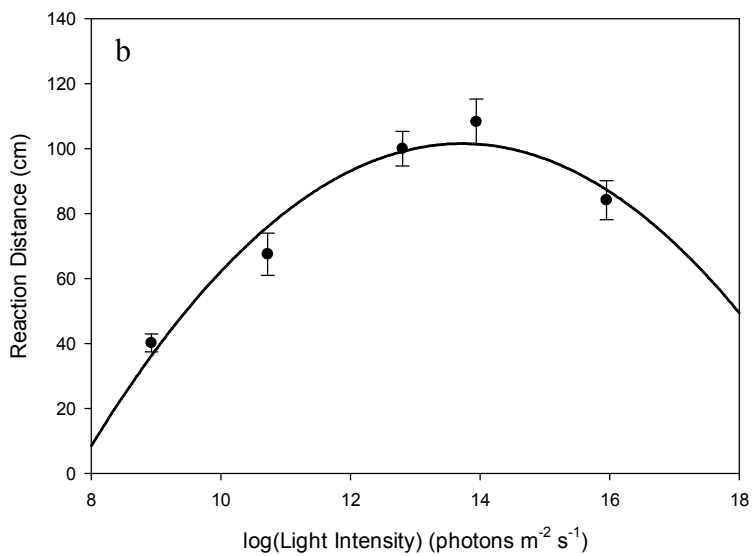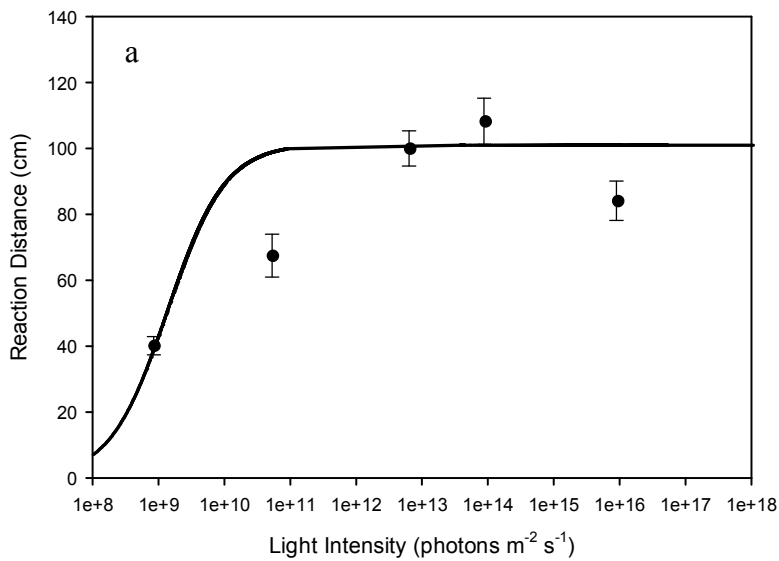
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Figure 2. Average peak reaction distance models for smallmouth bass using a) the Michalis-Menten function and b) a parabolic function pooled from both Round Goby and mottled sculpin trials. Michalis-Menten parameters were $R_{max} = 101.51$ and $\alpha = 1.33 \times 10^9$, with an $R^2 = 0.71$ while the parabolic function returned parameter values of $a = -434.3271$, $b = 78.1260$, and $c = -2.8476$, with an $R^2 = 0.90$. Note the common log scale for the Michaelis-Menten calculated with standard light intensity vs the common log scale of the parabola calculated with $\log_{10}$ light intensity. Error bars represent ± 1 SE.
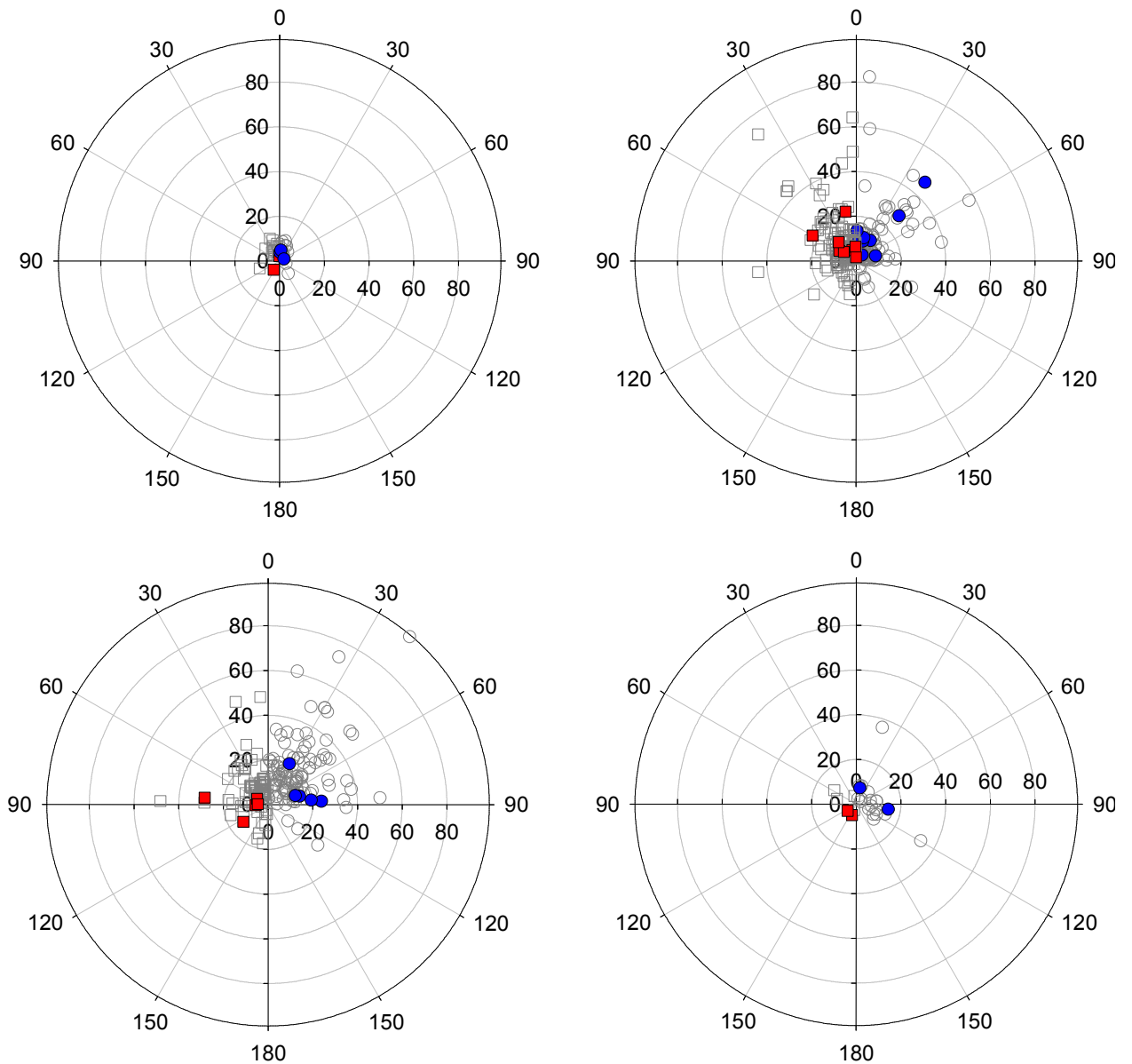
Figure 3. Reaction distances for burbot to mottled sculpin (left side, ■) or round gobies (right side, ●). Open shapes represent reactions to prey, while filled shapes represent successful captures. Each concentric circle represents 40 cm and angles are measured in degrees. The corresponding light levels are a) Dark (N_{MS}=16, N_{RG}=18), b) CT-6 (N_{MS}=151, N_{RG}=108), c) CT-4 (N_{MS}=88, N_{RG}=110), and d) Sunrise (N_{MS}=6, N_{RG}=20).
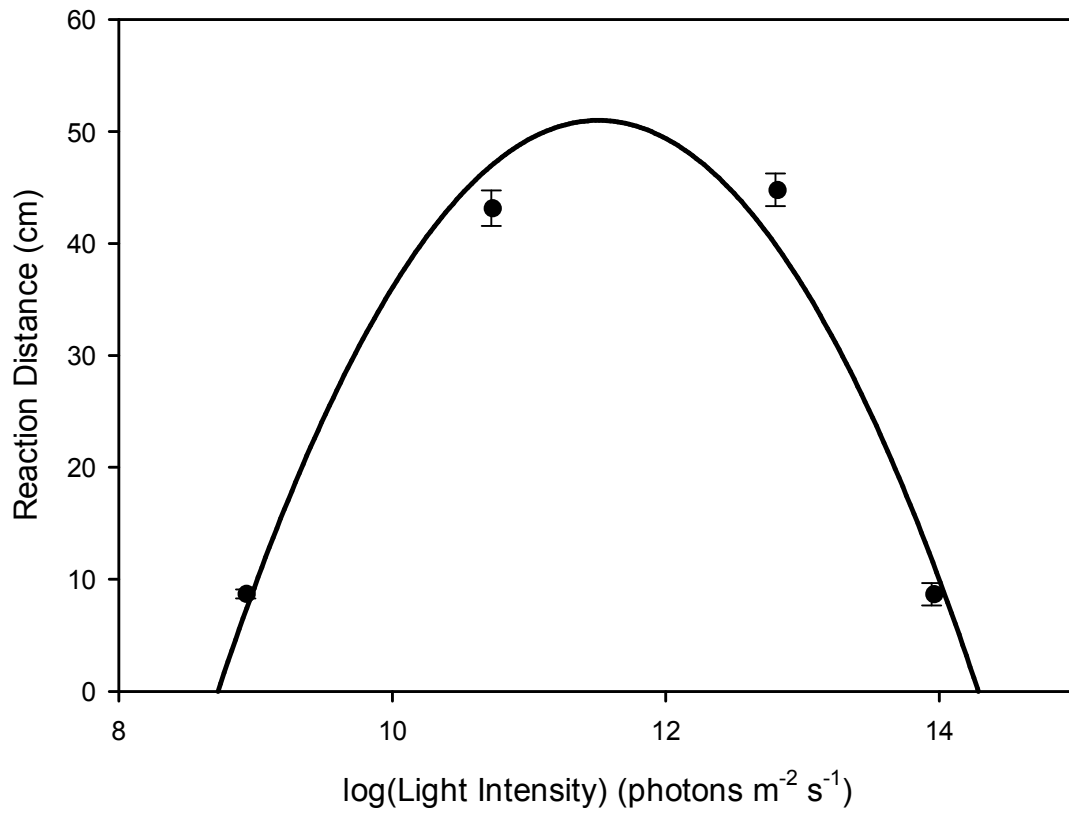
Figure 4. Parabolic function fitting the average peak reaction distance (cm) of Burbot across $\log_{10}$ light intensities, pooled from both Round Goby and mottled sculpin trials. Parameter estimates were a = -824.6265, b = 152.3739, and c = -6.6288, with an R^2 = 0.88. Error bars represent ± 1 SE.

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