Prey Behavior to Predator Growth: The Influence of Light Intensity on Predator-Prey Interactions in North Temperate Lakes and Rivers

A DISSERTATION SUBMITTED TO
THE FACULTY OF THE
UNIVERSITY OF MINNESOTA BY

Noland Otis Michels

IN PARTIAL FULFILLMENT OF THE
REQUIREMENTS FOR THE DEGREE OF
DOCTOR OF PHILOSOPHY

Dr. Allen Mensinger, Advisor
Dr. Thomas R. Hrabik, Advisor

August 2024

Acknowledgements

Thank you to the many people who have helped make this project a success; it would have been impossible without your help. First and foremost, thank you to my advisors Dr. Allen Mensinger and Dr. Thomas Hrabik for always pushing me to go a little deeper into an idea and providing me the freedom to pursue what interested me most. I would also like to thank my committee members Dr. Greg Sass and Dr. Donn Branstrator for their valuable input and broader questions that helped spark further interests.

Without the many field assistants collecting fish, this project would have been impossible. A huge thank you goes out to Brian Borkholder and Nick Bogyo, along with the rest of the Fond-du-Lac Tribal Management and 1854 Authority agency employees, who were always willing to help collect more fish when necessary. Similarly, thank you to Quinnlan Smith, Levi Feucht, Josh Schrope, Emily Fleissner, and Dr. Rosalyn Putland for their assistance in the field and in lab. I was always able to bounce ideas off of all of you to get new perspectives which has only improved this project as a whole.

I would also like to thank the various undergraduates who have helped on the various projects I have worked on, both written here as well as additional projects on top of my dissertation work. Greyson Wolf, Grace Dunlop, Macey MacLean, Nora Curtis, Lily Hall, Harry Redman, Dan Hebeisen, and Nathan Kamm; thank you for all of your hard work. All of your time and effort was invaluable.

I would also like to thank the Integrated Biosciences program for supporting me financially, as well as challenging me to take more holistic approaches in my research. Finally, the IBS program has put in me in contact with many lifelong friends who have helped me work through anything. Riley Pizza, Emily Fleissner, Rosalyn Putland, Quinn Smith, Levi Feucht, and Josh Schrope, thank you for always being there and I could not have completed this without you.

Most importantly, I want to thank my wonderful parents, Dan and Tamara Michels, who have encouraged me throughout my life. Without your support, none of this would have been possible.

Abstract

Abiotic and biotic conditions interact to influence fish behavior, which can scale up temporally to affect growth and population dynamics. My dissertation includes four unique studies that improve our knowledge of how predator-prey interactions change across species and diel periods, and the translation of individual interactions into effects on long-term growth rate. My first study tested the predator avoidance behaviors of invasive (round goby; *Neogobius melanostomus*) and native (mottled sculpin; *Cottus bairdii*) prey fishes from active (smallmouth bass, *Micropterus dolomieu*) and ambush (burbot; *Lota lota*) predators at multiple light intensities. Round goby were more successful at avoiding predators as they have an increased flight initiation distance, flee at angles closer to their theoretical optimal, and made more turns during an escape. Next, I examined the scotopic spectral sensitivity of adult walleye (*Sander vitreus*) and then observed age-0 walleye foraging behavior under their optimal wavelength. I found that walleye were most sensitive to 500-550 nm light. Under 525 nm light, age-0 walleye had the most reactions and attacks on prey from 1.58×10^{11} - 3.16×10^{13} photons m^{-2} s^{-1} (nautical-civil twilight). To test whether individual interactions translated to effects on growth, as well as the effect of light intensity, I tested the growth rates of age-0 walleye under 525 nm light at three intensities and three staining levels. I observed a higher growth rate in darker, heavily stained water and lowest growth rates were in bright, clear conditions. Lastly, I combined information from the previous chapters into an individual-based model on walleye foraging and tested whether light intensity, temperature, and prey density affected growth rates of a walleye population. Growth rate was greatly affected by temperature and prey density independently, but light intensity did not influence growth rate. Light intensity had a large influence on predator and prey behavior, but extrapolating these behavioral effects over time as measured by growth rate showed light intensity had limited effects.

Table of Contents

List of Tables

List of Figures

Forward

This is a doctoral dissertation submitted as partial fulfillment for the degree of Doctor of Philosophy from the University of Minnesota. Chapter 2 is currently published in Ecology of Freshwater Fishes. Chapter 3 is currently under review in Environmental Biology of Fishes. Chapter 4 is currently under review in the North American Journal of Fisheries Management. All of the chapters were prepared for publication with co-authors, so the collective “we” is used instead of “I” throughout the dissertation.

Michels, N. O., Hrabik, T. R., & Mensinger, A. F. 2024. Effects of predator species, composition and light environment on prey escape behaviours of invasive and native benthic fishes. Ecology of Freshwater Fish, 33: e12777.

Michels, N. O., Smith, Q. C., Rogers, L. S., Hrabik, T. R., Sass, G. G., Mensinger, A. F. *In review*. Foraging Behavior and Success of Walleye (*Sander vitreus*) Under Ecologically Relevant Downwelling Light Conditions. Submitted to Environmental Biology of Fishes.

Michels, N. O., Hrabik, T. R., Smith, Q. C., Sass, G. G., Mensinger, A. F. *Submitted*. The Effects of Light Intensity and Water Clarity on Growth Rates of Age-0 Walleye (*Sander vitreus*). Expected submission to North American Journal of Fisheries Management.

Chapter 1

Introduction

Predator-prey interactions often determine aquatic community structure with a multitude of factors affecting interactions, outcomes, and effects (Carpenter et al. 1985, Higham et al. 2015). These factors 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). 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).

Effect of Light Intensity on Fish Behavior

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 (Webb & Skadsen 1980, New et al. 2001, Michels et al. 2021). As light intensity increases, reaction distance often increases drastically and approaches an asymptote to the likes of a Michaelis-Menten curve (Hansen et al. 2013, Keyler et al.

2019, Michels et al. 2021). Alternatively, some species such as burbot (*Lota lota*) display a parabolic curve with a reduced reaction distance in full darkness and high light intensities (Michels et al. 2021). In predator-prey interactions, vision and mechanoreception are used to varying degrees and thus warrant further investigation into contributions of each sensory system in various environmental conditions.

Light intensity also affects the activity levels of predator and prey fishes. Piscivores have a variety of active foraging periods, ranging from extremely low light, crepuscular foraging observed for walleye (*Sander vitreus*; Einfalt et al. 2012, also see Chapter 3), lake trout (*Salvelinus namaycush*, Hansen et al. 2013; *Salvelinus namaycush siscowet*; Keyler et al. 2019), and burbot (Michels et al. 2021) to bright, midday conditions for smallmouth bass (*Micropterus dolomieu*; Webb 1983, Michels et al. 2021), largemouth bass (*Micropterus salmoides*; Anderson 1984), rainbow trout (*Oncorhynchus mykiss*, Webb 1983), and tiger muskellunge (*Esox* spp., Webb 1983). Alternatively, most prey species active foraging periods are strongly determined by predator presence (Webb 1982, Rahel & Stein 1988, Sih 1992). However, some prey species are bolder and have increased vigilance, which is shown by continuing foraging in the presence of predators rather than seeking shelter (McLean & Godin 1989, Sih 1992, Godin 1997). An increased boldness, especially when observed during interspecific interactions between prey species, is often rooted in a different behavioral escape strategy (Godin 1997).

Predator Avoidance and Escape Behaviors

Fishes often have a wide range of predator avoidance and escape behaviors including Mauthner neuron mediated rapid escape movements, directional avoidance, seeking and/or hiding in refuge/sediment, schooling or shoaling, crypsis, mimicry, and chemical cues that attract secondary predators (Webb 1982, Godin 1997, Savino & Stein 1989, Loennstedt & McCormick 2015, Nair et al. 2017). However, the outcome of predator-prey interactions is determined by relative sensorimotor performance (Cooper & Blumstein 2015). The mode of avoidance or combination of modes and success rate is often correlated with environmental conditions such as light intensity and habitat structure (Savino & Stein 1989). Following predator detection, prey may freeze or flee. Since prey may not flee when a predator is first detected, flight initiation distance (hereafter FID), which is the distance between predator and prey when the prey flees, is used as a measure of prey escape response (Ydenberg & Dill 1986). Previous research has shown that early detection and integration of those signals into an escape response were vital in avoiding predation (Walker et al. 2005, Catania 2009, McCormick et al. 2018). However, the vast majority of research regarding prey escape responses has focused on the initial startle response mainly because of the ease of the experimental approach (Domenici et al. 2011). The dynamic nature of a continually pursuing predator is lost in this approach and warrants further investigation.

Predators often attack a variety of prey species and face inter- and intraspecific competition for prey resources, but 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 and Beauchamp 1999, Mazur and Beauchamp 2003, Jönsson et al. 2013, Hansen et al. 2013, Keyler et al. 2015, 2019). Few predator-prey experiments have used multiple predator species (Webb 1984, Savino and

Stein 1989) or more than one predator in a trial (Sweka and Hartman 2003), and none have used multiple predator species simultaneously in trials observing individual predator-prey interactions. Chapter 2 tested the behavioral differences between invasive round goby (*Neogobius melanostomus*) and native mottled sculpin (*Cottus bairdii*) under predation risk by smallmouth bass and/or burbot at various light intensities.

Foraging Behavior

Predatory-prey interactions determine the structure and function of aquatic communities (Carpenter et al 1985, Kerfoot and Sih 1987). During a predator-prey interaction, sequential binary decisions predators make include location, pursuit, attack, and capture (O'Brien 1979). Location is defined as a predator orienting towards the prey (O'Brien 1979). Ambush predators, like walleye, wait until prey are within striking distance or occasionally pursue prey; pursuit may nor may not occur within an interaction (O'Brien 1979, Einfalt et al. 2012). Attack probabilities are correlated with distance, prey length and density, relative speeds of the predator and prey, predator satiation level (Sass & Motta 2002), and habitat (Einfalt and Wahl 1997, Gill and Hart 1998, Curio 2012, Einfalt et al. 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, Einfalt et al. 2012, 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). Reaction angle, which can be defined in the lateral or vertical plane, is less often used but can still produce useful data for evaluating the limitations of a certain sensory system in predator-prey interactions (Harper & Blake 1988, Chesney 2008, Michels et al. 2021, also see Chapter 3).

The spectrum of light in the aquatic environment also has a strong influence on fish behavior. Freshwater downwelling light is primarily composed of blue-green wavelengths (500-550 nm) that become red shifted as primary production increases (Jerome et al. 1983). The sensitivity hypothesis proposed by Munz and McFarland (1973) stated that a species' spectral sensitivity will generally match the spectrum of light in its environment. Red light is rapidly attenuated in aquatic systems (Jerlov 1968), which is one reason why fishes often have a decreased spectral sensitivity to red wavelength light (McComb et al. 2013, Harrington et al. 2015).

Reaction distance models have been generated previously for YOY walleye at midday under natural light (10:00 – 15:00) while testing the effects of sedimentary and algal turbidity (Nieman & Gray 2019) and larval walleye foraging in high and low light in turbid environments (Osborn 2008). Most studies have been conducted under white light. There have been no studies that have tested the effect of spectral sensitivity or specific light intensities on the reaction distance of walleye. Chapter 3 tested the spectral sensitivity and the foraging behavior under optimal optical conditions of age-0 walleye.

Foraging Success and the Translation to Growth

Once a successful foraging bout occurs, energy from the prey will be used towards metabolism, reproduction, growth, and specific dynamic action (SDA; i.e., the energetic cost of digestion; Kitchell et al. 1977). Over time, the summation of energy gained from foraging, after subtracting energy towards metabolism and SDA, goes towards somatic and reproductive growth. Understanding drivers of fish growth and their inherent variation on diel and seasonal scales is critical for fisheries managers. Growth rates in fishes reflect metabolic processes, and by elucidating whether specific abiotic, biotic, density-dependent, and density-independent factors influence growth, management agencies can better forecast how fish populations change over time (Brandt et al. 1992, Clarke & Johnston 1999, Pederson et al. 2017). Growth rates can be highly plastic and dependent on prey abundance (Hartman & Margraf 1992), the amount of energy available from prey (i.e. size, caloric density; Rand et al. 1994), the metabolic rate of the predator (Rice et al. 1983, Rand et al. 1994), and allocations of energetic reserves to somatic growth and reproduction (Auer et al. 2015). Growth rates are also influenced by environmental variables (Lorenzen 2016).

The effects of temperature on growth have been well documented (Fielder et al. 2007, Venturelli et al. 2010, Johnston et al. 2012, Peat et al. 2015) but the effect of light intensity, and thus foraging behavior and habitat, lack sufficient data for non-larval fishes. Light is a crucial environmental variable for the development, growth, and survival of many larval and juvenile fishes (Boeuf & Le Bail 1999, Downing & Litvak 1999). Growth rates can be influenced by light intensity (Downing & Litvak 1999), spectral composition (Ruchin 2005), and photoperiod (Boeuf & Falcôn 2001). The amount and spectral composition of downwelling light influences predator and prey behaviors in aquatic ecosystems. Visual predators often prefer specific light conditions that allow longer range detection of prey and enhance successful strikes. High intensity light can overwhelm photo receptors, particularly in fish with tapetum lucidum, while lower light conditions can limit detection range (Mazur & Beauchamp 2003, Hansen et al. 2013, Michels et al. 2021). Crepuscular and nocturnal species such as walleye are known to specialize in low light conditions (Einfalt et al. 2012, also see Chapter 3). Chapter 4 tested the effects of light intensity and staining level via tannin concentration on age-0 walleye growth rates over a 16-day period.

Individual Based Models

Individual-based models (IBMs) that have accurate environmental, population, diet, and growth data can be used to simulate spatially explicit effects of changing ecosystem conditions on fish populations in dynamic systems (Daewel et al., 2010). Hayes et al. (2009) noted the importance of determining specific habitat use of fishes when modeling processes and changes in population trends, as well as the relative importance of various environmental factors. Variation in habitat use and movement among individuals is important to population-level properties such as size structure, population size, and predator–prey interactions (DeAngelis et al., 1993, Maes et al., 2005, Rice et al., 1993). IBMs that can reproduce these ecological patterns may provide the most appropriate means for assessing the influences of changing habitat parameters on fish populations (Hayes et al., 2009). One way to elucidate independent influences of environmental variables on fish populations is through habitat sensitivity analyses (HSAs). HSAs compare a nominal model to environmental variables that are modified independently with a higher and lower scenario to test the effects of an individual variable on the outcome of interest (Kitchell et al. 1977). Chapter 5 combines data provided in Chapters 3 and 4 into an individual-based model of age-0 walleye foraging and independently tests the effects of light intensity, temperature, and prey density via HSA on the growth rates of a 100 individuals.

Background on Walleye

Walleye reach greatest abundance and size in cool, mesotrophic environments that have specific temperature, dissolved oxygen, and light ranges (Bozek et al. 2011). Bioenergetically optimal water temperatures range from 18 - 24°C (Koenst & Smith 1976, Hokanson 1977) and these temperatures are often incorporated into thermal-optical habitat area models (Lester et al. 2004, Chu et al. 2004, Jones et al. 2006, Hansen et al. 2019, Mahlum et al. 2023). Optimal temperatures vary between life stages. Young-of-year (YOY) walleye grow fastest at 25°C (Madon & Culver 1993), while larger juveniles and adults achieve optimal growth at about 22°C (Bozek et al. 2011). Walleye are crepuscular, increasing activity under low surface light intensities (4-1000 lux; Ryder 1977). Predicting light available at depth based on surface irradiance is difficult as light reflection, refraction, scattering, and absorbance due to algae, suspended sediments, dissolved organic carbon, and tannins can attenuate light and alter the spectrum. Walleye preference for low-light environments has been attributed to the presence of the *tapetum lucidum*, a retroreflective retinal layer that reflects light back through the retina. The *tapetum lucidum* increases retinal sensitivity but decreases visual acuity (Moore 1944, Zyznar & Ali 1975, Ali & Anctil 1977, Ali et al. 1977) resulting in walleye having greater visual sensitivity than prey that lack the adaptation (Ryder 1977, Vandenbyllaardt et al. 1991).

Light is a principal abiotic variable that controls temporal and spatial distributions of foraging walleye (Ryder, 1977). The vertical position of walleye in shallow (39 cm deep) tanks with surface illumination ranging from 2 to 200 lux was deeper at the highest intensity with movement to the middle of the tank at lower intensities. The greatest change in vertical position occurred during the transition from 2 to 20 lux (Scherer 1976). Lester et al. (2004) found that the highest angler catch per unit effort for walleye occurred at 28 lux, which is in accordance with Sherer's (1976) ~30 lux and Ryder's (1977) *in situ* experiments (4 – 100 lux). Most previous studies have reported light intensity in lux, which is based on human visual sensitivity. Quanta of light per area per time, such as photons m^{-2} s^{-1}, may be a more accurate measurement for fish (Johnsen 2012). Although lux measurement allows for a comparison with previous studies, reporting light intensity in photons m^{-2} s^{-1} (or cm^{-2}) delivers more precise information, such as the number of photons hitting the animal's eye of a certain wavelength per unit time (Johnsen 2012). Einfalt et al. (2012) observed increased walleye foraging behavior and prey capture with decreasing light levels (8.16×10^{13} - 3.16×10^{14} photons m^{-2} s^{-1}; 5-10 lux) and prey capture was greatest at night in vegetated habitat. Other factors identified that may affect foraging and prey capture were prior experience with the prey species (Wahl et al. 1995), prey morphology (Einfalt & Wahl 1997), predator length and prey density (Galarowicz & Wahl 2005), and habitat complexity (Vandenbyllaardt et al. 1991, Einfalt et al. 2012). No studies to date have examined walleye foraging behavior and success in light intensities < 8.16×10^{13} photons m^{-2} s^{-1} (~5 lux). Other species that specialize in low light foraging, such as lake trout, can use visual input as low as 3.05×10^9 photons m^{-2} s^{-1} (Keyler et al. 2019).

Walleye (*Sander vitreus*) show highly variable growth and survival throughout many aquatic ecosystems (Sass et al. 2004). This variability is often attributed to prey densities (Rose et al. 1999, Herbst et al. 2016) and available thermal-optical habitat (TOHA), which contains optimum light and temperature conditions for walleye (Lester et al. 2004, Mahlum et al. 2023). Walleye support an important subsistence fishery for First Nations and Native American communities, as well as a popular sport fishery across North America (Cook & Younk 1998). Understanding variable growth and survival are a priority for walleye management.

Overall, my dissertation uses four unique and novel studies to provide additional information about how environmental factors, specifically light intensity, affect predator-prey interactions, how the temporal scale of foraging translates to growth, and how increasing the spatial scale via modeling can help predict population-level changes. Chapter 2 provided detailed escape behaviors of invasive (round goby) and native (mottled sculpin) prey fishes from active (smallmouth bass) and ambush (burbot) predators at multiple light intensities. Chapter 3 examined the scotopic spectral sensitivity of walleye and their foraging behavior under optimal light conditions on fathead minnow (*Pimephales promelas*) at eight different times of day. Chapter 4 expanded upon Chapter 3 by testing the effect of light intensity and water clarity on walleye growth rate. Lastly, Chapter 5 combined information from Chapters 2, 3, and 4 into an individual-based model on walleye foraging and tested whether light intensity, temperature, and prey density affected growth rates of a walleye population. Understanding whether environmental factors such as light intensity influence predator-prey interactions at the species, diel, and population level was summarized in the final Chapter 6.

Chapter 2

Effects of predator species, composition and light environment on prey escape behaviors of invasive and native benthic fishes

---

Fishes often have a wide range of predator avoidance and escape defenses including Mauthner neuron mediated rapid escape movements, directional avoidance, seeking and/or hiding in refuge/sediment, schooling or shoaling, crypsis, mimicry, and chemical cues that attract secondary predators (Webb 1982, Godin 1997, Savino & Stein 1989, Lonnstedt & McCormick 2015, Nair et al. 2017a). However, the outcome of predator-prey interactions is determined by relative sensorimotor performance (Cooper & Blumstein 2015). The mode of avoidance or combination of modes and success rate is often correlated with the environmental conditions such as light intensity and habitat structure (Savino & Stein 1989). Furthermore, daily and seasonal changes in light intensity can change fish distribution and depth of potential interactions and thus alter modes of avoidance (Hrabik et al. 2006).

Following predator detection, prey may freeze or flee. Since prey may not flee when a predator is first detected, flight initiation distance (hereafter FID), which is the distance between predator and prey when the prey flees, is used as a measure of prey escape response (Ydenberg & Dill 1986). Previous work shows early detection of a predator and integration of predator characteristics (profile, swimming speed, size, etc.) into an escape response are vital in avoiding predation (Walker et al. 2005, Catania 2009, McCormick et al. 2018). Fast-start performance has also been shown to accurately predict survivorship (Langerhans 2009). However, the vast majority of work regarding prey escape responses focuses on the initial startle response mainly because of the ease of the experimental approach (Domenici et al. 2011). The dynamic nature of a continually pursuing predator is lost in this approach and warrants further investigation.

Predator profile, speed, and size affect prey escape behaviors (Karplus & Algom 1981, Webb 1984a, 1984b). As a predator approaches, the cost of remaining in a given space increases with both predator speed (Dill 1973, 1974, Fuiman 1993) and size (Dill 1974, Hurley & Hartline 1974, Helfman 1986, Ydenberg & Dill 1986, Lima & Dill 1990) as closer interactions often result in prey capture (Michels et al. 2021). Predators are classified into two broad categories; ambush lie-in-wait predators versus active search predators. To escape ambush or fast approaching predators, prey must react quickly (< 1 second; Webb 1976, Webb & Skadsen 1980, Harper & Blake 1991) to avoid the predator lunge. Conversely, due to the possibility of detection at greater distances, prey often have more time to avoid active-search predators as they approach more slowly and/or from farther distances (Dill 1973, Webb 1982, 1984a, 1986, Fuiman 1993). The initial FID has been shown to influence avoidance success more than escape speed (Nair et al. 2017b).

The effect of light intensity on predator foraging success is often dependent on the predator’s natural activity level (Benfield & Minello 1996, Vogel & Beauchamp 1999, Utne-Palm 1999, Utne-Palm 2002, Mazur & Beauchamp 2003), however the mechanisms of successful prey escapes under different light intensities has been vastly understudied. Increases in predation pressure, such as at dawn and dusk, often decrease prey activity (Helfman 1981, Hanych et al. 1983). However, few studies have examined prey activity levels in controlled settings when predators are present (Rahel & Stein 1988, Scharf et al. 2003), as well as escape mechanisms while also accounting for light intensity (Ranåker et al. 2014).

Comparisons of prey escape behavior between different fishes are rare (Webb 1984a, Webb 1986, Scharf et al. 2003), with few examples that include benthic prey (Augustyniak et al. 2022). Many comparisons are focused on the effect of stickleback armoring due to predator presence (McLean & Godin 1989, Marchinko 2009, Paccard et al. 2018). To examine behavioral differences, two benthic species comparable in both form and function were chosen, the mottled sculpin (*Cottus bairdii*; native) and the round goby (*Neogobius melanostomus*; invasive). Both species lack swim bladders and have mottled patterns, helpful when blending into rocky-gravel habitats (Kornis et al. 2012, Hoekstra & Janssen 1985). Habitat and diet overlap, which are both affected by prey responses to predator presence, drive competitive interactions between the two species where round gobies have an advantage (Dubs & Corkum 1996, Janssen & Jude 2001). Additionally, vision is often the predominant sensory system used to interpret light (Johnsen 2012). The visual systems of both round goby and mottled sculpin have not been described previously, although eye sizes are similar but mottled sculpin have a more pronounced dorsal postorbital ridge.

Our goal was to observe escape behaviors of two similar benthic prey species to understand why fewer invasive round gobies were consumed by predators than native mottled sculpin (Michels et al. 2021). Predators were chosen based on foraging strategy, with smallmouth bass (*Micropterus dolomieu*) chosen as an active forager while burbot

(*Lota lota*) was selected as a low-light, lie-in-wait predator. Additionally, to expand on the experiments performed by Rahel & Stein (1988), trials were tested at multiple light intensities to compare different photic environments as activity levels, especially when prey are most active foraging, may be more susceptible to predators. Our objectives were to 1) compare baseline activity levels of each prey in response to predator presence, 2) determine what species was more successful in avoiding and escaping each predator at each light intensity, and 3) determine what behavioral strategies increased prey survival. To address these objectives, we conducted experiments with differing combinations of predator and prey species under varying light conditions natural relevant wavelengths.

Methods

Fish Collections and Care:

Round gobies were collected using baited minnow traps and trawling in the Duluth-Superior Harbor and mottled sculpin were collected from tributaries connected to the St. Louis River and on the Fond du Lac Reservation via backpack electroshocking. 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 predators and prey populations overlap in their range, except for Harriet and Shagawa Lakes burbot which only have mottled sculpin. However, when first presented round gobies, they were readily consumed in small tanks. Unique predator characteristics (length, patterning, etc.) were recorded prior to trials to later test for predator population differences. All collections were made between May 15, 2018 and August 20, 2019 in water at depths ≤ 10 m. Smallmouth bass ($\bar{x}$= 379 ± 7.3 mm SD;

n = 18) and burbot ($\bar{x}$= 342 ± 4.2 mm SD; n = 16) ranged from 290-425 mm and 285-490 mm total length (T_L) respectively. Round gobies ranged from 60-74 mm ($\bar{x}$= 66.2 ± 0.7 mm SD; n=60) and mottled sculpin ranged from 64-78-mm ($\bar{x}$= 67.4 ± 0.9 mm SD; n=60) T_L, respectively. Fish were transported in coolers filled with a 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) and battery-operated air pumps. When needed, ice was placed in Ziploc bags to maintain the water temperature within ± 1.5°C of the water temperature fishes were collected during transport.

At the UMD holding facility, fish were segregated by species into 568 L 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 (Ammonia, Nitrites, Nitrates, pH) was tested daily via API freshwater test kits (Mars Fishcare Inc., Chalfront, PA) for the first week after fish introductions and twice weekly thereafter (Ammonia: 0-0.25 ppm; Nitrites: 0-0.5 ppm; Nitrates: 0-20 ppm; pH: 6.8-7.2). The burbot and smallmouth bass (predators) were fed ~150 g of live fathead minnows (*Pimephales promelas*) three times weekly while prey (round gobies and mottled sculpin) were provided with ~ 20 g of live California blackworms (*Lumbriculus variegatus*) three times per week.

Experimental and Trial Setup:

Foraging trials were conducted from June 15th, 2018 to November 9th, 2018 and June 14th, 2019 to September 18th, 2019. A 1900 L (2.3 m × 1.3 m × 0.7 m) fiberglass tank was filled with buffered pond water maintained at 16 °C to a depth of 0.5 m. The inside of the tank was lined with black cloth, rounded inserts placed in the corners, and with tan-brown pea gravel (52-157 mm; KolorScape^{TM}, Atlanta, GA) was placed on the bottom up to 2.5 cm in depth. No additional structure was added to the tank. Eight light engines equipped with cyan LED lights (Cree XLamp XR Series, Durham, NC) were mounted 1.2 m above the water surface and produced downwelling light centered at 510 nm with intensity adjusted via external controller. Video was recorded via three overhead and three lateral charged coupled device (CCD) infrared sensitive cameras (Vantage model LBC7081, Lorex Technology, Markham, ON) with additional light provided when needed by three 850 nm peak wavelength infrared LED lights (CMVision, Houston, TX). Videos were saved to a DVR (ECO2 series, LH130, Lorex Technologies, Markham, ON) and analyzed at a later date.

The light intensities for the experimental tank were adjusted to mimic the downwelling irradiance at a depth of 10 m 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.

Four 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), and sunrise (8.78×10^{13} photons m^{-2} s^{-1}) were tested. Civil twilight and sunrise irradiances were based on Kishida (1989; 34.3853° N, 132.4553° E). All values were converted to photons m^{-2} s^{-1} (Thimijan and 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, Sunrise, CT-4) 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.

Two piscivores per trial were used in a crossed design, with trials consisting of two smallmouth bass, two burbot, or one smallmouth bass and one burbot. Three trials were run per predator treatment for both prey species at all light intensities resulting in a total of 72 trials. Three control trials for each prey species and light intensity were recorded to establish baseline prey activity. Food was withheld for all fishes at least 24 hours prior to a trial. Two predators and twenty prey were acclimated for one hour in separate sections of the arena, 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. After acclimating for one hour, the divider was lifted and predators foraged for two hours, and the trial concluded with predator removal and tallying prey remaining. Predators were not reused until at least 24 hours had passed to allow for prey digestion. Predators were paired based on total length to reduce size effects, randomly assigned prey and light intensities, and each smallmouth was used for a maximum of five trials and burbot for seven trials. Between trials, a 30% water change was performed and filters were running to minimize the effect of kairomones. Up to four trials were run per day, with an average of 1.4 trials conducted per day.

Analyses

Video was recorded at 20 fps with 720 by 480-pixel resolution and data was analyzed frame by frame beginning with the frame immediately prior to predator orientation to the prey or prey escape initiation using ImageJ (NIH, v. 1.52a). A 20 × 20 cm plexiglass square was placed on the bottom of the tank for distance calibration in ImageJ. To minimize boundary effects, the limited number of reactions (~6%) to prey and prey escapes along the wall were not analyzed. A measurement was taken at 9 different foci for each camera to test differences in measurements (all were ± 1 cm), and the length-width distortion ratio was calculated and then the distortion ratio was embedded into ImageJ to accurately measure distance. All interactions were assumed to be on a linear plane based on two benthic prey, burbot being a benthic predator, and smallmouth bass spending >98% of time within 5 cm of the substrate.

Prey Activity Levels

Prey movements during trials with predators but not in close proximity were termed free movements. The frequency and distance of free movements were calculated in 5 min intervals at 0:00:00-0:05:00, 0:27:30-0:32:30, 0:57:30-1:02:30, 1:27:30-1:32:30, and 1:55:00-2:00:00 of the trials. A single movement was defined as the relocation distance via a single dart, multiple quick bouts (<1 second of rest in between swimming/darting) or continuous swimming. Prey must move >1 body length (T_L) to be considered a movement. Relocation distances were measured as the linear distance the prey's dorsal midpoint moved from the initial location to the final location. The number of movements and relocation distances were compared between control and predator trials within each light intensity in movements per fish per minute to account for prey already consumed.

Evasion Success

Prey evasion success was calculated as the inverse probability of the predator locating, attacking, capturing, and retaining prey (i.e. 1- $P_{Reaction}$, Michels et al. 2021), using the approach identified for prey detection by predators (O'Brien 1979, Richmond et al. 2004, Keyler et al. 2015, 2018). Descriptions of each stage are detailed in Michels et al. (2021), but below are brief definitions. Reactions were defined as predators orienting towards moving prey (O'Brien 1979). The predator's detection radius was the average peak reaction distance, which is the maximum reaction distance for each predator species per trial and averaging those distances, at each light intensity (Michels et al. 2021). Reactions were calculated as the number of moving prey that elicited predator reactions divided by the total number of prey moving within the predator's detection radius.

Immobile prey that were detected before moving were factored into the attack, capture, and retention calculations. Attacks were defined as a rapid burst of speed towards the prey, ending with the predators mouth open (O'Brien 1979). Attack success was calculated from the number of attacks divided by the total number of reactions to prey. Captures were defined as the prey being contained in the predator's mouth (O'Brien 1979) and retentions were defined as prey that were ingested (Richmond et al. 2004). Capture and retention success was calculated as the number of prey entering the predators mouth divided by the total number of attacks and the number of prey ingested divided by the number of captured prey, respectively.

Escape Metric Measurements

Flight initiation distance (FID) was the first metric of escape, measured at the frame immediately before 1) prey initiated an escape from an immobile position or 2) moving prey increasing swimming speeds (≥ 70 cm/second) and changing direction while in motion. FID was measured from the midpoint of the prey body to the closest point of the predator. An escape as defined here was limited to within the maximum reactive distance of the predator at the tested light intensity, which was defined by Michels et al. (2021). The number of prey fleeing during an attack (multiple individuals fleeing at the same time from the same predator) were tallied, but the FID was only measured for the first individual fleeing since subsequent escapes could be triggered by either escaping prey or the predator.

Escape trajectories (initial escape angle; Dill 1974, Domenici & Batty 1997, Domenici 2001, 2002) were measured from the prey body axis 150 ms after escape initiation compared to the predator body axis (Figure 1). Only prey that predators oriented towards before prey moved were analyzed for escape angles to account for differences between avoidance (maneuvering position before predator starts chase) and evasion (escape response to an attack; Weihs & Webb 1984). Location of the prey relative to predator body axis before an escape response was initiated was also taken.

Measured escape angles were then compared to optimal escape angles as calculated by equation 1 (Domenici 2002):

Eq. 2: $$D_{pred} = D_{prey}\left[\frac{U_{\mathrm{pred}}}{U_{\mathrm{prey}} \times \cos\alpha} - \tan\alpha\right]$$

where D_{pred} (distance to predator) is the FID of the prey, D_{prey} (distance prey must travel to leave the predator's reaction distance) is half of the predator's reaction distance, U_{pred} is the predator velocity and U_{prey} is the prey escape velocity (Fig. 1). U_{pred} was substituted using maximum linear speeds for smallmouth bass from Webb (1983), while U_{prey} for round goby and mottled sculpin were measured using linear escape accelerations from our prey escapes. U_{prey} was calculated as the linear distance traveled over 250 ms. D_{prey} was calculated for smallmouth bass from Michels et al. (2021), using 40 cm as the reactive radius for all light intensities (the radius where smallmouth made >75% of captures over all light intensities). This equation created a complex asymptotic curve, with the optimal escape angle (x-value) selected based on the trial average FID (y-value) for each light intensity. Burbot was excluded from the analysis due to switching predator foraging style across light intensities.

Once an escape is initiated, the number of turns an individual prey made during the flee was used as a proxy for the complexity of an escape, defined here as evasiveness.

A turn was defined as a directional change greater than 30° in less than 100 ms. These calculations were limited to the first prey to flee from a predator stimulus.

Statistical Analysis

All statistical analyses were performed using JMP Pro 16.0.0. All data are reported as mean ± standard error unless otherwise indicated. Differences between the number of reactions by predators to each prey species, as well as the difference in total prey consumed were tested via a Chi-square test. Prey activity measures were tested using Generalized Linear Models (GLM) on 1) the number of movements over time within trials (Poisson distribution with Log link function; tested against light intensity, predator factor (bass, burbot, mixed, none), prey species, all interactions among light intensity, predator, and prey, as well as time within trial) and 2) on the distances of free movements over time within trials (Normal distribution with Identity link function; tested same factors as above) and reported as mean ± standard error. Probability differences of avoiding predator reactions, attacks, captures, and retentions were tested using Generalized Linear Mixed Effects Models (Binomial distribution with Logit link function; tested against light intensity, predator species, prey species, all interactions among light intensity, predator, and prey, as well predator ID and trial ID as random factors). A GLMM was used to test the effects of light intensity, predator species, and prey species on the average FID (Normal distribution with Identity link function; tested against light intensity, predator species, trial type (BB, SMB, MIX), prey species, all interactions among light intensity, predator, and prey, as well as time within trial, trial ID and predator ID as random factors). A GLM (Normal distribution with Identity link function; tested for slope comparison against 1:1 regression line) was then used to compare the differences in optimal vs. the average observed escape angles between round gobies and mottled sculpin. Finally, differences in the number of turns made by round gobies and mottled sculpin during one escape were analyzed via GLMM (Poisson distribution with Log link function; tested against light intensity, predator species, trial type (BB, SMB, MIX), prey species, all interactions among light intensity, predator, and prey, as well as time within trial, trial ID and predator ID as random factors). All tests were analyzed with an alpha of 0.05 to indicate significance.

Results:

A total of 4877 predator prey interactions were observed, and 40.7% of the interactions elicited a response from a predator. Of the 1985 predator responses, 76% were elicited from smallmouth bass while burbot accounted for the remaining 24%. There was no significant difference in frequency of reactions to either prey species (χ^2=0.14, df=1, p=0.7) for either predator. Round goby were subjected to 380 attacks (54 burbot, 326 smallmouth bass) with 310 successful escapes (45 burbot, 265 smallmouth bass). Likewise, mottled sculpin endured 368 attacks (64 burbot, 304 smallmouth bass) with 250 successful escapes (49 burbot, 201 smallmouth bass). In total, significantly more mottled sculpin were consumed (18.3% of fish used) compared to round goby (8.5%; χ^2=92.47, df=1, p<0.0001).

Prey Behavior

Predator presence, light intensity, prey species, and time elapsed had a significant interaction (GLM: χ^2_{17}=114.37, p=0.0001; Fig. 2) on the number of free prey movements. The species of predator (GLM: χ^2_{17}=0.472 p=0.283) showed no effect. The total number of movements fish^{-1} minute^{-1} in experimental trials relative to control trials in the first 5 minutes was not significantly different (GLM: χ^2 =7.61, p=0.97) for round gobies but was for mottled sculpin GLM: χ^2_{17}=64.21, p<0.0001; Fig. 2; however, the number of movements fish^{-1} minute^{-1} was statistically lower than controls at the end of the two hours for round goby (74%; GLM: χ^2_{17}=72.43, p=0.007; Fig. 2) and mottled sculpin (95%; GLM: χ^2_{17}=399.4, p<0.0001; Fig. 2).

Distances traveled during these free movements were significantly affected by an interaction between light intensity and prey species (GLM: χ^2_{17}=2.89, p=0.038; Fig. 3). Round goby relocation distances were significantly greater at CT-4, over double the mottled sculpin distance (χ^2_{17}=2.43, p=0.0067; Fig. 3). Time along the trial did not have an effect movement distance (χ^2_{17}=0.091, p=0.72).

Avoidance Probabilities

The probability of avoiding a predator reaction was significantly affected by an interaction between light intensity, predator species, and prey species (GLMM: χ^2_{15}=10.46, p<0.015; Supplementary Table 2). Specifically, the probability of mottled sculpin being detected by burbot was significantly lower than round goby at dark (χ^2_{15}=4.55, p=0.033), CT-6 (χ^2_{15}=4.03, p=0.045), and CT-4 (χ^2_{15}=4.94, p=0.026). The probability of round goby being detected by smallmouth bass was significantly lower than mottled sculpin at CT-6 (χ^2_{15} =5.98, p<0.0001) and CT-4 (χ^2_{15}=7.89, p<0.0001), but significantly higher at dark (χ^2_{15} =1.47, p=0.0158); Supplementary Table 2). Predator ID (χ^2_{15} =0.023, p=0.856) and trial ID (χ^2_{15} =0.012, p=0.917) had no effect on the probability of a reaction.

Attack probabilities were also significantly affected by an interaction between light intensity, predator species, and prey species (GLMM: χ^2_{15}=11.47, p<0.0094). Mottled sculpin had a significantly lower probability of burbot attacks at dark compared to round goby ($\chi^2_{15, 3}$=4.23, p<0.0398). Mottled sculpin had a significantly greater probability of being attacked by smallmouth bass than round goby at CT-6 (χ^2_{15}=3.14, p<0.0481) and CT-4 (χ^2_{15}=3.79, p<0.0423). Predator ID (χ^2_{15} =0.003, p=0.927) and trial ID (χ^2_{15}=0.0028, p=0.943) had no effect on the probability of an attack.

Capture probabilities were not significantly different between prey species (GLMM: χ^2_{15}=0.850, p=0.357), predator species (χ^2_{15}=0.536, p=0.464), light intensity (χ^2_{15}=0.3.364, p=0.339), or any interactions (χ^2_{15}<2.176, p>0.53; Supplementary Table 3). The interaction between predator and prey on capture probability was marginally non-significant (χ^2_{15}=3.358, p=0.067). Predator ID (χ^2_{15}=0.179, p=0.66) and trial ID (χ^2_{15}=0.247, p=0.59) had no effect on the probability of a capture.

Retention probabilities were significantly affected by an interaction between predator species and prey species (GLMM: χ^2_{15}=10.36, p=0.0013). Mottled sculpin had a significantly greater probability of being retained and ingested by burbot than round goby (χ^2_{15}=10.36, p=0.0013), whereas smallmouth bass had a similar retention probability between prey species (χ^2_{15}=0.001, p=0.98. Predator ID (χ^2_{15}=0.371, p=0.32) and trial ID (χ^2_{15}=0.134, p=0.72) had no effect on the probability of prey being retained.

Initial Escape Metrics

To understand the differences observed in the probability of eliciting reactions from predators, the FID and initial escape direction of the prey were analyzed. A significant interaction existed between predator species, prey species, and light intensity (GLMM: χ^2_{17}=81.558, p<0.0001; Fig. 4; Supplemental Table 1). Round gobies significantly increased their FID in the presence of burbot at and CT-6 and CT-4 compared to mottled sculpin (χ^2_{17}=7.641, p<0.0004 and χ^2_{17}=18.742, p<0.0001, respectively; Fig. 4). Under predation by smallmouth bass, round goby significantly increased their FID compared to mottled sculpin at CT-6 (χ^2_{17}=4.317, p=0.0038), CT-4 (χ^2_{17}=17.653, p<0.0001), and Sunrise (χ^2_{17}=21.437, p<0.0001; Fig. 4). Time along trial (χ^2_{17}=0.153, p=0.70), trial type (χ^2_{17}=1.443, p=0.23), trial ID (χ^2_{17}=0.513, p=0.62) and predator ID (χ^2_{17}=0.843, p=0.47) did not have any significant effect.

Round gobies initiated their escape oriented away from smallmouth bass at an average escape angle of 38.2 ± 0.9° at dark followed by 66.4 ± 3.6°, 58.4 ± 2.4°, and 54.6 ± 3.0° at CT-6, CT-4, and sunrise, respectively. Plotting the observed escape angles against their theoretical optimums calculated from the FID resulted in an R^2 of 0.97 and was not significantly different from the 1:1 regression line (GLMM: χ^2_{11}=0.031, p=0.91; Fig. 5). Comparatively, mottled sculpin fled similar to round gobies at dark with an escape angle of 35.3 ± 1.5°, followed by 48.1 ± 1.8°, 29.8 ± 14.4°, and 17.2 ± 4.0° at CT-6, CT-4, and sunrise, respectively. However, comparing the observed and optimal escape angles resulted in a low R^2 of 0.13 and was significantly lower than the 1:1 regression line (GLMM: χ^2_{11}=14.27, p<0.0001; Fig. 5). Surprisingly, 9% of mottled sculpin's escapes were in the direction of the predator which was maladaptive as 89% of these movements resulted in ingested mottled sculpin.

Evasiveness

Once prey initiated an escape, directional changes resulted in increased path complexity. The predator species did not influence evasiveness (GLMM: χ^2_{17}=0.883, p=0.43), but light (χ^2_{17}=8.158, p=0.0429) and prey species (GLMM: χ^2_{17}=8.879, p=0.0029) both had separate, significant effects on evasiveness (Fig. 6). Specifically, dark had significantly lower turns per flee than the other light intensities (χ^2_{17}=8.144, p=0.0043; Fig. 6). Round goby also made significantly more turns per flee than mottled sculpin (χ^2_{17}=8.880, p=0.0029; Fig. 6). Time along trial (χ^2_{17}=0.247, p=0.54), trial type (χ^2_{17}=0.529, p=0.37), trial ID (χ^2_{17}=0.398, p=0.41) and predator ID (χ^2_{17}=0.913, p=0.29) did not have any significant effect.

Discussion:

This study is among the first to compare native and invasive benthic species escape behavior in the presence of two different predators under multiple light intensities. Round gobies were more elusive than native sculpin in virtually all escape metrics despite encountering two predatory species that they have co-existed with for a short period (<30 years, Bergstrom et al. 2008). The round goby's greater ability to avoid both ambush (burbot) and searching predators (smallmouth bass; burbot at both civil twilight conditions) provides additional information as why they have had such success in their establishment in the Laurentian Great Lakes basin. Overall, increased FID's and more optimal escape angles, paired with more complex escape paths increased the evasion success of round gobies compared to mottled sculpin.

Effect of Light on Escape Behavior

Our findings show that light intensity significantly affects escape metrics and avoidance success. In trials where round gobies were more likely to elicit reactions from predators (all burbot trials and smallmouth at dark), only the smallmouth bass-dark trials had more round gobies consumed than mottled sculpin (14 and 11, respectively), while all other trials had more mottled sculpin consumed. The predator's detection abilities, both visually and mechanosensory, factor heavily into the reaction probability (Luecke & O'Brien 1981), but the prey species' avoidance abilities (Svensson 1992, Trager et al. 1994) and environmental factors (Sih 1992) also play a role. Both prey species can be found in similar depths and light environments (Bergstrom & Mensinger 2009, Kornis et al. 2012), and often use structure like rip-rap and interstitial spaces to moderate light intensity as they do not often exhibit diel bank migrations but were noted to vertically migrate seasonally in Lake Ontario (Pennuto et al. 2021).

As light intensity increased, round gobies fled farther from approaching predators. This strategy is rewarded when prey escape a predator's detection zone without eliciting a predator response but can also increase the probability of detection by predators (Godin 1997). Longer FIDs often translate to increased survival (Dill 1973, Webb 1982, 1984a, 1986), but lower light intensities reduce the distance prey can visually detect predators (Pitcher & Turner 1986). We observed low FIDs at dark, which correlates to short range mechanosensory detection. As light intensity increased, round gobies increased their FID while also increasing their probability of escaping predator attacks after being detected. Alternatively, the probability of escaping predator attacks for mottled sculpin after detection was inversely proportional to light intensity which could be attributed to only slight variations in FID across light intensities.

There is debate as to whether fish escape direction is random to prevent predator learning of prey behaviors (Skajaa & Browman 2007) or optimized to a certain angle path to increase survival for each encounter (Weihs & Webb 1984, Webb 1986, Domenici & Blake 1993, Domenici & Batty 1994). When predictable prey were encountered, predators adjusted their behavior before prey even initiated a flee and ultimately attacked with greater acceleration than when prey were unpredictable, suggesting unpredictable escapes are less useful to prey than previously thought (Szopa-Comley & Ioannou 2022). However, Nair et al. (2017a) discovered that when attacked from the side, prey consistently escaped contralaterally to simulated predators whereas when attacked from caudal or rostral positions, there was an equal probability of escaping contra- or ipsilaterally. Kimura and Kawabata (2018) found that prey oriented 120-150 degrees off the predator's body axis had the highest probability of escaping a predator. Our results showed that prey escapes were non-random and either followed (round gobies, similar to angles in Kimura & Kawabata 2018) or did not follow (mottled sculpin) the predicted escape angles based on the FID (Domenici 2002). As light intensity increased, round goby FID changed along with the average escape direction, matching the optimal flee direction calculated. Conversely, mottled sculpin fled at approximately the same FID but the average escape angle was reduced as light intensity increased, fleeing closer to the predator's initial attack path, allowing more direct pursuit by the predator.

The evasiveness of round gobies also increased with light intensity, making more directional changes within a flee. Previous studies examining escapes found that more directional changes and increased variability in velocities during a flee increased escape success (Herbert-Read et al. 2017). Comparatively, mottled sculpin did not change direction as much and had a significantly greater probability of being captured by smallmouth bass (Michels et al. 2021). Mottled sculpin often reacted to predators via quick bouts of swimming followed by immobility, presumably trying to restore crypsis especially at higher light intensities.

A less complex path directed more in line with the predator's attack should be less successful in escaping predator attacks. Under predation by single-strike predators like burbot, instantaneous measures such as FID, escape direction, speeds, accelerations, and turning rates are important for determining whether prey survive (Webb 1976, 1982, Eaton & Emberley 1991, Fuiman 1993, Fuiman et al. 2006). When predators actively chase prey (smallmouth bass; Domenici et al. 2014, Neill & Cullen 1974), sustaining high levels of path complexity is a strong determinant of survival probability (Herbert-Read et al. 2017). Mottled sculpin turned fewer times, which led to smallmouth bass redetecting prey 77% of the time compared to 42% for round gobies, which may have contributed to more mottled sculpin being consumed.

Predator species effects

Round gobies and mottled sculpin were both more successful in avoiding attacks by burbot than by smallmouth bass. Lunging piscivores (ambush predators) such as burbot rarely pursue prey after an escape is initiated (Webb & Skadsen 1980, Webb 1984a & b, Harper & Blake 1991). The lack of follow-up attacks, as well as covering less ground than an active searching predator, explains the low number of attacks observed for burbot. Similarly, a variety of ambush piscivores are more likely to abort attacks when prey initiate a rapid escape compared to prey that remain immobile (Neill & Cullen 1974, Major 1978, Webb & Skadsen 1980, Webb 1981, 1984a, 1984b, 1986). However, smallmouth bass did not abort attacks but rather selected for moving and/or escaping prey.

Prey Behaviors

The effect of predator presence on prey activity levels and behavior have been well documented (Helfman 1993, Rahel & Stein 1988) while kairomones alone have been shown to have long-lasting effects on *Chaoborus* larval diel vertical migration behavior (Dawidowicz et al. 1990). We observed round gobies did not significantly alter the number of movements following initial predator introduction but did limit movement as these trials progressed. Conversely, mottled sculpin responded quickly to predator introduction by remaining motionless and continued this behavior throughout the trial. Johnny darters (*Etheostoma nigrum*) showed similar patterns as our mottled sculpin when under predation by smallmouth bass, reducing their activity by 94% (Rahel & Stein 1988). Darter activity was also reduced for at least 24 hours after a 30-minute exposure to smallmouth (Rahel & Stein 1988). With mottled sculpin movement drastically reduced, round gobies have more opportunities to access food and other resources while predators are nearby. This is consistent with the competitive exclusion hypothesis and underlies why round gobies are more successful competitors than many native fishes (Dubs & Corkum 1996, Bergstrom & Mensinger 2009). However, the distance traveled by both prey species did not vary between predator species or time during trial, thus providing evidence that only the number of movements is affected by predator presence. As round goby are more elusive prey for predators, this likely helps facilitate their invasion into new areas. Predators that were used here have coexisted with round goby for years, but in newly invaded locations naïve predators would likely heavily select for easier, native prey and thus may further facilitate a more successful invasion.

Caveats

Predator prey studies conducted in controlled conditions have several limitations. To ensure observation, participants are limited to confined areas, and walls and corners can alter fish behavior. While no three-dimensional refuge was provided, which could be available in their environments, the benthic species were able to use crypsis or partially bury into the substrate to avoid detection. However, very few fish either elected or were able to move into the sediment (< 0.2%) and furthermore these egressions were limited to < two minutes. For the immobile prey, it was difficult to discern if and when prey were detected until there were motor movements. Additionally, for mobile predators and/or prey, the methodology was limited to when the fish visibly reacted and not necessarily when sensory detection transpired. Additionally, using mottled sculpin collected from streams could induce different behaviors than lake-derived fish. To combat this, mottled sculpin were collected from tributaries within 75 m from the St. Louis River (comparable to a lentic environment) which had low stream discharge rates, thus in theory limiting the differences the environment may have on behavior. Our tank size was limiting in that the predators used, at least in width, was less than two reaction distances so prey relocation may have been at increased rates compared to a natural system. Alternatively, tank size was greater than two FID’s so boundary effects likely impacted prey behavior less than the predators. The next logical steps are to increase to a larger system, as well as implement substrate complexity and shelter for both predators and prey. Finally, in our analysis our random factors of Predator ID and Trial ID were not used in all models due to issues with degrees of freedom. Thus, issues with pseudo replication, either with the reuse of predators or multiple consecutive trials may have small effects on the theoretical optimal vs observed escape angle.

Summary

In the presence of predators, round gobies still move freely around the tank, although at reduced levels, whereas mottled sculpin rarely move. Round gobies thus have greater potential foraging time, increasing their access to shared diet items while mottled sculpin remain cryptic. The invasive round goby is also more successful avoiding and escaping predators than the native mottled sculpin, due in large part to variable FIDs that change with light intensity and predator species. Lastly, a more optimal escape direction away from the attacking predator and increased evasiveness when fleeing make for a more challenging, complex pursuit for predators that often results in a successful escape for round gobies.

Chapter 3

Foraging Behavior and Success of Walleye (*Sander vitreus*) Under Ecologically Relevant Downwelling Light Conditions

---

INTRODUCTION

Walleye (*Sander vitreus*) show highly variable growth and survival throughout many aquatic ecosystems (Sass et al. 2004). This variability is often attributed to prey densities (Rose et al. 1999, Herbst et al. 2016) and available thermal-optical habitat (TOHA), which contains optimum light and temperature conditions for walleye (Lester et al. 2004, Mahlum et al. 2023). Walleye support an important subsistence fishery for First Nations communities, as well as a popular sport fishery across North America (Cook & Younk 1998). Understanding variable growth and survival are a priority for walleye management.

Walleye reach greatest abundance and size in cool, mesotrophic environments that have specific temperature, dissolved oxygen, and light ranges (Bozek et al. 2011). Bioenergetically optimal water temperatures range from 18 - 24°C (Koenst & Smith 1976, Hokanson 1977) and these temperatures are often incorporated into thermal-optical habitat area models (Lester et al. 2004, Chu et al. 2004, Jones et al. 2006, Hansen et al. 2019, Mahlum et al. 2023). Optimal temperatures vary between life stages. Young-of-year (YOY) walleye grow fastest at 25°C (Madon & Culver 1993), while larger juveniles and adults achieve optimal growth at approximately 22°C (Bozek et al. 2011). Walleye are crepuscular, increasing activity under low surface light intensities (4-1000 lux; Ryder 1977). Predicting light available at depth based on surface irradiance is difficult as light reflection, refraction, scattering, and absorbance due to algae, suspended sediments, dissolved organic carbon, and tannins can attenuate light and alter the spectrum. Walleye preference for low-light environments has been attributed to the presence of the *tapetum lucidum*, a retroreflective retinal layer that reflects light back through the retina. The *tapetum lucidum* increases retinal sensitivity but decreases visual acuity (Moore 1944, Zyznar & Ali 1975, Ali & Anctil 1977, Ali et al. 1977) resulting in walleye having greater visual sensitivity than prey that lack the adaptation (Ryder 1977, Vandenbyllaardt et al. 1991).

Light is a principal abiotic variable that controls temporal and spatial distributions of foraging walleye (Ryder, 1977). The vertical position of walleye in shallow (39 cm deep) tanks with surface illumination ranging from 2 to 200 lux was deeper at the highest intensity with movement to the middle of the tank at lower intensities. The greatest change in vertical position occurred during the transition from 2 to 20 lux (Scherer 1976). Lester et al. (2004) found that the highest angler catch per unit effort for walleye occurred at 28 lux, which is in accordance with Sherer's (1976) ~30 lux and Ryder's (1977) *in situ* experiments (4 – 100 lux). Most previous studies have reported light intensity in lux, which is based on human visual sensitivity. Quanta of light per area per time, such as photons m^{-2} s^{-1}, may be a more accurate measurement for fish (Johnsen 2012). Although lux measurement allows for a comparison with previous studies, reporting light intensity in photons m^{-2} s^{-1} (or cm^{-2}) delivers more precise information, such as the number of photons hitting the animal's eye of a certain wavelength per unit time (Johnsen 2012). Einfalt et al. (2012) observed increased walleye foraging behavior and prey capture with decreasing light levels (8.16×10^{13} - 3.16×10^{14} photons m^{-2} s^{-1}; 5-10 lux) and prey capture was greatest at night in vegetated habitat. Other factors identified that may affect foraging and prey capture were prior experience with the prey species (Wahl et al. 1995), prey morphology (Einfalt & Wahl 1997), predator length and prey density (Galarowicz & Wahl 2005), and habitat complexity (Vandenbyllaardt et al. 1991, Einfalt et al. 2012). No studies to date have examined walleye foraging behavior and success in light intensities $< 8.16 \times 10^{13}$ photons m^{-2} s^{-1} (~5 lux).

Other species that specialize in low light foraging, such as lake trout, can utilize visual input as low as 3.05×10^9 photons m^{-2} s^{-1} (Keyler et al. 2019).

Predatory-prey interactions determine the structure and function of aquatic communities (Carpenter et al 1985, Kerfoot and Sih 1987). During a predator-prey interaction, sequential binary decisions predators make include location, pursuit, attack, and capture (O’Brien 1979). Location is defined as a predator orienting towards the prey (O’Brien 1979). As ambush predators, walleye wait until prey are within striking distance or occasionally pursue prey; pursuit may nor may not occur within an interaction (O’Brien 1979, Einfalt et al. 2012). Attack probabilities are correlated with distance, prey length and density, relative speeds of the predator and prey, predator satiation level (Sass & Motta 2002), and habitat (Einfalt and Wahl 1997, Gill and Hart 1998, Curio 2012, Einfalt et al. 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, Einfalt et al. 2012, 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). Reaction distance models have been generated for YOY walleye at midday under natural light (10:00 – 15:00) while testing the effects of sedimentary and algal turbidity (Nieman & Gray 2019) and larval walleye foraging in high and low light in turbid environments (Osborn 2008). Most studies have been conducted under white light. There have been no studies that have tested the effect of spectral sensitivity or specific light intensities on the reaction distance of walleye.

Although walleye are known for higher activity in low light intensities, particularly during twilight hours (Ryder 1977, Lester et al. 2004, Einfalt et al. 2012, Shaw et al. 2021), very little information exists on their foraging behaviors and activity levels below 5 lux. Our objectives were to: 1) develop a reaction distance model for juvenile walleye in clear water conditions ranging from dark to midday ($< 6.65 \times 10^8$ to 2.88×10^{17} photons m^{-2} s^{-1}; 0 – 750 lux); 2) observe predator success at each stage of the predator – prey interaction; and 3) measure the scotopic visual sensitivity of adult walleye.

MATERIALS AND METHODS

Fish collections and husbandry

We collected wild young-of-the-year (YOY) walleye via boat electrofishing on Shagawa Lake (Ely, MN) on September 18th, 2019 and September 28th, 2021. Fifteen adult walleye were also collected from Shagawa Lake on September 28th, 2021 for electroretinography experiments. Young-of-year walleye total length (T_L) ranged from 103-153 mm in 2019 (n=147) and 121-162 mm in 2021 (n=113). Adults ranged from 261-437 mm (n=16). We purchased fathead minnows (*Pimephales promelas*) from Marine General (Duluth, MN) or The Bait Box (Superior, WI). A representative sample of 100 fathead minnows from each location were used to measure prey T_L. Marine General fathead minnows ranged from 31-42 mm (average 37.4 mm). The Bait Box fathead minnows ranged from 32-40 mm (average 36.9 mm). We transported fishes in coolers filled with a 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 aeration. When needed, ice sealed in plastic bags were 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 18 °C under a 14h:10h day:night light cycle set at 3.16×10^{15} photons m^{-2} s^{-1}. 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. We fed all fishes three times per week with walleye provided live fathead minnows, while fathead minnows were fed fish flakes (TetraMin, Melle, Germany). All YOY walleye were tagged under anesthesia using 0.003% MS-222 buffered with sodium bicarbonate for ten minutes (Meerbeek et al. 2013). Fish were implanted with VI Alpha tags (Northwest Marine Technology, Anacortes, WA) using a single-shot syringe and the injection site was sealed with Nexaband surgical grade adhesive (Abbott Laboratories, Chicago, IL). Fish were released into a post-operative tank containing 1% API Stress Coat Plus (Mars Fishcare Inc., Chalfront, PA) and their behavior was observed for one-hour post-surgery. After one hour, fish were returned to the holding tanks.

Electroretinography

All electroretinography (ERG) testing was conducted on adult walleye in a room illuminated by dim red light (15 W light bulbs with Kodak GBX-2 dark red safelight filter). Each fish was anesthetized with a MS-222 solution (0.0075 - 0.0085%), buffered with sodium bicarbonate to a pH of 7.0, for 5 min. The fish was then placed on a moist sponge in the acrylic experimental tank (63 × 26 × 16 cm) and covered with a wet Kimwipe (Kimberly-Clark Professional; Roswell, GA, United States). The experimental tank was housed within an opaque metal faraday cage (77 × 67 × 97 cm) to prevent equipment light from reaching the fish. The buffered MS-222 solution was delivered to the fish via a gravity-fed tube placed in the buccal cavity of the fish to maintain the surgical plane of anesthesia.

We made a small incision through the limbus of the eye with a 0.3 mm 15° stab knife (Surgical Specialties; Westwood, MA, United States). A 0.64 mm diameter silver-silver chloride electrode was inserted into the incision, with the reference electrode placed within the nostril of the ipsilateral side. Electroretinography waveforms were amplified using a DAM50 bioamplifier (World Precision, Inc.; Sarasota, FL, United States; 1,000× gain; 1 Hz high pass, 3 kHz low pass), filtered with a digital 60 Hz notch filter, and recorded with a PowerLab 4SP (AD Instruments, Inc.; Colorado Springs, CO, United States) using Lab Chart7 Software (AD Instruments) on a Dell laptop.

A 100 W quartz tungsten-halogen Model 6333 lamp (Newport Corp.; Stratford, CT, United States) powered by a constant current power supply (Model 68938; Newport) produced the light stimulus. Stimulus duration (200 ms) was regulated with an electronic shutter (Model 76994; Newport) and controller (Model 76995; Newport). A dual filter wheel (Model 7736; Newport) containing neutral density filters from 0.1 to 3.0 regulated light intensity, with wavelength controlled by a monochromator (Model 77250; Newport). Light intensity was determined using a radiant power energy meter (Model 70260; Newport) and probe (Model 70268; Newport). A fiber optic light pipe (Model 77632; Newport) transmitted the light from the monochromator to the eye, completely illuminating it.

All fish were dark adapted for 30–60 min. We initiated test flashes at the 30 minute mark to determine if the retina was dark adapted, which was defined as the absence of "the a-wave" (hyperpolization) prior to the b-wave (depolarization) in the ERG waveform. If the a-wave remained, the fish was allowed to dark adapt for an additional 10 min, and the process was repeated until the a-wave was undetectable. Wavelengths between 400 and 700 nm were presented in 25 nm increments to the fish in random order with a flash duration of 200 ms and interflash interval of 30 s to reach ±10% of the criterion amplitude. The criterion response was determined by measuring the irradiance needed to elicit a b-wave response at 400 nm. Experiments were conducted during the fish's daytime light cycle to avoid circadian rhythm effects. Upon completion of the ERG, fish were revived by delivering buffered pondwater to the fish *via* a separate gravity-fed tube until gilling resumed, and fish were returned to their home aquaria.

Reaction Distance

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. Tank sides were lined with black cloth to reduce light reflection, and rounded inserts were placed in the corners to minimize corner effects. Three Plexiglas viewing windows in the side of the tank provided viewing access for cameras. Substrate consisted of light-colored sand (CaribSea, Fort Pierce, FL) up to 2.5 cm in depth. Eight light engines were mounted 1.2-m above the water surface and housed LED lights with a peak wavelength of 525 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 (Shenzhen Univivi Technology Co. Ltd, Hong Kong, China) 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 with the plexiglass viewing port. Videos were saved to a DVR (ECO2 series, LH130, Lorex Technologies, Markham, ON) and analyzed at a later date.

The light intensities for the experimental tank were adjusted to mimic the downwelling irradiance at a depth of 5 m for the following times: night (without astral light contribution; (< 6.65×10^{8} photons m^{-2} s^{-1}; 0 lux), nautical twilight (-9° solar altitude, 1.58×10^{11}; 0.05), civil twilight (-6° solar altitude: 3.16×10^{12}; 0.1 and -3° solar altitude: 3.16×10^{13}; 1), sunrise (3.16×10^{14}; 10), cloudy morning (1.58×10^{15}; 40), sunny morning (3.16×10^{15}; 100 lux), and a sunny afternoon (2.88×10^{17}; 750; Table 1). 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 surface irradiance, x is the depth, k is the attenuation coefficient (1.25 m^{-1} for moderate staining and/or suspended sediments), and I_x is the irradiance (light intensity) at depth. Nautical twilight, civil twilight, and sunrise irradiances were based on Kishida (1989; 34.3853° N, 132.4553° E), while the morning and afternoon irradiance were converted from values for a summer morning at 10:30 am with 0% (sunny) or 50% cloud cover (Fahnenstiel et al. 1984; 47.2855° N, -90.6879° W). All values were converted to photons m^{-2} s^{-1} (Thimijan and Heins, 1983; Harrington et al. 2015) for biological applicability (Johnsen 2014). Tank surface irradiances were measured using an International Light Technologies ILT1700 Research Radiometer with a SED033/F/HMR/W broadband silicon detector (Peabody, MA). Our 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.

Foraging trials were conducted from February 11th, 2020 to March 6th, 2020 and October 2nd, 2021 to June 2nd, 2022. Eight light intensities (Table 1) were tested with 10 trials each resulting in 80 trials. Food was withheld from all fishes at least 48 hours prior to a trial. 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. Each trial consisted of one walleye and three prey, with all fishes acclimated for at least 30 minutes in their respective sections of the arena. At the onset of each trial, the divider was lifted, and walleye were allowed to forage for 15 minutes, at which time the predator was removed and the number of remaining prey counted. Surviving prey were maintained in separate tanks for at least 24 hours between trials and used in a maximum of three trials. Predators were not tested again for at least 48 hours to allow for prey digestion and used in a maximum of two trials. No walleye was tested twice at the same light intensity.

We recorded video at 20 fps with 720 x 480-pixel resolution. We analyzed the video 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. A predator-prey interaction was defined as a predator detecting a moving or immobile prey, or prey that was not detected within the predator's detection radius.

Foraging success

We calculated foraging success as the probability of the predator locating, attacking, capturing, and retaining prey (O'Brien 1979, Richmond et al. 2004, Michels et al. 2021). All steps and measurements within a foraging interaction were categorized based on the criteria established in Michels et al. (2021). Briefly, location, hereafter reactions, were tallied as the number of prey that walleye oriented towards. An attack was defined as a rapid burst of speed by the predator towards the prey (Sweka and Hartman 2003) that included the predator opening its mouth during the terminal phase of the attack (O'Brien 1979). Captures were defined as prey held within the buccal cavity of the fish, and a retention was when prey were successfully ingested (Michels et al. 2021).

Reaction Distance Model

We defined reaction distance 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°.We used a non-linear regression on original light intensities to estimate the relationship between light intensity using approximate lux values and reaction distance for walleye with the following Michaelis-Menten equation:

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

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).

Statistical Analyses

Statistical analyses for reaction distances were performed in SigmaPlot 15.0 (SPSS inc.) on normally distributed data with the averages and standard errors shown unless noted otherwise. Visual sensitivity was quantitatively defined as ± 2 standard deviations from the peak sensitivity. The effect of light on the average reaction distance was tested via one-way ANOVA. Statistical analyses for reaction angles were performed in Oriana 4.02 (Kovach Computing Services) with mean angle and circular standard deviation (SD). A Moore's modified Rayleigh test was used as a nonparametric second order statistic to test for differences in the sub-grouped means, here using light intensity, to the population mean. Watson's U^2 test was used to test for homogeneity at each light intensity against dark. A p-value > 0.05 represented a homogenous reaction angle, whereas a p-value ≤ 0.05 represented a preferred direction following the predicted Von Mises distribution. All tests were analyzed with $\alpha = 0.05$ to indicate statistical significance.

RESULTS

Visual Sensitivity

Adult walleye exhibited relatively broad spectral sensitivity from 450 to 625 nm, with maximum spectral sensitivity at 500-550 nm (Figure 1). Spectral sensitivity markedly decreased at wavelengths < 450 nm and > 625 nm (Figure 1). Walleye could detect irradiances as low as 1.6 × 10^{-13} photons cm^{-2} s^{-1} (Figure 1).

Reaction Distance

Reaction distances increased asymptotically as light intensity increased. Dark trials, at 6.65 × 10^{8} photons m^{-2} s^{-1}, produced an average reaction distance of 12.5 ± 2.02 cm (0.94 body lengths calculated from T_L; Figure 2), with a maximum reaction distance of 21.2 cm (1.78 body lengths). As light intensity increased, the average reaction distance increased to 15.4 ± 1.95 cm at nautical twilight, 20.2 ± 4.48 cm at civil twilight (-6°) , and 27.1 ± 2.48 cm at 3.16 × 10^{13} photons m^{-2} s^{-1} at civil twilight (-3°). For civil twilight (-3°) and higher, the average reaction distance was significantly greater than dark and nautical twilight (One-Way ANOVA: $F_{7,23}$ =8.199, $P<0.001$) and approached an asymptote at 29.3 cm. Average reaction distance followed a Michaelis-Menten function with an R_{max} of 29.2726 and an α of 0.0319 (r^2=0.86 ; Figure 2).

Reaction angles were not uniformly distributed across light intensities (Moore's modified Rayleigh test: R_8=1.56, $P<0.001$; Figure 3), so individual comparisons were made using Watson's U^2 test. The average reaction angle in dark trials was 72.1 ±70.1° SD with no statistical directionality (Watson's U^2: U^2=0.291, P=0.012). The average reaction angle significantly shifted from anterolateral to anterior for trials with light present, beginning with 10.5 ± 46.9° SD at nautical twilight (Watson's U^2: U^2=0.023, $P>0.5$). The average reaction angle remained anterior at civil twilight (-6°; 18.5 ± 58.7°; Watson's U^2: U^2=0.033, $P>0.5$), civil twilight (-3°; 16.2 ± 52.9°; Watson's U^2: U^2=0.037, $P>0.5$), sunrise (5.43 ± 49.7°; Watson's U^2: U^2=0.029, $P>0.5$), cloudy morning (1.14 ± 41.3°; Watson's U^2: U^2=0.041, $P>0.5$), sunny morning (9.81 ± 36.1°; Watson's U^2: U^2=0.043, $P>0.5$), and sunny afternoon (3.36 ± 62.7°; Watson's U^2: U^2=0.016, $P>0.5$; Figure 3).

Foraging Success

Most reactions (54%) occurred in light intensities ranging from nautical twilight to civil twilight (-3°). Overall, YOY walleye oriented to prey 105 times, 15% of which ended with retained prey. Only 30% of reactions elicited an attack, and when an attack was attempted, the retention rate was 52%. Light intensity had little influence on the success of capturing prey, but at higher light intensities there were a limited the number of attacks. Young-of-year walleye only attacked prey that were ± 12 degrees off the predator's body axis after predator reaction and as long as prey did not change orientation once the walleye reacted. This resulted in 100% successful captures in cloudy morning, sunny morning, and sunny afternoon trials. If prey changed orientation, walleye would abort the pursuit.

DISCUSSION

Whether the light environment affects juvenile walleye foraging is critical to understanding the contribution of light in the estimation of thermal-optical habitat. We found that YOY walleye foraged at all light intensities tested but were more successful when attacking in very low light intensities that were less than in previously published interactions (Einfalt et al. 2012). Most prey were consumed from $1.58 \times 10^{11} – 3.16 \times 10^{13}$ photons m^{-2} s^{-1} (nautical twilight to civil twilight (-3°)) and was likely due to increased foraging activity based on the number of reactions and subsequent attacks, as well as the presence of the *tapetum lucidum* which increases visual sensitivity. The reduced number of attacks at higher light intensities may be driven by heightened prey awareness and detection distance that positions prey outside attack areas rather than a major decrease in walleye foraging activity as walleye still reacted to prey and moved around the tank. Higher light intensities may impair walleye vision, thus reducing the number of reactions to prey. Average reaction distances for juvenile walleyes followed a Michaelis-Menten function, rapidly increasing from 12.5 cm (0.94 body lengths calculated from TL) until civil twilight (-3°; ~1 lux), reaching an asymptote at 29.3 cm.

Visual Sensitivity of Adult Walleye

Adult walleye had a maximum spectral sensitivity in the blue-green range from 500-550 nm. Pothier and Ali (1978) found similar spectra for walleye (533 nm) via microspectrophotometer research on the porphyropsin within the eye. The spectral sensitivity was consistent with the sensitivity hypothesis proposed by Munz and McFarland (1973), which stated that a species' spectral sensitivity will generally match the spectrum of light in its environment. Freshwater systems contain more particulate matter, such as non-algal particulates and colored dissolved organic matter, that increase light attenuation and shift the downwelling spectral irradiance to longer wavelengths than in salt water (Effler et al. 2010). Walleye inhabit lakes ranging in productivity from oligotrophic to eutrophic (Raabe et al. 2020), but most commonly inhabit mesotrophic systems where algal particulates may also influence the downwelling spectral irradiance. Within these systems, downwelling light is red-shifted with green wavelengths having a greater intensity than blue wavelengths (Hienermann & Ali 1988), making walleye well-adapted to their environment.

Eye Size and Development in Juvenile Walleye

Visual acuity, or the ability to determine spatial detail, is strongly correlated to eye size in fishes (Caves et al. 2017). Many teleost fishes have a relatively fixed pupil, and pupil size is an important determinant of how much light enters the eye (Cronin et al. 2014, Vinterstare et al. 2020). Eye and lens growth is directly correlated in walleye (eye diameter and lens diameter), so the eye diameter to pupil diameter ratio remains constant (Wahl 1990). Nieman and Gray (2019) used similar length walleye and found no correlation between eye metrics and reaction distance within their clear water treatment, thus eye size likely did not influence reaction distance in our experiment.

The *tapetum lucidum* is a biological reflector system that is found behind the vertebrate retina in many species. The *tapetum lucidum* reflects light, allowing for an increased opportunity of photoreceptors to absorb light and enhances visual sensitivity at low light levels (Zyznar & Ali 1975, Braekevelt et al. 1989, Vandenbyllaardt et al. 1991). In walleye, the *tapetum lucidum* is well established in fish of 90 mm TL, and by 125-140 mm TL, has the same structure as adults (Braekevelt et al. 1989). Less than 5% of the fish in our growth experiment may not have fully developed *tapeta*; however, all walleye used in reaction distance trials were >125 mm TL.

Optical habitat on reaction distance and foraging behavior

The predator-prey trials conducted in darkness established the range of the lateral line. Strikes in the light outside of this range were attributed to visual input. Reaction distance of fishes has been well documented to change with the light intensity of the surrounding optical environment (Beauchamp et al. 1999, Hansen et al. 2013, Nieman & Gray 2019). The reaction distance and foraging behavior of walleye has not been observed under a range of light intensities. Our data suggested that peak walleye foraging occurs from nautical twilight to civil twilight (~0.05-1 lux), well below previous estimates which ranged from 5-10 lux (Lester et al. 2004, Metcalfe 2006, Einfalt et al. 2012). Increased foraging activity during this low light period directly corresponded to the rapid increase in average reaction distance. After civil twilight (-3°), the average reaction distance reached an asymptote at 29.3 cm and the number of reactions, attacks, and captures decreased. Previous research on juvenile walleye at midday light intensity observed average reaction distances of 50+ cm to prey (Nieman & Gray 2019). Our farthest reaction distance was 64 cm in a sunny afternoon trial (750 lux), but the average for 750 lux was just over 30 cm. Additionally, Nieman and Gray (2019) found that reaction distance decreased with the addition of sediment and algae, although no specific light intensities were reported.

When foraging at low light intensities, walleye would react to prey, pursue, and then attack if the prey could be localized. Recently, TOHA has been shown to affect small (post hatch

- <300 mm) and medium length walleye (300-450 mm) to a greater degree than larger adults (>450 mm; Mahlum et al. 2023). Our study which used small fish suggested that low light intensities were critical to increased foraging success of YOY walleye. Although capture success was not strongly correlated with light intensity, the number of reactions and subsequent attacks were strongly dependent on light intensity. At high light intensities, walleye were more selective of prey they attacked. Multiple interactions occurred where a walleye would react to prey, but then abort any pursuit within a few seconds if the prey was already oriented diagonally or horizontal to the walleye's body axis, or if the prey turned at any time during the pursuit or approach. After an attack was initiated, there was a high probability of capturing and retaining prey. Similar behaviors were noted in Einfalt et al. (2012), where walleye followed and pursued prey less in daylight conditions. Einfalt et al. (2012) attributed the reduced pursuing of prey in brighter conditions to the long distance between predator and prey being perceived as too far for probable capture or that prey gave off cues indicating detection of the predator (Magurran 1990). Although a small sample size from our experiment, distance was not the primary factor attributed to aborting a reaction to or pursuit of prey but rather prey orientation which likely served as feedback that prey may have detected the predator or would soon become aware of the predator's presence. By changing their foraging strategy to only pursuing and attacking prey oriented away from them, predators may optimize their foraging and reduce energy costs (Manatunge & Asaeda 1999, Ahrenstorff et al. 2009).

Limitations

The electroretinography measured the summed electrical response of the eye to a monochromatic flash and is a reliable indicator of spectral sensitivity. Due to variations in eye size and electrode placement, which can affect the signal amplitude, it should not be construed as a measure of absolute sensitivity. Our experiments indicated that walleye detected irradiance at

1.6×10^{-13} photons cm^{-2} s^{-1}. The behavior data showed that they used visual cues at an irradiance as low as 1.58×10^{-17} photons cm^{-2} s^{-1} , which suggested that behavioral measures were a more accurate indicator of their absolute visual sensitivity. Although walleye have been correctly characterized as visual predators, the presence of the *tapetum lucidum* is known to increase visual sensitivity at the expense of visual acuity (Ollivier et al. 2004). Image and/or movement detection seemed to be more important than clarity for this visual predator.

Our reaction distance experiment examined predator-prey interactions over a wide range of light levels in a moderately sized mesocosm under naturally relevant downwelling light. Our study had several limitations that need to be acknowledged. To ensure observation, fish were limited by the tank area, where corners and walls may influence behavior and predator-prey outcomes. Likewise, the size of the tank was about 2 reaction distances at the highest light intensity, which mitigates the issue of predators continuously seeing prey and thus skewing the number of reactions and reaction distances. Additionally, the methodology was limited to determining when the predator visibly reacted and/or pursued a prey and not when sensory detection first occurred. Finally, the reaction distance experiments were also limited to clear water conditions because any degree of staining occluded observation of the predator and prey.

Conclusions

Our findings showed that previous estimates of optimal light intensities for YOY walleye foraging were overestimated, and that most foraging activity was conducted at extremely low light intensities. At higher light intensities, walleye still predated but were more conservative about which prey they attacked. Our findings are helpful to management agencies interested in conserving optical habitat for walleye or predicting changes in growth due to changes in water quality.

Chapter 4

The Effects of Light Intensity and Water Clarity on Growth Rates of Juvenile Walleye (*Sander vitreus*)

Introduction:

Understanding drivers of fish growth and their inherent variation on diel and seasonal scales is critical for fisheries managers. Growth rates in fishes reflect metabolic processes, and by elucidating whether specific abiotic, biotic, density-dependent, and density independent factors influence growth, management agencies can better forecast how fish populations may change over time (Brandt et al. 1992, Clarke & Johnston 1999, Pederson et al. 2017). Growth rates can be highly plastic and dependent on prey abundance (Hartman & Margraf 1992), the amount of energy available from prey (i.e. size, caloric density; Rand et al. 1994), the metabolic rate of the predator (Rice et al. 1983, Rand et al. 1994), and allocations of energetic reserves to somatic growth and reproduction (Auer et al. 2015). Growth rates are also influenced by environmental variables (Lorenzen 2016).

Light is a crucial environmental variable for the development, growth, and survival of many larval and juvenile fishes (Boeuf & Le Bail 1999, Downing & Litvak 1999). Growth rates can be influenced by light intensity (Downing & Litvak 1999), spectral composition (Ruchin 2005), and photoperiod (Boeuf & Falcôn 2001). The amount and spectral composition of downwelling light influences both predator and prey behaviors in aquatic ecosystems. Visual predators often prefer specific light conditions that allow longer range detection of prey and enhance successful strikes. High intensity light can overwhelm photo receptors, particularly in fish with *tapetum lucidum*, while lower light conditions can limit detection range (Mazur & Beauchamp 2003, Hansen et al. 2013, Michels et al. 2021). Crepuscular and nocturnal species such as Walleye *Sander vitreus* are known to specialize in low light conditions (Einfalt et al. 2012, Michels et al. Chapter 3).

Light is the principal abiotic variable that controls temporal and spatial distributions of foraging Walleye (Ryder, 1977). Walleye display strong positive phototaxis in larval and early juvenile stages preferring high light intensities (7,800 lux until about 8 weeks; ~ 32 mm; Bulkowski & Meade 1983). Post 8 weeks in age, juvenile Walleye are attracted to low light intensities (~2-4 lux; Bulkowski & Meade 1983). The preference of large juvenile and adult Walleye for low-light environments has been attributed to the presence of the *tapetum lucidum*, a layer at the back of the retina which reflects unabsorbed photons back through the retina to enhance visual sensitivity but decreases visual acuity (Moore 1944, Zyznar & Ali 1975, Ali & Anctil 1977, Ali et al. 1977). The presence of the *tapetum lucidum* is hypothesized to enhance the visual sensitivity of Walleye in low light conditions (Ryder 1977, Vandenbyllaardt et al. 1991). In Walleye, the *tapetum lucidum* is evident in 90 mm TL fish, with longer fish (125-140 mm TL) possessing a fully developed structure (Braekevelt et al. 1989).

Our study tested for variation in growth rates of juvenile Walleye (*Sander vitreus*) under simulated light conditions in a laboratory foraging arena. Growth studies of Walleye at various life stages are prominent (Sass & Kitchell 2005, Moles et al. 2010, Venturelli et al. 2010, Johnston et al. 2012, Sheppard et al. 2018), but few have tested for the effects of light intensity on growth (Huh et al. 1976). Recent Walleye research has largely focused on thermal-optical habitat (TOHA), which is comprised of optimum light and temperature conditions for Walleye (Lester et al. 2004, Metcalfe 2006, Hansen et al. 2019, Mahlum et al. 2023, Vasquez 2024). Elucidating the relative contribution and importance of light intensity on TOHA and juvenile Walleye growth has not been directly tested. Our objective was to test whether light intensity influenced growth rates of juvenile Walleye. We tested for growth rate effects under multiple light intensities and staining treatments aligning with the lower (8 lux), upper (68 lux), and extreme (well above 68 lux) bounds of Walleye foraging activity based on angler catch per unit effort estimates presented by Lester et al. (2004). We hypothesized that juvenile Walleye growth rates would be higher under lower light conditions in stained environments. Recent studies indicate that recruitment bottlenecks occur on age-0 walleye (Gostiaux et al. 2022).

Methods:

Fish collections and husbandry

We collected wild age-0 Walleye via boat electrofishing (alternating current) on Shagawa Lake (Ely, MN) on September 18th, 2019 and September 28th, 2021. Age-0 Walleye total length (TL) ranged from 103-153 mm in 2019 (n=147) and 121-162 mm in 2021 (n=113). We purchased Fathead Minnow *Pimephales promelas* from Marine General (Duluth, MN) or The Bait Box (Superior, WI). A representative sample of 100 Fathead Minnow from each location were used to measure prey TL. Marine General

Fathead Minnow ranged from 31-42 mm (mean ± SE = 37.4 ± 1.2 mm). The Bait Box Fathead Minnow ranged from 32-40 mm (mean ± SE 36.9 ± 1.4 mm). We transported fishes in coolers filled with a 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 aeration. When needed, ice sealed in plastic bags were added to maintain water temperatures within ± 1.5°C of the water temperature at the collection site. In the laboratory, fish were separated by species into 568-L holding tanks and maintained at 18 °C under a 14h:10h day:night light cycle set at 3.16×10^{15} photons m^{-2} s^{-1}. 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. Age-0 Walleye were fed live Fathead Minnow three times per week. The Fathead Minnow were fed fish flakes (TetraMin, Melle, Germany) every other day. All age-0 Walleye were tagged under anesthesia using 0.003% MS-222 buffered with sodium bicarbonate for ten minutes (Meerbeek et al. 2013). Fish were implanted with VI Alpha tags using the VI Alpha Injector (Northwest Marine Technology, Anacortes, WA). The injection site was sealed with Nexaband surgical grade adhesive (Abbott Laboratories, Chicago, IL). Fish were released into a post-operative tank containing 1% API Stress Coat Plus (Mars Fishcare Inc., Chalfront, PA), their behavior was observed for one-hour post-surgery, and then they were returned to the holding tanks.

YOY Walleye Growth

We used a 1900-L (2.3 m × 1.0 m × 0.7 m) fiberglass tank with water depth maintained at 0.5 m to test for the effects of light and water staining on age-0 Walleye growth rates. Tank sides were lined with black cloth to reduce light reflection, and rounded inserts were placed in the corners to minimize corner effects. The tank was divided to create three equal sections that measured 0.80 m × 1.15 m via plexiglass dividers wrapped in black cloth, with a 30 cm × 10 cm mesh section just under the surface to allow water exchange between sections. Lights were left on a 14:10 day:night cycle and the water temperature was kept constant at 18°C, which is the average temperature of Northern Minnesota lakes in late summer and fall (Borkholder & Parsons 2001). Eight light engines were mounted 1.2-m above the water surface and housed LED lights with a peak wavelength of 525 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. Pea gravel on top of light-colored sand was used as substrate.

Growth trials were conducted from October 22nd, 2019 – January 15th, 2020 and November 11th, 2021 - January 10th, 2022. Trials were conducted for 16 days, with length (TL) and weight (g) of each fish taken on days 0, 8, and 16. Each replicate contained five age-0 Walleye and 20 minnows. Minnows were counted and replenished back to 20 total daily. Injured and dead minnows were removed and replaced with a fresh minnow. Food was withheld for 48 hours prior to trial initiation to clear the digestive tract. Upon trial completion, growth rates were calculated in g g^{-1} day^{-1}.

We selected three light intensities based on optimal foraging conditions estimated by Lester et al. (2004), with one tested intensity within the estimated optimal 8-68 lux (3.16×10^{14} photons m^{-2} s^{-1}, ~10 lux), one higher than the optimal (3.16×10^{15} photons m^{-2} s^{-1}, ~100 lux), and one extreme light intensity which was well above the estimated optimal (2.88×10^{17} photons m^{-2} s^{-1}, ~750 lux). Tank surface irradiances were measured using an International Light Technologies ILT1700 Research Radiometer with a SED033/F/HMR/W broadband silicon detector (Peabody, MA). We tested three different staining levels within each light intensity equating to clear, moderately stained, and heavily stained Minnesota lakes. Staining was achieved through the addition of 10 or 20 mg L^{-1} of sodium humate ($C_9H_8Na_2O_4$, HuminFeed, Düsseldorf, Germany) to the pondwater solution (deionized water, NaCl, KCl, and $CaCl_2{\cdot}2H_20$) for the moderate and heavy staining, respectively.

We collected absorbance values at 440 and 525 nm using a Spectronic 20 Genesys spectrophotometer (Spectronic-Unicam, USA). Absorbance values at 440 were used to calculate the a_{440}. The a_{525} was also measured and used to calculate the extinction coefficient (k) values for each staining level as only 525 nm light was present during trials. To calculate extinction coefficients, the Beer's Law equation was used:

Eq 1. $A_\lambda = \varepsilon \text{bc}$

where A_λ is the absorbance value at 525 nm, ε is molar absorptivity, *b* is the path length in m, and *c* is the concentration in moles/L. Beer's Law can also be used to calculate light at depth using the following equation:

Eq 2. $I_x = I_0e^{-kz}$

where I_0 is the surface irradiance, z is the depth, k is the extinction coefficient, and I_x is the irradiance (light intensity) at depth. Because b is the light path and equal to 1 m, A_λ was simplified to $\varepsilon * c$. Since k represents the attenuation of light per m and we only used FDOM (fine dissolved organic matter), all light attenuation was via absorption and was not scattering via particulate matter. Thus, the absorbance equaled attenuation and we could substitute $\varepsilon * c$ for k.

The staining conditions tested included three treatments: clear (no sodium humate added), moderate staining (10 mg L^{-1}), and heavy staining (20 mg L^{-1}). The corresponding a_{440} values were 0.6 m^{-1} in the clear treatment, 13.8 m^{-1} in moderate staining, and 28.3 m^{-1} in heavily stained water (Figure 1). The a_{525} values were 0.5 m^{-1} in the clear treatment, 8.06 m^{-1} in moderate staining, and 16.8 m^{-1} in heavily stained water. The extinction coefficients calculated from the A_{525} values were 0.2 for clear water, 3.5 for moderate staining, and 7.3 for the heavily stained condition.

Analyses

Age-0 Walleye growth was analyzed via a classification regression tree (CART) model in JMP Pro 16.0.0 (SAS, Cary, NC). A CART model was chosen because with two different year classes of age-0 Walleye, year class can be a predictor variable and the predictor's importance is quantified based on which node it appears, if any. The second caveat was Walleye length, as later trials contained longer Walleye based on average length and length range. As a result, age-0 Walleye starting total length was used as a second predictor variable. The remaining variables used in the CART model were fish ID (the alphanumeric tag used to test for outliers), starting weight, light intensity, and staining level. The dendrogram was grown until additions contributed < 0.015 to the R^2 value.

Results:

Age-0 Walleye Growth

As light intensity at depth increased, age-0 Walleye growth rates decreased non-linearly following a quadratic function ($y_{growth} = -0.0685 + 0.0139x - 0.0005x^2$; $r^2 = 0.88$; Figure 2). When comparing similar light intensities at depth, the darker stained water resulted in a higher growth rate in all cases. For example, comparing 3.16×10^{15} photons m^{-2} s^{-1} (~ 100 lux) in heavily stained water to 3.16×10^{14} photons m^{-2} s^{-1} (~10 lux) with moderately stained water resulted in greater growth rates in the heavily stained condition, but greater light intensity at the surface and at depth (Figure 2). The CART model indicated that the most variance in age-0 Walleye growth was best explained by light intensity at the surface followed by the staining level at 2.88×10^{17} photons m^{-2} s^{-1} (~750 lux) and then the lower light intensities (Figure 3). Walleye growth was positive, ranging from 0.0092 g g^{-1} day^{-1} at 9.44×10^{15} photons m^{-2} s^{-1} (~750 lux surface intensity) in clear water to 0.0223 g g^{-1} day^{-1} at 1.58×10^{15} photons m^{-2} s^{-1} (~10 lux surface intensity) in heavily stained water. Growth was greatest in low light conditions and heavily stained waters.

Discussion:

Light is a key determinant influencing suitable thermal-optical habitat for walleye and other fishes. As such, whether the light environment affects juvenile Walleye growth rates is critical to understanding the contribution of light in the estimation of thermal-optical habitat. We found that age-0 Walleye gained weight at all light intensities tested but grew more rapidly in very low light intensities and heavily stained water. The greatest explanation of variance in the age-0 Walleye growth rates was separating the high light intensity from the lower two intensities. Next, the CART model identified the heavily stained treatments in the lower two light intensities, followed by parsing the heavily stained treatment in the highest light intensity. It is important to note that only the surface light intensity was included in the CART model, and as tannin concentration increased, more light was being absorbed generating a lower light environment at depth. For example, the light intensity at depth for 10 lux trials in heavily stained water (8.21×10^{12} photons m^{-2} s^{-1}) was 97% lower than in clear water (3.01×10^{14} photons m^{-2} s^{-1}). Growth was greater in heavily stained water when compared to moderate staining or clear water, although growth was positive in all treatments tested. As light intensity decreased, growth rates increased within a condition and across conditions. If age-0 Walleye growth is a predictor of survival, our findings may be able inform management about which Walleye lakes may have the greatest production potential and compare that to currently estimated production.

Optical habitat on growth

Thermal-optical habitat has long been implicated as a crucial factor to understanding Walleye population declines (Chu et al. 2004, Hansen et al. 2019, Raabe et al. 2020). However, the effect of light intensity on Walleye growth has never been tested on large juveniles and has only been modeled (Lester et al. 2004). More recently, TOHA has been shown to affect small- (0-300 mm) and medium-length Walleye (300-450 mm) to a greater degree than larger adults (>450 mm; Mahlum et al. 2023). Our findings, which aligned with the small length class above, suggested that light only significantly affected growth rates when the light intensity was 2.88×10^{17} photons m^{-2} s^{-1} (~750 lux) in clear water conditions. Growth rates became more variable at the highest light intensity, but any degree of staining aided in almost doubling the growth rate. It should also be noted that growth rates for all individuals were positive, increasing in length and weight regardless of light treatment.

Linking Light Intensities to Environment

Light intensity is a strong determinant of fish behavior, and because Walleye are visually mediated predators, the availability and suitability of optical habitat matters. We quantified the a_{440} values of the staining levels, but these values may be of limited utility for many management agencies. Secchi depth is often used as a measure of water transparency. To better represent how a_{440} and Secchi depth may roughly translate, we summarized data from Brezonik et al. (2019) which contains recorded a_{440} values and Secchi depth from the same location on a given date. Our low staining level a_{440} equaled 0.6 m^{-1} (~ 2.8 m Secchi depth), medium was 13.8 m^{-1} (~ 0.8 m Secchi depth), and high was 28.3 m^{-1} (~ 0.4 m Secchi depth). However, variation in Secchi depth was much greater in clear-water conditions, ranging from 1.8 m to over 6 m (Brezonik et al. 2019). Multiple factors can be attributed to changes in Secchi depth such as phytoplankton, runoff entering the lake, seasonal turnover, wind events, and dissolved organic carbon and tannins. All the factors above affect the light environment in different ways, as some absorb light while others attenuate, reflect or refract light.

Limitations

Our age-0 Walleye growth experiment examined the long-term result of previously studied predator-prey interactions under similar conditions (Michels et al. Chapter 4). The largest limitation of our study was that food was provided *ad libitum*; thus, our growth rates represented conditions when prey abundance was not a limiting factor. Growth rates in fish are often correlated with prey abundance (Hartman & Margraf 1992, Rosenfeld & Taylor 2009). In the stained treatments, the reaction distance of Walleye was likely reduced (Nieman & Gray, 2018). Thus, the growth rates observed here described a system that would often have high prey fish abundances. Lastly, consumed prey were only counted once per day, so the relative contributions of foraging during day vs night cannot be directly linked to growth rates.

Conclusions

Our findings showed that optimal light conditions for wild age-0 Walleye growth mainly involved avoiding high light intensities in clear water. Lower light intensities in clear water treatments produced high growth rates, so structural habitat to help avoid high light is likely beneficial in clear systems. Moderate to heavily stained systems are likely to produce higher age-0 Walleye growth rates if prey abundances of preferred prey are high. Our findings are helpful to management agencies interested in determining what optical habitat and water quality conditions are best for juvenile Walleye growth rates.

Chapter 5

Effects of light intensity, temperature, and prey density on age-0 Walleye (*Sander vitreus*): Insight from a habitat sensitivity analysis using an individual-based model

---

Introduction:

Predator-prey interactions often determine aquatic community structure with a multitude of factors affecting interactions, outcomes, and effects (Carpenter et al. 1985, Higham et al. 2015). These factors 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). 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.

Light is the principal abiotic variable that controls temporal and spatial distributions of foraging fishes, including walleye (*Sander vitreus*; Ryder, 1977). Post 8-weeks of age, juvenile walleye > 32 mm are attracted to low light intensities (~2-4 lux; Bulkowski & Meade 1983). In mesocosms, (39 cm deep), the vertical position of juvenile walleye with surface illumination ranging from 2 - 200 lux was deeper at the highest intensity, with movement to the middle of the tank at lower intensities (Scherer 1976). The greatest change in vertical position of juvenile walleye occurred during the transition from 2 to 20 lux (Scherer 1976). Lester et al. (2004) found that the highest angler catch per unit effort for walleye occurred at 28 lux, which is in accordance with Sherer's (1976) ~30 lux and Ryder's (1977) *in situ* experiments (4 – 100 lux). Einfalt et al. (2012) observed increased walleye foraging behavior and prey capture success with decreasing light levels ($8.16 \times 10^{13} – 3.16 \times 10^{14}$ photons m^{-2} s^{-1}; 5-10 lux), and prey capture was greatest at night in vegetated habitat. However, recent research by Vasquez (2024) showed that adult walleye will remain in littoral areas in natural systems even if well above their optimal light intensity, and noted that temperature was a much stronger determinant of walleye location.

Walleye reach greatest abundance and size in cool, mesotrophic environments that have specific temperature, dissolved oxygen, and light ranges (Bozek et al. 2011). Bioenergetically optimal water temperatures for growth range from 18 - 24°C (Koenst & Smith 1976, Hokanson 1977). Optimal growth temperatures vary between life stages. Age-0 walleye grow fastest at 25°C (Madon & Culver 1993), while larger juveniles and adults achieve optimal growth at about 22°C (Bozek et al. 2011). These temperatures are often incorporated into thermal-optical habitat area models (Lester et al. 2004, Chu et al. 2004, Jones et al. 2006, Hansen et al. 2019, Mahlum et al. 2023), but no models have tested the individual effects of light and temperature on walleye growth.

Individual-based models (IBMs) that have accurate environmental, population, diet, and growth data can be used to simulate spatially explicit effects of changing ecosystem conditions on fish populations in dynamic systems (Daewel et al. 2010). Hayes et al. (2009) noted the importance of determining specific habitat use of fishes when modeling processes and changes in population trends, as well as the relative importance of various environmental factors. Variation in habitat use and movement among individuals is important to population-level properties such as size structure, abundance, and predator–prey interactions (DeAngelis et al. 1993, Maes et al. 2005, Rice et al. 1993). IBMs that can simulate these ecological patterns may provide the most appropriate means for assessing the influences of changing habitat parameters on fish populations (Hayes et al. 2009).

Our goal was to test for the individual effects of light intensity, temperature, and prey density on age-0 walleye growth. We simulated interactions using an age-0 walleye IBM under four scenarios: 1) the nominal scenario where light intensity, temperature, and prey density all mimicked realistic bounds from a reference lake; 2) a temperature scenario that increased and decreased the temperature by 20% compared to the nominal condition; 3) a light intensity scenario where the tannins in the lake were increased and decreased by 20%; and 4) a prey density scenario where the number of prey per acre was increased and decreased by 20%. Under each scenario, simulated walleye exhibited free movements in response to the varying prey and environmental conditions experienced by each individual. These scenarios provide detailed information on the individual effects each variable had on age-0 walleye growth rates.

Methods:

Model Structure:

Our IBM included a population of 100 juvenile walleye that were followed for 60 days. The population existed in a 300-acre lake with a maximum depth of 8 m, with

Escanaba Lake in Vilas County, WI serving as the reference lake (Sass et al. 2022). Individual lengths were randomly drawn from a measured length distribution of age-0 walleye (100-165 mm; Michels Chapters 3 & 4) and fit to a length-weight relationship generated from initial starting weights (Michels Chapter 4). Juvenile walleye in the model move, forage, and grow with decisions made in that order. Movement and foraging occurred every 15 minutes, whereas growth occurred on a daily timestep. Walleye and yellow perch (*Perca flavescens*; prey) mortality and reproduction were not included as these processes were not central to the goals of our study. Instead, growth rate and prey consumption of the simulated walleye were tracked while performing a habitat sensitivity analysis. Abiotic conditions included temperature and light profiles mimicking inland lakes, which were used in developing the movement, foraging, and growth sub-models.

The juvenile walleye abundance used was not estimated to mimic empirical age-0 numbers in inland lakes. The model was designed to identify consumption and growth by individual juvenile walleye over a realistic length distribution, rather than the entire population to avoid issues with starvation and mortality. Model output included information on walleye foraging and growth. Foraging output included daily and total consumption of prey. Growth output included daily and total biomass change for each individual in g g^{-1} day^{-1}.

Prey Abundance:

We derived prey abundances from estimates of age-0 yellow perch in Escanaba Lake, WI (Sass pers. comm.). Estimated age-0 yellow perch densities during 2012-2022 ranged from 20 – 110 individuals $hectare^{-1}$. We designed the nominal model around an average prey abundance year with about 74 yellow perch hectare^{-1}. Choosing a relatively higher prey density allowed us to more directly test our goal, while minimizing walleye density-dependent effects such as competition for prey.

Foraging:

Foraging commenced each hour after an individual juvenile walleye moved to its new location. Walleye foraging was modeled using the encounter rate model of Gerritsen and Strickler (1977) and Mason and Patrick (1993). These models have frequently been used to simulate foraging by Great Lakes predators (Hrabik et al. 2014). We chose to use the model as it has been applied in the past (Mason and Patrick, 1993). In this case, the foraging rate potential (FRP) was assessed for each prey as:

Eq. 1: $FRP = \left(\frac{\pi R_j^2}{3}\right)\left(\frac{3V_j^2+V_i^2}{V_j}\right) d_i$

where V (m h^{-1}) is the swimming velocity of predator j or prey i, and d_i is the density of prey (number m^{-3}) i, and R_j is the reaction distance of predator j (juvenile walleye; m). R_j follows the formulation of Michels et al. (Chapter 3) for juvenile walleye and was dependent upon light availability:

Eq. 2: $R_j = \frac{R_{max} \cdot l}{a+l}$

where R_j 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). Light intensity at the surface was calculated from multiple different sources. Nautical twilight, civil twilight, and sunrise irradiances were based on Kishida (1989; 34.3853° N, 132.4553° E), while the morning and afternoon irradiance were converted from values for a summer morning at 10:30 am with 0% (sunny) or 50% cloud cover (Fahnenstiel et al. 1984; 47.2855° N, -90.6879° W). All values were converted to photons m^{-2} s^{-1} (Thimijan and Heins 1983; Harrington et al. 2015) for biological applicability (Johnsen 2014). We calculated light intensity at depth z using the Beer–Lambert equation (Hutchinson 1957):

Eq. 3: . $I_z = I_0 e^{-kz}$

where k is the extinction coefficient used in Michels et al. (Chapter 4).

Predator swimming velocity followed Peake et al. (2000) and was dependent upon the mass of a given juvenile walleye (updated daily) and temperature. Determination of yellow perch movements were based on the swimming speed in Otto & Rice (1974). Although prey selection was based on a random draw of prey lengths (below), determination of an encounter rate had to occur beforehand, and thus necessitated using constant prey lengths for calculation of FRP. The FRP produced a non-integer value that was rounded to produce the number of individual prey of each species that a predator encountered in that hour.

Prey selection followed the algorithm presented in Mason et al. (1998). In this algorithm, prey capture and consumption are determined by probability as determined by prey length and an optimal capture probability. The probability of capture success (P_c) decreases to zero at the maximum predator gape and at small prey lengths:

Eq. 4: $P_C = C_{opt}Fk^2e^{2(1-r)}$

where $C_{opt}F$ is the probability of capturing optimal length prey and r represents the length-dependent capture probabilities, shown as:

Eq. 3: $r = \frac{(S_{max} - S_{ratio})}{(S_{max} - S_{opt})}$

where S_{max} is the maximum prey to predator length ratio, S_{ratio} is the encountered prey length to predator length ratio (prey length divided by predator length), and S_{opt} is the optimum prey to predator length ratio (Mason et al. 1998, Hrabik et al. 2014). Values for S_{max} (0.5) and S_{opt} (0.25) were taken from Mason et al. (1998) and assumed to be constant. The length of prey input into S_{ratio} was determined from a random draw from a length–frequency distribution of age-0 yellow perch observed in Escanaba Lake, WI in 2019 (Sass pers. comm.). C_{opt} was estimated via capture success of age-0 walleye on fathead minnows (*Pimephales promelas*; Michels et al. Chapter 3) and was also a function of light intensity. If the light intensity was between 1.58×10^{11} - 3.16×10^{13} photons m^{-2} s^{-1}, C_{opt} was 0.22; otherwise, C_{opt} was 0.09. If prey were captured as determined by a random draw, the length of the prey was converted to mass using length–weight relationships (Mills et al. 1989, Post & McQueen 1994) and stored for use in the growth sub model at the end of each day. A satiation point was added to the model after initial test simulations produced unrealistically high growth rates. Previous age-0 walleye growth rate experiments showed cyclical consumption, averaging three prey consumed every 48 hours per juvenile walleye (Michels et al. Chapter 4). We used this as our satiation benchmark, and the time of initial consumption was recorded. If satiated, 48 hours after the first prey was consumed the walleye was able to resume foraging.

Movement:

Walleye movement was evaluated every 15 minutes. We simulated fish movement (vertical and horizontal) using an approach similar to Railsback et al. (1999)

and Hrabik et al. (2014). Fish were able to evaluate prey conditions in all adjacent cells and move accordingly based on prey density. Evaluation of cells was based on a modification of the FRP model:

Eq. 4: $Q_z = C_{opt}F \cdot FRP_z + [FRP_z \cdot b \cdot \varepsilon(\mu, \sigma)]$

where $C_{opt}F$ is the probability of capturing optimal length prey, FRP is the foraging rate potential as described previously at that given depth, b is the random integer to give directionality to the movement (1, 0, -1), and $\varepsilon(\mu, \sigma)$ to give a random movement to ensure not all juvenile walleye occupy the same strata within the lake, typically at the thermocline. We included a measure of random movement drawn from a normal distribution ($\mu = 5$, $\sigma = 3$), whose direction was determined by b to ensure that all juvenile walleye did not occupy the same x-y plane or depth. Our movement algorithm had two assumptions: 1) a lack of mortality risk in evaluating neighboring cells; and 2) stained water conditions did not significantly reduce reaction distance.

Prey movement was also evaluated every 15 minutes. Yellow perch were randomly distributed within the simulated lake, and movement was restricted to only one cell from the original starting position. Prey movement was updated after walleye movement to partially simulate predator avoidance.

Growth:

Growth was computed daily for each fish using a bioenergetic scaling factor. Estimated total prey mass consumed by an individual juvenile walleye over an entire simulation period, or 60 days, was input into a ‘Wisconsin’ bioenergetics model (Fish Bioenergetics 4.0; Deslauriers et al. 2017) for juvenile walleye (parameters from Madon

& Culver 1993). Total weight gained was divided by the total input to get a temperature-dependent scaling factor at 18, 22, and 26 °C. Temperature was input as a constant throughout the simulation. Next, the weight of prey consumed for an individual juvenile walleye on a given day was multiplied by the bioenergetic scaling factor to determine weight gained, which was then added to the starting weight for that day. The following calculation was used to calculate the specific growth rate:

Eq. 5: $\left(\frac{w_{final} - w_{initial}}{w_{initial}}\right) \div t$

where w_{final} is final weight after day 60, $w_{initial}$ is the initial starting weight, and t is time in days to get g g^{-1} day^{-1}.

Model Calibration:

Our goal was for the nominal model to fit growth rates observed in laboratory-based studies with age-0 walleye (Michels et al. Chapter 4). We used the empirical data presented in Chapter 4 to adjust some model parameters, while also maintaining a pattern-oriented approach. Specifically, the following adjustments were made to the model to test the empirically fit data. The temperature was maintained at 18 °C with a day-night light cycle of 14:10. Light intensity at depth was constant throughout the water column. Lastly, prey abundance was drastically overestimated to observe modeled growth rates under *ad libitum* feeding conditions. The latter portion was specifically designed to ensure the satiation factor was accurate. Once the modified model was calibrated, the light cycle, light intensity at depth, and prey abundance were all reset to nominal conditions.

Habitat Sensitivity Analysis:

Three independent habitat components were tested using an HSA: temperature, water clarity influenced by staining, and prey abundance. The nominal model tested had a prey abundance of 74 age-0 yellow perch hectare^{-1}, water clarity had an a_{440} value of 13.8 m^{-1} (k = 3.5), and a temperature of 22 °C (temperature-dependent scaling factor: 0.18). Next, each component was individually tested via ± 20% of the nominal value while all other components remained at the nominal value (Kitchell et al. 1977). Each simulation scenario was run over 50 iterations.

Statistics:

To test model calibration, the modified nominal model was compared to the juvenile walleye growth rates from Chapter 4. Individual Two-Sample T-tests were run within each light intensity and staining condition to test for differences between the model output and the empirical growth rates. For the habitat sensitivity analysis, a One-Way ANOVA was used to test for differences within one parameter across scenarios (i.e. nominal vs. high vs. low). Normality and equal variance assumptions were tested via Shapiro-Wilk and Brown-Forsythe tests, respectively. Averages and standard deviations are reported. All statistical tests were performed in SigmaPlot 15.0 (SPSS inc.) and analyzed with an $\alpha = 0.05$ to indicate statistical significance.

Results:

Model Calibration:

The model produced juvenile walleye growth rates statistically similar to the empirical growth rates (Figure 1). At 2.88×10^{17} photons m^{-2} s^{-1} in clear water, the model output had a slightly higher value than the empirical growth rate, but the difference was not statistically significant (Two-Sample T-test: $t_{64} = 1.93$, p=0.062). All other t-tests resulted in p-values > 0.42.

Habitat Sensitivity Analysis:

Prey density and temperature each had separate significant influences on growth rates of age-0 walleye. Growth rates in the high prey density scenario were significantly higher than in the low prey density scenario (One – Way ANOVA: $F_{2,147} = 7.445$, p<0.001) with a difference of 41% between the two scenarios (Figure 2). Neither high (p=0.19) nor low (p=0.14) prey densities were different from the nominal model. The cold temperature scenario also had a significantly higher growth rate (81%) compared to the warmer temperature (One – Way ANOVA: $F_{2,147} = 4.897$, p=0.009), but the temperature scenarios were not significantly different from the nominal model (cold: p=0.23; warm: p=0.41; Figure 2). Different staining conditions did not influence growth rate (One – Way ANOVA: $F_{2,147} = 0.0123$, p=0.988), although increased staining considerably increased variability in the model output (Figure 2).

Discussion:

Elucidating the influences of individual environmental variables on fish growth can be particularly difficult, but individual-based modeling represents an approach that helps predict the effects of any one variable while holding others constant. Testing for the effects of prey density, temperature, and light intensity on age-0 walleye growth rates showed that certain variables were disproportionally important. Our model was able to accurately predict age-0 walleye growth rates when compared to empirical growth rates observed in laboratory conditions (Michels et al. Chapter 4). The IBM suggested that temperature and prey density each had significant, independent effects on growth rates of age-0 walleye. Light intensity did not influence growth rate as hypothesized, although increased staining levels produced much greater variability across iterations.

Temperature changes had the greatest effect on the growth rates of age-0 walleye, resulting in an 81% difference comparing the +20% and -20% scenarios. Colder water consistently increased growth rates, whereas warmer water was more variable, with some simulations resulting in increased growth rates. Adult walleye in Lake Erie have grown close to double the rate compared to Lake Huron, but with similar temperature regimes, food availability was the driver of the faster growth (Madenjian et al. 2018). However, temperature-dependent bioenergetics likely played a factor as well. Gut evacuation rates for larval walleye are higher at 20 °C than 15 °C and 25 °C (Johnston & Mathias 1996), and the bioenergetic scaling factor was greater in our 18 °C scenario than the nominal model (22 °C). Thus, more energy from a prey item was allocated towards growth in our colder temperatures. Our warm water scenario had the greatest bioenergetic scaling factor (26 °C), but if prey were not consumed, energetic costs were also highest. In our IBM, yellow perch and walleye were randomly distributed to start, so it may have taken multiple time-steps to days for walleye to encounter suitable prey densities. Initial location of suitable prey densities may explain the high variability observed in our high-temperature scenario.

Prey density also had a significant influence on age-0 walleye growth rates, resulting in a 41% increase between low and high prey densities. High prey density scenarios had significantly higher growth rates than low prey density scenarios as hypothesized. However, low prey density had high variability, likely rooted in the random distribution of predators and prey. In low prey density scenarios, juvenile walleye may have needed to search longer to find suitable prey densities, so incurring a cost at the start in some iterations. In other iterations, most juvenile walleye may have started in close proximity to clusters of prey in the low prey density scenario. Fox and Flowers (1990) found that age-0 walleye had density-dependent growth, with walleye at higher densities (60 fish m^{-3}) having significantly reduced stomach content biomass than either 20 or 40 fish m^{-3}. However, Fox and Flowers (1990) attributed at least part of the density-dependent growth to density-dependent activity; that is, being more metabolically active at higher walleye densities to capture sufficient prey and also avoid predation by a cohort (McIntyre, 1987). With our low prey density scenario, intra-specific competition between walleye was likely minimal, but may still occur if several walleye were following the same cluster of prey. Thus, density-dependent activity may be one reason for the more variable growth rates at low prey densities.

Light intensity did not influence growth rates of age-0 walleye. However, variability in growth in the increased staining scenario reached a standard error 25% above and below the nominal model. This variability, paired with the lack of statistical difference among scenarios, showed that light intensity did not have a direct effect on age-0 walleye growth. More specifically, light intensity may have confounding effects when paired with either temperature or prey density. Our nominal model was based on a good prey abundance year in Escanaba Lake, WI, but prey densities of age-0 yellow perch within the last 10 years have occasionally been below 25 individuals hectare^{-1} (Sass pers. comm.). In our model, light intensity influenced the reaction distance and capture probability ($C_{opt}F$) of juvenile walleye. Reaction distance of fishes has been well documented to change with the light intensity of the surrounding optical environment (Beauchamp et al. 1999, Hansen et al. 2013, Nieman & Gray 2019). Lower light intensities due to staining in the simulated lake essentially allowed for a longer time spent foraging at higher prey capture probabilities. With high prey abundance, increased prey capture probabilities were less important as there were increased chances to capture prey. Thus, light intensity did not influence growth rates, as prey were still being captured regardless of a specific light intensity.

Thermal-Optical Habitat

As discussed in Chapter 3, age-0 walleye foraging increased at low light intensities and became more selective at higher light intensities. Recently, TOHA has been shown to affect small (post hatch - <300 mm) and medium length walleye (300-450 mm) to a greater degree than larger adults (>450 mm; Mahlum et al. 2023). Our Chapter 4 study, which used small fish, suggested that low light intensities were critical to increased foraging success of age-0 walleye. Chapter 4 provided evidence that growth rates were higher in dark, heavily stained environments and that extremely bright environments reduced the growth rates of age-0 walleye. However, after testing the IBM output of growth rate under the conditions set in Chapter 4, there was no difference between the empirical growth rates and the model. Likewise, age-0 walleye behavior was not encoded to avoid higher light intensities, nor select for lower light intensities. Recent research by Vasquez (2024) showed that walleye >310 mm did not select for a specific light habitat. Our results support and extend this claim to juvenile walleye, demonstrating that light intensity may be a confounding factor, but not a direct driver of age-0 walleye growth rates.

Limitations:

Our IBM examined predator-prey interactions over multiple scenarios that independently manipulated prey density, light intensity, and temperature. Our IBM had several limitations that need to be acknowledged. To start, walleye digestion and egestion rates are temperature-dependent. The satiation factor we used was calculated from our growth study (3 prey every 48 hours; Chapter 4), which should also be temperature-dependent. For the sake of consistency between scenarios, the satiation factor was kept constant. We did not have sufficient data to predict whether the satiation constant would change as temperature increased. Thus, the high temperature scenario results may underestimate growth as more prey could be consumed than what was observed in the model. Second, we used a simplified model system that included only one predator and prey species. Natural systems and their food webs are often more complex, with various larger piscivores foraging on age-0 walleye and age-0 yellow perch that would influence walleye abundance via mortality. Various prey species also spawn at different times of the year, creating a seasonal gradient of prey sizes for age-0 walleye to consume, and not just the simplified, yet relevant, system we depicted here. Our main goal was to observe the independent effects of prey density, light intensity, and temperature on juvenile walleye growth rates, so a simplified system let us address the core question.

Conclusions:

Our findings showed that temperature and prey density had separate, significant effects on juvenile walleye growth. Light intensity did not have an effect, but may become a confounding factor that may exacerbate suboptimal temperature or prey density conditions. Thus, our findings suggest that more management focus should be directed towards efforts in keeping optimal thermal habitat and good prey abundances. Our findings are helpful to management agencies interested in conserving age-0 walleye habitat and/or predicting changes in growth due to environmental changes like climate change.

Chapter 6

Conclusions

The objective of my dissertation was to test whether environmental factors, specifically light intensity, affected predator-prey interactions, whether the temporal scale of foraging translated to growth, and whether increasing the spatial scale via modeling could help predict population-level changes. Chapter 2 examined the detailed escape behaviors of invasive (round goby) and native (mottled sculpin) prey fishes from active (smallmouth bass) and ambush (burbot) predators at multiple light intensities. Chapter 3 examined the scotopic spectral sensitivity of walleye and their foraging behavior under optimal light conditions on fathead minnow (*Pimephales promelas*) at eight different times of day. Chapter 4 expanded upon Chapter 3 by testing for the effect of light intensity and water clarity on walleye growth rate. Lastly, Chapter 5 combined information from Chapters 2, 3, and 4 into an individual-based model on walleye foraging and tested whether light intensity, temperature, and prey density affected growth rates of a population of age-0 walleye. Understanding whether environmental factors such as light intensity influence predator-prey interactions at the species, diel, and population level is summarized in the final Chapter 6. In addition to the results provided by each independent study, a discussion summarizing all of these studies collectively provides a synthesis of the importance of light intensity on fish behavior.

Effects of Light Intensity on Prey Behavior

Our findings showed that light intensity significantly affected escape metrics and avoidance success. When round gobies elicited more reactions from predators (all burbot trials and smallmouth bass at dark), only the smallmouth bass in dark trials had more round gobies consumed than mottled sculpin. All other trials had more mottled sculpin consumed. The predator's detection abilities, visually and mechanosensory, factored heavily into the reaction probability (Luecke & O'Brien 1981), but the prey species avoidance abilities (Svensson 1992, Trager et al. 1994) and environmental factors (Sih 1992) also played a role. Both prey species can be found in similar depths and light environments (Bergstrom & Mensinger 2009, Kornis et al. 2012), and often use structure like rip-rap and interstitial spaces to moderate light intensity as they do not often exhibit diel bank migrations but were noted to vertically migrate seasonally in Lake Ontario (Pennuto et al. 2021).

As light intensity increased, round gobies fled farther from approaching predators, fled closer to theoretical optimal angles, and made more turns during a flee. This FID strategy is rewarded when prey escape a predator's detection zone without eliciting a predator response but can also increase the probability of detection by predators (Godin 1997). Longer FIDs often translate to increased survival (Dill 1973, Webb 1982, 1984a, 1986), but lower light intensities reduce the distance prey can visually detect predators (Pitcher & Turner 1986). We observed low FIDs at dark, which correlates to short range mechanosensory detection. As light intensity increased, round gobies increased their FID while also increasing their probability of escaping predator attacks after being detected. Alternatively, the probability of escaping predator attacks for mottled sculpin after detection was inversely proportional to light intensity, which could be attributed to only slight variations in FID across light intensities. There is debate as to whether fish escape direction is random to prevent predator learning of prey behaviors (Skajaa & Browman 2007) or optimized to a certain angle path to increase survival for each encounter (Weihs & Webb 1984, Webb 1986, Domenici & Blake 1993, Domenici & Batty 1994). When predictable prey were encountered, predators adjusted their behavior before prey even initiated a flee and ultimately attacked with greater acceleration than when prey were unpredictable, suggesting that unpredictable escapes are less useful to prey than previously thought (Szopa-Comley & Ioannou 2022). However, Nair et al. (2017a) discovered that when attacked from the side, prey consistently escaped contralaterally to simulated predators, whereas when attacked from caudal or rostral positions, there was an equal probability of escaping contra- or ipsilaterally. Kimura and Kawabata (2018) found that prey oriented 120-150 degrees off the predator's body axis had the highest probability of escaping a predator. Our results showed that prey escapes were non-random and either followed (round gobies, similar to angles in Kimura & Kawabata 2018) or did not follow (mottled sculpin) the predicted escape angles based on the FID (Domenici 2002). As light intensity increased, round goby FID changed along with the average escape direction, matching the optimal flee direction calculated. Conversely, mottled sculpin fled at about the same FID but the average escape angle was reduced as light intensity increased, fleeing closer to the predator's initial attack path, allowing more direct pursuit by the predator.

The evasiveness of round gobies also increased with light intensity, making more directional changes within a flee. Previous studies examining escapes found that more directional changes and increased variability in velocities during a flee increased escape success (Herbert-Read et al. 2017). Comparatively, mottled sculpin did not change direction as much and had a significantly greater probability of being captured by smallmouth bass (Michels et al. 2021). Mottled sculpin often reacted to predators via quick bouts of swimming followed by immobility, presumably trying to restore crypsis especially at higher light intensities.

A less complex path directed more in line with the predator's attack should be less successful in escaping predator attacks. Under predation by single-strike predators like burbot, instantaneous measures such as FID, escape direction, speeds, accelerations, and turning rates are important for determining whether prey survive (Webb 1976, 1982, Eaton & Emberley 1991, Fuiman 1993, Fuiman et al. 2006). When predators actively chase prey (smallmouth bass; Domenici et al. 2014, Neill & Cullen 1974), sustaining high levels of path complexity is a strong determinant of survival probability (Herbert-Read et al. 2017). Mottled sculpin turned fewer times, which led to smallmouth bass redetecting prey 77% of the time compared to 42% for round gobies, which may have contributed to more mottled sculpin being consumed.

Effect of Light Intensity on Foraging Success

The age-0 walleye predator-prey trials conducted in darkness established the range of the lateral line. Strikes in trials with light present outside of the lateral line distance were attributed to visual input. Reaction distance of fishes has been well documented to change with the light intensity of the surrounding optical environment (Beauchamp et al. 1999, Hansen et al. 2013, Nieman & Gray 2019). The reaction distance and foraging behavior of juvenile walleye has not been observed under a range of light intensities. Our data suggested that peak walleye foraging occurs from nautical twilight to civil twilight (~0.05-1 lux), well below previous estimates which ranged from 5-10 lux (Lester et al. 2004, Metcalfe 2006, Einfalt et al. 2012). Increased foraging activity during this low light period directly corresponded to the rapid increase in average reaction distance. After civil twilight (-3°; 3.16×10^{13} photons m^{-2} s^{-1}; 1 lux), the average reaction distance reached an asymptote at about 29 cm and the number of reactions, attacks, and captures decreased. Previous research on juvenile walleye at midday light intensity observed average reaction distances of > 50 cm to prey (Nieman & Gray 2019). Our farthest reaction distance was 64 cm in a sunny afternoon trial (750 lux), but the average for 750 lux was just over 30 cm. Nieman and Gray (2019) also found that reaction distance decreased with the addition of sediment and algae, although no specific light intensities were reported.

When foraging at low light intensities, juvenile walleye would react to prey, pursue, and then attack if the prey could be localized. Although capture success was not strongly correlated with light intensity, the number of reactions and subsequent attacks were strongly dependent on light intensity. At high light intensities, walleye were more selective of prey they attacked. Multiple interactions occurred where a walleye would react to prey, but then abort any pursuit within a few seconds if the prey was already oriented diagonally or horizontal to the walleye's body axis, or if the prey turned at any time during the pursuit or approach. After an attack was initiated, there was a high probability of capturing and retaining prey. Similar behaviors were noted in Einfalt et al.

(2012), where walleye followed and pursued prey less in daylight conditions. Einfalt et al. (2012) attributed the reduced pursuing of prey in brighter conditions to the long distance between predator and prey being perceived as too far for probable capture or that prey gave off cues indicating detection of the predator (Magurran 1990). Although a small sample size from our experiment, distance was not the primary factor attributed to aborting a reaction to or pursuit of prey, but rather prey orientation, which likely served as feedback that prey may have detected the predator or would soon become aware of the predator's presence. By changing their foraging strategy to only pursuing and attacking prey oriented away from them, predators may optimize their foraging and reduce energy costs (Manatunge & Asaeda 1999, Ahrenstorff et al. 2009).

Effect of Light Intensity on Growth

Growth is ultimately the surplus of energy gained from foraging after subtracting energy towards metabolism and SDA. Growth rates in fishes reflect metabolic processes, and by elucidating whether specific abiotic, biotic, density-dependent, and density independent factors influence growth, management agencies can better forecast how fish populations may change over time (Brandt et al. 1992, Clarke & Johnston 1999, Pederson et al. 2017). The effects of temperature on growth have been well documented (Fielder et al. 2007, Venturelli et al. 2010, Johnston et al. 2012, Peat et al. 2015) but the effect of light intensity, and thus foraging behavior and habitat, lack sufficient data for non-larval fishes. From Chapter 3, we found that adult walleye were most sensitive to 500-550 nm wavelength light. Because our age-0 fishes were almost all possessing fully developed *tapeta lucidum*, our fish should have comparable sensitivities to the adult fish. The greatest explanation of variance in the age-0 walleye growth rates was separating the high light intensity from the lower two light intensities. The CART model then parsed the heavily stained treatments in the lower two light intensities, followed by identifying the heavily stained treatment in the highest light intensity. Light at depth was a critical component to directly comparing growth rates, as comparing surface light intensity and staining did not generate a clear pattern. It should also be noted that our growth studies were conducted under light intensities that were well above the optimal foraging light intensity for the age-0 walleye. Based on light at depth, only the lowest surface light intensity at the highest staining level was within the optimal foraging light intensity. Light intensity does affect walleye growth rate, but *ad libitum* food scenarios are at best seasonal, but often rare in natural systems.

Effect of Light Intensity, Temperature, and Prey Density on Growth Rate

Growth rates can be highly plastic and dependent on prey abundance (Hartman & Margraf 1992), the amount of energy available from prey (i.e. size, caloric density; Rand et al. 1994), the metabolic rate of the predator (Rice et al. 1983, Rand et al. 1994), and allocations of energetic reserves to somatic growth and reproduction (Auer et al. 2015). Metabolism is a function of temperature, so by its very nature, temperature should have a significant effect on growth rate. The effects of temperature on growth have been well documented (Fielder et al. 2007, Venturelli et al. 2010, Johnston et al. 2012, Peat et al. 2015) and walleye optimal growth is well studied (Madon & Culver 1993, Galarowicz & Wahl 2003, Bozek et al. 2011). As explained above and in Chapter 4, light intensity and water clarity had a significant effect on age-0 growth rate. However, the magnitude of the effect of light intensity on growth rate needed to be compared to temperature and prey density in a simulated natural system. The individual-based model (IBM) was generated using information from Chapters 2, 3, and 4 to address this question.

The habitat sensitivity analysis (HSA) allowed us to independently manipulate a single environmental variable by ± 20% to test its individual effect on growth rate. Temperature had the greatest influence on growth rate followed by prey density, but light intensity did not have an effect on growth rate. One reason for this potential null effect of light intensity compared to Chapter 4 results is that ± 20% had a minor change on the extinction coefficient (k). The nominal model used a moderately stained lake ($k = 3.5\ m^{-1}$), but Chapter 4 was comparing clear, moderately stained, and heavily stained water, which was double the amount of sodium humate ($k = 7.3\ m^{-1}$). In the HSA, the low staining k was set to $2.8\ m^{-1}$ and the high staining k was set at $4.2\ m^{-1}$. The growth experiment in Chapter 4 may exaggerate the significance of light intensity on growth rate due to the stark contrast between conditions, although they are still within the bounds of natural systems observed in Minnesota (Brezonik et al. 2019). The model was tested against the empirical data from Chapter 4, and no differences were observed, so light intensity may still have an effect specifically when comparing extreme conditions (i.e. clear water lake vs. heavily stained lake; $k = 7.3\ m^{-1}$).

The Importance of Light Intensity in Thermal-Optical Habitat

Thermal-optical habitat (TOHA) has long been implicated as a crucial factor to understanding walleye population declines (Chu et al. 2004, Hansen et al. 2019, Raabe et al. 2020). Light is a crucial environmental variable for the development, growth, and survival of many larval and juvenile fishes (Boeuf & Le Bail 1999, Downing & Litvak 1999). Growth rates can be influenced by light intensity (Downing & Litvak 1999), spectral composition (Ruchin 2005), and photoperiod (Boeuf & Falcôn 2001). Recently, TOHA has been shown to affect small- (0-300 mm) and medium-length walleye (300-450 mm) to a greater degree than larger adults (>450 mm; Mahlum et al. 2023). Our findings, which aligned with the small length class above, suggested that light only significantly affected growth rates when the light intensity was 2.88×10^{17} photons m^{-2} s^{-1} (~750 lux) in clear water conditions. Growth rates became more variable at the highest light intensity, but any degree of staining aided in almost doubling the growth rate. It should also be noted that growth rates for all individuals were positive, increasing in length and weight regardless of light treatment. However, the staining levels we tested also covered a moderate staining scenario and two extremes: clear and heavily stained water. The IBM identified temperature and prey density as two environmental variables that have a significant effect on age-0 walleye growth rate. Similarly, walleye behavior was not encoded to avoid higher light intensities, nor select for lower light intensities. Under this model, if light intensity had a significance to TOHA, one would hypothesize that the model should overperform in the model under high light conditions when compared to empirical data. However, there was no difference between the model output when tested against the empirical data. Research by Vasquez (2024) supports this claim with adult walleye, suggesting that temperature should be the predominant environmental factor regarding walleye management. Our research supports this claim, while supporting that lake water clarity could serve as a benefit if adequate prey abundances are moderate to high.

Collectively, these studies have improved and advanced our understanding of how predator-prey interactions and growth are affected by light. Consistent patterns include: (1) prey behavior is light and predator dependent, (2) light intensity affects age-0 walleye foraging behavior, (3) as light intensity affects foraging behavior, age-0 walleye growth rate is also affected by light intensity, and (4) although light intensity may be important, it is likely a confounding variable that can magnify the effects of a changing temperature or prey base of a lake.

Tables

Table 1. Time of day corresponding to light intensities at 5m depth. Light intensities were calculated from surface irradiances published in the literature using Beer's Law with an extinction coefficient (k) of 1.25 m^{-1}.

Time of Day	Light Intensity (photons m^{-2} s^{-1})	Light Intensity (lux)
Dark	6.65×10^{8}	0
Nautical Twilight	1.58×10^{11}	0.05
Civil Twilight (-6°)	3.16×10^{12}	0.1
Civil Twilight (-3°)	3.16×10^{13}	1
Sunrise	3.16×10^{14}	10
Cloudy Morning	1.58×10^{15}	40
Sunny Morning	3.16×10^{15}	100
Sunny Midday	2.88×10^{17}	750

Table 2. Model parameters and values used in the walleye (*Sander vitreus*) individual based model.

Parameter	**Definition**	**Value**	**Unit**	**Source**
NA	Density of yellow perch	74	Individuals hectare^{-1}	Sass (pers. comm)
$C_{opt}F_{optL}$	Optimal capture probability of walleye (optimal light intensity)	0.22		Chapter 4
$C_{opt}F_{other}$	Optimal capture probability of walleye (outside of optimal light intensity)	0.09		Chapter 4
S_{max}	Maximum prey to predator length ratio	0.5		Mason et al. (1998)
S_{opt}	Optimum prey to predator length ratio	0.25		Mason et al. (1998)
NA	Bioenergetic scaling factor (18, 22 26°C)	0.20, 0.18, 0.23		Fish Bioenergetics 4.0
V_1	Swimming speed of yellow perch	0.25	m s^{-1}	Otto & Rice (1974)
V_P	Swimming speed of predator (walleye)	0.35	m s^{-1}	Peake et al. (2000)
k	Extinction coefficient	3.5	m^{-1}	Chapter 4

Figures

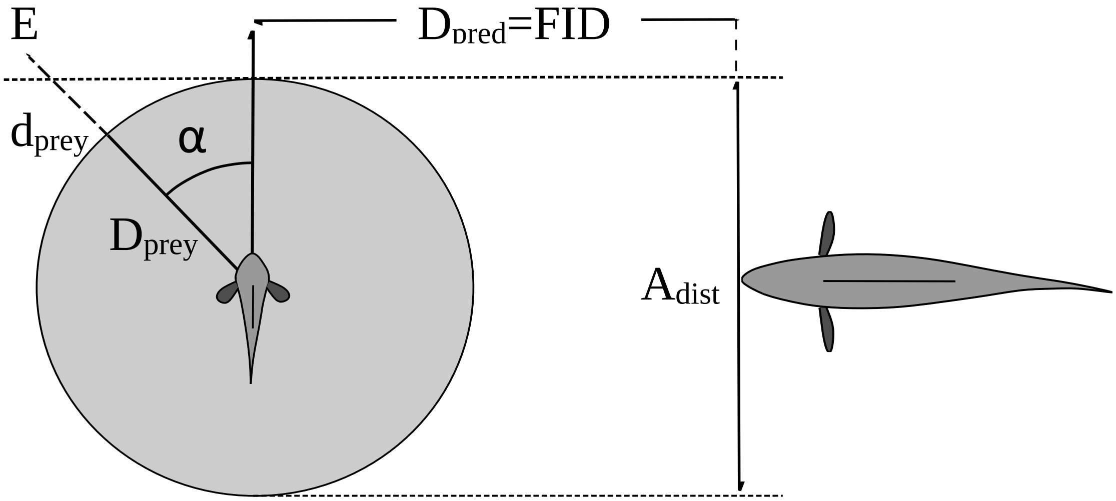

Fig. 1. Geometric breakdown of a prey escape. Shaded circle represents the minimum distance, with a radius of D_{prey}, that prey must move to avoid the predator's attack distance (A_{dist}; here 80 cm). Escapes occur at E by fleeing D_{prey} (1/2 of predator's attack distance) plus d_{prey} (residual distance) cm away to reach escape point E via escaping at angle α. This all depends on when the prey initiates the escape (D_{pred}; measured as FID). Figure was modified from the original figure in Domenici (2002).

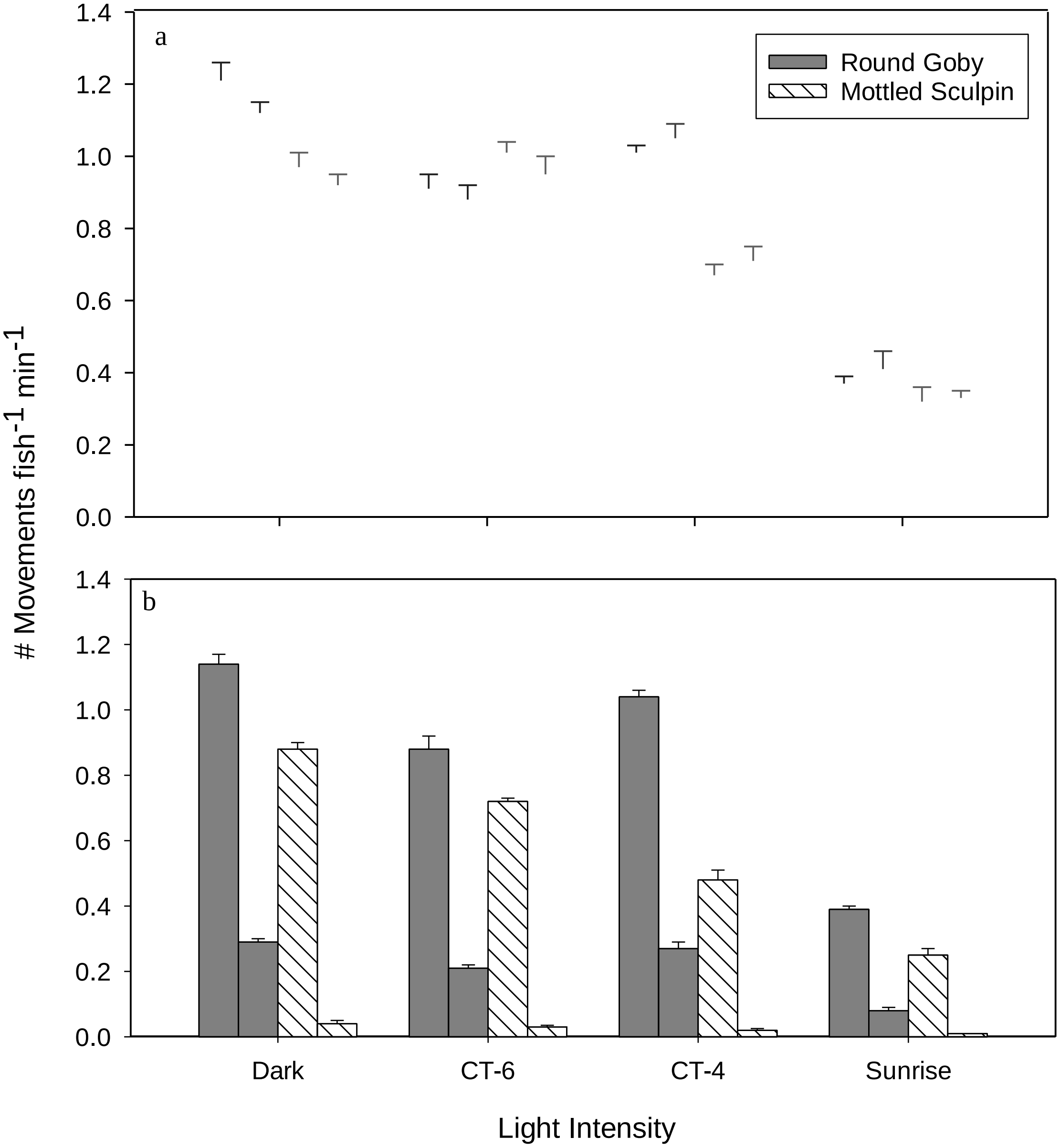

Fig. 2. The number of free movements over time for each prey species under a) no predation and b) when predators were in the tank. Within each species and light intensity, the left bar represents the start of the trial, and the right bar represents after two hours. Predator species had no effect on the number of free movements (GLM: $\chi^2{}_{17}$=0.051 p=0.254). Predator presence, light intensity, and time elapsed had a significant interaction for both round goby (GLM: $\chi^2{}_{17}$=58.47, p=0.002) as well as mottled sculpin (GLM: $\chi^2{}_{17}$=82.42, p<0.001). Averages are shown ± 1 SE.

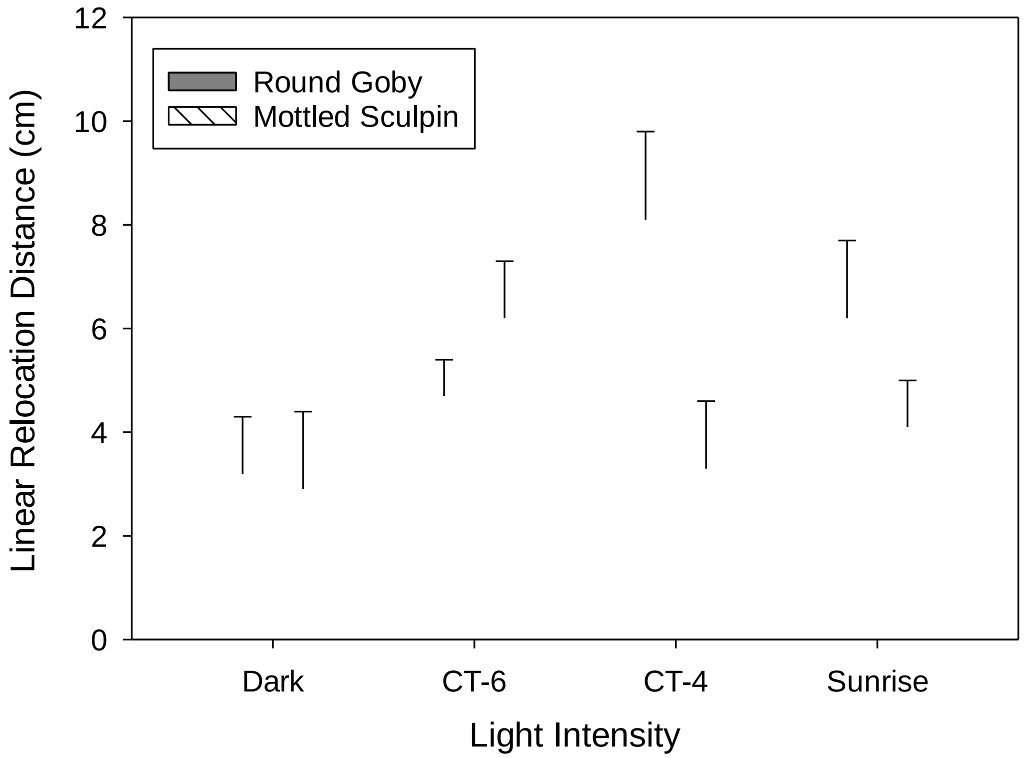

Fig. 3. Linear distance traveled during free movements when predators were in the tank. Distances were measured as the midpoint of the prey body at the frame before movement to the frame after the movement concluded. Distances traveled during these free movements were significantly affected by an interaction between light intensity and prey species (GLM: χ^2_{17}=2.89, p=0.038). Averages are shown ± 1 SE.

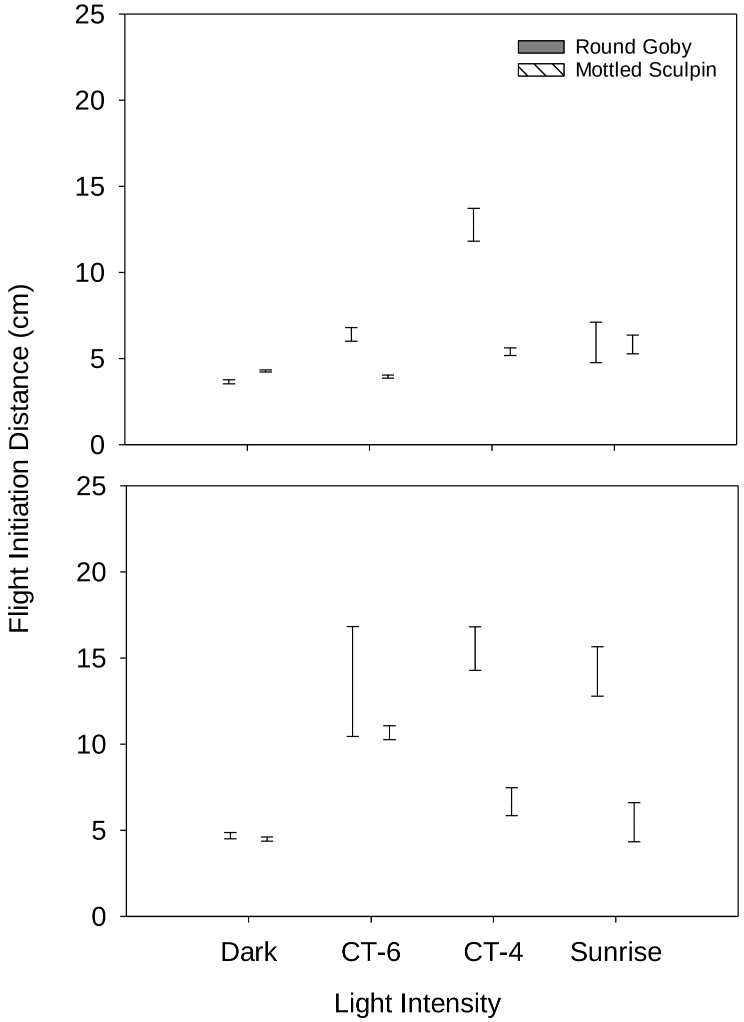

Fig. 4. Flight initiation distances of round goby and mottled sculpin from a) burbot and b) smallmouth bass at different light intensities. A GLMM was used to test the effects of light intensity, predator species, and prey species on FID (Normal distribution with Identity link function; tested against light intensity, predator species, trial type (BB, SMB, MIX), prey species, all interactions among light intensity, predator, and prey, as well as time within trial and predator ID as random factors). A significant interaction existed between predator species, prey species, and light intensity (GLMM: $\chi^2{}_{17}=81.558$, $p<0.0001$). Round gobies significantly increased their FID in the presence of burbot at CT-4 compared to mottled sculpin ($\chi^2{}_{17}=18.742$, $p<0.0001$). Under predation by smallmouth bass, round goby significantly increased their FID compared to mottled sculpin at CT-6 ($\chi^2{}_{17}=32.937$, $p<0.0001$), CT-4 ($\chi^2{}_{17}=24.555$, $p<0.0001$), and Sunrise ($\chi^2{}_{17}=99.389$, $p<0.0001$). Averages are shown with ± 1 SE.

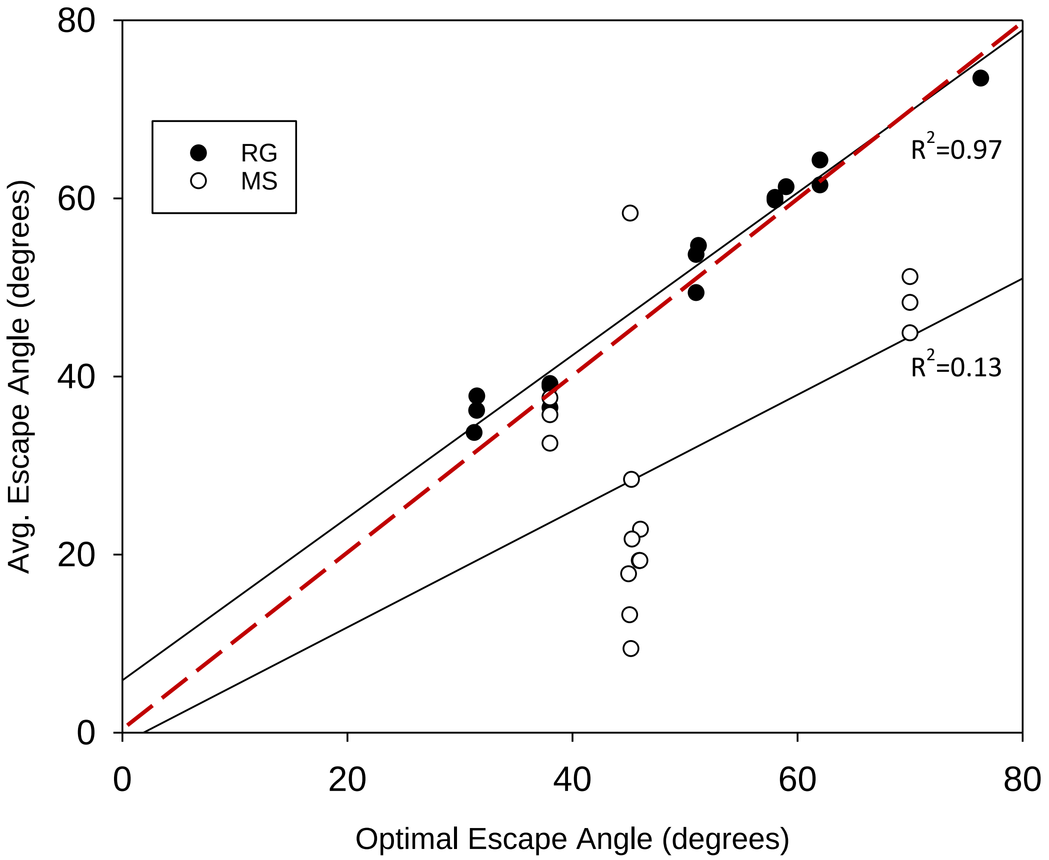

Fig. 5. Comparison of observed and optimal escape angles between round goby (●) and mottled sculpin (○). Red dashed line represents the one-to-one ratio. Optimal angles were calculated using Equation 1 originally from Domenici (2002). A GLM (Normal distribution with Identity link function; tested against 1:1 regression line) was then used to compare the differences in optimal vs. observed escape angles between round gobies and mottled sculpin. Round goby escape angles were not significantly different from the theoretical optimal angles (GLMM: χ^2_{11}=0.031, p=0.91); however, mottled sculpin escape angles were significantly lower than the theoretical optimal (GLMM: χ^2_{11}=14.27, p<0.0001)

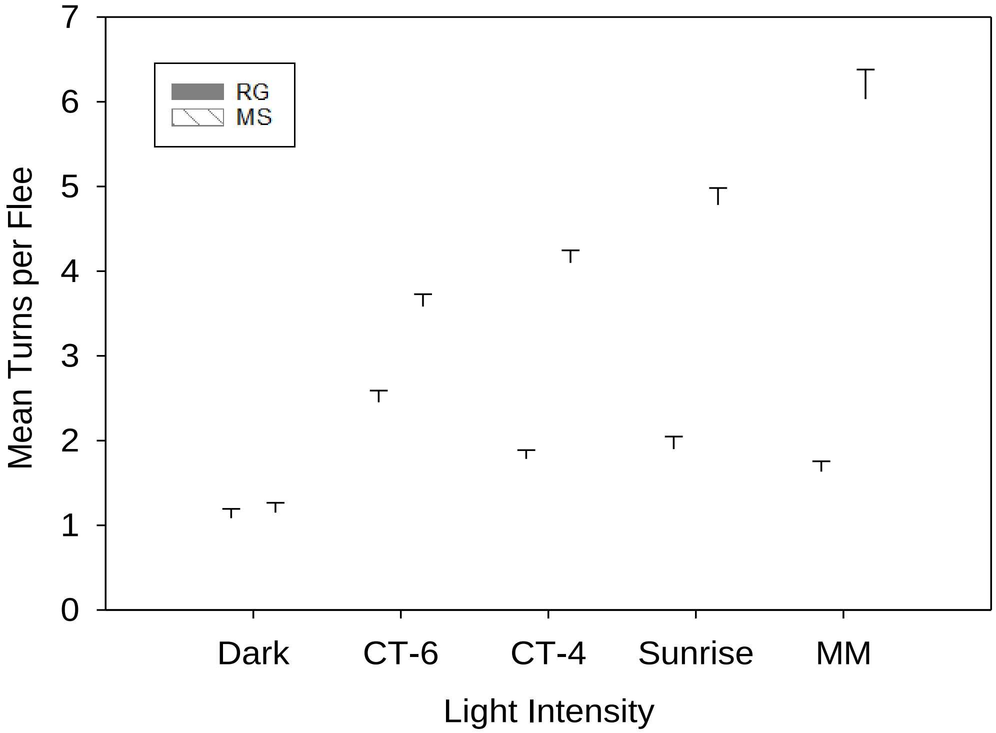

Fig. 6. Number of directional changes performed by round gobies and mottled sculpin while fleeing from predators. Directional changes were defined by angular changes >30° within 0.25 seconds, not counting the escape initiation. A GLM was used to test the effects of light intensity, predator species, and prey species on FID (Poisson distribution with Log link function; tested against light intensity, predator species, trial type (BB, SMB, MIX), prey species, all interactions among light intensity, predator, and prey, as well as time within trial and predator ID as random factors). The predator species did not influence evasiveness (GLM: $\chi^2{}_{17}$=0.883, p=0.43), but light ($\chi^2{}_{17}$=8.158, p=0.0429) and prey species (GLM: $\chi^2{}_{17}$=8.879, p=0.0029) both had separate, significant effects on evasiveness. Error bars represent one standard error.

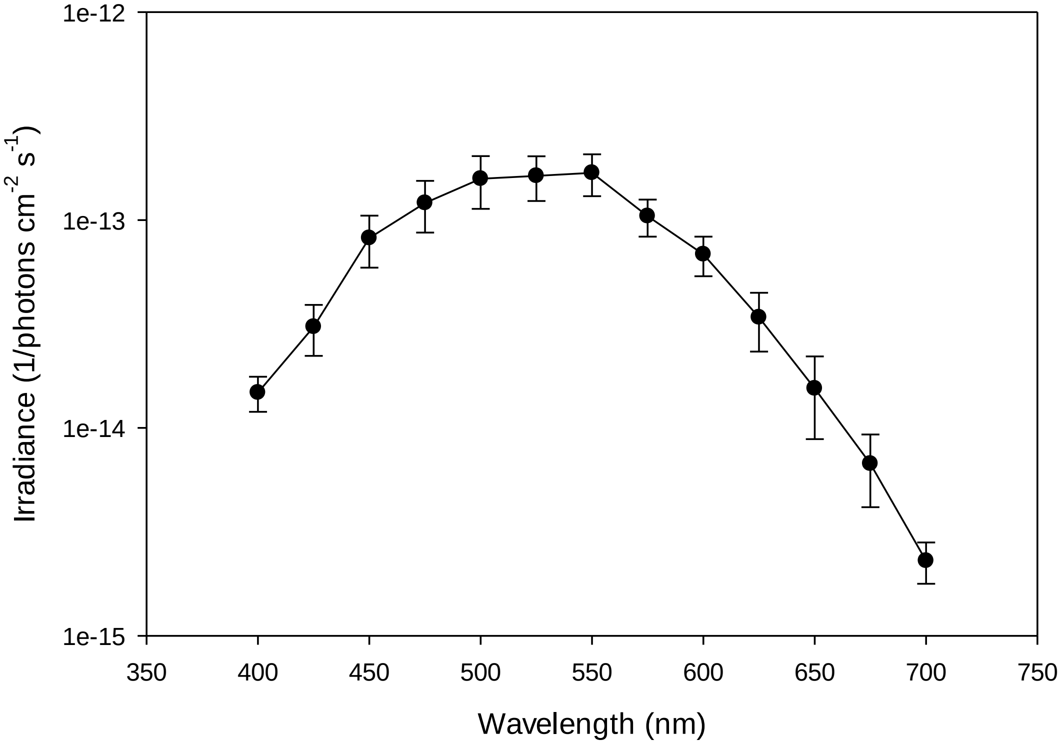

Fig. 7. Average irradiance (1/photons cm^{-2} s^{-1}) needed to invoke the criterion response for adult walleye (*Sander vitreus*) from 400-700 nm. Adult sizes tested ranged from 261-437 mm. Relative spectral sensitivity was tested via electroretinography. Error bars represent ± 1 standard error. n=14.

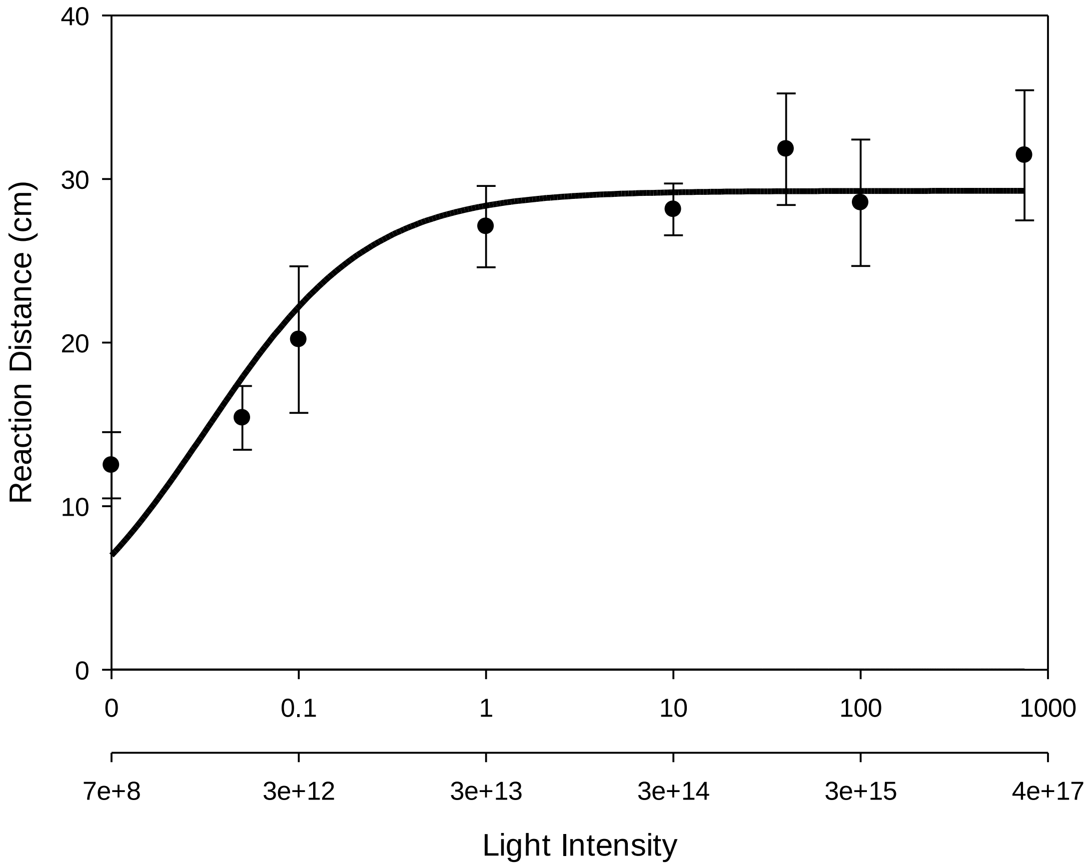

Fig. 8. Average reaction distance of young-of-year walleye (*Sander vitreus*) to fathead minnows (*Pimephales promelas*) at multiple light intensities. Trials spanned 15 minutes with one predator and three prey. A Michaelis-Menten function was fitted with an R_{max} of 29.2726 and an α of 0.0319 (r^2=0.86). The top x-axis is shown as lux, while the bottom axis is shown in photons m^{-2} s^{-1}. Each light intensity had an n=10, and error bars represent ±1 SE.

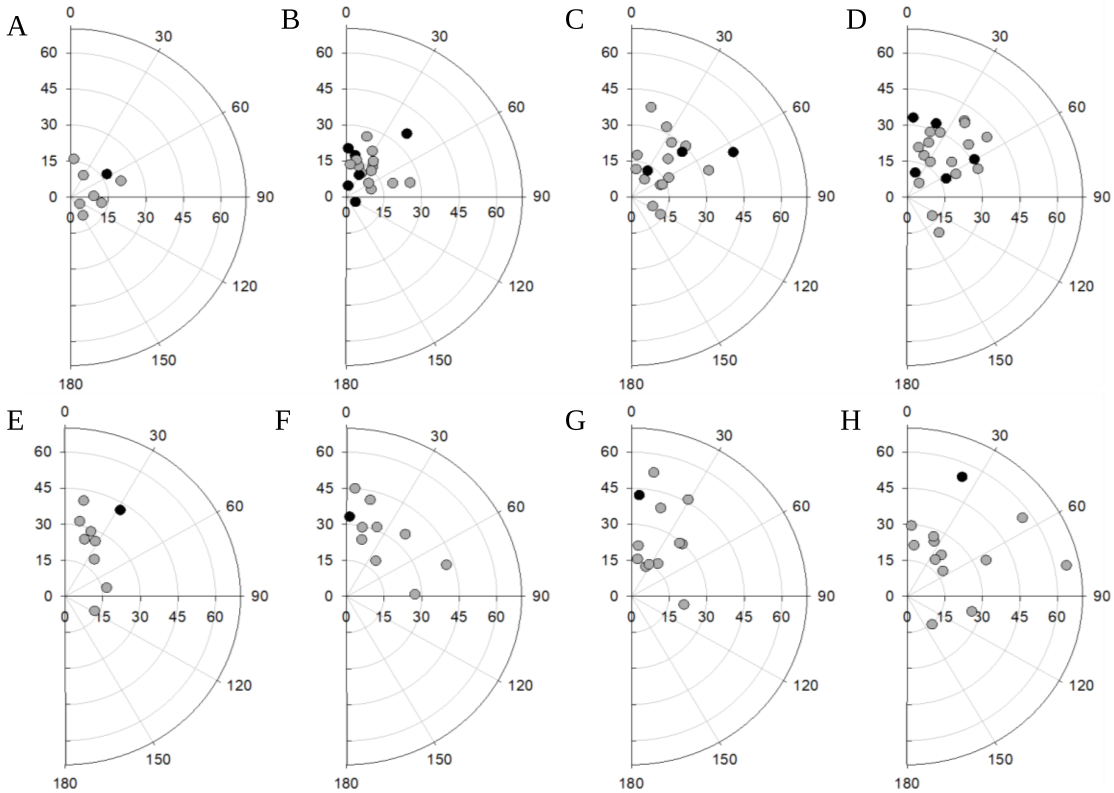

Fig. 9. Young-of-year walleye (*Sander vitreus*) reaction distances and angles to fathead minnows under eight different light intensities. The light intensities are as follows: A) dark, B) nautical twilight, C) civil twilight (-6°), D) civil twilight (-3°), E) sunrise, F) cloudy morning, G) sunny morning, and H) sunny afternoon. Reaction distance (x- and y-axis, measured in cm) was calculated as the distance from the midpoint of the prey's body to the location between the predator's eyes one frame prior to the initiation of a reaction. The reaction angle (circular axis, measured in degrees) was the angle formed between the reaction distance line and the line anterior to the predator's body axis. Grey circles represent reactions, while black circles represent reactions that resulted in a successful capture of prey. Each light intensity included 10 trials, with walleye foraging for 15 minutes.

Concentration	0 mg L^{-}	10 mg L^{-}	20 mg L^{-}
a_{440} value	0.6 m^{-1}	13.8 m^{-1}	28.3 m^{-1}

Fig. 10. Staining levels used in experimental trials and their associated a_{440} value. Staining was created by adding sodium humate ($C_9H_8Na_2O_4$) to the pondwater solution (deionized water, NaCl, KCl, and $CaCl_2 \cdot 2H_20$). Fathead Minnow were added to show differences in appearance due to staining.

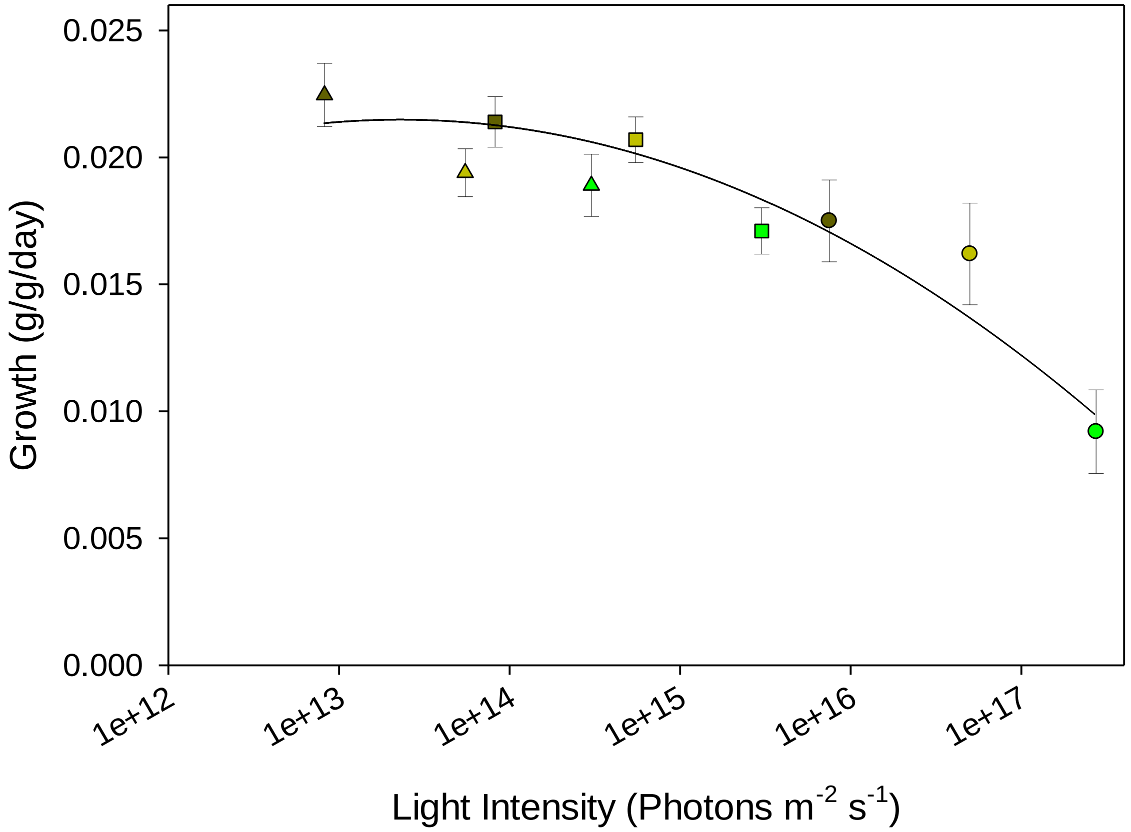

Fig. 11. Wild age-0 Walleye growth compared to light intensity at depth. Temperature was held at 18°C. Light intensity at depth was calculated using the Beer-Lambert equation ($I_z = I_0 e^{-kz}$) with k-values of 0.1 (green), 3.5 (gold), and 7.3 (brown) calculated from spectrophotometry and a depth (z) equal to 0.5 m. Shapes represent the light intensity at the surface of the water with triangles representing 3.16×10^{14}, squares 3.16×10^{15}, and circles 2.88×10^{17} photons m^{-2} s^{-1}. The regression equation was $y_{growth} = -0.0685 + 0.0139x - 0.0005x^2$ with an r^2 of 0.88. Error bars represent ±1 SE.

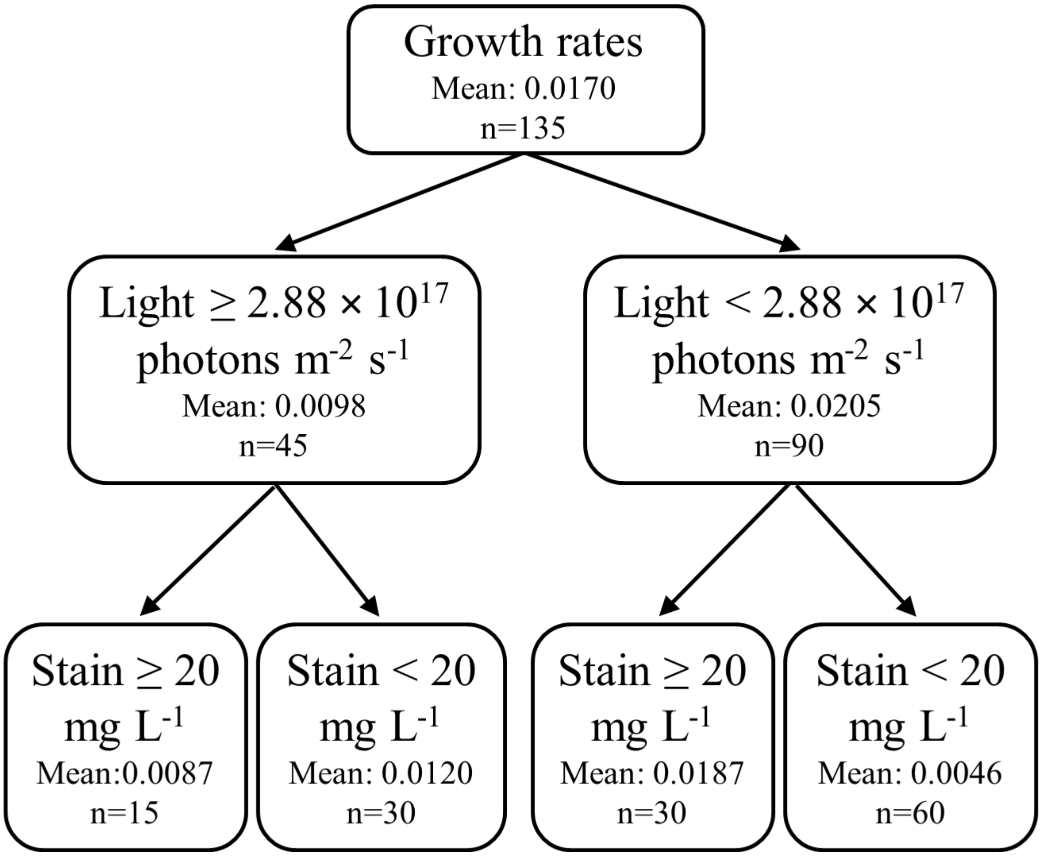

Fig. 12. Dendrogram of wild age-0 Walleye growth rates (g/g/day) produced from the CART model. Variables incorporated were light intensity, staining level, starting total length, starting mass, year class, and fish ID. The dendrogram was grown until additions were < 0.015 to the R^2. Model fit was R^2=0.64 with an AIC of -1088.3.

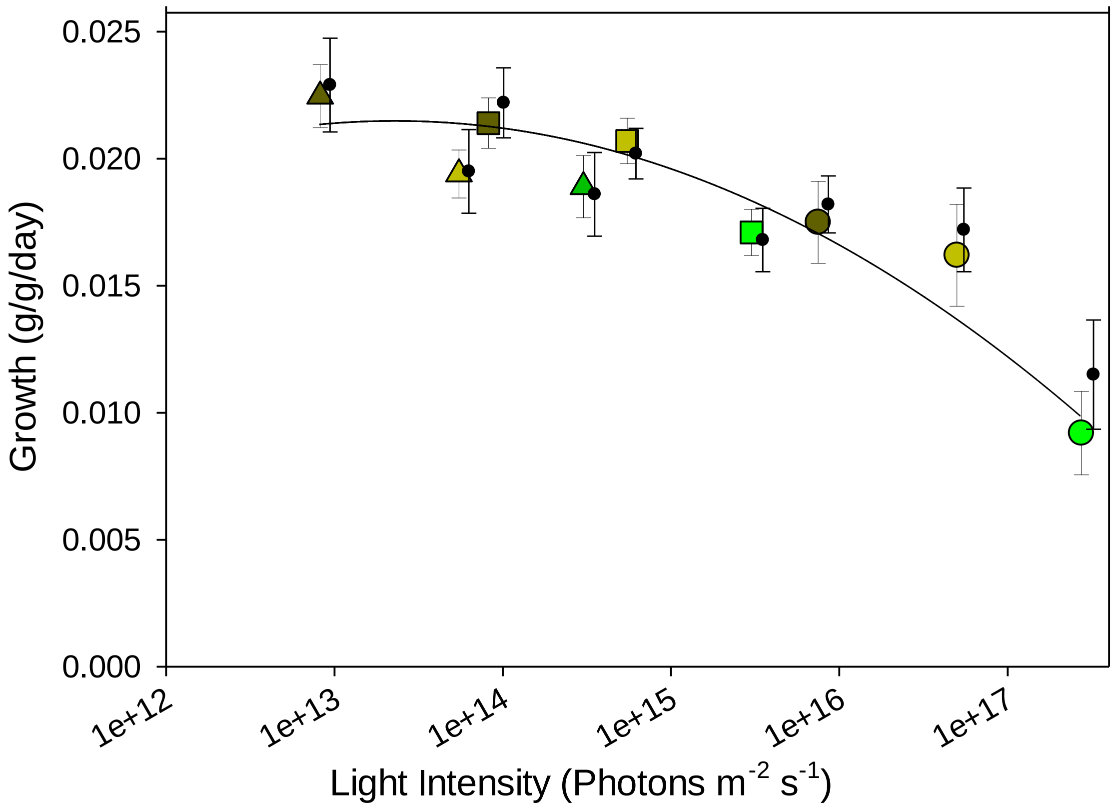

Fig. 13. IBM calibration to empirical growth rates observed in Chapter 4. Light intensity at depth was calculated using the Beer-Lambert equation ($I_z = I_0 e^{-kz}$) with k-values of 0.1 (green), 3.5 (gold), and 7.3 (brown) calculated from spectrophotometry and a depth (z) equal to 0.5 m. Shapes represent the light intensity at the surface of the water with triangles representing 3.16×10^{14}, squares are 3.16×10^{15}, and circles are 2.88×10^{17} photons m^{-2} s^{-1}. The IBM was modified to have constant light intensity at depth with temperature at 18° C to match empirical data. Black dots represent model output average for the scenario. Model results are jittered. Error bars represent ±1 SE.

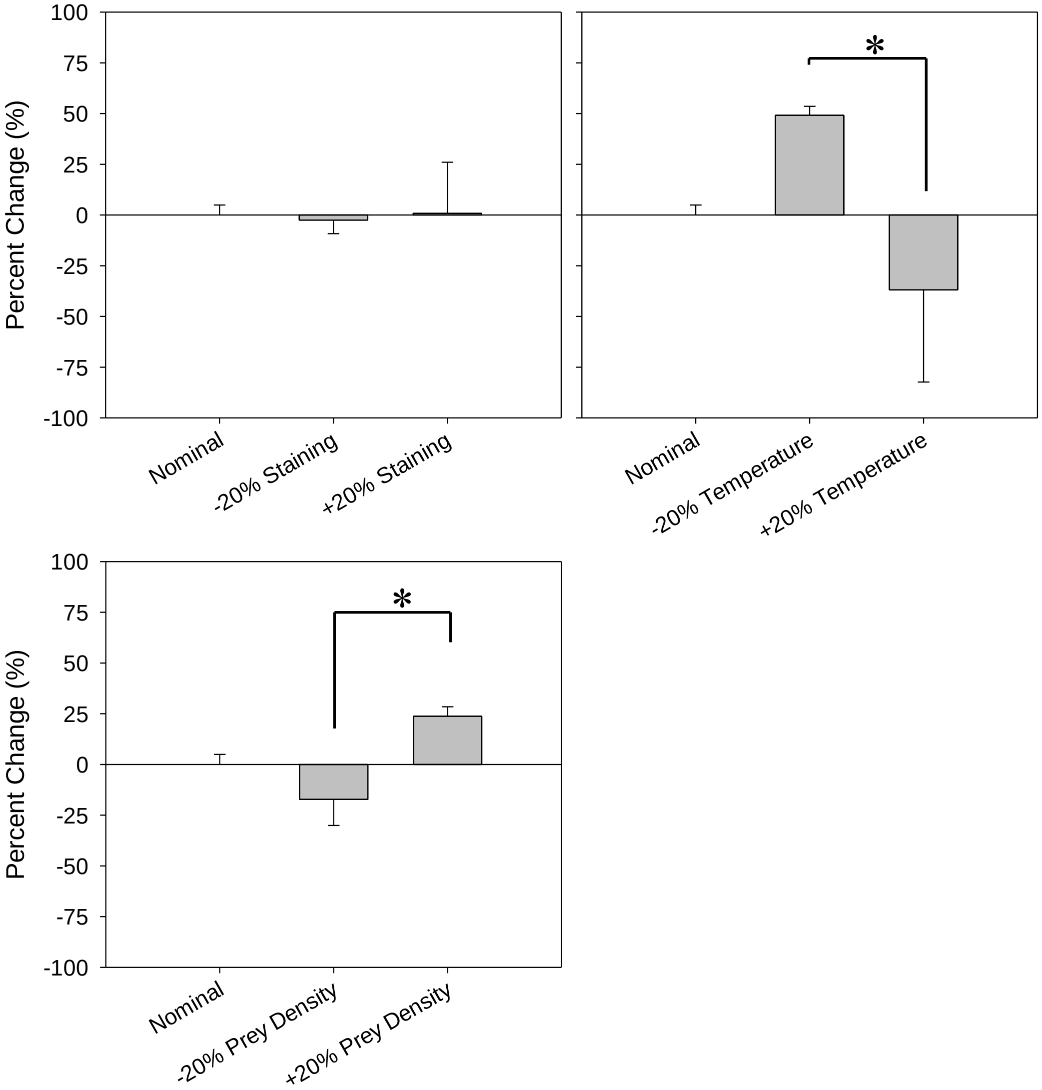

Fig. 14. Model output of the habitat sensitivity analysis for A) light intensity, B) temperature, and C) prey density on YOY walleye growth. Model outputs for ± 20% of the nominal model were compared along with the nominal model (30 prey acre^{-1}, 22°C, k=1.5 for staining level). One-way ANOVAs were run to test for statistical significance within each scenario. Temperature ($F_{2,147} = 4.897$, $p=0.009$) and prey density ($F_{2,147} = 7.445$, $p<0.001$) both had separate, significant effects on walleye growth rates. Light intensity did not affect growth rate ($F_{2,147} = 0.0123$, $p=0.988$). Error bars represent ± 1 SE. Asterisks denote statistical significance at the 0.05 level.

References

Ahrenstorff, T.D., Sass, G.G., and Helmus, M.R. 2009. The influence of littoral zone coarse woody habitat on home range size, spatial distribution, and feeding ecology of largemouth bass (Micropterus salmoides). Hydrobiologia 623(1): 223–233. doi:10.1007/s10750-008-9660-1.

Ali, M., Ryder, R., and Anctil, M. 1977. Photoreceptors and Visual Pigments as Related to Behavioral Responses and Preferred Habitats of Perches (Perca spp.) and Pikeperches (Stizostedion spp.). Journal of the Fisheries Research Board of Canada 34: 1475–1480. doi:10.1139/f77-212.

Ali, M.A., and Anctil, M. 1977. Retinal Structure and Function in the Walleye (Stizostedion vitreum vitreum) and Sauger (S. canadense). J. Fish. Res. Bd. Can. 34(10): 1467–1474. NRC Research Press. doi:10.1139/f77-211.

Auer, S. K., K. Salin, A. M. Rudolf, G. J. Anderson, and N. B. Metcalfe. 2015. The optimal combination of standard metabolic rate and aerobic scope for somatic growth depends on food availability. Functional Ecology 29(4):479–486.

Augustyniak, M., Kołacka, K., Kobak, J., Hliwa, P., Kłosiński, P., Poznańska-Kakareko, M., Jermacz, Ł., Kakareko, T., 2023. Differences in predator-avoidance behavior between two invasive gobies and their native competitors. Current Zoology 69, 727–737. https://doi.org/10.1093/cz/zoac082

Beauchamp, D.A., Baldwin, C.M., Vogel, J.L., and Gubala, C.P. 1999. Estimating diel, depth-specific foraging opportunities with a visual encounter rate model for pelagic piscivores. Canadian Journal of Fisheries and Aquatic Sciences 56(S1): 128–139.

doi:10.1139/cjfas-56-S1-128.

Benfield, M.C., Minello, T.J., 1996. Relative effects of turbidity and light intensity on reactive distance and feeding of an estuarine fish. Environ Biol Fish 46, 211–216. https://doi.org/10.1007/BF00005223

Bergstrom, M.A., Evrard, L.M., Mensinger, A.F., 2008. Distribution, Abundance, and Range of the Round Goby, *Apollina melanostoma*, in the Duluth-Superior Harbor and St. Louis River Estuary, 1998–2004. Journal of Great Lakes Research 34, 535–543. https://doi.org/10.3394/0380-1330(2008)34[535:DAAROT]2.0.CO;2

Bergstrom, M.A., Mensinger, A.F., 2009. Interspecific Resource Competition between the Invasive Round Goby and Three Native Species: Logperch, Slimy Sculpin, and Spoonhead Sculpin. Transactions of the American Fisheries Society 138, 1009–1017. https://doi.org/10.1577/T08-095.1

Boeuf, G., and J. Falcôn. (2001). Photoperiod and growth in fish. Vie Milieu 51 (4):247-266.

Boeuf, G., and P.-Y. Le Bail. 1999. Does light have an influence on fish growth? Aquaculture 177(1–4):129–152.

Borkholder, B. D., and B. G. Parsons. 2001. Relationship between Electrofishing Catch Rates of Age-0 Walleyes and Water Temperature in Minnesota Lakes. North American Journal of Fisheries Management 21(2):318–325.

Bozek, M.A., Baccante, D.A., and Lester, N.P. (2011). Walleye and Sauger Life History.

Braekevelt, C. R., D. B. Mclntyre, and F. J. Ward. (1989). Development of the retinal tapetum lucidum of the Walleye (Stizostedion vitreum vitreum).

Brandt, S. B., D. M. Mason, and E. V. Patrick. 1992. Spatially-explicit Models of Fish Growth Rate. Fisheries 17(2):23–35.

Brezonik, P. L., R. M. Hozalski, and J. C. Finlay. 2019, January 15. Combined UMN-MPCA 2014-2017 lake data on Secchi depth, CDOM, Chlorophyll and total suspended solids.

Bulkowski, L., and J. W. Meade. 1983. Changes in Phototaxis during Early Development of Walleye. Transactions of the American Fisheries Society 112(3):445–447.

Carpenter, S.R., Kitchell, J.F., and Hodgson, J.R. 1985. Cascading Trophic Interactions and Lake Productivity. BioScience 35(10): 634–639. [American Institute of Biological Sciences, Oxford University Press]. doi:10.2307/1309989.

Catania, K.C., 2009. Tentacled snakes turn C-starts to their advantage and predict future prey behavior. Proceedings of the National Academy of Sciences 106, 11183–11187. https://doi.org/10.1073/pnas.0905183106

Caves, E.M., Sutton, T.T., and Johnsen, S. 2017. Visual acuity in ray-finned fishes correlates with eye size and habitat. Journal of Experimental Biology: jeb.151183. doi:10.1242/jeb.151183.

Chu, C., Minns, C.K., Moore, J.E., and Millard, E.S. 2004. Impact of Oligotrophication, Temperature, and Water Levels on Walleye Habitat in the Bay of Quinte, Lake Ontario. Transactions of the American Fisheries Society 133(4): 868–879. Taylor & Francis. doi:10.1577/T03-095.1.

Clarke, A., and N. M. Johnston. 1999. Scaling of metabolic rate with body mass and temperature in teleost fish. Journal of Animal Ecology 68(5):893–905.

Cooper, W.E., Blumstein, D.T., 2015. Escaping From Predators: An Integrative View of Escape Decisions. Cambridge University Press.

Cronin, T.W., Johnsen, S., Marshall, N.J., and Warrant, E.J. 2014. Visual Ecology. Princeton University Press.

Curio, E. 2012. The Ethology of Predation. Springer Science & Business Media.

Daewel, U., Peck, M.A., Schrum, C., 2010. Life history strategy and impacts of environmental variability on early life stages of two marine fishes in the North Sea: an individual-based modeling approach. Can. J. Fish. Aquat. Sci. 68, 426–443.

DeAngelis, D.L., Rose, K.A., Crowder, L.B., Marschall, E.A., Lika, D.l, 1993. Fish cohort dynamics: application of complementary modeling approaches. Am. Nat. 142, 604–622.

DeBoom, C.S., and Wahl, D.H. 2013. Effects of Coarse Woody Habitat Complexity on Predator–Prey Interactions of Four Freshwater Fish Species. Transactions of the American Fisheries Society 142(6): 1602–1614. doi:10.1080/00028487.2013.820219.

Deslauriers, D., Chipps, S. R., Breck, J. E., Rice, J. A., & Madenjian, C. P. 2017. Fish Bioenergetics 4.0: An R-Based Modeling Application. Fisheries, 42: 586–596.

Dill, L.M., 1973. An avoidance learning submodel for a general predation model. Oecologia 13, 291–312.

Dill, L.M., 1974. The escape response of the zebra danio (Brachydanio rerio) II. The effect of experience. Animal Behaviour 22, 723–730. https://doi.org/10.1016/S0003-3472(74)80023-0

Dill, L.M., 1990. Distance-to-cover and the escape decisions of an African cichlid fish, Melanochromis chipokae. Environ Biol Fish 27, 147–152. https://doi.org/10.1007/BF00001944

Domenici, P., 2001. The scaling of locomotor performance in predator–prey encounters: from fish to killer whales. Comparative Biochemistry and Physiology Part A: Molecular & Integrative Physiology 131, 169–182. https://doi.org/10.1016/S1095-6433(01)00465-2

Domenici, P., 2002. The Visually Mediated Escape Response in Fish: Predicting Prey Responsiveness and the Locomotor Behaviour of Predators and Prey. Marine and Freshwater Behaviour and Physiology 35, 87–110. https://doi.org/10.1080/10236240290025635

Domenici, P., Batty, R.S., 1994. Escape manoeuvres of schooling Clupea harengus. Journal of Fish Biology 45, 97–110. https://doi.org/10.1111/j.1095-8649.1994.tb01086.x

Domenici, P., Batty, R.S., 1997. Escape behaviour of solitary herring (Clupea harengus) and comparisons with schooling individuals. Marine Biology 128, 29–38. https://doi.org/10.1007/s002270050065

Domenici, P., Blagburn, J.M., Bacon, J.P., 2011. Animal escapology I: theoretical issues and emerging trends in escape trajectories. Journal of Experimental Biology 214, 2463–2473. https://doi.org/10.1242/jeb.029652

Domenici, P., Blake, R.W., 1993. Escape trajectories in angelfish (Pterophyllum eimekei). Journal of Experimental Biology 177, 253–272.

Domenici, P., Wilson, A.D.M., Kurvers, R.H.J.M., Marras, S., Herbert-Read, J.E., Steffensen, J.F., Krause, S., Viblanc, P.E., Couillaud, P., Krause, J., 2014. How sailfish use their bills to capture schooling prey. Proceedings of the Royal Society B: Biological Sciences 281, 20140444. https://doi.org/10.1098/rspb.2014.0444

Downing, G., and M. K. Litvak. 1999. The Influence of Light Intensity on Growth of Larval Haddock. North American Journal of Aquaculture 61(2):135–140.

Dubs, D.O.L., Corkum, L.D., 1996. Behavioral Interactions Between Round Gobies (Neogobius melanostomus) and Mottled Sculpins (Cottus bairdi). Journal of Great Lakes Research 22, 838–844. https://doi.org/10.1016/S0380-1330(96)71005-5

Eaton, R.C., Emberley, D.S., 1991. How stimulus direction determines the trajectory of the Mauthner-initiated escape response in a teleost fish. Journal of Experimental Biology 161, 469–487.

Eaton, R.C., Lee, R.K.K., Foreman, M.B., 2001. The Mauthner cell and other identified neurons of the brainstem escape network of fish. Progress in Neurobiology 63, 467–485. https://doi.org/10.1016/S0301-0082(00)00047-2

Effler, S.W., Perkins, M., Peng, F., Strait, C., Weidemann, A.D., and Auer, M.T. 2010. Light-absorbing components in Lake Superior. Journal of Great Lakes Research 36(4): 656–665. doi:10.1016/j.jglr.2010.08.001.

Einfalt, L.M., and Wahl, D.H. 1997. Prey selection by juvenile walleye as influenced by prey morphology and behavior. Can. J. Fish. Aquat. Sci. 54(11): 2618–2626. doi:10.1139/f97-172.

Einfalt, L.M., Grace, E.J., and Wahl, D.H. 2012. Effects of simulated light intensity, habitat complexity and forage type on predator–prey interactions in walleye Sander vitreus. Ecology of Freshwater Fish 21(4): 560–569. doi:10.1111/j.1600-0633.2012.00576.x.

Fahnenstiel, G.L., Schelske, C.L., and Moll, R.A. 1984. In Situ Quantum Efficiency of Lake Superior Phytoplankton. Journal of Great Lakes Research 10(4): 399–406. doi:10.1016/S0380-1330(84)71856-9.

Fox, M. G., & Flowers, D. D. 1990. Effect of Fish Density on Growth, Survival, and Food Consumption by Juvenile Walleyes in Rearing Ponds. Transactions of the American Fisheries Society, 119: 112–121.

Fuiman, L.A., 1993. Development of predator evasion in Atlantic herring, Clupea harengus L. Animal Behaviour 45, 1101–1116. https://doi.org/10.1006/anbe.1993.1135

Fuiman, L.A., Magurran, A.E., 1994. Development of predator defences in fishes. Rev Fish Biol Fisheries 4, 145–183. https://doi.org/10.1007/BF00044127

Fuiman, L.A., Rose, K.A., Cowan, J.H., Smith, E.P., 2006. Survival skills required for predator evasion by fish larvae and their relation to laboratory measures of performance. Animal Behaviour 71, 1389–1399. https://doi.org/10.1016/j.anbehav.2005.11.013

Gerritsen, J., Strickler, J., 1977. Encounter probabilities and community structure in zooplankton: a mathematical model. J. Fish. Res. Board Can. 34, 73–82.

Gill, A.B., and Hart, P.J.B. 1998. Stomach capacity as a directing factor in prey size selection of three-spined stickleback. Journal of Fish Biology 53(4): 897–900. doi:10.1111/j.1095-8649.1998.tb01844.x.

Godin, J.-G.J. 1997. Behavioural ecology of fishes: adaptations for survival and reproduction. Behavioural Ecology of Teleost Fishes: 1–9. Oxford University Press New York.

Grant, J.W.A., Noakes, D.L.G., 1987. Escape Behaviour and Use of Cover by Young-of-the-Year Brook Trout, Salvelinus fontinalis. Can. J. Fish. Aquat. Sci. 44, 1390–1396. https://doi.org/10.1139/f87-167

Hansen, A.G., Beauchamp, D.A., and Schoen, E.R. 2013. Visual Prey Detection Responses of Piscivorous Trout and Salmon: Effects of Light,Turbidity,and Prey Size. Trans Am Fish Soc 142(3): 854–867. doi:10.1080/00028487.2013.785978.

Hansen, G. J. A., L. A. Winslow, J. S. Read, M. Treml, P. J. Schmalz, and S. R. Carpenter. 2019. Water clarity and temperature effects on Walleye safe harvest: an empirical test of the safe operating space concept. Ecosphere 10(5):e02737.

Hanych, D.A., Ross, M.R., Magnien, R.E., Suggars, A.L., 1983. Nocturnal Inshore Movement of the Mimic Shiner (Notropis volucellus): a Possible Predator Avoidance Behavior. Can. J. Fish. Aquat. Sci. 40, 888–894. https://doi.org/10.1139/f83-115

Harper, D.G., Blake, R.W., 1991. Prey Capture and the Fast-Start Performance of Northern Pike Esox Lucius. Journal of Experimental Biology 155, 175–192.

Harrington, K.A., Hrabik, T.R., and Mensinger, A.F. 2015. Visual Sensitivity of Deepwater Fishes in Lake Superior. PLoS One 10(2). doi:10.1371/journal.pone.0116173.

Hartman, K. J., and F. J. Margraf. 1992. Effects of Prey and Predator Abundances on Prey Consumption and Growth of Walleyes in Western Lake Erie. Transactions of the

American Fisheries Society 121(2):245–260.

Hayes, D., Jones, M., Lester, N., Chu, C., Doka, S., Netto, J., Stockwell, J., Thompson, B., Minns, C.K., Shuter, B., Collins, N., 2009. Linking fish populations dynamics to habitat conditions: insights from the application of a process-oriented approach to several Great Lakes species. Rev. Fish Biol. Fish. 19, 295–312.

Helfman, G.S., 1981. Twilight Activities and Temporal Structure in a Freshwater Fish Community. Can. J. Fish. Aquat. Sci. 38, 1405–1420. https://doi.org/10.1139/f81-187

Helfman, G.S., 1986. Fish Behaviour by Day, Night and Twilight, in: Pitcher, T.J. (Ed.), The Behaviour of Teleost Fishes. Springer US, Boston, MA, pp. 366–387. https://doi.org/10.1007/978-1-4684-8261-4_14

Helfman, G.S., 1993. Fish Behavior by day, night and twilight, in: Behavior of Teleost Fishes. Chapman & Hall, London, pp. 479–512.

Herbert-Read, J.E., Ward, A.J.W., Sumpter, D.J.T., Mann, R.P., 2017. Escape path complexity and its context dependency in Pacific blue-eyes (*Pseudomugil signifer*). The Journal of Experimental Biology 220, 2076–2081. https://doi.org/10.1242/jeb.154534

Herbst, S.J., Roth, B.M., Hayes, D.B., and Stockwell, J.D. 2016. Walleye Foraging Ecology in an Interconnected Chain of Lakes Influenced by Nonnative Species. Transactions of the American Fisheries Society 145(2): 319–333. doi:10.1080/00028487.2015.1121924.

Hoekstra, D., Janssen, J., 1985. Non-visual feeding behavior of the mottled sculpin, Cottus bairdi, in Lake Michigan. Environ Biol Fish 12, 111–117.

https://doi.org/10.1007/BF00002763

Hokanson, K.E.F. 1977. Temperature Requirements of Some Percids and Adaptations to the Seasonal Temperature Cycle. J. Fish. Res. Bd. Can. 34(10): 1524–1550. NRC Research Press. doi:10.1139/f77-217.

Holbrook, B.V., Hrabik, T.R., Branstrator, D.K., and Mensinger, A.F. 2013. Foraging mechanisms of age-0 lake trout (Salvelinus namaycush). Journal of Great Lakes Research 39(1): 128–137. doi:10.1016/j.jglr.2012.12.008.

Howick, G.L., and O'Brien, W.J. 1983. Piscivorous Feeding Behavior of Largemouth Bass: An Experimental Analysis. Transactions of the American Fisheries Society 112(4): 508–516. doi:10.1577/1548-8659(1983)112<508:PFBOLB>2.0.CO;2.

Hrabik, T. R., Roth, B. M., & Ahrenstorff, T. 2014. Predation risk and prey fish vertical migration in Lake Superior: Insights from an individual based model of siscowet (Salvelinus namaycush). Journal of Great Lakes Research, 40: 730–738.

Hrabik, T.R., Jensen, O.P., Martell, S.J.D., Walters, C.J., Kitchell, J.F., 2006. Diel vertical migration in the Lake Superior pelagic community. I. Changes in vertical migration of coregonids in response to varying predation risk. Can. J. Fish. Aquat. Sci. 63, 2286–2295. https://doi.org/10.1139/f06-124

Huh, H. T., H. E. Calbert, and D. A. Stuiber. 1976. Effects of Temperature and Light on Growth of Yellow Perch and Walleye Using Formulated Feed. Transactions of the American Fisheries Society 105(2):254–258.

Hurley, A.C., Hartline, P.H., 1974. Escape response in the damselfish Chromis cyanea (Pisces: Pomacentridae): A quantitative study. Animal Behaviour 22, 430–437.

https://doi.org/10.1016/S0003-3472(74)80041-2

Hutchinson, G.E. 1957. A Treatise on Limnology VOLUME II INTRODUCTION TO LAKE BIOLOGY AND THE LIMNOPLANKTON. Limnology.

Janssen, J., Jude, D.J., 2001. Recruitment Failure of Mottled Sculpin Cottus bairdi in Calumet Harbor, Southern Lake Michigan, Induced by the Newly Introduced Round Goby Neogobius melanostomus. Journal of Great Lakes Research 27, 319–328. https://doi.org/10.1016/S0380-1330(01)70647-8

Johnsen, S. 2012. The Optics of Life: A Biologist's Guide to Light in Nature. Princeton University Press.

Johnston, T. A., & Mathias, J. A. 1996. Gut evacuation and absorption efficiency of walleye larvae. Journal of Fish Biology, 49: 375–389.

Johnston, T. A., W. Lysack, and W. C. Leggett. 2012. Abundance, growth, and life history characteristics of sympatric Walleye (Sander vitreus) and Sauger (Sander canadensis) in Lake Winnipeg, Manitoba. Journal of Great Lakes Research 38:35–46.

Jones, M.L., Shuter, B.J., Zhao, Y., and Stockwell, J.D. 2006. Forecasting effects of climate change on Great Lakes fisheries: models that link habitat supply to population dynamics can help. Can. J. Fish. Aquat. Sci. 63(2): 457–468. doi:10.1139/f05-239.

Karplus, I., Algom, D., 1981. Visual Cues for Predator Face Recognition by Reef Fishes. Zeitschrift für Tierpsychologie 55, 343–364. https://doi.org/10.1111/j.1439-0310.1981.tb01277.x

Kerfoot, W.C., and Sih, A. 1987. Predation: Direct and Indirect Impacts on Aquatic Communities. University Press of New England.

Keyler, T.D., Hrabik, T.R., Austin, C.L., Gorman, O.T., and Mensinger, A.F. 2015. Foraging mechanisms of siscowet lake trout (Salvelinus namaycush siscowet) on pelagic prey. Journal of Great Lakes Research 41(4): 1162–1171. doi:10.1016/j.jglr.2015.09.016.

Keyler, T.D., Hrabik, T.R., Mensinger, A.F., Rogers, L.S., and Gorman, O.T. 2019. Effect of light intensity and substrate type on siscowet lake trout (Salvelinus namaycush siscowet) predation on deepwater sculpin (Myoxocephalus thompsonii). Hydrobiologia 840(1): 77–88. doi:10.1007/s10750-019-3944-5.

Kimura, H., Kawabata, Y., 2018. Effect of initial body orientation on escape probability of prey fish escaping from predators. Biology Open 7, bio023812. https://doi.org/10.1242/bio.023812

Kishida, Y.A. 1989. Changes in light intensity at twilight and estimation of the biological photoperiod. Japan Agr. Res. Qrtly 1(22): 247–252.

Kitchell, J. F., D. J. Stewart, and D. Weininger. 1977. Applications of a bioenergetics model to Yellow Perch (Perca flavescens) and Walleye (Stizostedion vitreum vitreum). Journal of the Fisheries Research Board of Canada 34:1922–1935.

Koenst, W.M., and Smith Jr., L.L. 1976. Thermal Requirements of the Early Life History Stages of Walleye, Stizostedion vitreum vitreum, and Sauger, Stizostedion canadense. J. Fish. Res. Bd. Can. 33(5): 1130–1138. NRC Research Press. doi:10.1139/f76-141.

Kornis, M.S., Mercado-Silva, N., Zanden, M.J.V., 2012. Twenty years of invasion: a review of round goby Neogobius melanostomus biology, spread and ecological implications. Journal of Fish Biology 80, 235–285. https://doi.org/10.1111/j.1095-

8649.2011.03157.x

Krause, J., Godin, J.-G.J., 1995. Predator preferences for attacking particular prey group sizes: consequences for predator hunting success and prey predation risk. Animal Behaviour 50, 465–473. https://doi.org/10.1006/anbe.1995.0260

Langerhans, R.B., 2009. Morphology, performance, fitness: functional insight into a post-Pleistocene radiation of mosquitofish. Biol Lett 5, 488–491. https://doi.org/10.1098/rsbl.2009.0179

Lester, N.P., Dextrase, A.J., Kushneriuk, R.S., Rawson, M.R., and Ryan, P.A. 2004. Light and Temperature: Key Factors Affecting Walleye Abundance and Production. Transactions of the American Fisheries Society 133(3): 588–605. doi:10.1577/T02-111.1.

Lima, S.L., Dill, L.M., 1990. Behavioral decisions made under the risk of predation: a review and prospectus. Can. J. Zool. 68, 619–640. https://doi.org/10.1139/z90-092

Loennstedt, O.M., McCormick, M.I., 2015. Damsel in distress: captured damselfish prey emit chemical cues that attract secondary predators and improve escape chances. Proc. R. Soc. B-Biol. Sci. 282, 20152038. https://doi.org/10.1098/rspb.2015.2038

Lorenzen, K. 2016. Toward a new paradigm for growth modeling in fisheries stock assessments: Embracing plasticity and its consequences. Fisheries Research 180:4–22.

Luecke, C., O’Brien, W.J., 1981. Prey Location Volume of a Planktivorous Fish: A New Measure of Prey Vulnerability. Can. J. Fish. Aquat. Sci. 38, 1264–1270. https://doi.org/10.1139/f81-168

Lundvall, D., Svanbäck, R., Persson, L., and Byström, P. 1999. Size-dependent predation in piscivores: interactions between predator foraging and prey avoidance abilities. Canadian Journal of Fisheries and Aquatic Sciences 56(7): 1285–1292. doi:10.1139/cjfas-56-7-1285.

Madenjian, C. P., Hayden, T. A., Peat, T. B., Vandergoot, C. S., Fielder, D. G., Gorman, A. M., Pothoven, S. A., Dettmers, J. M., Cooke, S. J., Zhao, Y., & Krueger, C. C. 2018. Temperature regimes, growth, and food consumption for female and male adult walleye in Lake Huron and Lake Erie: a bioenergetics analysis. Canadian Journal of Fisheries and Aquatic Sciences, 75: 1573–1586.

Madon, S. P., and D. A. Culver. 1993. Bioenergetics model for larval and juvenile Walleyes: an in situ approach with experimental ponds. Transactions of the American Fisheries Society 122:797–813.

Maes, J., Limburg, K.E., Van De Putte, A., Ollevier, F., 2005. A spatially explicit, individualbased model to assess the role of estuarine nurseries in the early life history of North Sea herring, Clupea harengus. Fish. Oceanogr. 14, 17–31.

Magurran, A.E. 1990. The adaptive significance of schooling as an anti-predator defence in fish. Annales Zoologici Fennici 27(2): 51–66. Finnish Zoological and Botanical Publishing Board.

Mahlum, S., Vitense, K., Corson-Dosch, H., Platt, L., Read, J.S., Schmalz, P.J., Treml, M., and Hansen, G.J.A. 2023. Connecting habitat to species abundance: the role of light and temperature on the abundance of walleye in lakes. Can. J. Fish. Aquat. Sci. 80(2): 273–286. doi:10.1139/cjfas-2022-0109.

Major, P.F., 1978. Predator-prey interactions in two schooling fishes, Caranx ignobilis and Stolephorus purpureus. Animal Behaviour 26, 760–777. https://doi.org/10.1016/0003-3472(78)90142-2

Manatunge, J., and Asaeda, T. (1999). Optimal foraging as the criteria of prey selection by two centrarchid fishes.

Marchinko, K.B., 2009. Predation's Role in Repeated Phenotypic and Genetic Divergence of Armor in Threespine Stickleback. Evolution 63, 127–138. https://doi.org/10.1111/j.1558-5646.2008.00529.x

Martel, G., Dill, L.M., 1995. Influence of Movement by Coho Salmon (Oncorhynchus kisutch) Parr on Their Detection by Common Mergansers (Mergus merganser). Ethology 99, 139–149. https://doi.org/10.1111/j.1439-0310.1995.tb01095.x

Mason, D. M., & Patrick, E. V. 1993. A Model for the Space–Time Dependence of Feeding for Pelagic Fish Populations. Transactions of the American Fisheries Society, 122: 884–901.

Mason, D. M., Johnson, T. B., & Kitchell, J. F. 1998. Consequences of prey fish community dynamics on lake trout (*Salvelinus namaycush*) foraging efficiency in Lake Superior. Canadian Journal of Fisheries and Aquatic Sciences, 55: 1273–1284.

Mazur, M.M., Beauchamp, D.A., 2003. A comparison of Visual Prey Detection Among Species of Piscivorous Salmonids: Effects of Light and Low Turbidities. Environmental Biology of Fishes 67, 397–405. https://doi.org/10.1023/A:1025807711512

McCormick, M.I., Allan, B.J.M., Harding, H., Simpson, S.D., 2018. Boat noise impacts risk assessment in a coral reef fish but effects depend on engine type. Sci Rep 8, 3847. https://doi.org/10.1038/s41598-018-22104-3

McIntyre, D. B. 1987. Changes in Feeding Behaviour and the Occurrence of Cannibalism in the Early Life History of Walleye (Stizostedion vitreum vitreum). University of Manitoba.

McLean, E.B., Godin, J.-G.J., n.d. Distance to Cover and Fleeing from Predators in Fish with Different Amounts of Defensive Armour. Oikos 55.

Meerbeek, J.R., Larscheid, J.G., Hawkins, M.J., and Scholten, G.D. 2013. Retention of Large-Format, Soft Visible Implant Alphanumeric Tags in Walleye. N American J Fish Manag 33(1): 26–31. doi:10.1080/02755947.2012.739984.

Metcalfe, B.W. 2006. Influence of Light Intensity on Activity and Habitat Utilization of Walleye {Sander vitreus) in Two Northwestern Ontario Lakes. Master's Thesis, Lakehead University, Thunder Bay, Ontario.

Michels, N.O., Hrabik, T.R., and Mensinger, A.F. 2021. Comparison of Multipiscivore Foraging Success on Native and Invasive Prey Fish under Variable Light Intensities. Transactions of the American Fisheries Society 150(3): 361–374. doi:10.1002/tafs.10293.

Mills, E. L., Pol, M. V., Sherman, R. E., & Culver, T. B. 1989. Interrelationships Between Prey Body Size and Growth of Age-0 Yellow Perch. Transactions of the American Fisheries Society, 118: 1–10.

Miner, J.G., and Stein, R.A. 1996. Detection of Predators and Habitat Choice by Small Bluegills: Effects of Turbidity and Alternative Prey. Transactions of the American Fisheries Society 125(1): 97–103. doi:10.1577/1548-8659(1996)125<0097:DOPAHC>2.3.CO;2.

Moles, M. D., B. W. Robinson, T. A. Johnston, R. A. Cunjak, T. D. Jardine, J. M. Casselman, and W. C. Leggett. 2010. Morphological and trophic differentiation of growth morphotypes of Walleye (Sander vitreus) from Lake Winnipeg, Canada. Canadian Journal of Zoology 88(10):950–960.

Moore, G.A. 1944. The retinae of two north American teleosts, with special reference to their tapeta lucida. J. Comp. Neurol. 80(3): 369–379. doi:10.1002/cne.900800306.

Munz, F.W., and McFarland, W.N. 1973. The significance of spectral position in the rhodopsins of tropical marine fishes. Vision Research 13(10): 1829-IN1. doi:10.1016/0042-6989(73)90060-6.

Nair, A., Changsing, K., Stewart, W.J., McHenry, M.J., 2017a. Fish prey change strategy with the direction of a threat. Proceedings of the Royal Society B: Biological Sciences 284, 20170393. https://doi.org/10.1098/rspb.2017.0393

Nair, A., Nguyen, C., McHenry, M.J., 2017b. A faster escape does not enhance survival in zebrafish larvae. Proc. R. Soc. B-Biol. Sci. 284, 20170359. https://doi.org/10.1098/rspb.2017.0359

Neill, S.R.J., Cullen, J.M., 1974. Experiments on whether schooling by their prey affects the hunting behaviour of cephalopods and fish predators. Journal of Zoology 172, 549–569. https://doi.org/10.1111/j.1469-7998.1974.tb04385.x

Nieman, C.L., and Gray, S.M. 2019. Visual performance impaired by elevated sedimentary and algal turbidity in walleye Sander vitreus and emerald shiner Notropis atherinoides. Journal of Fish Biology 95(1): 186–199. doi:10.1111/jfb.13878.

O'Brien, W.J., 1979. The Predator-Prey Interaction of Planktivorous Fish and Zooplankton: Recent research with planktivorous fish and their zooplankton prey shows the evolutionary thrust and parry of the predator-prey relationship. American Scientist 67, 572–581.

Ollivier, F.J., Samuelson, D.A., Brooks, D.E., Lewis, P.A., Kallberg, M.E., and Komáromy, A.M. 2004. Comparative morphology of the tapetum lucidum (among selected species). Veterinary Ophthalmology 7(1): 11–22. doi:10.1111/j.1463-5224.2004.00318.x.

Osborn, J.C. (2008). Effects of Light and Turbidity on Foraging Efficiency of Larval Walleye Sander Vitreus.

Ota, D., Francese, M., Ferrero, E.A., 1999. Vision in the grass goby, Zosterisessor ophiocephalus (Teleostei, Gobiidae): A morphological and behavioural study. Italian Journal of Zoology 66, 125–139. https://doi.org/10.1080/11250009909356247

Otto, R. G., & Rice, J. O. 1974. Swimming Speeds of Yellow Perch (*Perca flavescens*) Following an Abrupt Change in Environmental Temperature. Journal of the Fisheries Research Board of Canada, 31: 1731–1734.

Paccard, A., Wasserman, B.A., Hanson, D., Astorg, L., Durston, D., Kurland, S., Apgar, T.M., El-Sabaawi, R.W., Palkovacs, E.P., Hendry, A.P., Barrett, R.D.H., 2018. Adaptation in temporally variable environments: stickleback armor in periodically breaching bar-built estuaries. Journal of Evolutionary Biology 31, 735–752. https://doi.org/10.1111/jeb.13264

Peake, S., McKinley, R. S., & Scruton, D. A. 2000. Swimming performance of walleye (Stizostedion vitreum). Canadian Journal of Zoology, 78.

Pedersen, E. J., D. Goto, J. W. Gaeta, G. J. A. Hansen, G. G. Sass, M. J. Vander Zanden, T. A. Cichosz, and A. L. Rypel. 2018. Long-term growth trends in northern Wisconsin Walleye populations under changing biotic and abiotic conditions. Canadian Journal of Fisheries and Aquatic Sciences 75(5):733–745.

Pennuto, C.M., Mehler, K., Weidel, B., Lantry, B.F., Bruestle, E., 2021. Dynamics of the seasonal migration of Round Goby (Neogobius melanostomus, Pallas 1814) and implications for the Lake Ontario food web. Ecology of Freshwater Fish 30, 151–161. https://doi.org/10.1111/eff.12568

Pitcher, T.J., Turner, J.R., 1986. Danger at dawn: experimental support for the twilight hypothesis in shoaling minnows. Journal of Fish Biology 29, 59–70. https://doi.org/10.1111/j.1095-8649.1986.tb04999.x

Post, J. R., & McQueen, D. J. 1994. Variability in First-Year Growth of Yellow Perch (*Perca flavescens*): Predictions from a Simple Model, Observations, and an Experiment. Canadian Journal of Fisheries and Aquatic Sciences, 51: 2501–2512.

Pothier, F., and Ali, M.A. 1978. [Scotopic visual pigments in 3 Percidae: Perca flavescens, Stizostedion vitreum and S. canadense]. Rev Can Biol 37(2): 91–100.

Raabe, J.K., VanDeHey, J.A., Zentner, D.L., Cross, T.K., and Sass, G.G. 2020. Walleye inland lake habitat: considerations for successful natural recruitment and stocking in North Central North America. Lake and Reservoir Management 36(4): 335–359. doi:10.1080/10402381.2019.1697771.

Radabaugh, D.C., 1989. Seasonal colour changes and shifting antipredator tactics in darters. Journal of Fish Biology 34, 679–685. https://doi.org/10.1111/j.1095-8649.1989.tb03349.x

Rahel, F.J., Stein, R.A., 1988. Complex predator-prey interactions and predator intimidation among crayfish, piscivorous fish, and small benthic fish. Oecologia 75, 94–98. https://doi.org/10.1007/BF00378819

Railsback, S., Lamberson, R., Harvey, B., & Duffy, H. 1999. Movement rules for individual-based models of stream fish. Ecological Modelling, 123: 73–89.

Ranaker, L., Persson, J., Jonsson, M., Nilsson, P.A., Bronmark, C., 2014. Piscivore-Prey Fish Interactions: Mechanisms behind Diurnal Patterns in Prey Selectivity in Brown and Clear Water. PLoS One 9, e102002. https://doi.org/10.1371/journal.pone.0102002

Rand, P. S., B. F. Lantry, R. O˙Gorman, R. W. Owens, and D. J. Stewart. 1994. Energy Density and Size of Pelagic Prey Fishes in Lake Ontario, 1978–1990: Implications for Salmonine Energetics. Transactions of the American Fisheries Society 123(4):519–534.

Rice, J. A., J. E. Breck, S. M. Bartell, and J. F. Kitchell. 1983. Evaluating the constraints of temperature, activity and consumption on growth of largemouth bass. Environmental Biology of Fishes 9(3–4):263–275.

Rice, J.A., Miller, T.J., Rose, K.A., Crowder, L.B., Marschall, E.A., Trebitz, A.S., et al., 1993. Growth rate variation and larval survival: inferences from an individual-based size dependent predation model. Can. J. Fish. Aquat. Sci. 50, 133–142.

Richmond, H.E., Hrabik, T.R., and Mensinger, A.F. 2004. Light intensity, prey detection and foraging mechanisms of age 0 year yellow perch. Journal of Fish Biology 65(1): 195–205. doi:10.1111/j.0022-1112.2004.00444.x.

Rose, K.A., Rutherford, E.S., McDermot, D.S., Forney, J.L., and Mills, E.L. 1999. Individual-Based Model of Yellow Perch and Walleye Populations in Oneida Lake. Ecological Monographs 69(2): 127–154. doi:10.1890/0012-9615(1999)069[0127:IBMOYP]2.0.CO;2.

Rosenfeld, J. S., and J. Taylor. 2009. Prey abundance, channel structure and the allometry of growth rate potential for juvenile trout. Fisheries Management and Ecology 16(3):202–218.

Ruchin, A. B. 2004. Influence of Colored Light on Growth rate of Juveniles of Fish. Fish Physiology and Biochemistry 30(2):175–178.

Ryder, R.A. 1977. Effects of Ambient Light Variations on Behavior of Yearling, Subadult, and Adult Walleyes (Stizostedion vitreum vitreum). J. Fish. Res. Bd. Can. 34(10): 1481–1491. NRC Research Press. doi:10.1139/f77-213.

Sass, G. G., & Motta, P. J. (2002). The effects of satiation on strike mode and prey capture kinematics in the largemouth bass, Micropterus salmoides. *Environmental Biology of Fishes*, *65*, 441-454.

Sass, G. G., and J. F. Kitchell. 2005. Can growth be used as a surrogate measure of

Walleye (*Sander vitreus*) abundance change? Canadian Journal of Fisheries and Aquatic Sciences 62(9):2159–2168.

Sass, G. G., Hewett, S. W., Beard Jr, T. D., Fayram, A. H., & Kitchell, J. F. 2004. The role of density dependence in growth patterns of ceded territory walleye populations of northern Wisconsin: effects of changing management regimes. North American Journal of Fisheries Management, 24(4): 1262-1278.

Sass, G. G., Shaw, S. L., & Renik, K. M. (2022). Celebrating 75 years of Wisconsin's Northern Highland fishery research area: the past, present, and future. *Fisheries*, *47*(2), 55-67.

Savino, J.F., Stein, R.A., 1989. Behavioural interactions between fish predators and their prey: effects of plant density. Animal Behaviour 37, 311–321. https://doi.org/10.1016/0003-3472(89)90120-6

Scharf, F.S., Buckel, J.A., McGinn, P.A., Juanes, F., 2003. Vulnerability of marine forage fishes to piscivory: effects of prey behavior on susceptibility to attack and capture. Journal of Experimental Marine Biology and Ecology 294, 41–59. https://doi.org/10.1016/S0022-0981(03)00260-0

Scharf, F.S., Manderson, J.P., and Fabrizio, M.C. 2006. The effects of seafloor habitat complexity on survival of juvenile fishes: Species-specific interactions with structural refuge. Journal of Experimental Marine Biology and Ecology 335(2): 167–176. doi:10.1016/j.jembe.2006.03.018.

Scherer, E. 1976. Overhead-Light Intensity and Vertical Positioning of the Walleye, Stizostedion vitreum vitreum. J. Fish. Res. Bd. Can. 33(2): 289–292. NRC Research

Press. doi:10.1139/f76-042.

Sheppard, K. T., B. J. Hann, and G. K. Davoren. 2018. Growth rate and condition of Walleye (Sander vitreus), Sauger (Sander canadensis), and dwarf Walleye in a large Canadian lake. Canadian Journal of Zoology 96(7):739–748.

Sih, A., 1992. Prey Uncertainty and the Balancing of Antipredator and Feeding Needs. The American Naturalist 139, 1052–1069.

Skajaa, K., Browman, H.I., 2007. The escape response of food-deprived cod larvae (Gadus morhua L.). Journal of Experimental Marine Biology and Ecology 353, 135–144. https://doi.org/10.1016/j.jembe.2007.01.014

Stein, R.A., 1979. Behavioural response of prey to fish pred- ators. Pages 343-353 in R. H. Stroud and H. Clepper, ed- itors. Predator-prey systems in fisheries management. Sport Fishing Institute, Washington, D.C., USA.

Svensson, J.-E., 1992. The influence of visibility and escape ability on sex-specific susceptibility to fish predation in Eudiaptomus gracilis (Copepoda, Crustacea). Hydrobiologia 234, 143–150.

Szopa-Comley, A.W., Ioannou, C.C., 2022. Responsive robotic prey reveal how predators adapt to predictability in escape tactics. Proc Natl Acad Sci U S A 119, e2117858119. https://doi.org/10.1073/pnas.2117858119

Thimijan, R.W., and Heins, R.D. 1983. Photometric, radiometric, and quantum light units of measure: a review of procedures for interconversion. HortScience 18(6): 818–822.

Trager, G., Achituv, Y., Genin, A., 1994. Effects of prey escape ability, flow speed, and predator feeding mode on zooplankton capture by barnacles. Marine Biology 120, 251–259.

Utne-Palm, A.C., 1999. The effect of prey mobility, prey contrast, turbidity and spectral composition on the reaction distance of Gobiusculus flavescens to its planktonic prey. Journal of Fish Biology 54, 1244–1258. https://doi.org/10.1111/j.1095-8649.1999.tb02052.x

Utne-Palm, A.C., 2002. Visual feeding of fish in a turbid environment: Physical and behavioural aspects. Marine and Freshwater Behaviour and Physiology 35, 111–128. https://doi.org/10.1080/10236240290025644

Vandenbyllaardt, L., Ward, F.J., Braekevelt, C.R., and McIntyre, D.B. 1991. Relationships between Turbidity, Piscivory, and Development of the Retina in Juvenile Walleyes. Transactions of the American Fisheries Society 120(3): 382–390. doi:10.1577/1548-8659(1991)120<0382:RBTPAD>2.3.CO;2.

Vasquez, B. R. 2024. Evaluating Walleye (Sander vitreus) thermal and optical habitat occupancy in northern wisconsin lakes using two forms of technology. University of Wisconsin-Stevens Point.

Venturelli, P. A., N. P. Lester, T. R. Marshall, and B. J. Shuter. 2010. Consistent patterns of maturity and density-dependent growth among populations of Walleye (Sander vitreus): application of the growing degree-day metric. Canadian Journal of Fisheries and Aquatic Sciences 67(7):1057–1067.

Vinterstare, J., Hulthén, K., Nilsson, D.E., Nilsson, P.A., and Brönmark, C. 2020. More than meets the eye: Predator-induced pupil size plasticity in a teleost fish. J Anim Ecol 89(10): 2258–2267. doi:10.1111/1365-2656.13303.

Vogel, J.L., and Beauchamp, D.A. 1999. Effects of light, prey size, and turbidity on reaction distances of lake trout (*Salvelinus namaycush*) to salmonid prey. Canadian Journal of Fisheries and Aquatic Sciences 56(7): 1293–1297. doi:10.1139/f99-071.

Wahl, C. (1990). Development of the retinal mosaic in the walleye (Stizostedion vitreum) and the yellow perch (Perea flavescens), including daily changes in morphology. Cornell University.

Wahl, D.H., Einfalt, L.M., and Hooe, M.L. 1995. Effect of Experience with Piscivory on Foraging Behavior and Growth of Walleyes. Transactions of the American Fisheries Society 124(5): 756–763. doi:10.1577/1548-8659(1995)124<0756:EOEWPO>2.3.CO;2.

Walker, J.A., Ghalambor, C.K., Griset, O.L., McKenney, D., Reznick, D.N., 2005. Do faster starts increase the probability of evading predators? Functional Ecology 19, 808–815. https://doi.org/10.1111/j.1365-2435.2005.01033.x

Webb, P.W., 1976. The effect of size on the fast-start performance of rainbow trout Salmo gairdneri, and a consideration of piscivorous predator-prey interactions. Journal of Experimental Biology 65, 157–177.

Webb, P.W., 1981. Responses of northern anchovy, Engraulis mordax, larvae to predation by a biting planktivore, Amphiprion percula. Fishery Bulletin 79.

Webb, P.W., 1982. Avoidance responses of fathead minnow to strikes by four teleost predators. Journal of Comparative physiology 147, 371–378.

Webb, P.W., 1983. Speed, acceleration and manoeuvrability of two teleost fishes. Journal of Experimental Biology 102, 115–122.

Webb, P.W., 1984a. Body and Fin Form and Strike Tactics of Four Teleost Predators Attacking Fathead Minnow (Pimephales promelas) Prey. Can. J. Fish. Aquat. Sci. 41, 157–165. https://doi.org/10.1139/f84-016

Webb, P.W., 1984b. Body form, locomotion and foraging in aquatic vertebrates. American Zoologist 24, 107–120.

Webb, P.W., 1986. Effect of Body Form and Response Threshold on the Vulnerability of Four Species of Teleost Prey Attacked by Largemouth Bass (Micropterus salmoides). Can. J. Fish. Aquat. Sci. 43, 763–771. https://doi.org/10.1139/f86-094

Webb, P.W., Gerstner, C.L., Minton, S.T., 1996. Station-Holding by the Mottled Sculpin, Cottus bairdi (Teleostei: Cottidae), and Other Fishes. Copeia 1996, 488–493. https://doi.org/10.2307/1446874

Webb, P.W., Skadsen, J.M., 1980. Strike tactics of Esox. Can. J. Zool. 58, 1462–1469. https://doi.org/10.1139/z80-201

Weber, M.J., Dettmers, J.M., Wahl, D.H., Czesny, S.J., 2010. Effects of Predator–Prey Interactions and Benthic Habitat Complexity on Selectivity of a Foraging Generalist. Transactions of the American Fisheries Society 139, 1004–1013. https://doi.org/10.1577/T09-100.1

Weihs, D., Webb, P.W., 1984. Optimal avoidance and evasion tactics in predator-prey interactions. Journal of Theoretical Biology 106, 189–206.

Ydenberg, R.C., Dill, L.M., 1986. The economics of fleeing from predators. Advances in the Study of Behavior.

Zyznar, E.S., and Ali, M.A. 1975. An interpretative study of the organization of the visual cells and tapetum lucidum of Stizostedion. Can. J. Zool. 53(2): 180–196. NRC Research Press. doi:10.1139/z75-023.