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Visual sensitivity, foraging behavior, and success of walleye (*Sander vitreus*) under ecologically relevant downwelling light conditions

Noland O. Michels · Quinnlan C. Smith · Loranzie S. Rogers · Thomas R. Hrabik · Greg G. Sass · Allen F. Mensinger

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Abstract Successful foraging of piscivores is often dependent upon light availability in their visual habitat and is often influenced by a number of abiotic and biotic factors. In north-temperate lakes, dissolved organic carbon concentrations vary greatly, thus likely influencing foraging success. To understand the impact this has on the walleye (*Sander vitreus*), we sought to study foraging success at various light intensities under physiologically relevant downwelling light conditions in a laboratory foraging arena. Using electroretinography to determine physiologically relevant light conditions in adult walleye, we found that fish exhibit broad spectral sensitivity that was greatest from 500 to 550 nm. Under optimal light conditions (525 nm), we next determined the reaction distance and foraging success of age-0 walleye at various light intensities. The average reaction distance of age-0 walleye increased rapidly from 12 cm in complete darkness to 27 cm at civil twilight (1 lx or 3.16×10^{13} photons m^{-2} s^{-1}) and then plateaued, ranging from 28 to 30 cm at higher light intensities. Prey capture success of age-0 walleye was greatest under low light conditions, averaging 20.5% from nautical twilight to civil twilight at −3° solar altitude (0.05–1 lx or 1.58×10^{11}–3.16×10^{13} photons m^{-2} s^{-1}) and declined to 10–12% as light intensity increased and in full darkness. Walleye may be best suited for environments with predominantly green downwelling light and age-0 foraging was most successful at nautical and civil twilight. In north-temperate lakes, dissolved organic carbon concentrations can fluctuate interannually due to climate change. Defining preferred juvenile walleye foraging conditions allows for predictions of climate change influences on walleye habitat and age-0 recruitment.

Keywords Walleye · Thermal-optical habitat · Foraging · Reaction distance · Spectral sensitivity

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N. O. Michels (✉) · Q. C. Smith · T. R. Hrabik · A. F. Mensinger
Department of Biology, University of Minnesota-Duluth, 1035 Kirby Drive, 207 SSB, Duluth, MN 55812, USA
e-mail: miche498@d.umn.edu

L. S. Rogers
Department of Psychology, University of Washington, Seattle, WA 98195, USA

G. G. Sass
Escanaba Lake Research Station, Office of Applied Science Wisconsin Department of Natural Resources, 3110 Trout Lake Station Drive, Boulder Junction, WI 54512, USA

Introduction

Changes in aquatic environmental conditions, such as fluctuating levels of primary production, suspended sediments, and dissolved organic carbon (DOC), can

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greatly alter visual habitats and influence the behavior of visually-mediated piscivores and their prey (Heinermann and Ali 1988; Mazur and Beauchamp 2003; Hansen et al. 2013; Ranåker et al. 2012; Ranåker et al. 2014). In north-temperate freshwater lakes, DOC (Stasko et al. 2012) and colored dissolved organic matter (CDOM, predominantly humic and tannic substances; Brezonik et al. 2019) concentrations are becoming more variable due to climate change and changing precipitation patterns, thus influencing the aquatic visual environment (Karlsson et al. 2009; Thrane et al. 2014). The sensitivity hypothesis, proposed by Munz and McFarland (1973), states that a species' spectral sensitivity will generally match the spectrum of light available in its environment. Therefore, it is important to understand how changes in the optical environment, especially light attenuation, and the resulting light intensity and predominant wavelengths of light at depth, influence predator–prey interactions.

Predatory-prey interactions determine the structure and function of aquatic communities (Carpenter et al. 1985; Kerfoot and Sih 1987). During these interactions, predators make numerous sequential binary decisions for successful prey capture (O'Brien 1979). For example, location, defined as a predator orienting towards the prey (O'Brien 1979), attacks, defined as periods of rapid acceleration towards a prey item, and the probability of attacking a prey item, which is correlated with distance, prey length and density, relative speeds of the predator and prey, predator satiation level (Sass and Motta 2002), and habitat (Einfalt and Wahl 1997; Gill and Hart 1998; Curio 2012; Einfalt et al. 2012), have all been shown to influence predator foraging. 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 and Wahl 2013). To understand how these decision factors and environmental conditions (e.g., increased turbidity; Vogel and Beauchamp 1999) influence predator foraging success, predictive models rely on reaction distance, which is the distance between predator and prey at the time of initial predator orientation and is a metric to describe a predator's effective search distance (Howick and O'Brien 1983; Miner and Stein 1996; Vogel and Beauchamp 1999).

For many piscivores, successful prey capture depends on light intensity (Mazur and Beauchamp 2003; Keyler et al. 2019; Michels et al. 2021). Light is a principal abiotic variable that controls temporal and spatial distributions of foraging walleye (*Sander vitreus*; Ryder 1977), a popular piscivorous game fish and culturally significant species for Native American and First Nations people. Walleye inhabit lakes ranging in productivity but most commonly inhabit mesotrophic systems where algal particulates may also influence the downwelling spectral irradiance. Within behavioral paradigms, walleye have been observed to inhabit deeper depths under high surface light intensities (up to 200 lx) and migrated to mid-water depths under low surface light intensities (up to 20 lx) (Scherer 1976), indicating that light intensity plays an important role in water column position and activity. For context, surface illumination of a natural lake can range from 0 lx (no lunar input; new moon phase) to upwards of 32,000 lx during bright, midday conditions (Ryder 1977) Furthermore, the catch per unit effort while angling for walleye is highest at 28 lx, which is in accordance with Scherer (1976) ~ 30 lx and Ryder's (1977) in situ experiments (4–100 lx).

Walleye selection 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, which increases retinal sensitivity but decreases visual acuity, or the ability to determine spatial detail (Moore 1944; Zyznar and Ali 1975; Ali and 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). Visual acuity is strongly correlated to eye size in fishes (Caves et al. 2017), and many teleost fishes have a relatively fixed pupil, thus making pupil size 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). However, the presence of the *tapetum lucidum* is known to increase visual sensitivity at the expense of visual acuity (Ollivier et al. 2004), so understanding the visual sensitivity of walleye is needed to better understand optical foraging habitat. Other low light foraging specialists, such as lake trout, can utilize visual input as low as 3.05×10^9 photons m^{-2} s^{-1} (0.001 lx, Keyler et al. 2019). Thus, to characterize the optimal optical habitat for

walleye foraging, their visual sensitivity must also be examined.

Fish growth is a function of temperature that results from successfully capturing prey over a given period (Kitchell et al. 1977). In North American north-temperate lakes, walleye exhibit highly variable growth and survival across 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 optimal light and temperature conditions for walleye (Lester et al. 2004; Mahlum et al. 2023). Thermal preferences of walleye are well described (Koenst and Smith 1976; Hokanson 1977; Madon and Culver 1993), and these temperatures are often incorporated into TOHA models (Lester et al. 2004; Chu et al. 2004; Jones et al. 2006; Hansen et al. 2019; Mahlum et al. 2023). However, the optical preferences of walleye are not well described, and optical area estimations in TOHA models have largely been assumed. Walleye are crepuscular, increasing activity under low surface light intensities (4–1000 lx; Ryder 1977; light at depth modeled by Lester et al. 2004). Understanding variable growth and survival of walleye, especially at early life stages, in the context of a changing climate is a priority for walleye management. However, to better understand variable growth, the foraging behavior and resulting consumption, or lack thereof, should be examined in detail.

Age-0 walleye foraging behavior and reaction distance have been previously described by Einfalt et al. (2012) and Nieman and Gray (2019), respectively. Notable observations were 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 lx) and greatest prey capture at night in vegetated habitat (Einfalt et al. 2012). Numerous biotic (e.g., prior experience with the prey species, prey morphology, predator length, prey density) and abiotic (e.g., habitat complexity, temperature, turbidity, pH, dissolved oxygen concentrations) have been shown to influence prey capture success (Vandenbyllaardt et al. 1991; Wahl et al. 1995; Einfalt and Wahl 1997; Moore and Townsend 1998; Anderson et al. 2001; Mazur and Beachamp 2003; Galarowicz and Wahl 2005; Einfalt et al. 2012; Chaturvedi and Misra 2019). Reaction distance measurements of age-0 walleye under natural midday light (10:00–15:00) testing the effects of sedimentary and algal turbidity (Nieman and Gray 2019) and larval walleye foraging in high and low light in turbid environments (Osborn 2008) have previously been conducted. However, these, and most other studies, have been conducted in artificial light environments (e.g., white light or red light) and no studies have tested the effect of spectral sensitivity or specific light intensities on the reaction distance of walleye. By understanding the interaction between predominant wavelengths in the aquatic visual system, spectral sensitivity, light intensities at depth, and the reaction distance at specific intensities, we can more accurately model the optimal optical habitat and better predict available TOHA for age-0 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 lx, which for other low light specialists is where most foraging occurs (Keyler et al. 2019). Our ultimate goal was to determine the best optical conditions for walleye foraging for use in improved TOHA models. Our objectives were to (1) measure the scotopic visual sensitivity of adult walleye; (2) develop a reaction distance model for age-0 walleye in clear water conditions ranging from dark to midday ($<6.65\times10^{8}$ to 2.88×10^{17} photons m^{-2} s^{-1}; 0–750 lx); and (3) observe predator success at each decision of the predator – prey interaction (locate, attack, capture, retain).

Materials and methods

Fish collections and husbandry

We collected wild age-0 walleye via boat electrofishing on Shagawa Lake (Ely, MN) on September 18, 2019 and September 28, 2021. Fifteen adult walleye were also collected from Shagawa Lake on September 28, 2021 for electroretinography experiments. Young-of-year walleye total length (T_L) ranged from 103 to 153 mm in 2019 (120 ± 5.1 mm, reported as mean ± standard deviation; $n=147$) and 121–162 mm in 2021 (133 ± 11.2 mm; $n=113$). Adults ranged from 261–437 mm (317 ± 46 mm; $n=15$). We purchased fathead minnows (*Pimephales promelas*) from Marine General (31–42 mm, avg. 37.4 ± 2.7 mm; Duluth, MN) or The Bait Box (32–40 mm,

avg. 36.9 ± 2.1 mm; Superior, WI). A representative sample of 100 fathead minnows from each location were used to measure prey T_L. 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 five 568-L holding tanks (4 walleye tanks, 1 fish per 15 L; 1 fathead minnow tank, 1 fish per 3 L) and maintained at 18 °C in a controlled environmental chamber under a 14h:10h day:night light cycle set at 3.16×10^{15} photons m^{-2} s^{-1}. Water temperature was checked manually daily for the first two weeks, and then weekly thereafter with an average recorded temperature of 18.1 ± 0.2 °C. Recirculated water was filtered via sponges, activated charcoal and zeolite, and nitrogen-fixing bacteria 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 age-0 walleye were tagged under anesthesia using 30 mg/L 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. All fish were acclimated for > 2 weeks to laboratory conditions before experimentation began.

Visual sensitivity

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). The experimental tank was housed within an opaque metal faraday cage (77 × 67 × 97 cm) to prevent equipment light from reaching the fish. Electroretinography waveforms were amplified using a DAM50 bioamplifier (World Precision, Inc.; Sarasota, FL, USA; 1000 × 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, USA) using Lab Chart7 Software (AD Instruments) on a Dell laptop. A 100-W quartz tungsten-halogen Model 6333 lamp (Newport Corp.; Stratford, CT, USA) 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. For a visual reference of the setup used, see Supplemental Fig. 1.

Each fish was anesthetized with a MS-222 solution (75–85 mg/L), 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 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, USA). 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.

All fish were dark adapted for 30–60 min. We initiated test flashes at the 30-min mark to determine if the retina was dark adapted, which was defined as the absence of "the a-wave" (hyperpolarization) 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

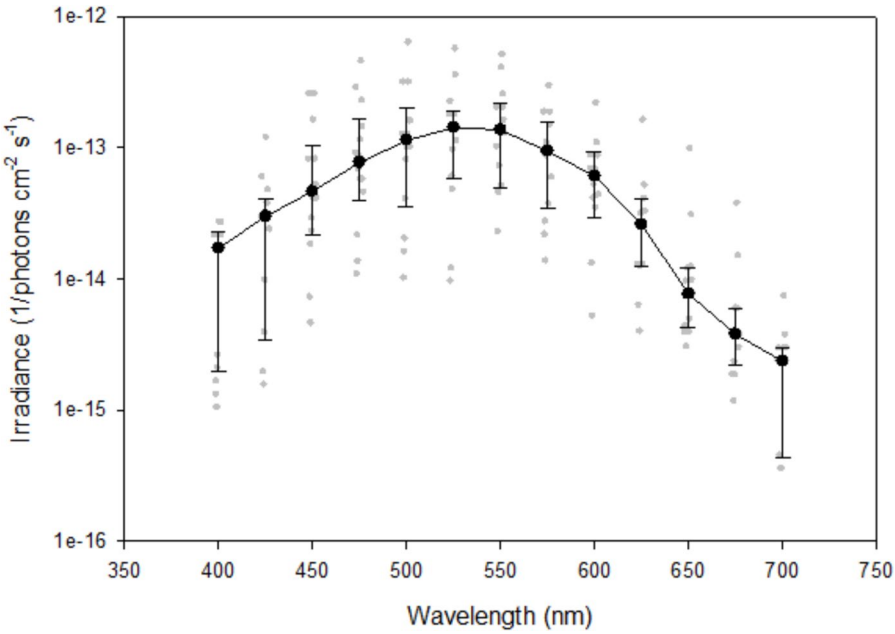

Fig. 1 Median irradiance (1/photons cm^{-2} s^{-1}) needed to invoke the criterion response for adult walleye (*Sander vitreus*) from 400 to 700 nm. Adult sizes tested ranged from 261 to 437 mm. Relative spectral sensitivity was tested via electroretinography. Error bars represent the 25% and 75% interquartile ranges. $n = 14$

a flash duration of 200 ms and inter-flash 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 (Supplemental Fig. 2). 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. The 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.

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; ($< 6.65 \times 10^8$ photons m^{-2} s^{-1}; 0 lx), nautical twilight (−9° solar altitude, 1.58×10^{11}; 0.05 lx), civil twilight (−6° solar altitude: 3.16×10^{12}; 0.1 lx and −3° solar altitude: 3.16×10^{13}; 1 lx), sunrise (3.16×10^{14}; 10 lx), cloudy morning (1.58×10^{15}; 40 lx), sunny morning (3.16×10^{15}; 100 lx), and a sunny afternoon (2.88×10^{17}; 750 lx; Table 1). 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,

Table 1 Time of day corresponding to light intensities at 5 m 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

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). Tank surface irradiances were calculated using the Beer-Lambert equation (Hutchinson 1957):

$$I_x = I_0 e^{-kx} \quad (1)$$

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 2012). 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 layers of black fabric, black plastic, and aluminum foil to keep out all external light.

Foraging trials were conducted from February 11, 2020 to March 6, 2020 and October 12, 2021 to June 2, 2022. The water temperature in the experimental tank was equal to the holding tanks (avg. 18.0 ± 0.02 °C). Eight light intensities (Table 1) were tested with 10 trials each resulting in 80 trials. Food was withheld from all fishes at least 48 h 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 min 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 min, 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 h between trials and used in a maximum of three trials. No walleye was tested under multiple conditions ($n = 80$) but were retained for future experiments. Water changes were made daily within the experimental tank (30%), with three filters (Penn Plax Cascade 1500, Hauppauge, NY) rated for 1324 L/h running for an hour between trials. During the acclimation, no behavioral differences between trials were observed for either predator or prey.

We recorded video at 20 fps with 720 × 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

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:

$$R_d = R_{max} \times l \times (\alpha + l)^{-1} \quad (2)$$

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; Keyler et al. 2019).

Statistical analyses

Visual sensitivity was tested across wavelengths via Kruskal–Wallis one way ANOVA on ranks. The effect of light on the average reaction distance was tested via one-way ANOVA in SigmaPlot 15.0 (SPSS inc.) on normally distributed data with the averages and standard errors shown unless noted otherwise. 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 non-parametric 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 650 nm, with maximum spectral sensitivity at 500–550 nm (Fig. 1). Spectral sensitivity significantly decreased at wavelengths < 450 nm and > 650 nm (Kruskal–Wallis One Way ANOVA on Ranks: $H_{12} = 107.77$, $p < 0.001$, Fig. 1). The lowest irradiance needed to elicit a response in a single walleye was 6.4×10^{-13} photons cm^{-2} s^{-1} (Fig. 1), or a light intensity of 1.56×10^{-13} photons m^{-2} s^{-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; Fig. 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

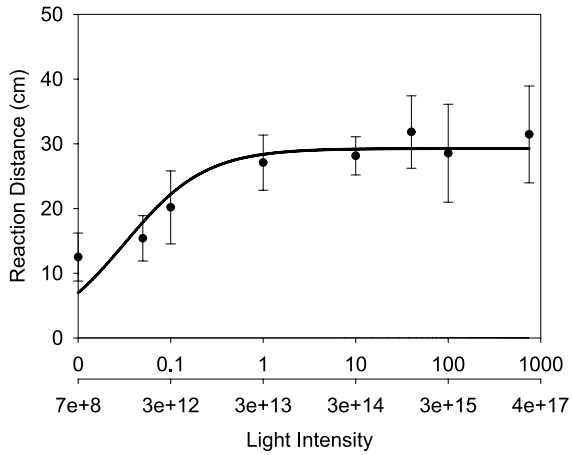

Fig. 2 Average reaction distance of young-of-year walleye (*Sander vitreus*) to fathead minnows (*Pimephales promelas*) at multiple light intensities. Trials spanned 15 min with one predator and three prey. A Michaelis–Menten function was fitted with an R_{max} of 29.2726 and an α of 0.0319 ($r^2 = 0.86$). 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 95% confidence intervals

(−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 ($r^2=0.86$; Fig. 2).

Reaction angles were not uniformly distributed across light intensities (Moore's modified Rayleigh test: $R_8=1.56$, $P<0.001$; Fig. 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

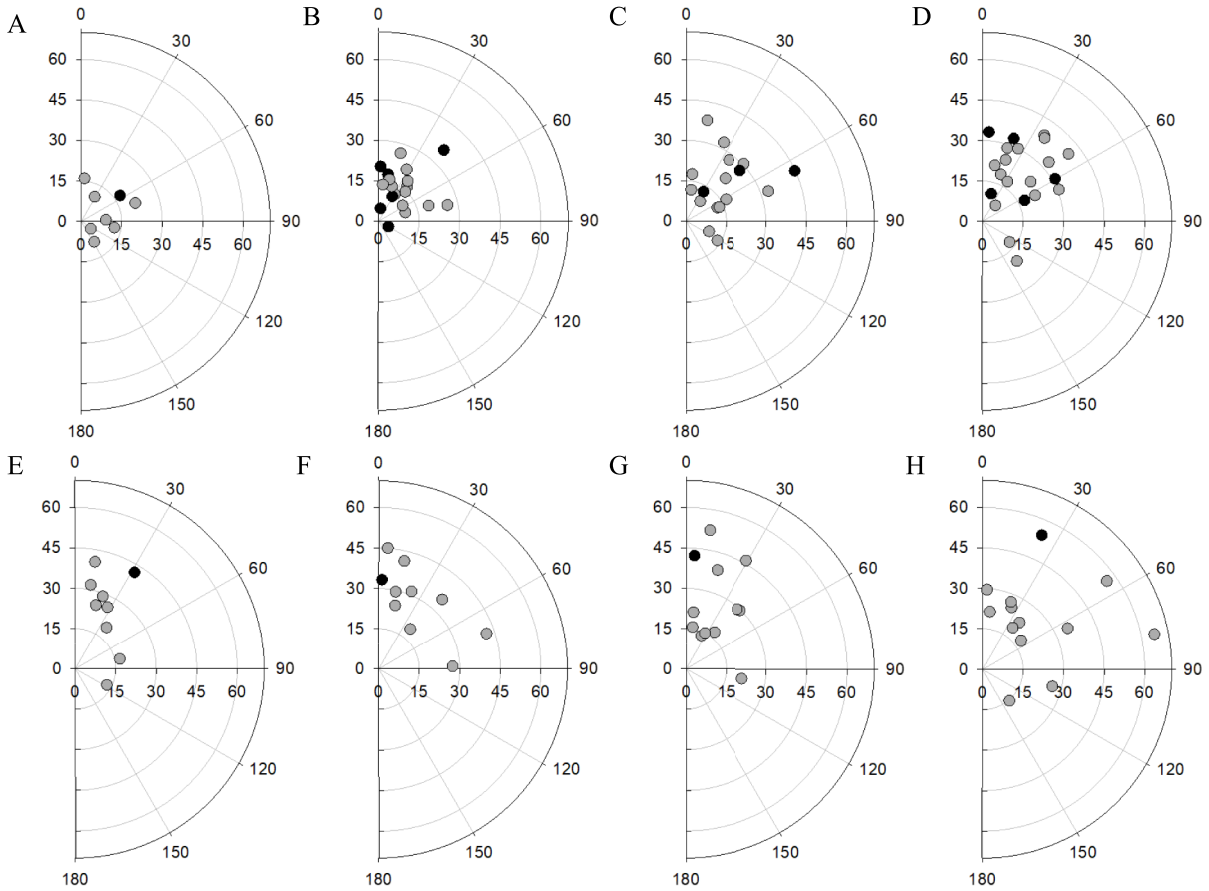

Fig. 3 Young-of-year walleye (*Sander vitreus*) reaction distances and angles to fathead minnows (*Pimephales promelas*) under eight different light intensities. The light intensities are as follows: **A** dark, **B** nautical twilight, **C** civil twilight (−6°), **D** civil twilight (−3°), **E** sunrise, **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 min

($3.36 \pm 62.7°$; Watson's U^2: $U^2 = 0.016$, $P > 0.5$; Fig. 3).

Foraging success

Overall, age-0 walleye oriented to prey 105 times, 15% of which ended with retained prey (16 prey consumed; Table 2). Most reactions (54%) occurred in light intensities ranging from nautical twilight to civil twilight (−3°). 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. Age-0 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

Understanding how the optical environment influences foraging is critical to developing thermal-optical habitat models, yet it has remained understudied. We found that age-0 walleye foraged at all light intensities tested but were most successful under lower light intensities than those in previously published interactions (Einfalt et al. 2012). Most prey were consumed from 1.58×10^{11}–3.16×10^{13} photons m^{-2} s^{-1} [nautical twilight to civil twilight (−3°)], likely due to increased foraging activity. The decrease in attacks at higher light intensities was likely driven by heightened prey awareness and increased detection distance, as prey responded to predators at distances beyond predator striking distances. Higher light intensities may also impair walleye vision, thus reducing the number of reactions to prey. Furthermore, average juvenile walleye reaction distances followed a Michaelis–Menten function, rapidly increasing from 12.5 cm (0.94 body lengths calculated from TL) until civil twilight −3°; ~ 1 lx), reaching an asymptote at 29.3 cm.

Table 2 Age-0 walleye (*Sander vitreus*) reactions, attacks, captures, and retentions of fathead minnows (*Pimephales promelas*). Walleye foraging was observed for 15 min. Trials were conducted under eight light intensities, each with 10 replicates

Light level (photons m^{-2} s^{-1})	Reaction	Attack	Capture	Retention
6.65×10^{8}	8	3	1	1
1.58×10^{11}	19	8	5	4
3.16×10^{12}	17	5	3	2
3.16×10^{13}	21	7	5	5
3.16×10^{14}	9	2	1	1
1.58×10^{15}	10	3	1	1
3.16×10^{15}	9	2	1	1
2.88×10^{17}	12	1	1	1

Visual sensitivity of adult walleye

Adult walleye had a maximum spectral sensitivity in the blue-green range from 500 to 550 nm. This aligns with previous research by Pothier and Ali (1978), which found similar spectra for walleye porphyropsin (533 nm) via microspectrophotometer. Walleye often inhabit mesotrophic systems (Raabe et al. 2020) where downwelling light is red-shifted, with green wavelengths having the greatest intensity (Heinermann and Ali 1988). A peak sensitivity for walleye of 525 nm is consistent with the sensitivity hypothesis proposed by Munz and McFarland (1973), suggesting walleye are well-adapted to a green-dominated optical environment.

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 adult walleye detected irradiances as low as 1.6×10^{-13} photons cm^{-2} s^{-1}; however, age-0 walleye behavioral sensitivity was as low as 1.58×10^{-17} photons cm^{-2} s^{-1}, suggesting 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). The reduced visual acuity may have exacerbated effects at higher light intensities, which may partially explain reduced foraging activity. Through our foraging experiments,

image and/or movement detection seemed to be more important than locating and differentiating immobile prey for this visual predator.

Eye size and development in juvenile walleye

Eye size likely did not influence reaction distance in our experiment, as previous research used similar-sized walleye and found no correlation between eye metrics and reaction distance (Nieman and Gray 2019). In walleye, the *tapetum lucidum* is well established in 90-mm TL fish, and by 125-–14- mm TL, juveniles have the same structure as adults (Braekevelt et al. 1989). Less than 5% of the fish in our reaction distance experiment may not have had 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; therefore, strikes in the light outside of this range can be attributed to visual input. The 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 and Gray 2019). The reaction distance and foraging behavior of walleye have not previously been investigated across variable light intensities. Our data suggests that peak walleye foraging occurs from nautical twilight to civil twilight (~ 0.05–1 lx), well below previous estimates, which ranged from 5 to 10 lx (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 intensities observed average reaction distances of 50 + cm to prey (Nieman and Gray 2019). Our farthest reaction distance was 64 cm in a sunny afternoon trial (750 lx), but the average for 750 lx was just over 30 cm. Furthermore, Nieman and Gray (2019) found that reaction distance decreased with the addition of sediment and algae, although no specific light intensities were reported.

Our reaction distance experiment examined predator–prey interactions over a wide range of light levels in a moderately sized laboratory foraging arena under naturally relevant downwelling light. However, several limitations must 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 two 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.

When foraging at low light intensities, walleye would react to prey, pursue, and then attack if the prey can 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, suggests that low light intensities were critical to increased foraging success of age-0 walleye. Although capture success was not strongly correlated with light intensity, the number of reactions and subsequent attacks were dependent upon light intensity. At high light intensities, walleye were more selective of the prey they attacked. Multiple interactions occurred where a walleye would react to prey but abort any pursuit within seconds if the prey was oriented diagonally or horizontally 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 pursuit of prey in high-light conditions to the increased predator–prey distance being perceived as too far for probable capture, or that prey gave off cues indicating predator detection (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 and Asaeda 1998; Ahrenstorff et al. 2009).

Conclusions

Our findings show that previous estimates of optimal light intensities for age-0 walleye foraging were overestimated and that most foraging activity occurred at extremely low light intensities (~ 0.05–1 lx). At higher light intensities, walleye still predated but were more conservative about which prey they attacked. In a changing climate, turbidity, DOC concentrations, or other ecological variables are modifying the optical aquascape. Our findings highlight the importance of low-light habitat for age-0 walleye and provide valuable data that can help produce more accurate thermal-optical habitat models.

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Data availability Data are available from the Data Repository for the University of Minnesota (DRUM).

Declarations All procedures used in our study were approved by the Institutional Animal Care and Use Committee (IACUC) protocol #2103-38889A and in accordance with the Guide for the Care and Use of Laboratory Animals.

Competing interest The authors declare no competing interests.

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