Visual Sensitivity, Behavior, and Habitat of Select North American Fishes


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


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


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May 2018

**Acknowledgements**

Foremost, I must thank Dr. Tom Hrabik for his continued motivation while completing my dissertation. Through many life events, Tom has managed to remain supportive and kept my best interests in mind, both personal and academic.  Thank you for this opportunity, experience, and for serving as my advisor.

 I also would like to thank my committee members for their time and expertise. Each member has helped me along this journey and has been supportive in their own way.  Dr. Allen Mensinger, while providing critical, helpful reviews of my writing has also provided me with many unforgettable teaching experiences at renown institutions including the MBL at Woods Hole, and Friday Harbor Labs. Dr. Owen Gorman has provided continuous valuable insight into my research and assistance with the writing process; his mentorship is sincerely appreciated. Finally, Dr. Joel Hoffman has always made time to discuss research, personal growth, and provide in depth feedback that has challenged my critical thinking.  Thanks to each of you.

While there are many people at UMD who helped with my research that must be thanked, critical assistance was provided by Loranzie Rogers, Dr. Bryan Matthias, Michael Joyce, and Dr. Brooke Vetter.  Loranzie provided unfaltering dedication to my research while Bryan offered his knowledge, reviews and modeling expertise willingly. Michael, Bryan, and Brooke, without your senior expertise and general support along the way, this dissertation would not have been possible.  You know how much you helped, and I thank you all.

"The setting of the sun is a difficult time for all fish."

— Ernest Hemingway, *The Old Man and the Sea*

## Dedication

This dissertation is dedicated to my wife, Brigitta, for her endless love and support and to my son, Everett, for his unfaltering ability to make me smile.

**Abstract**

This dissertation examines how both physiological and behavioral techniques can be used to address the visual capabilities of three low-light foraging species, the walleye (*Sander vitreus*), siscowet lake trout (*Salvelinus namaycush siscowet*), and deepwater sculpin (*Myoxocephalus thompsonii*). Visual physiology studies can reveal the specific wavelengths fish have adapted to detect at low light intensities while behavioral studies determine the minimal light intensities needed to forage, which may ultimately reveal habitat characteristics important to individual species. Our first study used electroretinography to determine the scotopic spectral sensitivity of the walleye dark-adapted retina (peak sensitivity 500-550 nm) in addition to the approximate maximum depths where visually mediated behavior may occur during the day (77.5 m) and at night (11.3 m) for $k_{PAR} = 0.3$. For our second study, we found that siscowet lake trout reaction distance to deepwater sculpin increased with increasing light intensity (up to $6.0 \times 10^9$ photons $m^{-2}$ $s^{-1}$, thereafter remaining constant), but was not affected by substrate type. Third, we determined that the average number of deepwater sculpin movements per trial increased with decreasing light intensity in the presence of siscowet lake trout, where both activity and reaction distance were suppressed at upper light intensities. Finally, we used solar/lunar patterns to predict how siscowet lake trout visual foraging habitat changes on a daily and seasonal basis. Our model predicted the deepest daytime foraging depths in summer (232.9 m), while the deepest nighttime foraging depths were predicted in winter (32.1 m). Collectively, the findings of these visual studies allow for the

improvement of foraging models as well as defining foraging habitat that describes when

and where fish may forage.

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      This doctoral dissertation is a submission to the faculty of the University of Minnesota in partial fulfillment of the requirements for the degree of Doctor of Philosophy in the Integrated Biosciences Program at the University of Minnesota. Chapter 2 has been submitted for publication and is co-authored by Thomas R. Hrabik, Kelly A. Harrington, Loranzie S. Rogers and Allen F. Mensinger.  Chapter 3 is a manuscript that will be submitted as part of a special issue of Hydrobiologia associated with the International Charr Symposium held in Duluth, MN in June, 2018 and is co-authored by Thomas R. Hrabik, Loranzie S. Rogers, Owen T. Gorman, and Allen F. Mensinger. Chapter 4 is being prepared as a note and the co-authors are Thomas R. Hrabik, Loranzie S. Rogers, and Owen T. Gorman. Finally, chapter 5 is currently in preparation for publication and is co-authored by Thomas R. Hrabik and Bryan G. Matthias.

**Chapter 1: Introduction**

The vast majority of fishes have well-developed eyes and rely on vision as a sensory modality (Guthrie, 1986). Visual detection is used by fishes for recognition of heterospecifics, including predators and prey, as well detection of conspecifics, such as members of a school or potential mates (Lagler et al., 1977). Fish are often the primary visual predators within aquatic systems and use vision to distinguish an object's size, color, brightness, texture, hue, and contrast (Guthrie, 1986). However, the importance of each distinguishable characteristic to a species' foraging success is dependent upon both the type of visually mediated behavior and the characteristics of the water medium (Confer et al., 1978; O'Brien, 1987; Aksnes and Utne, 1997). Additionally, these characteristics and the corresponding optical environment affect visual detection to varying degrees on an hourly, daily, monthly, and seasonal basis (Ryler & Olla, 1999).

The visual capabilities of fishes can be determined through physiological or behavioral studies (Denton & Warren, 1957; Douglas & Hawryshyn, 1990) which may reveal visual adaptation to a fish's environment or provide insight into the predator-prey interactions that drive overall ecosystem structure, respectively. Visual perception requires the detection of light (Gibson, 2014) and freshwater fishes exist in a broad range of light environments from extreme low-light to highly illuminated. Selective pressures have driven various visual adaptations in fishes (Collin, 1997), which are often a product of their respective habitat and temporal niche (i.e., deep water and crepuscular behavior; Guthrie & Muntz, 1993). Visual physiology studies can reveal the specific wavelengths fish have adapted to detect, as well as the minimal light intensities they are able to perceive. In conjunction with visual physiology, *in situ* behavioral foraging trials

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involving variation in light intensity reveal the dynamics of foraging characteristics pertaining to the threshold of visual detection which are useful when delineating fish visual habitat on spatial and temporal scales.

The visual sensitivity hypothesis states that a fish's visual sensitivity will generally match the spectrum of light available in its environment (Munz & McFarland, 1973). A variety of studies have found that visual sensitivity in predatory fish correlates to the intensity of downwelling light within their foraging habitat (Locket, 1974; Warrant & Locket, 2004; Land & Nilsson, 2012).  Due to light attenuation properties in water, the shortest and longest wavelengths of the visible spectrum are the first to diminish with increasing depth.  Clear, freshwater systems favor blue wavelengths at greater depths (Wetzel, 2001), while more turbid deepwater conditions favor green downwelling light (Jerlov 1968; Munz 1976; Walmsley et al. 1979).  As fish generally have visual sensitivity that correlates to the wavelengths and intensities of light available where they forage (e.g., Denton and Warren, 1957; McFarland & Munz, 1975; Harrington et al., 2015), scotopic visual sensitivities are expected to match a species' respective light environment. While many studies of fish vision have investigated spectral sensitivity using electroretinography (measures electrical response of visual pigments to light) or microspectrophotometry (measures spectral absorbance of visual pigments), few have compared the visual sensitivities of fishes to a detailed profile of the light available in the natural environment (Warrant, 2004).

After a species' scotopic sensitivity has been determined, foraging studies can be conducted using the spectrum or wavelengths of light to which the species showed peak sensitivity. Behavioral studies like these can help determine the degree to which

environmental characteristics modify prey detection (Beauchamp et al., 1999), specifically, the effects of light intensity (Mazur & Beauchamp, 2003; Hansen et al., 2013; Keyler et al., 2015) and substrate type (Houtman & Dill, 1994; Ellis et al., 1997; Sowersby et al., 2015). Light can influence the daily timing and success of foraging events by visually foraging fishes (Aksnes & Utne, 1997; Boscarino et al., 2010), and substrate can affect prey behavior and crypsis (Ellis et al., 1997; Ruxton et al., 2004; Stevens & Cuthill, 2006). Both of these factors can affect prey detection and therefore the reaction distance, or the distance at which a fish first responds to prey (Munz & McFarland 1977; Ruxton et al., 2004). Reaction distance is an important metric in visual foraging models, and minor errors in reaction distance estimates will influence the accuracy of a model's predictions (Vogel & Beauchamp, 1999).

Finally, once the preferred light intensity of a species has been determined, it may be possible to delineate their foraging habitat (Melnikow et al., 1981). Both the spatial and temporal distributions of pelagic fishes may be determined by available light if other limiting abiotic factors (e.g. oxygen, temperature) and biotic factors (e.g. prey and predator density) have been taken into account (McFarland, 1986; De Robertis, 2002; Boscarino et al., 2009). Distributions of pelagic fishes in general may therefore be a product of the available foraging habitat which is associated with both solar (Munz & McFarland, 1977; Helfman, 1981) and lunar (Gliwicz, 1986) light changes, which vary on daily and seasonal scales (Boscarino et al., 2010). Given that an organism shows a high correlation between light intensity and depth inhabited, and the light intensity preference of that organism is known, it may be possible to predict the spatial and

temporal foraging patterns that describe when and where organisms feed based on daily and seasonal solar or lunar intensities.

Due to the properties of freshwater, light attenuates quickly (compared to open ocean) and consequently many predator and prey interactions occur in low light environments. To determine the role vision plays in meditating predator prey interactions at low light levels, it is necessary to understand both the physiological and behavioral aspects of visual detection. The objective of this dissertation is to use physiological and behavioral methods to address fish vision, specifically the intensities and wavelengths detected using dark-adapted vision and how fishes forage for prey under varying abiotic factors, which can ultimately be used to delineate optimal visual habitat.

In Chapter 2, electroretinography was used to determine the scotopic spectral sensitivity of the walleye (*Sander vitreus*) dark-adapted retina. In addition to peak spectral sensitivity data, visual depth profiles were constructed, representative of the approximate maximum depths where visually-mediated behavior may occur. The scotopic spectral sensitivity data can be used to describe habitat preferences and help explain the spatial foraging locations and temporal foraging patterns that describe when and where the species forages. Chapter 3 addressed the foraging characteristics of siscowet lake trout (*Salvelinus namaycush siscowet*) under varying light intensities including reaction distance, angle of attack and foraging success in response to benthic prey, the deepwater sculpin (*Myoxocephalus thompsonii*). The association between light intensity and reaction distance can be used to develop a predictive detection model for siscowet lake trout. Additionally, trials were conducted using different tank substrates (sand, gravel, black fabric) to examine the potential effect of deepwater sculpin crypsis

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which may alter prey detection. In Chapter 4, deepwater sculpin behavior was in turn

examined by determining deepwater sculpin activity levels and reaction distance to

siscowet lake trout at varying light intensities, and on different substrates.  In Chapter 5,

siscowet lake trout foraging data from Keyler et al. (2015) was used to develop a model

to predict the depths at a given time that siscowet lake trout may occupy within Lake

Superior.  This model was used to delineate changes in visual foraging habitat for

siscowet lake trout on both diel scale and seasonal scales, and iii) due to hypothetical

changes associated with climate warming that alters light penetration.  Finally, Chapter 6

provides a summary of the primary conclusions from each chapter and discusses their

implications as well as where future research efforts should be focused.

**Chapter 2: Evaluating the Scotopic Visual Sensitivity of Walleye (*Sander vitreus*)**

**and Implications for Foraging Habitat**

**Synopsis**

To investigate the role scotopic vision plays in the foraging behavior of walleye *Sander vitreus*, electroretinography (ERG) was used to determine the spectral sensitivity of the dark-adapted retina of the species. *S. vitreus* displayed peak scotopic spectral sensitivity from 500 to 550 nm defined by a significant increase in sensitivity from 475 to 500 nm, no significant change between 500 to 550 nm, and a significant decrease from 550 to 575 nm. The results support the visual pigment sensitivity hypothesis, where a species' spectral sensitivity matches the wavelengths of downwelling light available within their habitat. Vision depth profiles were created based on the light intensity necessary to elicit an ERG response and represent potential maximum depths where *S. vitreus* may use vision to forage, and may be useful in delineating *S. vitreus* habitat. Based on ERG measurements, *S. vitreus* can detect light during the day to a depth of 77.5 m in clearer water ($k_{PAR} = 0.3$), while in more turbid systems ($k_{PAR} = 1.2$), visual detection is possible to a depth of 12.8 m. Under lunar illumination *S. vitreus* can detect light to a depth of at least 11.3 m ($k_{PAR} = 0.3$) and 1.9 m ($k_{PAR} = 1.2$). The scotopic spectral sensitivity data presented can be used to describe the species' habitat preferences and explain the spatial foraging locations and temporal foraging patterns of *S. vitreus*.

**Introduction**

Visual foraging of fishes can influence the structure and stability of aquatic ecosystems (Carpenter *et al.*, 1985). Freshwater fishes inhabit a broad range of photohabitats in which selective pressures have driven various visual adaptations (Collin

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1977).  The latitude, season, time of day, and physical properties of water affect the downwelling light available in aquatic ecosystems, which ultimately determine the spectrum and intensity of light available for visually mediated behavior (Horodysky 2010).  Fishes, therefore, have visual systems that are commonly adapted to the light environment within their respective habitats and temporal niche (i.e., diurnal or crepuscular behavior; Guthrie & Muntz, 1993).  Visual adaptation to the aquatic environment is most apparent within fishes' retinae (Land & Nilson, 2012). Fish may use photopic vision, mediated by cone photoreceptors in well-lit conditions, whereas scotopic vision involves rod photoreceptors and occurs under low-light conditions. The visual capabilities of freshwater fishes under low-light conditions have previously been investigated in predator-prey studies (Richmond *et al*., 2004; Vinyard & O'Brien, 1976; Confer *et al*., 1978; Henderson & Northcote, 1985).  However, physiology studies can additionally reveal the wavelengths fish have adapted to detect, as well as the minimal light intensities they are able to perceive, which are useful when delineating fish visual habitat on spatial and temporal scales.

Walleye *Sander vitreus* are native to the freshwater lakes and rivers of the northern latitudes within North America (Scott & Crossman, 1973) and are the largest member of the *Percidae* family within the continent (Sloss *et al*., 2004).  While previous studies (see Ali & Anctil, 1968; Zyznar & Ali, 1974; Ali & Anctil, 1977) have addressed *S. vitreus* photopic visual characteristics, very few have examined physiologically the scotopic visual capabilities that allow for visually mediated behavior.  In particular, there is little known about the scotopic spectral sensitivity that may influence activity patterns, habitat preference, foraging strategies, and interspecific competition.

*S. vitreus* are a crepuscular fish (Scherer, 1976; Ryder, 1977) reputed for their low-light visual capabilities based on the presence of a well-developed *tapetum lucidum* (Moore, 1944; Ali & Anctil, 1968; Zyznar & Ali, 1974; Ali & Anctil, 1977). The *tapetum lucidum* acts to reflect photons that initially were not absorbed back on to the photoreceptors, which increases visual sensitivity although lowers visual acuity. As *S. vitreus* mature, they undergo ontogenetic shifts in habitat and visual function (Eschmeyer, 1950; Braekefelt *et al*., 1989), where mature *S. vitreus* avoid higher light intensities during the day (Scherer 1976). While mature *S. vitreus* tend to be demersal in both lotic and lentic environments (Barton 2011), the specific depths and corresponding light intensities where visually mediated foraging may be used in different systems is less clear. Lester *et al.* (2004) defines the optimal *S. vitreus* light intensity range as 8 to 68 lux (noon during summer) corresponding to depths of approximately 12-18 m within a mesotrophic body of water (4 m Secchi depth; Carlson & Simpson, 1996). The evolution of the *S. vitreus* visual system allows for foraging in low-light environments (Disler & Smirnov, 1977; Ali & Anctil, 1978; Kelso, 1978), but the limits of *S. vitreus* visual detection and the associated approximate depths and light intensities within other systems need to be also investigated.

Despite numerous studies on the anatomical structures of the *S. vitreus* eye, little is known about how morphological specialization translates to physiologically determined scotopic visual and spectral sensitivity. The visual pigment sensitivity hypothesis posits that spectral sensitivity will match the spectrum of light available in the environment (Munz & McFarland, 1973). The colors that can be visually distinguished by a species are strongly related to the specific environmental niche occupied (Bedore *et*

*al*., 2013), therefore leading to a spectral sensitivity that correlates to the available wavelengths of light (Denton & Warren, 1957; McFarland & Munz, 1975; Cresitelli *et al*., 1985; Partridge *et al*., 1988; Harrington *et al*., 2015). Ali *et al*. (1977) previously investigated scotopic sensitivity in *S. vitreus* via *in-situ* microspectrophotometry, which measures the spectral absorbance of isolated visual pigments when exposed to monochromatic light, and determined peak absorbance for rods at 533 nm; however, it does not account for the *in-vivo* neural processing in intact animals. Electroretinography (ERG) has the additional capability of measuring the *in-vivo* neural response, or the difference in retinal electrical potential associated with the cellular depolarization that occurs with the detection of light (Shiells *et al*., 1981).

Additionally, ERG can be used to approximate the minimum amount of light *S. vitreus* can detect and the depths where vision may be used to forage. Studies have found that visual sensitivity in predatory fish typically correlates to the intensity of light within the foraging habitat (Locket, 1974; Warrant & Locket, 2004; Land & Nilsson, 2012; Harrington *et al*., 2015, Keyler *et al*., 2015), with benthic fish often showing greater sensitivity to low-light (Horodysky *et al*., 2010). Examining scotopic visual sensitivity via ERG provides a unique opportunity to study visually mediated behavior by correlating scotopic spectral sensitivity to estimated irradiance at depth within varying aquatic habitats. While many studies of fish vision have investigated spectral sensitivity using electroretinography or microspectrophotometry, few have compared the visual sensitivities of fishes to a detailed profile of the light available in the natural environment (Warrant & Locket, 2004).

The scotopic spectral sensitivity data presented can be used to describe *S. vitreus* habitat preferences and explain the spatial foraging locations and temporal foraging patterns. Furthermore, information on visual sensitivity in fish and its correlation with habitat preference is useful when developing foraging models for individual species (Horodysky *et al.*, 2010; Hrabik *et al.*, 2014). The objectives of this research therefore were to determine *S. vitreus*: i) scotopic spectral sensitivity, ii) visual depth profiles representative of the light intensities at depths sufficient for vision, and iii) potential spatial differences within varying aquatic system owing to variances in visual sensitivity.

**Materials and Methods**

*Fish Collection and Culture: S. vitreus* were collected via angling between June 15 2015 and July 8 2015 from Spirit Lake on the St. Louis River estuary along the NE shore of Spirit Island from depths between 3.0 to 3.5 m. Water surface temperatures on collection days ranged from 21.1 to 23.1°C and secchi depth was consistently ~ 0.7 m. *S. vitreus* were collected in accordance to the State of Wisconsin Department of Natural Resources Scientific Collecting policy, permit No. SCP-NOR-073-0527.

Collected *S. vitreus* were temporarily stored and transported in a cooler (96.2 L) treated with 0.026% Stresscoat® (Mars Fishcare North America Inc., Chalfont, PA). During both collection and transport, water was continually aerated via 8 cm Deluxe Bubble Disks (Penn Plax, Hauppauge, NY). Fish were housed in recirculating tanks in a 16.0°C cold room (to minimize fungal and bacterial growth) at the University of Minnesota Duluth (Duluth, MN) and were separated into six 568 L mechanically, chemically, and biologically filtered (1500 Penn-Plax Cascade™ filters) tanks (Miller Manufacturing, Eagan, MN). Tanks were subjected to a 12h:12h (L:D) photoperiod with

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a light intensity of ~$3.48 \times 10^{13}$ photons m$^{-2}$ s$^{-1}$ (roughly equivalent to 1.9 lx) for the

diurnal segment (0600 to 1800 h), which emulates nautical twilight (Johnsen 2012). Light

intensity was measured using the International Light Technologies ILT1700 Research

Radiometer (Peabody, MA) and a SED033/F/HMR/W broadband silicon detector

(Peabody, MA).  Fish were used for experimentation within 5 days of capture.

     *Experimental Preparation:* Electroretinography (ERG) was used to determine the

scotopic spectral sensitivity of *S. vitreus* (*n*=9).  Fish ranged from 31 to 44 cm and

averaged 36.9 ± 1.4 cm (Mean ± S.E.) in total length ($L_T$). Since fish were > 30 cm $L_T$

(Chevalier 1973; tested range: 31 to 44 cm $L_T$), aged 3-5 years (Olson, Wisconsin Dept.

of Natural Resources, 2018, personal communication) they all should possess functional

scotopic visual capabilities (Braekefelt *et al*., 1989; Vandenbyllaardt *et al*., 1991).

Experimental procedures were performed in a darkroom within a sheet metal Faraday

cage to eliminate electromagnetic interference and to eliminate external light sources

from the equipment in the room. To limit variation due to retinomotor movements,

experiments were conducted between 1200 and 1900 hours to account for endogenous

timekeeping mechanisms, or internal biological clocks (Cahill & Besharse 1995; Li &

Dowling 1998). For experimentation, fish were placed in a holding tank (50 L) with

chilled (16°C) recirculating water prior to anesthetization with 0.002% MS-222 in a

buffered $d_iH_20$ solution (7.0 to 7.4 pH) consisting of 1.1% potassium phosphate

monobasic and 2.5% sodium phosphate dibasic (Sigma Chemical Co., St. Louis, MO). To

ensure that the fish were properly anesthetized, a tail pinch was administered prior to an

intramuscular injection (0.1% bodyweight) of pancuronium bromide (muscle relaxant)

dissolved in 0.9% NaCl.  Fish were then secured between moistened sponges in an

acrylic experimental tank (37 x 15 x 11 cm) within the Faraday cage (77 x 67 x 96 cm).

*S. vitreus* were submerged to the ventral border of the eye and received a chilled (16 °C)

(420 W Teco SeaChill Aquarium Chiller, Teco model SCTR20, Ravenna, Italy),

buffered, MS-222 (0.002%) water solution that flowed over the gills via an intraoral tube

to maintain anesthesia.  All fish husbandry and experimentation conformed to the

University of Minnesota animal care protocols and were approved by the Institutional

Animal Care and Use Committee Protocol ID: 1504-32496A in addition to the

recommendations within the Guide for the Care and Use of Laboratory Animals of the

National Institutes of Health.

*Electroretinogram Procedure:* A 100 W quartz-tungsten halogen lamp (Newport

model 6333, Stratford, CT) powered by a constant current power supply (Newport model

68938) provided the light stimulus for the ERG (Fig. 1).  Square-wave light pulses (3.0,

3.0 and 5.0 ms delay, rise and fall times, respectively) were regulated by a controller

(Oriel® Instruments model 76995, Stratford, CT), which controlled an electric shutter

(Oriel® Instruments model 76994) responsible for modulating stimulus duration.  The

light from the lamp transited through a monochromator (Newport model 77250), passed

through a series of 0.1 to 5.0 neutral density filters (Newport FSR-OD series filters:

wavelength range 400 to 900 nm, neutral transmission 400 to 700 nm) and into a fiber

optic light pipe (Newport model 77632) positioned to illuminate the entire fish eye.  A

small incision was made at the limbus of the eye with a microsurgical knife (Sharpoint™,

Reading, PA) and an Ag-AgCl 0.13 mm diameter wire (A-M Systems, Inc., Cat. No.

781500, Carlsborg, WA) recording electrode was inserted within the vitreous body. A

reference electrode with the same specifications was placed within the nare of the fish.

After electrode insertion, *S. vitreus* were dark-adapted for a minimum of 30 min (Note: no increase in b-wave amplitude to a test stimulus was noted after 20 min dark adaptation). The stimulus consisted of a 200 ms flash of monochromatic light of wavelengths starting at 400 nm and proceeding in 25 nm increments to 700 nm. The presentation order of the wavelengths was randomly determined before each trial. An interstimulus duration of 30 seconds was sufficient to achieve the same b-wave amplitude for consecutive flashes and avoid photobleaching. The light intensity of the flash was measured using an Ophir radiant energy meter (model 70260) and probe (model 70268) and the ERG response was amplified by a World Precision Instrument, Inc. amplifier (model DAM50, Sarasota, FL) with a 10 Hz low pass filter and 10 kHz high pass filter. Data was recorded using PowerLab 4SP (AD Instruments, Castle Hill, Australia) and LabChart7 software (LabChart 7 v. 7.3.7, ADInstruments, Castle Hill, Australia).

The response of the dark-adapted retina was determined by measuring the amplitude of the b-wave rom baseline to peak. Shorter wavelength light ($\leq$ 425 nm) consistently elicited lower b-wave amplitudes, and therefore the minimal criterion response of 100 $\mu$V amplitude was established at 400 nm. Neutral density filters were used to reduce light intensity for tested wavelengths until a 100 $\mu$V b-wave response was obtained. The spectral sensitivity curve was generated based on the irradiance necessary to invoke the criterion response at each tested wavelength.

*Visual Depth Profile Calculation:* The minimum light intensities determined from the scotopic spectral sensitivity calculations and solar/lunar surface irradiances were used to calculate the depths sufficient to elicit the criterion b-wave response. Calculations

follow the methods of Keyler *et al*. (2015), which applies the Beer-Lambert equation (Hutchinson 1957):

$$I_x = I_o e^{-kx} \tag{1}$$

Where surface irradiance, $I_o = 9.57 \times 10^{19}$ photons m$^{-2}$ s$^{-1}$ is the surface intensity from solar radiation in summer for Lake Superior (Fahnenstiel *et al*., 1984). Surface intensity values from solar radiation for Lake Superior were used since all *S. vitreus* were captured from the mouth of the St. Louis river estuary, which is the confluence of the St. Louis River with Lake Superior. Unfortunately, Lake Superior surface irradiance from lunar radiation is reported in lux, which correlates to human vision and is not appropriate to use for fish vision calculations. Therefore, following Harington *et al.* (2015), the surface irradiance from lunar radiation, $I_o = 1.35 \times 10^{10}$ photons m$^{-2}$ s$^{-1}$ was used from Cramer et al. (2013) who reported wavelength specific surface irradiance for moonlight in Arizona. Spectral irradiance attenuation coefficients reported by Jerome *et al*. (1983) were used to determine various vertical attenuation coefficients *k* for calculating light at depth. Light attenuation *k* varies within systems due to light-absorbing particulates such as dissolved organic carbon compounds and suspended sediments (Guthrie & Muntz, 1993). The vertical attenuation coefficients of $k_{PAR} = 0.3$ and 0.5 were derived from Lake Superior data representing a clear-water system, while attenuation coefficients from Lake Ontario of $k_{PAR} = 0.8$ and 1.2 were used to represent a higher turbidity system (Jerome *et al*., 1983).

*Statistical analysis:* Statistical tests were performed using JMP software (JMP v.10.0, Statistical Analysis System Institute Inc., Cary, NC). Data were tested for normality and homoscedasticity before performing parametric tests. Normality was tested using a Shapiro-Wilk test, while equal variances were tested using a Brown-Forsythe test. All statistical tests used a significance value of $\alpha = 0.05$.

**Results**

*Visual Spectral Sensitivity:* The irradiance (photons $cm^{-2} s^{-1}$) necessary to meet the criterion response at each wavelength was used to create the scotopic spectral sensitivity curve for the dark-adapted *S. vitreus* retina. There was a significant effect of wavelength on the average irradiance (photons $cm^{-2} s^{-1}$) needed to invoke the criterion response (Fig. 2; ANOVA, $F_{12,104} = 7.90$, p<0.0001). *S. vitreus* displayed peak sensitivity from 500 to 550 nm, defined by a significant increase in sensitivity from 475 to 500 nm (Tukey's HSD, p <0.05), no significant changes between 500 to 550 nm, and a significant decrease from 550 to 575 nm (Tukey's HSD, p <0.05). Irradiance to invoke the criterion response followed a parabolic curve from 400 to 700 nm with minimum sensitivity occurring at 700 nm.

*Visual Depth Profiles:* To determine the maximum depth where sufficient irradiance exists to elicit the criterion ERG response, "visual depth profiles" were created to approximate the depth within a given body of water where visually-mediated behavior may occur under solar and lunar surface irradiances. Results indicate dark-adapted *S. vitreus* under daytime conditions can detect light as deep as 77.5 m ($k_{PAR} = 0.3$) and 47.5 m ($k_{PAR} = 0.5$) respectively (Fig. 3). With increased turbidity of $k_{PAR} = 0.8$ and 1.2, *S. vitreus* visual detection decreased to 19.6 m and 12.8 m, respectively (Fig. 3). At night, *S.*

*vitreus* can detect light to depths of 11.3 m, 6.9 m, 2.9 m, and 1.9 m for respective $k_{PAR}$

values of 0.3, 0.5, 0.8 and 1.2 (Fig. 4).

**Discussion**

Using ERG, peak scotopic spectral sensitivity for *S. vitreus* was determined from

500 to 550 nm.  Based on the spectral sensitivity results, inferences about visual

capabilities at varying depths under solar and lunar illumination can be made for different

aquatic systems. *S. vitreus* have the capability to detect solar light (noon on a summer's

day) to at least 77.5 m in a system where $k_{PAR} = 0.3$, 12.8 m in a more turbid system

where $k_{PAR} = 1.2$, and to 11.3 m and 1.9 m, during the night under lunar illumination

(waning gibbous, 2 days post-full) for respective $k_{PAR}$ values.

*Electroretinography:* While many have noted that *S. vitreus* have adapted to

feeding in low-light environments due to the presence of a *tapetum lucidum* (Ali &

Anctil, 1977; Ryder, 1977; Kelso, 1978; Wahl, 1994; Barton, 2011), very few studies

have determined the minimum visual sensitivity required for vision.  In this study, the

ERG was used to determine scotopic sensitivity in a dark-adapted retina. B-wave

responses originating from Müller cell and bipolar cell depolarization indicated sufficient

irradiance was detected by the photoreceptors to trigger the bipolar cell response.  As the

bipolar cells represent a direct link between photoreceptors and the ganglion cells which

synapse to central visual centers, activation of this cascade indicates sufficient light may

be available to mediate visual behavior. Due to the absence of a-waves (associated with

the cone photoreceptors and photopic vision), b-wave responses are most likely due to

rod photoreceptors and represent scotopic vision.  However, eye size, morphology and

electrode placement can affect the ERG response, and therefore the minimum light intensities detected for tested wavelengths should be viewed as conservative estimates.

Low-light vision is a product of the scotopic spectral sensitivity of the retina, the spectral transmission of the ocular media and the visual pigments of the fishes' retina. While the transmission of the ocular media in *S. vitreus* has yet to be investigated, the lens and cornea of the European perch (*Perca fluviatilis*) reduce radiation below 500 nm from reaching the retina, effectively limiting harmful UV radiation (Douglas & McGuigan, 1988). Due to phylogenetic similarities within the family *Percidae*, similar absorption traits may be true for the *S. vitreus*, explaining the findings of depressed sensitivity at shorter wavelengths for this species.

Ali *et al*. (1977) previously investigated the scotopic visual pigment in *S. vitreus* and found that rods absorb maximally ~ 533 nm. These findings align with the scotopic spectral sensitivity data, which determined peak sensitivity from 500 to 550 nm. Additionally, Ali *et al*. (1977) found that *S. vitreus* peak cone absorption, which is associated with photopic vision, occurred at 560 nm for single cones and ~630 nm for double cones providing further support that that rod sensitivity was being measured with little or no contribution from cone photoreceptors.

*Visual Pigment Sensitivity Hypothesis:* Results support the visual pigment sensitivity hypothesis, which states that a fish will be sensitive to the wavelengths of light available in its environment due to visual pigment adaptation (Clarke 1936). *S. vitreus* displayed significantly higher sensitivity (500 to 550 nm) to the prevailing downwelling wavelengths within typical mesotrophic freshwater environments (Jerlov 1968), where they are most abundant, when compared to eutrophic and oligotrophic systems (Regier *et*

*al*. 1969; Kitchell *et al*. 1977; Leach *et al*. 1977; Schupp 1978). Physical and chemical properties of water, such as light-absorbing particles affect how certain wavelengths attenuate; with an increase in turbidity, green (~ 530 nm) wavelengths penetrate deepest in the water column (Wetzel 2001). With greater turbidity and/or increasing depth, the input of rod photoreceptors will predominate even during daytime hours in low-light conditions and fishes will predominantly rely on scotopic vision in these dim-light environments.

Unfortunately, many fish vision papers use lux when referring to light intensity which is an inappropriate measure for fish vision (Johnsen 2012) as it is based on human sensitivity (Boscarino *et al*., 2010) while irradiance is more accurate for determining fish visual sensitivity. Additionally, species-specific lux units that account for scotopic spectral sensitivity are useful for describing the sensitivity of a single species, but are less useful when making interspecies comparisons. (see Widder & Frank, 2001; Cohen & Forward, 2005; Boscarino *et al*., 2010).

*Visual Depth Profiles*: Spectral sensitivity can assist in making inferences about a fish's visual depth capabilities. Mature *S. vitreus* prefer depths associated with light intensity ranging from 8 to 68 lux (Lester *et al*. 2004) and temperature between 20 to 24°C (Hokanson, 1977). ERG results indicate *S. vitreus* dark-adapted spectral sensitivity can detect solar light to depths of at least 77.5 m ($k_{PAR}$ = 0.3), 47.5 m ($k_{PAR}$ = 0.5), 19.6 m ($k_{PAR}$ = 0.8), and 12.8 m ($k_{PAR}$ = 1.2) under optimal daytime conditions. Under lunar conditions (waning gibbous, 2 days post-full), *S. vitreus* can detect moonlight to depths of 11.3 m ($k_{PAR}$ = 0.3), 6.9 m ($k_{PAR}$ = 0.5), 2.9 m ($k_{PAR}$ = 0.8), and 1.9 m ($k_{PAR}$ = 1.2). Previous studies that have investigated the spatial and temporal aspects of *S. vitreus*

distribution have reported that the observed depths occupied are shallower than the depth estimates at which vision is possible (Table 1). For example, within mesotrophic bodies of water (4 m Secchi depth) where *S. vitreus* are most abundant (Regier *et al*. 1969; Kitchell *et al*. 1977; Leach *et al*. 1977; Schupp 1978), Lester *et al*. (2004) proposes the *S. vitreus* depth range is from 12-18 m for a summer's day at noon. This study suggests *S. vitreus* could use vision to depths of at least 47.5 m within a comparable mesotrophic system ($k_{PAR} = 0.5$), almost 30 m deeper than the predictions from Lester *et al*. (2004). However, it is important to reiterate that these results represent the approximate maximum depths where light detection is possible and additional illumination may be needed to mediate predator-prey interactions. Additionally, abiotic factors (e.g. oxygen, temperature) and biotic factors (e.g. prey/predator density; McFarland, 1986; De Robertis, 2002; Boscarino *et al*., 2009) will influence the actual depths occupied within different systems.

Fishes feed where prey are located and will forage in suboptimal light conditions if necessary to optimize prey capture (Crowder & Cooper, 1982). In order for *S. vitreus* to use visual cues during predator-prey interactions, they may need to forage at shallower depths where both increased illumination and prey fishes, such as yellow perch *P. flavescens*, are found (Table 1). While there is limited info on nocturnal walleye distribution, the maximum depths at which light detection is possible more closely align with maximum fish depth. As nocturnal foraging relies predominantly on rod photoreceptors, the depth distribution model suggests that nocturnal depths may be more accurate. However, additional information on walleye nocturnal depth distribution will be needed to validate the model.

*Species comparison:* The siscowet lake trout *Salvelinus namaycush siscowet* is a low-light predator that is found within the offshore waters of Lake Superior. *S. namaycush siscowet* perform diel vertical migration (DVM), as they typically occupy depths >80 m during the day (Harvey *et al.*, 2003) and move higher in the water column at night (Jensen *et al.*, 2006; Hrabik *et al*., 2006; Stockwell *et al*., 2010; Gorman *et al*., 2012a). Due to both the depth occupied during the day and DVM behavior, *S. namaycush siscowet* exist in a low-light environment to which they have evolved enhanced scotopic visual capabilities with the ability to detect light at depths > 300 m in Lake Superior ($k_{PAR}$ = 0.1; Harrington *et al*., 2015). Harrington *et al*. (2015) determined *S. namaycush siscowet* can detect solar light as deep as 75.0 m ($k_{PAR}$ = 0.3), which closely matches the 77.5 m depth estimated for *S. vitreus*. At night, *S. namaycush siscowet* are capable of detecting light to 8.0 m, while *S. vitreus* should detect light to 11.2 m. This comparison provides physiologically-based support for empirical claims of *S. vitreus* as a low-light forager capable of feeding throughout the night in shallower waters (Ryder 1977; Wydoski and Whitney 1979). Ultimately, the habitat preferences and scotopic visual capabilities of each species are a result of adaptations to the light environment owing to each species' respective habitat and temporal niche.

*Conclusions:* The determined scotopic visual sensitivity of *S. vitreus* supports the visual pigment sensitivity hypothesis as *S. vitreus* show visual adaptation to their light environment. Collectively, visual physiology studies, specifically electroretinography, can reveal the specific wavelengths *s. vitreus* have adapted to detect at low-light intensities, as well as the minimal light intensities they may be able to perceive. These results may reveal habitat characteristics important to the species, which are useful when

delineating *s. vitreus* visual habitat on spatial and temporal scales. Additionally, *in situ* behavioral foraging trials that vary abiotic factors such as light may additionally reveal the dynamics of foraging characteristics pertaining to the threshold of visual detection. Behavioral studies are useful to determine how visual physiology translates to a species' visually-mediated foraging capabilities. Previous studies have shown that an asymptotic relationship exists between light intensity and predator reaction distance to prey (Vogel & Beauchamp, 1999; Mazur & Beauchamp, 2003; Keyler *et al*., 2015). Future studies should investigate the light intensities for which visual foraging is possible, which can clarify predator-prey interactions at low-light levels. Studies of this nature may validate the scotopic sensitivity results reported here and expand the knowledge relating to functional vision for *S. vitreus* and related fishes.

**Acknowledgments**

**Figure 1**. Schematic drawing of electroretinography setup. From left to right: (A) Constant current power supply, (B) electric shutter control, (C) quartz-tungsten halogen lamp, (D) neutral density filters, (E) monochromator, (F) Faraday cage, (G) fiber optic light pipe, (H) recording electrodes, (I) signal amplifier (G-I within circular enlargement), (J) PowerLab, (K) personal computer, (L) chilled water lines.
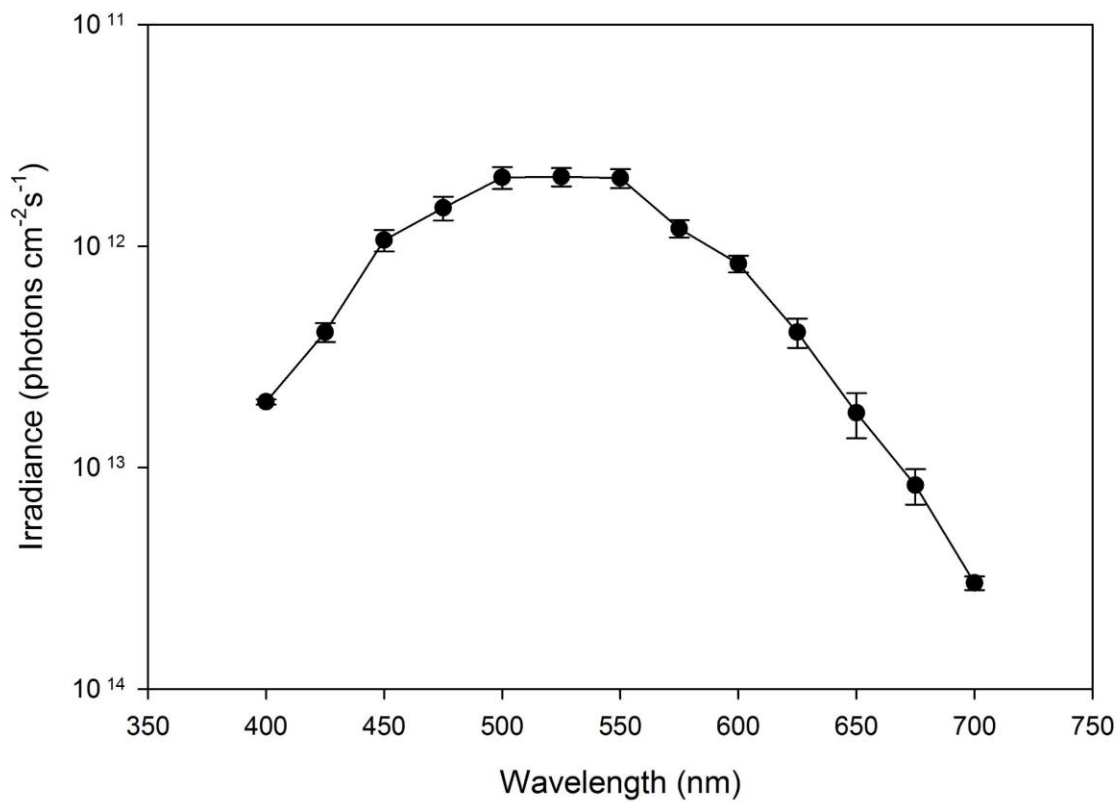
**Fig. 2.** The average irradiance (photons $cm^{-2} s^{-1}$) needed to invoke the criterion response versus wavelength (nm) for *S. vitreus* ($n = 9$). Error bars represent ±S.E.
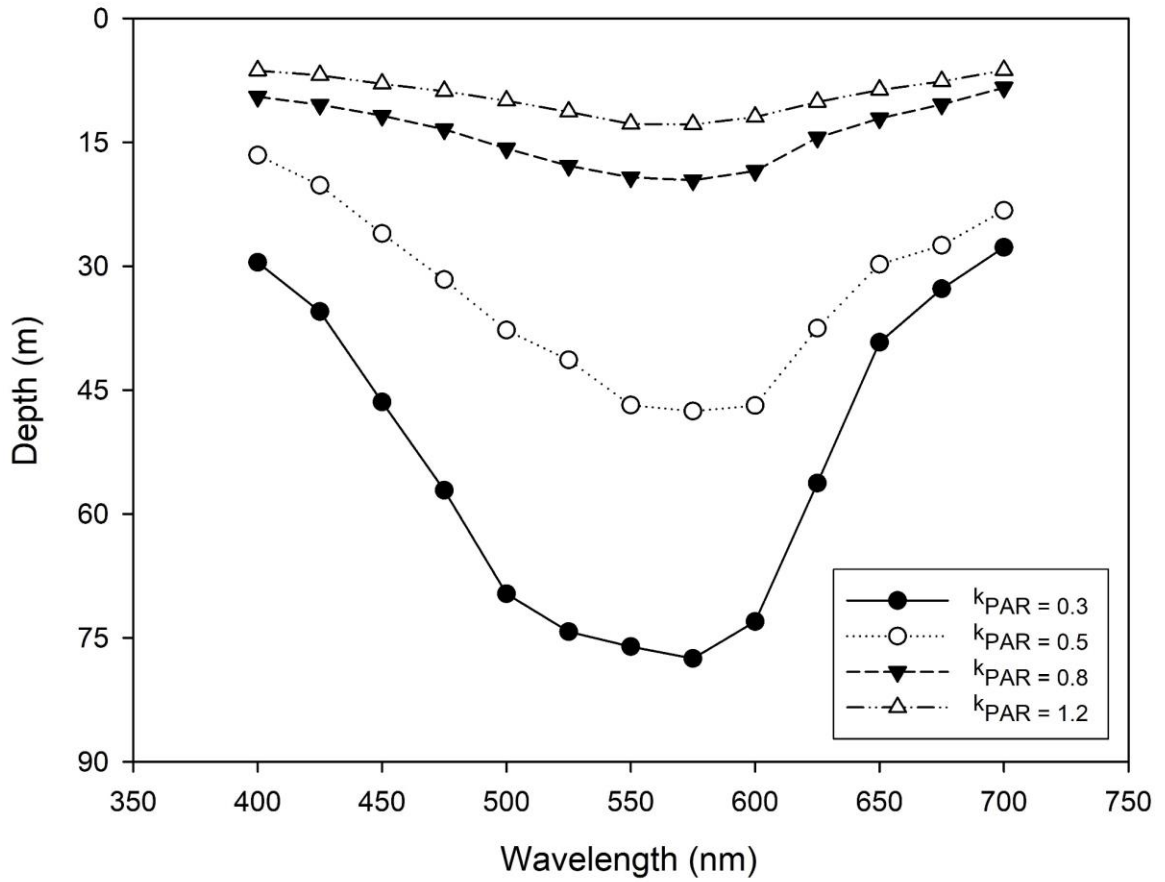
**Fig. 3**. The maximum depth (m) under solar conditions at which sufficient downwelling irradiance is available to elicit the criterion b-wave amplitude at light attenuation coefficients of $k_{PAR} = 0.3$, $k_{PAR} = 0.5$, $k_{PAR} = 0.8$ and $k_{PAR} = 1.2$.
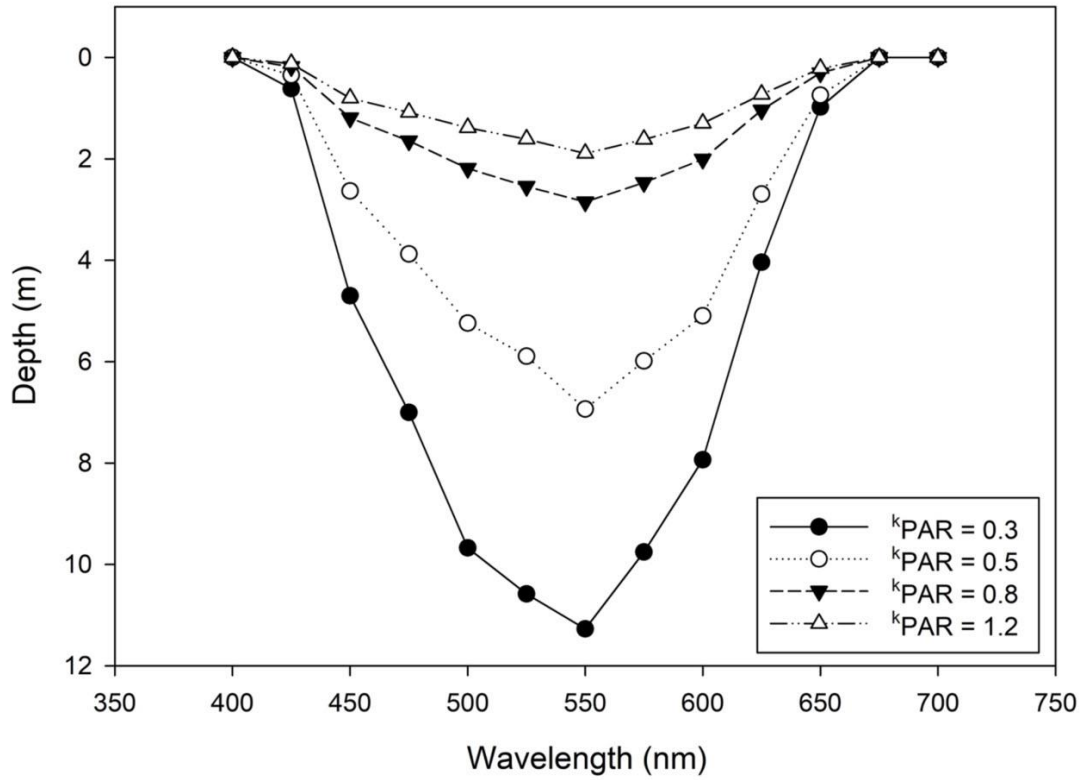
**Fig. 4.** The maximum depth (m) under lunar conditions at which sufficient downwelling irradiance is available to elicit the criterion b-wave amplitude at light attenuation coefficients of $k_{PAR} = 0.3$, $k_{PAR} = 0.5$, $k_{PAR} = 0.8$ and $k_{PAR} = 1.2$.

**Table I:** Summary of studies comparing water type, maximum water depth (m), and actual fish depths (m) for day/night to our predicted maximum depths (m) where visually mediated behavior may be possible during summer.  Predicted max. depths values are from *S. vitreus* visual depth profiles. Dashes (-) indicate undetermined depth values.

| Species | Author | Water type | Max water depth | Day-actual fish depth | Day-predicted max. depth | Night-actual fish depth | Night-predicted max. depth |
|---|---|---|---|---|---|---|---|
| *S. vitreus* | Lester *et al.* (2004) | mesotrophic | 20 | 12-18 [‡] | 47.5 | - | - |
| | Byrne *et al.* (2009) | mesotrophic | 51 | 10 [†] | 47.5 | 7 [†] | 6.9 |
| | Williams (1997) | mesotrophic | 76 | 6 | 47.5 | - | - |
| | Kelso (1978) | oligotrophic | 30 | 5-10 | 77.5 | - | - |
| | Haxton (2015) | oligotrophic | 200 | 6-12 | 77.5 | - | - |
| | Dendy (1948) | eutrophic | 53 | 3 [‡] | 12.8 | - | - |
| | Clark-Kolaks (2009) | eutrophic | 18 | 6 [†] | 12.8 | - | - |
| | Holt *et al.* (1977) | eutrophic | 25 | 5 | 12.8 | - | - |
| *P. flavescens* | Rudstam & Magnuson (1985) | mesotrophic | 36 | 7 | - | - | - |
| | Rudstam & Magnuson (1985) | oligotrophic | 20 | 18 | - | 12 | - |
| | Lyons (1987) | oligotrophic | 20 | 3-4 | - | - | - |

[†], max. depth; [‡] predicted dep

# Chapter 3: Foraging Mechanisms of Siscowet Lake Trout (*Salvelinus namaycush siscowet*) on the Benthic Deepwater Sculpin (*Myoxocephalus thompsonii*): Effect of Light Intensity and Substrate Type on Predator-Prey Interactions

**Synopsis**

The foraging characteristics of siscowet lake trout (*Salvelinus namaycush siscowet*) on deepwater sculpin (*Myoxocephalus thompsonii*) were studied under ecologically relevant light intensities ($9.0 \times 10^8$ to $1.62 \times 10^{11}$ photons m$^{-2}$ s$^{-1}$) and on varying substrates (gravel, sand, and black fabric). Siscowet reaction distance was directly correlated with increasing light intensity until saturation at to $6.0 \times 10^9$ photons m$^{-2}$ s$^{-1}$, thereafter remaining constant for the tested light intensities. Reaction distances were not affected by substrate type. A predictive model for reaction distance to benthic prey was developed to determine reaction distances for siscowet in various photic environments. Prey capture increased with increasing light intensity with the overall probability of prey capture and siscowet reaction distance increasing with light intensity. Siscowet reaction distance to deepwater sculpin did not significantly differ between 60° increments along the siscowet midline (forward, lateral or rear visual sectors) and siscowet remained active at all non-zero light levels. Results suggest siscowet can visually forage on benthic prey at great depth in Lake Superior and may not exhibit diminished reaction distances (≤ 27 cm) to sculpin until depths exceed 200 m ($6.00 \times 10^9$ photons m$^{-2}$ s$^{-1}$). At lower light levels, they may rely entirely on additional sensory modalities.

**Introduction**

Predator-prey interactions influence the distribution and abundance of freshwater species (Kerfoot & Sih, 1987). Both the habitat characteristics and the physical-chemical environment (Cooper & Crowder, 1979; Kitchell, 1979; Crowder et al., 1981) affect the outcome of these interactions, which are ultimately a determining factor in the structure of aquatic communities (Carpenter et al., 1985; Beauchamp et al., 2007). Encounters between piscivorous fishes and their prey depend upon the degree to which the environmental characteristics modify detection (Beauchamp et al., 1999). Changing light intensity, (Mazur & Beauchamp, 2003; Hansen et al., 2013; Keyler et al., 2015) can have a strong influence on predator-prey interactions in fishes and substrate type (Houtman & Dill, 1994; Ellis et al., 1997; Sowersby et al., 2015) can additionally influence interactions between benthic species. Light can influence the daily movements and success of visually foraging fishes (Aksnes & Utne, 1997; Boscarino et al., 2010) while substrate can affect fish behavior and crypsis (Ellis et al., 1997; Ruxton et al., 2004; Stevens & Cuthill, 2006). These environmental characteristics can alter prey detection and the distance at which a fish first responds to prey (Munz & McFarland 1977; Ruxton et al., 2004).

Reaction distance is a critical measurement for evaluating prey detection (Howick & O'Brien, 1983; Miner & Stein, 1996; Vogel & Beauchamp, 2013) and is an important metric in visual foraging models. These models are useful for predicting predation effects, foraging success, and fish distributions in response to environmental changes such as decreased water clarity (Vogel & Beauchamp, 1999). To estimate the volume of water searched during foraging (e.g. volume of a cylinder), these models typically use the

square, or another exponent, of the reaction distance (Eggers, 1977). Therefore, minor errors in reaction distance estimates will influence the accuracy of model predictions (Vogel & Beauchamp, 1999). For example, the use of reaction distances for a piscivore detecting pelagic prey in a benthic foraging model may overestimate reaction distance, and therefore search volume, due to differences in prey behavior and the additional substrate component. Current model simulations of predator-prey interactions without accurate prey detection are inherently biased (Roth et al., 2008); among information on visual and spectral sensitivity, improvements may be made by accounting for how predation is influenced by differences in light intensity, prey type and associated habitat (e.g. benthic vs. pelagic).

A thorough examination of predator-prey interactions between species that occupy the offshore benthic environment is needed to determine how perception of prey can vary between benthic and pelagic environments. Within the Lake Superior offshore system, the siscowet (*Salvelinus namaycush siscowet*), a deepwater morphotype of lake trout, is the most abundant piscivore (Gorman et al., 2012a,b). Siscowet perform diel vertical migration (DVM), characterized by moving shallower in the water column at night to consume kiyi (*Coregonus kiyi*) which are in turn following migrating mysid shrimp (*Mysis relicta*; Gorman et al., 2012a; Hrabik et al., 2006; Jensen et al., 2006). During the day, siscowet move to deeper water and are found between 80 m (Harvey et al., 2003) and 400 m (Sitar et al., 2008) where they prey upon deepwater sculpin (*Myoxocephalus thompsonii*). Deepwater sculpin (hereafter sculpin) are a benthic, profundal species which represent the bulk of demersal prey in the deepest areas of the lake, ~11% of the total fish biomass in Lake Superior (Gorman et al., 2012a,b; Sierszen,

2014), and comprise up to 70% of the siscowet diet by mass (Issac, 2010; Stockwell et al., 2010). Due to the greater depths where siscowet forage on sculpin, these predator-prey interactions take place within a light-limited environment.

Our objectives were to determine the visual foraging characteristics of siscowet on the benthic deepwater sculpin under ecologically relevant light intensities ranging from $9.0 \times 10^8$ to $1.62 \times 10^{11}$ photons m$^{-2}$ s$^{-1}$ and on various substrates (gravel, sand, and black fabric). We determined siscowet reaction distance to prey, angle of attack, forage activity, and foraging success. Finally, a predictive model of benthic prey detection was developed for siscowet using the association between light intensity and reaction distance. By studying both the effects of light and substrate, we can determine the importance of each factor as well as include interactions not apparent in one factor experiments (Vogel & Beauchamp, 1999). This work examines the less-studied interactions between a benthic/pelagic predator and a benthic prey that occupy a low-light environment.

**Materials and Methods**

*Fish Collection and Husbandry:* Siscowet lake trout (N=5) and deepwater sculpin (N=215) were collected in collaboration with the US Geological Survey (Ashland, WI) aboard the R/V *Kiyi* via bottom trawls. Sculpin were collected on 19 May 2015, 24 June 2015, and 31 July 2015 while siscowet were collected on 18 November 2015. Ten-minute trawls (12 m Yankee bottom trawl) were performed east of Stockton Island on Lake Superior (Latitude: 6° 54.751' Longitude: 90° 30.611') at depths between 110 and 120 m within the demersal stratum. Trawls were towed on contour between 1000 and 1300 hours. The surface temperature was 7.4°C for the May cruise, but >10°C for the

June and July cruises resulting in thermal shock for collected sculpins. Ice was added to collection boxes to minimize these effects and there was sufficient survival to conduct foraging trials. A more detailed account of collection and immediate care of fishes post-trawl can be found in Gorman and Keyler (2016).

To minimize transport stress (e.g. Carmichael et al. 1984), siscowet and sculpin were transferred to temporary tanks (100 L) for 5 minutes containing 4-6°C, oxygenated water with 0.5% NaCl (Instant Ocean® Aquarium Systems Inc., Mentor, OH), 24 mg/L Stresscoat® (Mars Fishcare North America Inc., Chalfont, PA), and 15 mg/L MS-222, tricaine methanesulfonate (Sigma Chemical Co., St. Louis, MO). Upon transfer to temporary tanks, siscowet swim bladders were then immediately vented using a sterilized (70% ethanol emersion) 14-gauge veterinary needle (QC Supply, Schuyler, NE). Needle insertion sites were cleansed with Betadine® iodine tincture (Purdue Products L.P., Stamford, CT). Fish were then transferred to continuously oxygenated transport tanks (284 L) consisting of a 0.5% NaCl, 24 mg/L Stresscoat®, and 15 mg/L MS-222 chilled lake water solution for truck transport from Ashland WI to the permanent housing facilities at the University of Minnesota Duluth (Duluth, MN).

Fish were separated by species and housed at the university in four oxygenated poly 568 L stock tanks (Miller Manufacturing Company, Glencoe, MN) treated with 0.5% NaCl, 24 mg/L Stresscoat®, 5 mg/L MS-222. Tank water was mechanically filtered (700L/hour) by canister filters (Penn-Plax Cascade™) with biological media. Seven days post-fish introduction, oxygenation of water ceased and carbon filtration was initiated. All tanks were maintained in cold rooms at an ambient 5.5°C with a diel photo period of 14 h light : 10 h dark and a light intensity of $3.05 \times 10^9$ photons m$^{-2}$ s$^{-1}$ for the diurnal

segment.  Additionally, ammonia, nitrite, and pH levels were maintained at <1 ppm, <10 ppm, and ~7.2, respectively and recorded twice daily for the first two weeks and then daily thereafter.  To limit exposure to ambient light, cold room doors were lined with foil and black cloth baffling was suspended from floor to ceiling at cold room entrance.  All husbandry and tank maintenance was conducted under low intensity red light (Sunbeam 40 W, 630-700 nm, $\sim 1.62 \times 10^{13}$ photons m$^{-2}$ s$^{-1}$) to limit disturbance to fish.  All fish husbandry and experimentation conformed to the University of Minnesota animal care protocols and were approved by the Institutional Animal Care and Use Committee Protocol ID: 1504-32496A in addition to the recommendations within the Guide for the Care and Use of Laboratory Animals of the National Institutes of Health.

*Foraging Arena:* An 1892 L rectangular (2.28 m x 1.0 m) fiberglass tank with water temperature maintained at 5.5°C was used for the foraging arena. The inside of the tank was lined with black cloth and water depth maintained at 0.4 m.  Two Penn-Plax canister filters on each end of the tank mechanically, chemically and biologically filtered tank water, until testing periods when filters were inactivated.  One siscowet and one sculpin were separated by an opaque acrylic lift gate before trial initiation (Fig. 1) which was then manually raised by a technician positioned behind suspended black fabric to eliminate observer interference.

*Substrates:* Three different substrates were used independently for each round of trials (5 light intensities), including gravel (KolorScape$^{TM}$, Atlanta, GA), sand (Quikrete, Atlanta, GA), and black fabric (ProMat Inc., Maryville, TN). Using the Wentworth scale (Wentworth, 1922), gravel and sand substrates were classified by diameter (mm) of grain. Diameters of gravel measured 8-16 mm, and sand measured 0.5-1 mm, designating the

substrates *medium gravel* and *course sand* by Wentworth class, respectively.  Substrates

were washed and applied to tank bottom creating a level (5 cm deep for non-fabric

substrates) surface.

*Lighting and Recording:* The experimental lighting, tested light intensities, and

recording procedures follow Keyler et al. (2015).  Briefly, 500-510 nm cyan LED lights

(Cree XLamp XR Series, Durham, NC) replicating downwelling light within Lake

Superior (Jerome et al., 1983) were mounted above the foraging arena.  Light intensities

were manipulated via a controller (outside of cold room) and required the application of

neutral density filters (FOTGA, Hong Kong, CH). For the upper light intensities

$(1.86{\times}10^{11}$ and $1.62{\times}10^{13}$ photons m$^{-2}$ s$^{-1}$) a 0.3 neutral density filter (FOTGA, Hong

Kong, CH) was placed over the light source. To reach the lowest light intensities tested (6

$\times 10^9$ to $9 \times 10^8$ photons m$^{-2}$ s$^{-1}$), a combination of 0.6 and 0.9 neutral density filters were

added in addition to the 0.3 filter to lower light levels to desired levels.

Light intensities were measured at the water's surface using an International Light

Technologies ILT1700 Research Radiometer (Peabody, MA) and a SED033/F/HMR/W

broadband silicon detector which measures light intensity in watts cm$^{-2}$ s$^{-1}$.  Infrared LED

lights (CMVision, Houston, TX) provided additional illumination for the three wide-

angle cameras (Vantage, night vision, model LBC7081) suspended above the tank for a

top-down perspective.  Foraging recordings were digitally saved to a DVR (ECO2 series,

LH130, Lorex Technologies, Markham, ON).

The five tested light intensities were $9.00{\times}10^8$, $3.05{\times}10^9$, $6.00{\times}10^9$, $1.86{\times}10^{11}$,

and $1.62{\times}10^{13}$ photons m$^{-2}$ s$^{-1}$ approximately equivalent to 0.0001, 0.0005, 0.001, 0.01,

and 1 lux, respectively, where $9.00{\times}10^8$ photons m$^{-2}$ s$^{-1}$ (0.0001 lux) represents total

darkness (no light source, sealed, blackened room). Conversion of measurements from watts cm$^{-2}$ s$^{-1}$ to photons m$^{-2}$ s$^{-1}$ were calculated using the methods of Harrington et al. (2015). To determine the depth ($x$) within Lake Superior that correlates to each tested light intensity, the Beer-Lambert equation was used (Hutchinson, 1957):

$$I_x = I_0 e^{-kx} \tag{2}$$

Where $I_0$ is the average Lake Superior summer solar surface irradiance from Fahnenstiel et al. (1984), and $k$ is the attenuation value for Lake Superior waters. For lunar surface irradiance, values from Arizona (Cramer et al., 2013) were used since Lake Superior surface irradiance is reported in lux, an inappropriate unit for fish visual studies (Johnsen, 2012).

*Foraging Trials:* Foraging trials were conducted between 2 February 2016 and 23 March 2016 after collected siscowet resumed actively foraging for prey. Each siscowet (N=5) was tested twice at each light intensity (N =5) on each substrate (N =3) for a total of 150 trials. Each fish received a visible implant alpha tag (VI Alpha, Northwest Marine Technology, Inc., Shaw Island, WA) implanted superficially in the transparent tissue posterior to the left eye and anterior to the operculum for individual fish identification. Tags were implanted in dermal tissue and did not affect or interfere with vision. Siscowet were small sexually mature adults ranging from 420-510 mm in total length ($L_T$) aged approximately 12-17 years (Gorman, U.S. Geological Survey, 2018, personal communication) while sexually mature adult sculpin used in foraging trials (N= 150) were an average of 79.0 ±0.58 mm $L_T$. Prior to a trial, a 20 x 20 cm acrylic square

outlined in red striping tape (3M, St. Paul, MN) was temporarily placed on the bottom of the tank (removed before trial start) and a brief recording is made to aid in digitally analyzing distance of predator/prey movements. One naïve (not previously used in a trial) sculpin was then introduced to the foraging arena while a siscowet was placed within the holding area of the tank; both were acclimated to the testing light intensity for a minimum of 30 min. After acclimation, the gate was lifted, recording started and the trial commenced lasting 10 min or until prey capture.

*Data Analysis and Foraging Parameters:* Digital foraging images were analyzed using ImageJ software (NIH, v. 1.5p) to determine predator reaction distance to prey and *vice versa* as well as siscowet angle of attack. Angle of attack was calculated as the angle of the sculpin off-axis from the longitudinal axis of the siscowet from midpoint of predator eyes to midpoint of prey body just prior to locating (turning of head) and orientating toward prey. For siscowet, we determined reaction distance as the distance from the midpoint of the siscowet's eyes to the midpoint of the sculpin body calculated at the moment of first detection and orientation toward prey. Foraging success was calculated as the overall probability of a siscowet locating, pursuing, attacking, and retaining the sculpin; whether sculpin were moving or stationary prior to attack was also recorded (Richmond et al., 2004; also see Keyler et al., 2015). Siscowet activity was also monitored and the siscowet defined as 'active' if moving around the arena for $\geq 50\%$ of the trial.

*Modeling and Statistical Analysis:* The reaction distance for siscowet to sculpin was fit to a Michaelis–Menten saturation function (O'Neill et al., 1989) in order to

demonstrate the relationship between reaction distance ($R_d$ cm) and light intensity ($L_i$, photons m$^{-2}$ s$^{-1}$).  This model is represented by:

$$R_d = \frac{R_{max}L_i}{\alpha + L_i} \tag{3}$$

Where $R_{max}$ is equal to the maximum reaction distance (cm) and $\alpha$ is equal to the half saturation constant (photons m$^{-2}$ s$^{-1}$).  The model has successfully described the relationship between reaction distance and light intensity for siscowet to golden shiners (*Notemigonus crysoleucas*) in Keyler et al. (2015).

When examining the proportion of siscowet orientations among 60° increments between foraging arena substrates, we determined whether proportions were different in the 3x3 contingency table (3 substrates x 3 60° increments) using Fisher's exact test. We then made pairwise comparisons to determine whether substrates differed using pairs of 2x2 contingency tables (2 substrates x 2 60° increments). Because the ±120–180° were clearly different for all substrates, we only performed 3 pairwise tests, comparing each pair of substrates for the ±0–60° and ±60–120° segments using a Fisher's exact test.  To reduce the chance of type-I error with multiple comparisons, a Bonferroni correction was used and the significance level of 0.017 was used instead of 0.05 for those tests. We used 60° increments to provide higher N values in order to determine statistical differences not detected between 30° increments.

Statistical analysis was performed using JMP software (JMP $^{®}$ Pro v.12.0.1, Statistical Analysis System Institute Inc., Cary, NC).  Data were tested for homoscedasticity and normality prior to performing parametric tests. Normality was

tested using a Shapiro-Wilk test and equal variances were tested using a Brown-Forsythe test. All statistical tests used a significance value of $\alpha$=0.05. Pooled results are representative of 150 trials while those listed by substrate represent 50 trials.

**Results**

Light intensity significantly influenced siscowet reaction distance (Fig. 2; Two-way ANOVA, $F_{11,180}$=3.22, p=0.0005; light intensity main effect, $F_{3,180} = 9.12$, p<0.0001). Reaction distance increased asymptotically with light intensity for all substrates from $9.00 \times 10^8$ to $6.0 \times 10^9$ photons m$^{-2}$ s$^{-1}$ and leveled at higher light intensities (Tukey's HSD, p=0.0146). Although reaction distance tended to be higher on black fabric compared to gravel and sand (Fig. 2a), the effect was not significant at the $\alpha$=0.05 level (Substrate effect, $F_{2,180}$=2.79, p=0.064). Additionally, the interaction between light intensity and substrate was not significant ($F_{6,180}$=0.01, p=0.996).

A Michaelis–Menten function was used to estimate the relationship between light intensity ($L_i$, photons m$^{-2}$ s$^{-1}$) and reaction distance ($R_d$, cm) to benthic prey. Data were pooled because there was no significant effect of substrate on reaction for all substrates. The model accounted for 97% of the variability in reaction distance (Fig. 3; Non-linear regression, $R^2 = 0.97$, $t_3$= 24.01, p=0.0016). The estimates of model parameters were $R_{max}$ = 44.02 and $\alpha = 1.83 \times 10^9$.

Siscowet orientations to sculpin were not equally distributed among 60° increments for black fabric (Fig. 4; $\chi2 = 54.74$, $d.f. = 2$, $p < 0.0001$), gravel ($\chi2 = 39.97$, $d.f. = 2$, $P < 0.0001$), or sand ($\chi2 = 27.11$, $d.f. = 2$, $p < 0.0001$). For fabric and gravel, significantly more orientations towards prey occurred within the forward sector from $\pm$0–60° (fabric N=56, gravel N=46) than for lateral sector, $\pm$60–120° (fabric N=20, gravel

N=21) and rear sector, ±120–180° (fabric N=4, gravel N=3). For sand, no orientations towards prey occurred for the rear sector, but nearly equal number of orientations occurred in front (N=26) and lateral (N=28) sectors. Although siscowet were generally more likely to orient to prey within ±60° of their midline, siscowet reaction distance to sculpin was the same across 60° increments and substrates (Two-way ANOVA, $F_{7,196}$=1.96, p=0.0617).

There was no significant difference in prey capture between foraging arena substrates (Fig. 5; $\chi2 = 3.167$, $d.f. = 2$, $p =0.21$). Siscowet had 24% overall foraging success (36 prey captures) for pooled light intensity and substrate data. There was an increase in foraging success with increasing light intensity from 0% (0 captures) at $9.00 \times 10^8$ photons m$^{-2}$ s$^{-1}$ to 43% success (13 captures) at $1.62 \times 10^{13}$ photons m$^{-2}$ s$^{-1}$. There was a significant positive correlation between overall probability of prey capture and reaction distance at each light intensity (Fig. 6; Spearman's rank correlation coefficient, $\rho$(rho)=0.9, $p= 0.037$). Below $6.0 \times 10^9$ photons m$^{-2}$ s$^{-1}$, both reaction distance and probability of capture begin to decline for all 3 substrates and in the dark tested trials, all reactions were ≤ 20 cm with no captures (Fig. 7). Finally, foraging success was independent of siscowet activity at all non-zero light levels. Siscowet showed ≥ 50% activity for approximately 80% of trials on all substrates for non-zero light levels; however, activity declined to 53% in dark trials. There was no significant difference in activity between substrates (Table I; $\chi2 = 1.632$, $d.f. = 2$, $p =0.44$).

**Discussion**

Light can determine the timing and success of visual foraging in fishes (Aksnes & Utne, 1997; Boscarino et al., 2010). Due to diurnal migration behavior, and the depths of

water inhabited, siscowet consistently occupy a low-light environment. Our study reveals that siscowet are capable of extreme low-light intensity foraging, even when compared to other lake trout morphotypes (see Vogel & Beauchamp, 1999; Mazur & Beauchamp, 2003). Siscowet reaction distance within our trials increased with light intensity up to $6.0 \times 10^9$ photons m$^{-2}$ s$^{-1}$, after which reaction distance remained constant with additional increases in light intensity following the Michaelis–Menten saturation function.  The number of prey captures also increased with increasing light intensity, with the majority of orientations toward prey occurring on average within the siscowet's forward sector ($\pm 0$–60°). Finally, there was a strong positive correlation between overall probability of prey capture and reaction distance at each light intensity.  While substrate is known to influence prey behavior and crypsis, (Ellis et al., 1997; Ruxton et al., 2004; Stevens & Cuthill, 2006) neither siscowet reaction distance nor prey capture were affected by substrate type in our trials, a possible product of decreased contrast perception at lower light intensities.

The effect of light intensity on prey detection and foraging success is critical when defining spatial and temporal limits of a species' niche (Beauchamp et al., 2003). On a clear summer's day, the highest tested light intensity in our study correlates to a depth of ~130 m within Lake Superior; however, siscowet occupy the demersal zone during the day and are typically found below 150 m (Stockwell et al., 2006).  Our results suggest siscowet can visually forage well below 150 m and would not exhibit diminished reaction distance to prey until depths >200 m ($6.00 \times 10^9$ photons m$^{-2}$ s$^{-1}$) within Lake Superior (using solar light intensities predicted at depth from Keyler et al., 2015). At the second lowest light intensity, ($3.05 \times 10^9$ photons m$^{-2}$ s$^{-1}$, equivalent to ~205 m) siscowet

may visually forage, however reaction distances (~27 cm) and prey capture (10%) were reduced (Fig. 8). Siscowet in the dark trials displayed reaction distances ($\leq 20$ cm) consistent with other dark-tested species suggesting mechanosensory detection of prey, which is limited to half the body length of the predator (Price & Mensinger, 1999; Palmer et al., 2005; Keyler et al., 2015). Siscowet in the dark profundal zone of Lake Superior (Below $3.05 \times 10^9$ photons m$^{-2}$ s$^{-1}$) likely discontinue visual foraging and rely on other sensory modalities such as mechanosensory or chemosensory detection of prey.

At night, siscowet vertically migrate higher in the water column to within approximately 30 m of the surface (Ahrenstorff et al., 2011). Since siscowet generally occupy offshore waters >80 m depth (Harvey et al., 2003), and sculpin are most abundant at depths >90 m (Kraft & Kitchell, 1986), migrating siscowet will predominantly forage for kiyi when shallower at night (Gorman et al., 2012a, Hrabik et al., 2006). Keyler et al. (2015) determined that under lunar illumination, siscowet would not exhibit diminished reaction distance to pelagic prey until depths >46 m ($6.00 \times 10^9$ photons m$^{-2}$ s$^{-1}$). Given that kiyi are found between 30-40 m depth at night (Hrabik et al., 2006; Ahrenstorff et al., 2011), successful capture of kiyi by siscowet is possible under moonlight conditions.

In contrast to nighttime foraging, successful foraging by siscowet during the day within the dark profundal zone of Lake Superior is likely a product of the greater density and biomass of sculpins at depths >100 m (Stockwell et al., 2010; Gorman et al., 2012a,b; Pratt et al., 2016). Trawl data and stomach analysis confirms the consumption of sculpin by siscowet during the day when deeper in the water column (Gorman, U.S. Geological Survey, 2017, personal communication), despite siscowet foraging efficiency being reduced at light intensities of $3.05 \times 10^9$ photons m$^{-2}$ s$^{-1}$ and lower. It is known that

some predators will forage in suboptimal conditions if prey densities are high (Crowder & Cooper, 1982), which compensates for increased search time (Ware, 1973). To optimize foraging, siscowet must obtain the most energy (prey) per unit effort, which includes both the time and energy spent foraging (Werner & Hall, 1974). Due to their DVM behavior, siscowet effectively change foraging habitats throughout a 24-hour period, a strategy many animals use to optimize their foraging (Werner and Hall, 1979; Mittelbach, 1981; Werner et al., 1981). Lack of prey higher in the water column during the day likely drives siscowet into deeper and darker waters where prey densities are higher (Ahrenstorff et al., 2011) and successful foraging is possible.

Siscowet show both physiological and morphological visual adaptations for foraging within the dark, deep, offshore waters of Lake Superior. Generally, fishes are sensitive to the spectrum of light that is available within their environment (Munz & McFarland, 1973). Accordingly, lake trout have a 512 nm visual pigment (rhodopsin) and a 539 nm pigment (porphyropsin) (Munz & McFarland, 1965) that matches the downwelling spectra within Lake Superior, which varies between 500 and 550 nm seasonally (Jerome, 1983). Harrington et al. (2015) conducted electroretinography, which additionally accounts for *the in-vivo* neural processing associated with vision. The study determined maximum sensitivity at 525 nm with relatively broad sensitivity from 500 to 550 nm, again optimally aligning with the seasonal downwelling spectra. Morphologically, siscowet vison may be improved by their large eyes that are positioned higher on the head (when compared to the other morphotypes), effectively improving light capture (Meer et al., 1984), and binocular vision (Bond, 1996). Individually, a single fish eye has ~180° field of view (Land & Nilsson, 2012); however the binocular

field of vision (binocular overlap) is small for fishes and is limited to ~35° (Duke-Elder, 1958). Binocular vision is useful in that it provides stereopsis, or depth perception, which aids in prey capture. To optimize use of binocular vision, siscowet in our trials generally oriented to prey head-on upon detection, maneuvering to employ binocular vision within the forward sector (±0–60°; Vogel & Beauchamp, 1999).

The fewest sculpin captures occurred on the gravel substrate (from $6.00 \times 10^9$ - $1.62 \times 10^{13}$ photons $m^{-2}$ $s^{-1}$); although this result was not significantly different at the alpha of 0.05 level, but was at the 0.10 level. The narrow band of wavelengths provided by the LED lighting (500-510 nm) used in trials decreased contrast, likely obscuring camouflage effects at the lower tested light levels. For the upper tested light intensities, gravel likely provided the greatest camouflage by offering disruptive patterning complimenting the sculpin's coloration patterns to aid in crypsis. The disruptive pattern of the sculpin, including a brown body with dark dorsal saddles, banded pectoral fins, spotted sides and pelvic fins, and blotchy dorsal and anal fins (Scott & Crossman, 1973), may have hindered siscowet foraging success (Muntz 1990; De Robertis et al., 2003). Prey species employ a variety of strategies to avoid predator detection including crypsis (Ellis et al., 1997; Ruxton et al., 2004; Stevens & Cuthill, 2006), the use of cover (Mittelbach, 1981; Cerri & Fraser, 1983; Sass et al., 2006) and reducing activity when predators are present (Dill, 1983; Dill & Fraser, 1984; Sih, 1986; Prejs 1987). Crypsis is an especially effective tactic for benthic species, and substrates that offer sufficient camouflage can alter the prey response to predators (Houtman & Dill, 1994; Sowersby et al., 2015). Foraging trials that involve benthic species like sculpin must therefore consider the

foraging arena substrate to encourage normal predator-prey response behavior, and ultimately ensure the determination of more accurate foraging parameters.

It is possible that our tested substrates did not facilitate natural sculpin behavior, which could lead to variability in siscowet detection. The consistency of the natural lakebed of Lake Superior is complex, but can be generalized as soft gray clay in the eastern basin and red clay in the western basin (Gorman, U.S. Geological Survey, 2017, personal communication). The use of clay substrate in our trials proved impractical due to high turbidity which obscured foraging recordings. Sand offered similar uniformly colored habitat, however, clay may have additionally allowed sculpin to burrow to better hide, which was not observed on the sand substrate. For example, slimy sculpin (*Cottus cognatus*) have been observed burrowing into looser sediments when approached by divers (Brandt, 1986). Burrowing behavior in sculpin would likely significantly decrease siscowet reaction distance and foraging success.

Future behavioral studies examining the response of prey fishes to piscivorous species, not just predators to prey, would help to provide a more comprehensive understanding of predator-prey interactions within the offshore system. By simultaneously determining prey response through metrics such as reaction distance, we may be able to determine whether a species has a first detection advantage. Sculpin, for example, may detect siscowet first given their eyes being oriented upward, allowing them to silhouette potential predators from their benthic position. Additionally, a comparison between the foraging mechanisms of siscowet on benthic and pelagic prey should be made to examine how piscivory may vary among systems (Beauchamp et al. 1999). Reaction distances for benthic species may be less since these species sit below the

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siscowet's plane of vision, when compared to pelagic species. These considerations would allow for more accurate foraging models (Schindler, 2003; Jensen et al., 2006; Hansen et al., 2013), which can provide better estimates of foraging success, distribution of benthic/pelagic fishes, and information on how apex predators like siscowet influence community structure.

**Acknowledgements**
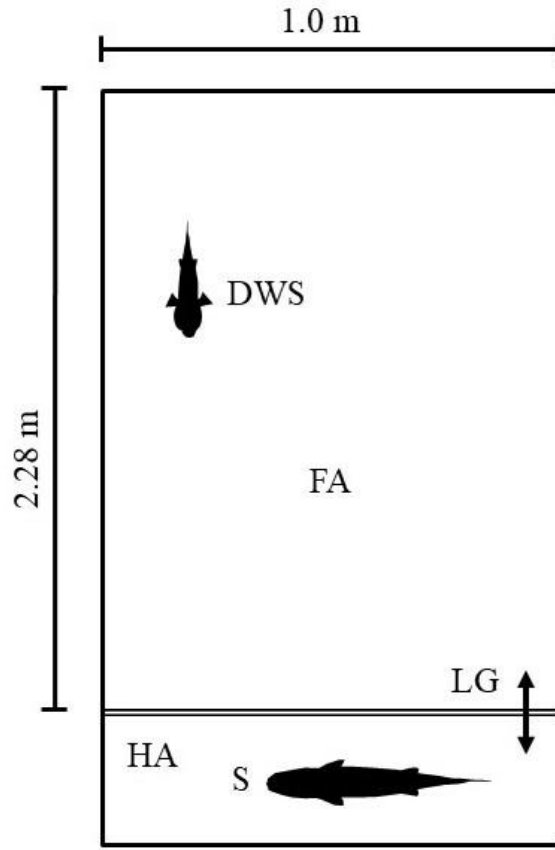
**Figure 1**: Top-view schematic of experimental foraging arena. Post-acclimation to trial light intensity, siscowet (S) were released from the holding area (HA) by raising the lift gate (LG) whereupon the siscowet entered the foraging arena (FA) to interact with the prey (DWS).
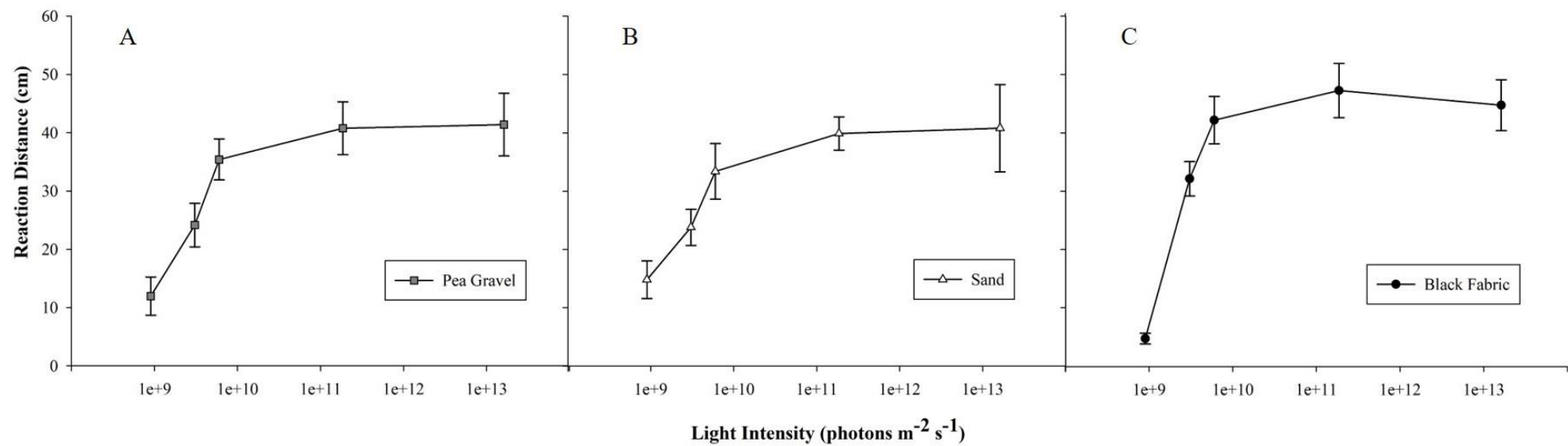
**Figure 2**:   Average reaction distance (cm) of siscowet in response to *Myoxocephalus thompsonii* at varying light intensity on (A)

gravel, (B) sand, and (C) black fabric substrates.  Error bars are ± 1 SE.
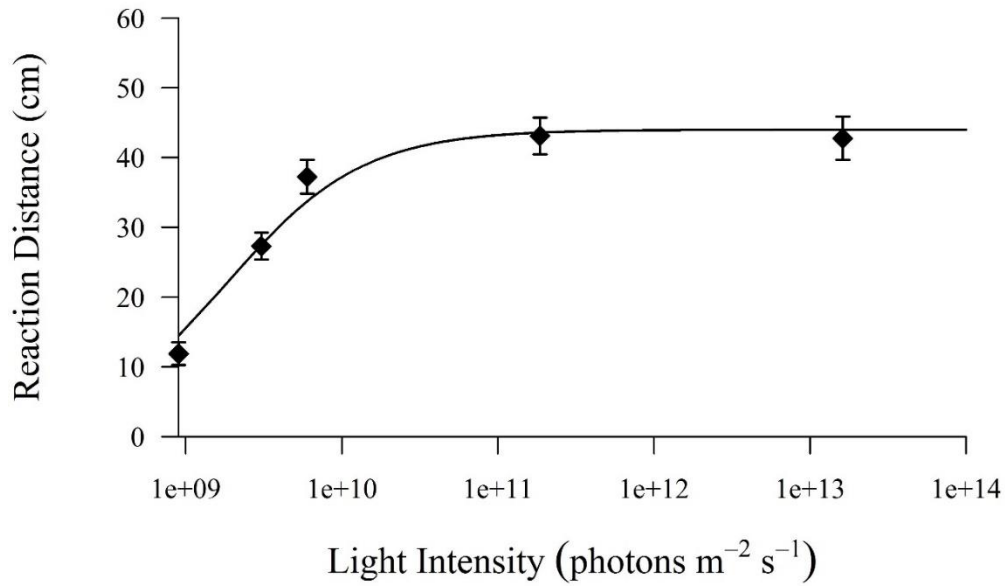
**Figure 3**: Michaelis–Menten function fitting data for the average reaction distance (cm) of siscowet in response to *Myoxocephalus thompsonii* at varying light intensity where $R_{max} = 44.02$ and $\alpha = 1.83 \times 10^9$ ($R^2 = 0.97$). Results are for pooled substrate data. Error bars for both panels are $\pm 1$ SE.
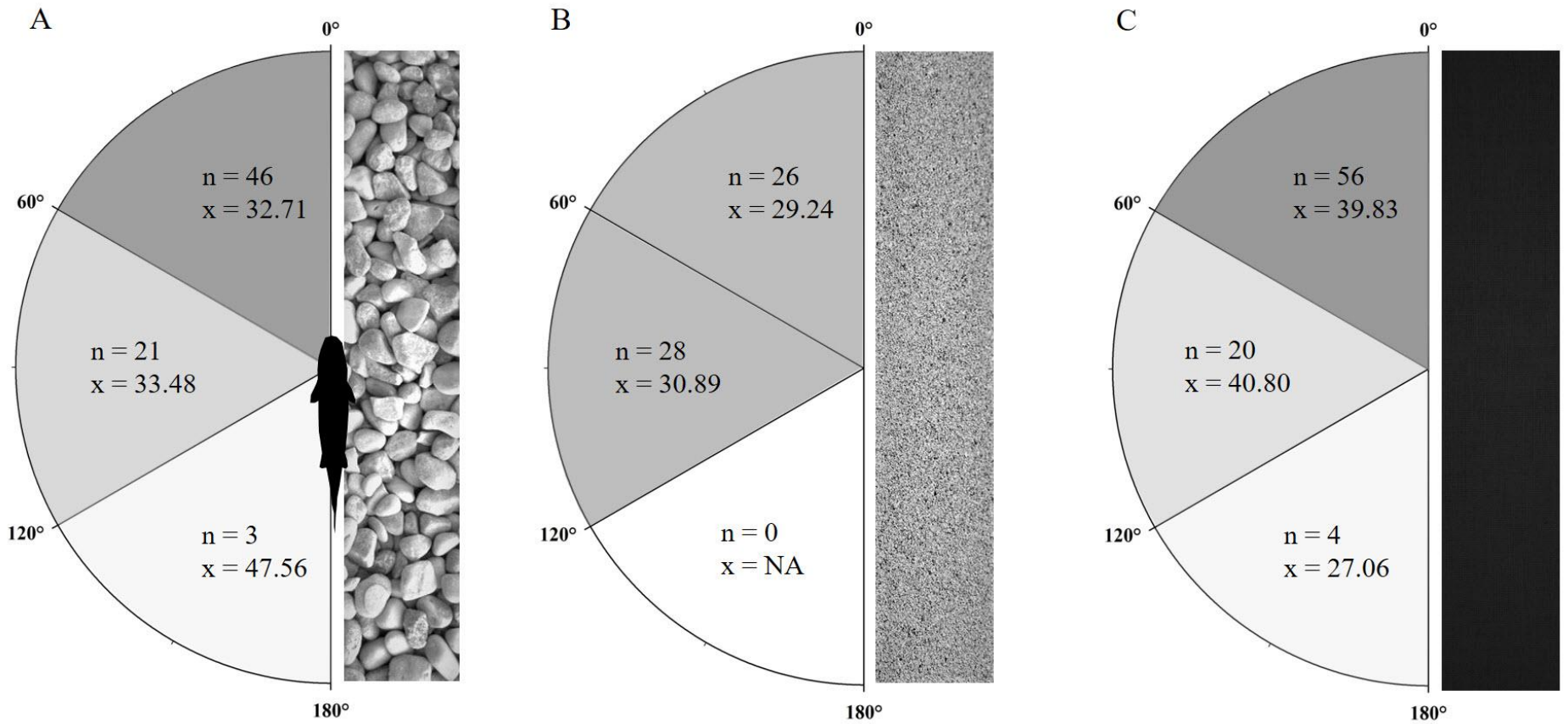
**Figure 4**: Average reaction distance (x) and total number of orientations (n) plotted within 60° increments for combined light intensities on (A) gravel, (B) sand, and (C) black fabric substrates. The solid fish figure in the middle (left panel) represents the orientation of the fish relative to degrees off axis of prey. The degree of shading for each 60° increment indicates a higher proportion of orientations.
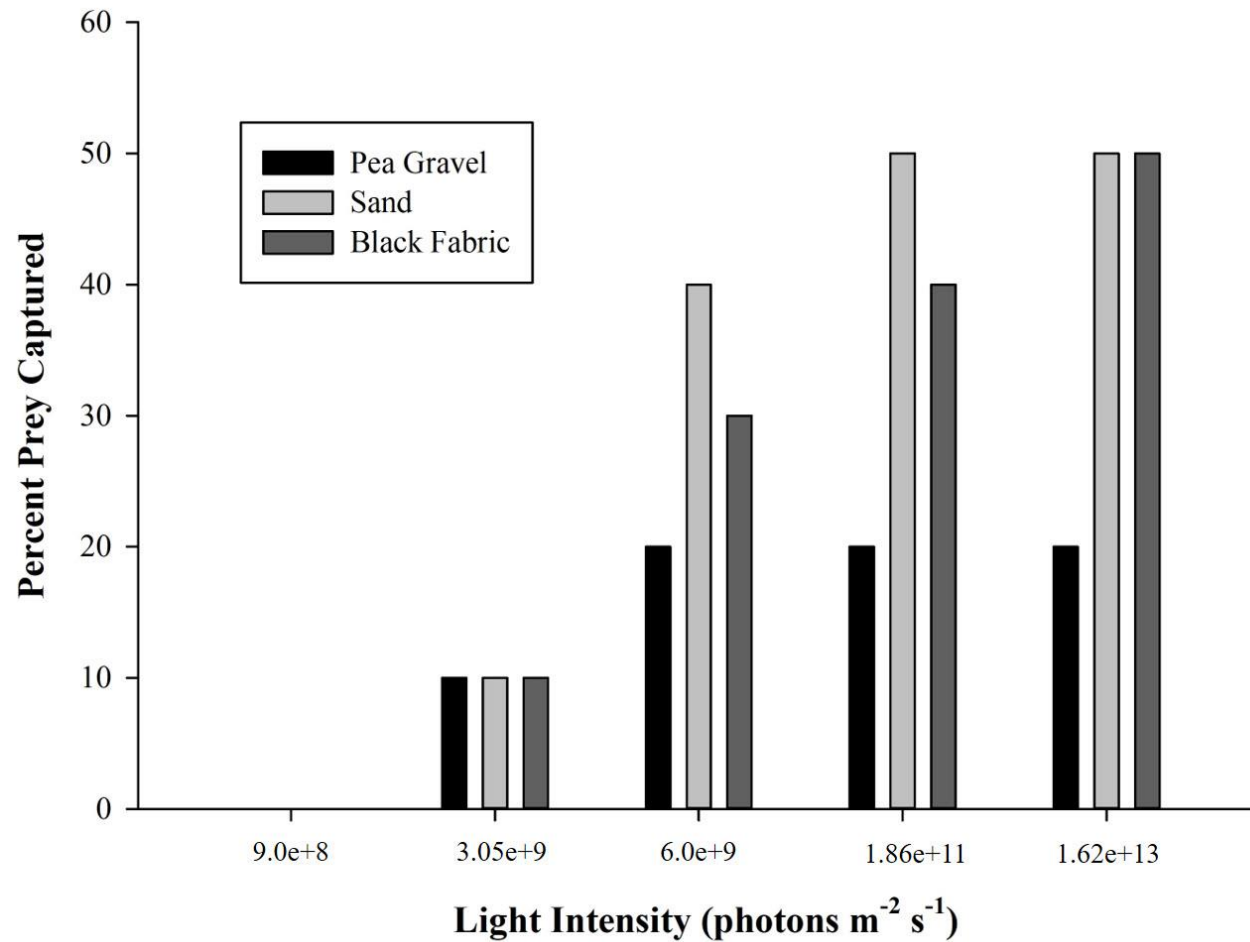
**Figure 5:** Percentage of benthic prey captured by siscowet at varying light intensity on gravel (black bars), sand (light grey bars) and

black fabric (dark grey bars) substrates. N=10 for each substrate light intensity combination; $\chi2 = 3.167$, *d.f.* = 2, *p* =0.21.
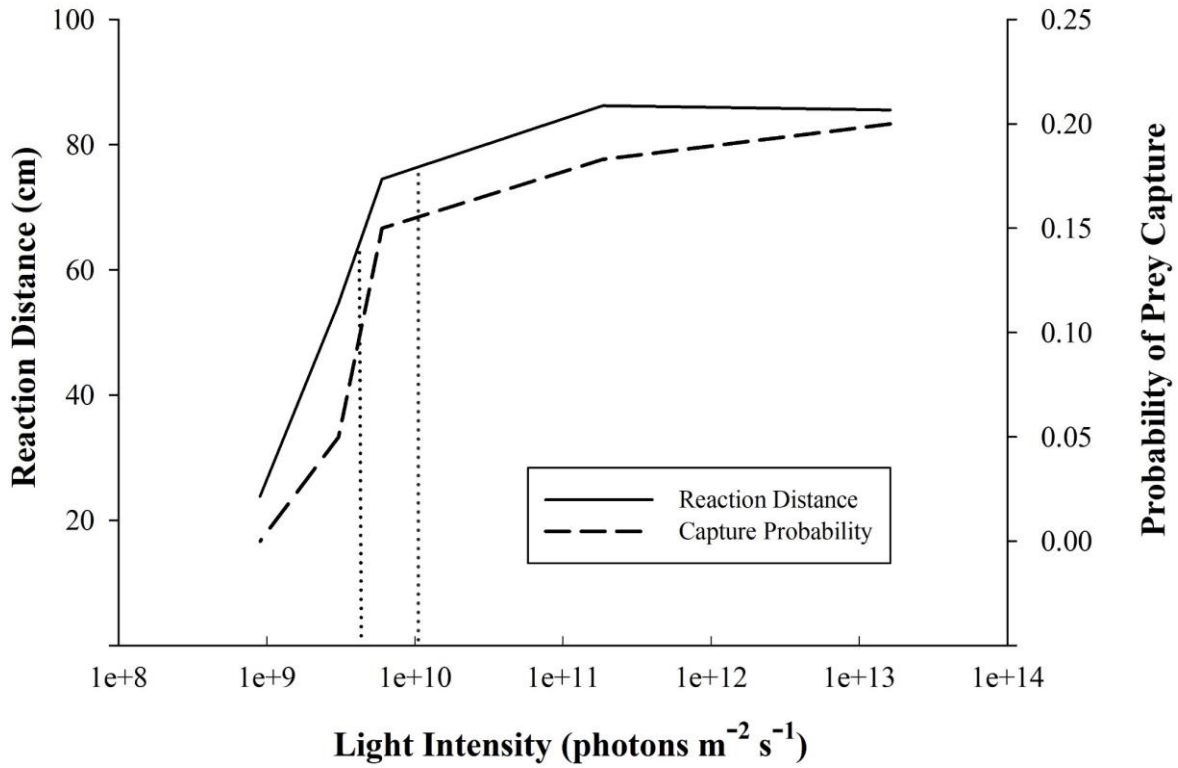
**Figure 6**: Correlation of prey capture probability (solid line) to siscowet reaction distance (dashed line) at corresponding light intensities for pooled substrates. Spearman's rank correlation coefficient, ρ=0.9. Grey, dotted vertical lines indicate light intensity range where both capture probability and reaction distance decline.
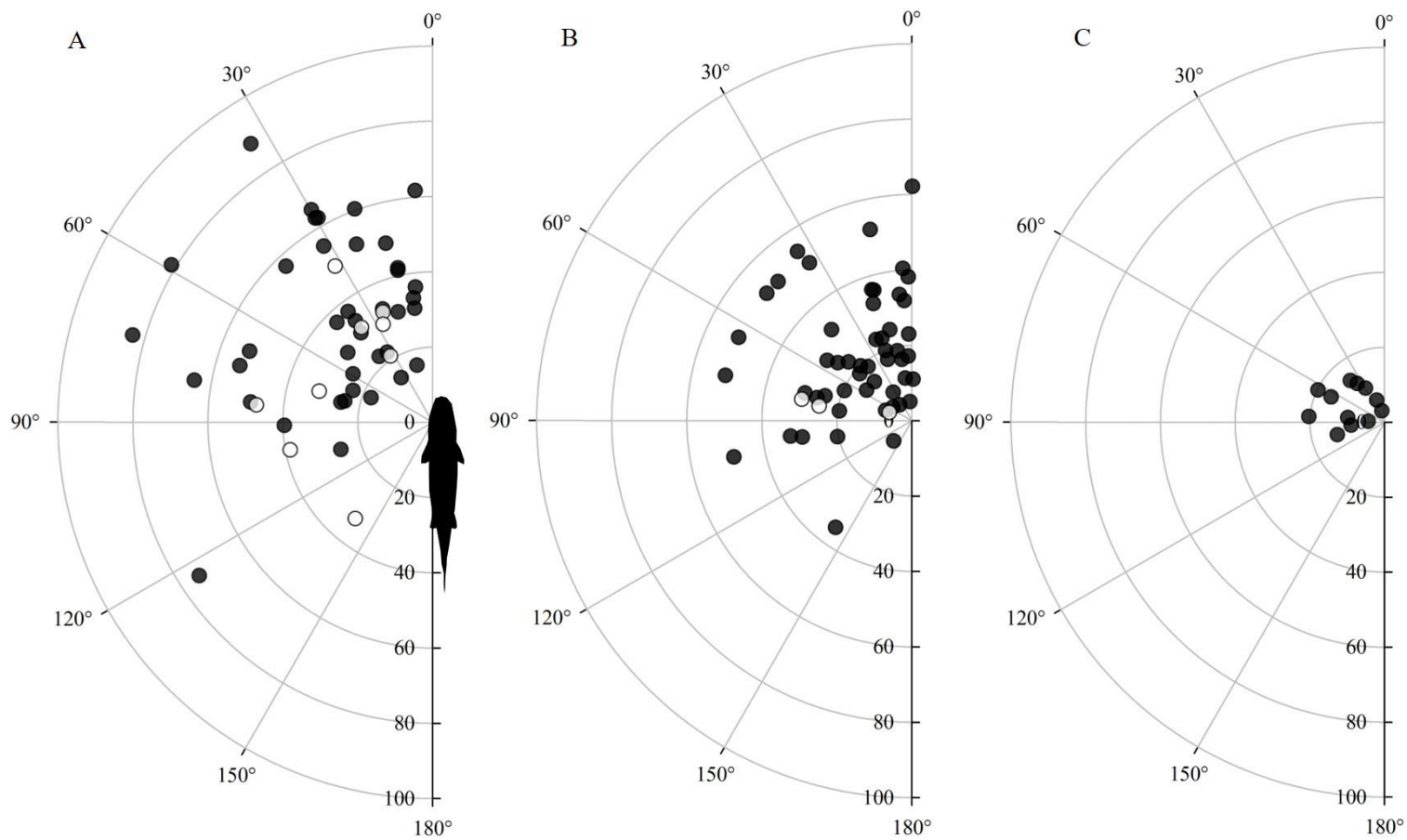
**Figure 7**: Polar plot diagram of reaction distance (cm) and angle of attack for siscowet lake trout in response to benthic prey for pooled substrates at three light intensities ranging from high to low (A) $1.86\times10^{11}$ (B) $3.05\times10^9$ and (C) $9.00\times10^8$ photons m$^{-2}$ s$^{-1}$. Solid shapes (●) represent orientation toward prey and open shapes (○) represent a capture. Each concentric circle represents 20 cm distance.
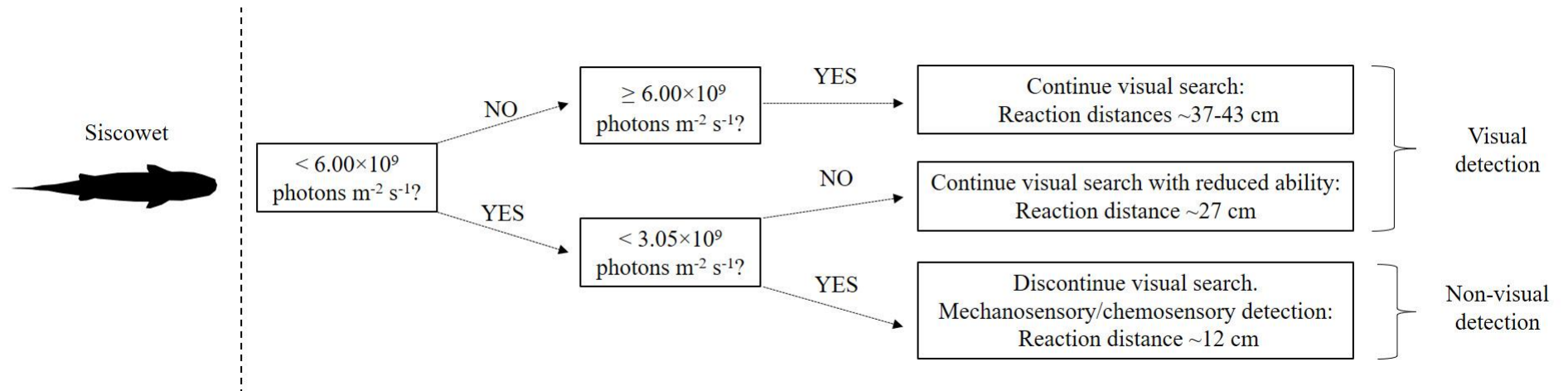
**Figure 8**: Siscowet prey hunting mode decision tree depicting the behavior and average reaction distance (cm) (for combined substrate data) as determined by the 5 tested light intensities (photons $m^{-2}$ $s^{-1}$).

**Table I**:  Percent of trials per substrate that siscowet showed >50% activity at varying light intensity. Activity is defined as actively foraging demonstrated by constantly swimming within the foraging arena.

| Substrate | Photons $m^{-2}$ $s^{-1}$ | Percent of trials (n=10) with >50% siscowet activity |
|---|---|---|
| Pea Gravel | $1.62 \times 10^{13}$ | 80 |
| | $1.86 \times 10^{11}$ | 70 |
| | $6.0 \times 10^{9}$ | 80 |
| | $3.05 \times 10^{9}$ | 80 |
| | $9.00 \times 10^{8}$ | 20 |
| Sand | $1.62 \times 10^{13}$ | 80 |
| | $1.86 \times 10^{11}$ | 70 |
| | $6.0 \times 10^{9}$ | 80 |
| | $3.05 \times 10^{9}$ | 90 |
| | $9.00 \times 10^{8}$ | 50 |
| Black Fabric | $1.62 \times 10^{13}$ | 80 |
| | $1.86 \times 10^{11}$ | 80 |
| | $6.0 \times 10^{9}$ | 100 |
| | $3.05 \times 10^{9}$ | 90 |
| | $9.00 \times 10^{8}$ | 90 |
| Average | $1.62 \times 10^{13}$ | 80 |
| | $1.86 \times 10^{11}$ | 73 |
| | $6.0 \times 10^{9}$ | 86 |
| | $3.05 \times 10^{9}$ | 86 |
| | $9.00 \times 10^{8}$ | 53 |

## Chapter 4: Deepwater Sculpin (*Myoxocephalus thompsonii*) Behavior: The Effect of Light Intensity and Predator Presence

**Synopsis**

The behavioral response of deepwater sculpin (*Myoxocephalus thompsonii*) to siscowet lake trout (*Salvelinus namaycush siscowet*) was studied under ecologically relevant light intensities ($9.0 \times 10^8$ to $1.62 \times 10^{11}$ photons m$^{-2}$ s$^{-1}$) that approximated downwelling wavelengths and on varying substrates (gravel, sand, and black fabric). Sculpin displayed suppressed activity in the presence of siscowet lake trout at the upper tested light intensities ($6.0 \times 10^9$ to $1.62 \times 10^{13}$ photons m$^{-2}$ s$^{-1}$). The average number of sculpin movements per trial increased with decreasing light intensity (up to $3.05 \times 10^9$ photons m$^{-2}$ s$^{-1}$ where after the number of movements remained similar) and the greatest increase in sculpin movement occurred from $6.0 \times 10^9$ to $3.05 \times 10^9$ photons m$^{-2}$ s$^{-1}$, the same light intensity threshold where siscowet reaction distance and prey capture both show the greatest decline. Deepwater sculpin reaction distance to siscowet was affected by both light intensity and foraging arena substrate. Sculpin reaction distance to siscowet showed a parabolic trend with increasing light intensity characterized by lower reaction distances in the dark, peaking at mid-range light intensities (between $3.05 \times 10^9$ and $6.0 \times 10^9$ photons m$^{-2}$ s$^{-1}$) and declining again at the upper tested light intensities. Reducing activity in the presence of predators is a common tactic for many cryptic species, and sculpin likely restricted movements to avoid detection by siscowet at greater light intensities.

**Introduction**

Light intensity (Emery, 1973; Clark & Levy, 1988; Helfman, 1993), substrate composition (Sowersby et al., 2015) and predator presence (Godin, 1986; Prejs, 1987;

Magnhagen, 1988) are a few recognized determinants of activity levels in fishes. Fish

behaviors that increase movement or activity are commonly associated with trade-offs

related to predator avoidance, foraging, and mating (Sih, 1980; Dill & Fraser, 1984;

Milinski, 1986). These movements are often influenced by the time of the day, and at

dusk, diurnal fishes reduce activity while nocturnal or crepuscular species become more

active (Helfman, 1981). Light intensities that inhibit the foraging of visual predators

allow fish that many be vulnerable to visual predation an opportunity to perform risk

taking behavior including foraging or mate seeking (Gregory & Northcote, 1993). While

many studies have examined the behavioral effects of light intensity or predator presence

independently, very few simultaneously measure both (see Endler, 1987; Cerri, 1993;

Sogard & Olla, 1993) which; more accurately represents natural environmental

conditions.

The risk of predation is a well-known determinant of activity levels in fishes

(Milinski & Heller, 1978; Dill, 1983; Metcalfe et al., 1987; Magnhagen, 1988). To

minimize detection by a predator, fish can use cover (Mittelbach, 1981; Cerri & Fraser,

1983; Werner et al., 1983; Schlosser, 1987; Sass et al., 2006) or reduce activity (Dill,

1983; Dill & Fraser, 1984; Godin, 1986; Sih, 1986; Prejs 1987). Movement increases

visibility to potential visual predators; therefore, some fishes decrease activity levels

when predators are nearby to lower encounter rates (Sih, 1987) while others flee. For

example, some gobiid fishes reduce foraging when a predator is present (Magnhagen,

1988). Similarly, banded killifish (*Fundulus diaphanus*) initiate fewer foraging attempts

in the presence of a predator (Godin, 1986) as do small tropical stream fishes (Prejs,

1987). This tactic is often associated with cryptic coloration, the morphological

adaptation of matching one's environment to avoid predator detection (Ellis et al., 1997; Ruxton et al., 2004; Stevens & Cuthill, 2006). Tidepool sculpins (*Oligocottus maculosus*), for instance, display cryptic coloration and reduce their movement by up to 65% on substrates that offer camouflage (Houtman & Dill, 1994).  These risk-minimizing adaptations help maximize the probability of survival for prey (Mange1 & Clark, 1986; McNamara & Houston 1986).

Light intensity is also a key determinant of activity levels in fishes (Emery, 1973; Clark & Levy, 1988; Helfman, 1993).  To reduce visual detection by predators, some fishes decrease activity during certain periods of the day (Emery, 1973; Helfman, 1993). The importance of light on predator-prey interactions is widely accepted (Eggers, 1977; O'Brien, 1987; Beauchamp et al., 1999) and light intensity is a major factor in determining the distance at which predators and prey can detect each other (Munz & McFarland 1977).  Detection distance decreases with light intensity (Howick & O'Brien, 1983; Miner & Stein, 1996; Vogel & Beauchamp, 2013, Keyler et al., 2015) and many prey fishes exhibit diel activity patterns associated with light intensities that minimize risk (Helfman, 1978).  While some fishes may reduce activity or swimming velocities during periods of low light (Helfman, 1993), others may take advantage of reduced visibility to predators to perform necessary daily behaviors, such as foraging (Scherer, 1976; Ryder, 1977; Wright & O'Brien, 1984).

Deepwater sculpin (*Myoxocephalus thompsonii*) are a benthic species that exist in low-light environments within Lake Superior.  They are a glacial relict representing ~11% of the total biomass within the lake (Gorman et al., 2012a,b), and are most abundant at depths greater than 90 m (Kraft & Kitchell, 1986). Deepwater sculpin

(hereafter sculpin) are a component of the offshore food web and primarily consume *Mysis relicta* and *Diporeia* (O'Brien et al., 2009). They also link profundal energy sources to upper level predators such as siscowet lake trout (*Salvelinus namaycush siscowet*; Madenjian et al., 1998). Additionally, sculpin are the most important component of the siscowet diet, comprising approximately 70% by mass (Issac, 2010; Stockwell et al., 2010). Siscowet perform diel vertical migration (DVM) characterized by moving shallower in the water column at night to consume kiyi (*Coregonus kiyi*) (Gorman et al., 2012a; Hrabik et al., 2006; Jensen et al., 2006; Stockwell et al., 2010) and returning to deeper water where they interact primarily with sculpin (Ahrenstorff et al., 2011; Gamble et al., 2011; Gorman et al., 2012a; Hrabik et al., 2014; Isaac et al., 2012).

To minimize risk, sculpin may restrict daily activities to periods when siscowet a) are absent from the profundal zone due to DVM, or b) visual detection of prey is reduced due to decreased light intensity. Our objectives therefore were to determine the effects of varying light intensities ranging from $9.0 \times 10^8$ to $1.62 \times 10^{11}$ photons m$^{-2}$ s$^{-1}$ as well as examine the effect of various substrates (gravel, sand, and black fabric) on sculpin activity in the presence of siscowet lake trout. These behavioral trials involving siscowet and the benthic deepwater sculpin will provide insight on predator-prey dynamics between two of the most abundant fish species in Lake Superior that contribute to overall ecosystem function.

**Materials and Methods**

*Fish Collection and Husbandry:* Siscowet lake trout (*n*=5) and deepwater sculpin (*n*=215) were collected with assistance from the US Geological Survey (Ashland, WI) aboard the R/V *Kiyi* via bottom trawls. Sculpin were collected on 19 May 2015, 24 June

2015, and 31 July 2015 while siscowet were collected on 18 November 2015. Ten minute trawls (12 m Yankee bottom trawl) were performed east of Stockton Island on Lake Superior (Latitude: 6° 54.751 Longitude: 90° 30.611) at depths between 110 and 120 m within the demersal stratum. Trawls were towed on contour between 1000 and 1300 hours. The surface temperature was 7.4°C for the May cruise, but >10°C for the June and July cruises resulting in thermal shock for collected fishes. Ice was added to collection boxes to minimize these effects and there was sufficient survival to conduct foraging trials. A more detailed account of collection and immediate care of fishes post-trawl can be found in Gorman and Keyler (2016).

To minimize transport stress as recommended by Carmichael et al. (1984), collected fish were transferred to temporary tanks (100 L) for 5 minutes containing chilled (4-6°C), oxygenated water with 0.5% NaCl (Instant Ocean® Aquarium Systems Inc., Mentor, OH), 24 mg/L Stresscoat® (Mars Fishcare North America Inc., Chalfont, PA), and 15 mg/L MS-222, tricaine methanesulfonate (Sigma Chemical Co., St. Louis, MO). Upon transfer to temporary tanks, siscowet swim bladders were then immediately vented using a sterilized (70% ethanol emersion) 14-gauge veterinary needle (QC Supply, Schuyler, NE). Needle insertion sites were cleansed with Betadine® iodine tincture (Purdue Products L.P., Stamford, CT). Fish were then transferred to continuously oxygenated transport tanks (284 L) consisting of a 0.5% NaCl, 24 mg/L Stresscoat®, and 15 mg/L MS-222 chilled lake water solution for truck transport from Ashland WI to the permanent housing facilities at the University of Minnesota Duluth (Duluth, MN).

Fish were separated by species and housed at the university in four oxygenated poly 568 L stock tanks (Miller Manufacturing Company, Glencoe, MN) treated with 0.5

NaCl, 24 mg/L Stresscoat®, 5 mg/L MS-222. Tank water was mechanically filtered (700L/hour) by canister filters (Penn-Plax Cascade™) with biological media. Seven days post-fish introduction, oxygenation of water ceased and carbon filtration was initiated. All tanks were maintained in cold rooms at an ambient 5.5°C with a diel photo period of 14 h light : 10 h dark and a light intensity of $3.05 \times 10^9$ photons $m^{-2} s^{-1}$ for the diurnal segment. Additionally, ammonia, nitrite, and pH levels were maintained at <1 ppm, <10 ppm, and ~7.2, respectively and recorded twice daily for the first two weeks and then daily thereafter. To limit exposure to ambient light, cold room doors were lined with foil and black cloth baffling was suspended from floor to ceiling at cold room entrance. All husbandry and tank maintenance was conducted under low intensity red light (Sunbeam 40 W, 630-700 nm, ~ $1.62 \times 10^{13}$ photons $m^{-2} s^{-1}$) to limit disturbance to fish. Experimental procedure and use of siscowet lake trout and sculpin conformed to the University of Minnesota animal care protocols and were approved by the Institutional Animal Care and Use Committee.

*Foraging Arena:* An 1892 L rectangular (2.28 m x 1.0 m) fiberglass tank in a 5.5°C cold room was used for the foraging arena. Sides were lined with black landscaping cloth and water depth maintained at 0.4 m. Two Penn-Plax canister filters on each end of the tank mechanically, chemically and biologically filtered tank water, until testing periods when filters were inactivated. Siscowet and sculpin were separated by an opaque acrylic lift gate before trial initiation (Fig. 1) which was then manually raised by a technician positioned behind suspended black fabric to eliminate observer interference.

*Substrates:* Three different substrates were used independently for each round of trials (5 light intensities), including gravel (KolorScape™, Atlanta, GA), sand (Quikrete,

Atlanta, GA), and black fabric (ProMat Inc., Maryville, TN). Using the Wentworth scale (Wentworth, 1922), gravel and sand substrates were classified by diameter (mm) of grain. Diameters of gravel measured 8-16 mm, and sand measured 0.5-1 mm, designating the substrates *medium gravel* and *course sand* by Wentworth class, respectively.  Substrates were washed and applied to tank bottom creating a level (5 cm deep for non-fabric substrates) surface.

 *Lighting and recording:* Lighting set up, tested light intensities, and recording procedures follow Keyler et al. (2015).  Briefly, 500-510 nm cyan LED lights (Cree XLamp XR Series, Durham, NC) replicating downwelling light within Lake Superior (Jerome et al., 1983) were mounted above the foraging arena.  Light intensities were manipulated via a controller (outside of cold room) and the lowest tested light intensities ($6\times10^9$ – $9\times10^8$ photons m$^{-2}$ s$^{-1}$) required the application of neutral density filters (FOTGA, Hong Kong, CH) to the LED light engines to decrease light emission.  Light intensities were measured at the water's surface using an International Light Technologies ILT1700 Research Radiometer (Peabody, MA) and a SED033/F/HMR/W broadband silicon detector which measures light intensity in watts cm$^{-2}$ s$^{-1}$.  Infrared LED lights (CMVision, Houston, TX) provided additional illumination for the three wide-angle cameras (Vantage, night vision, model LBC7081) suspended above the tank for a top-down perspective.  Foraging recordings were digitally saved to a DVR (ECO2 series, LH130, Lorex Technologies, Markham, ON).

 The five tested light intensities were $9.00\times10^8$, $3.05\times10^9$, $6.00\times10^9$, $1.86\times10^{11}$, and $1.62\times10^{13}$ photons m$^{-2}$ s$^{-1}$ approximately equivalent to 0.0001, 0.0005, 0.001, 0.01, and 1 lux, respectively, where $9.00\times10^8$ photons m$^{-2}$ s$^{-1}$ (0.0001 lux) represents total

darkness (no light source, sealed, blackened room). Conversion of measurements from watts $cm^{-2}$ $s^{-1}$ to photons $m^{-2}$ $s^{-1}$ were calculated using the methods of Harrington et al. (2015).

*Foraging Trials:* Foraging trials were conducted between 2 February 2016 and 23 March 2016. Each siscowet ($n=5$) was tested twice at each light intensity ($n=5$) on each substrate ($n=3$) for a total of 150 trials. Each fish received a visible implant alpha tag (VI Alpha, Northwest Marine Technology, Inc., Shaw Island, WA) implanted superficially in the transparent tissue posterior to the left eye for individual fish identification. Siscowet were small adults ranging from 420-510 mm $L_T$ while adult sculpin used in foraging trials ($n=150$) showed very little variation in size and were an average of 79.0 ±0.58 mm $L_T$. Prior to a trial, a 20 x 20 cm acrylic square is temporarily placed on the bottom of the tank (removed before trial start) and a brief recording is made to aid in digitally analyzing distance of predator/prey movements. Sculpin were then introduced to the foraging arena while a siscowet was placed within the holding area of the tank; both were acclimated to the testing light intensity for a minimum of 30 min. After acclimation, the gate is lifted, recording begins and the trial commences lasting 10 min or until prey capture.

*Sculpin behavior:* To determine the effect of substrate and light intensity on sculpin behavior, the number of sculpin movements was calculated for each trial. A movement was defined as a transition from rest to a change in any direction in the water column and ends when the sculpin rests. Additionally, we examined whether sculpin showed a preference for either of the three tested substrates. An additional poly 568 L stock tank (Miller Manufacturing Company, Glencoe, MN) within a cold room (5.5°C) subjected to the same filtration, photo period and light intensity described above, was divided into

equal thirds of gravel, sand, and fabric substrates.  One 48 hr trial was conducted where sculpin were released into the tank at 0700 hours and the number of sculpin (n=13) was counted at 12, 24, and 48 hr intervals.

*Statistical and data analysis:* Digital foraging images were analyzed using ImageJ software (NIH, v. 1.5p) to determine predator reaction distance to prey.  Sculpin reaction distance was determined just prior to an escape response and measured as the distance from sculpin rostrum to the nearest point on the siscowet.  Statistical analysis was performed using JMP software (JMP $^{®}$ Pro v.12.0.1, Statistical Analysis System Institute Inc., Cary, NC).  Data were tested for homoscedasticity and normality prior to performing parametric tests. Normality was tested using a Shapiro-Wilk test and equal variances were tested using a Brown-Forsythe test.  All statistical tests used a significance value of $\alpha$=0.05.  Pooled results are representative of 150 trials while those listed by substrate represent 50 trials.

**Results**

Light intensity and siscowet presence influenced sculpin movement during trials (Fig. 1; Two-way ANOVA, $F_{14,135}$=11.89, p<0.0001) and the average number of movements per trial decreased incrementally for each light intensity above $3.05\times10^9$ photons $m^{-2}$ $s^{-1}$ (Light intensity effect, $F_{4,135}$ = 39.28, p<0.0001). The greatest increase in sculpin movement occurred from $6.0\times10^9$ to $3.05\times10^9$ photons $m^{-2}$ $s^{-1}$ (Tukey's HSD, p<0.0001).  Correspondingly, we also see a significant decline in both siscowet reaction distance (Fig. 2a; Tukey's HSD, p=0.0146) and siscowet prey capture (Fig. 2b) at the $6.0\times10^9$ to $3.05\times10^9$ photons $m^{-2}$ $s^{-1}$ transition.  There was neither a substrate effect

($F_{2,135}=0.09$, p=0.9144) nor an interaction effect ($F_{8,135}=1.13$, p=0.3446) of light intensity on sculpin movement.

Light intensity and foraging arena substrate influenced sculpin reaction to siscowet (Fig. 3; Two-way ANOVA, $F_{14,367}=4.87$, p<0.0001). For all substrates, sculpin reaction distance initially increased with increasing light intensity and then decreased at the upper light levels ($1.86\times10^{11}$, and $1.62\times10^{13}$ photons m$^{-2}$ s$^{-1}$; light intensity effect, $F_{4,367} = 4.97$, p=0.0007). Sculpin reaction distance to siscowet was significantly higher for the gravel substrate (Fig. 9a) when compared to sand (Fig. 3b) and black fabric (Fig. 3c; Substrate effect, $F_{2,367}=11.89$, p<0.0001; gravel : sand, Tukey's HSD, p<0.0001; gravel : black fabric, Tukey's HSD, p=0.0003;  Interaction effect, $F_{8,367}=2.91$, p=0.0036).

Sculpin showed a significant preference for the gravel compared to sand and black fabric substrates ($\chi2 = 14.31$, *d.f.* = 2, *P* =0.0008). The ratio of substrate preference by sculpin was 8:3:2 for gravel, sand, and black fabric, respectively, and the same ratio was recorded at each of the three time intervals (12, 24 and 48 hr) despite sculpin actively moving on the preferred substrate.

**Discussion**

Reducing activity (Dill, 1983; Dill & Fraser, 1984; Godin, 1986; Sih, 1986; Prejs 1987) and/or matching the surrounding environment (Ellis et al., 1997; Ruxton et al., 2004; Stevens & Cuthill, 2006) are two successful tactics prey fishes employ to avoid detection by predators. While there was no effect of substrate on sculpin movement for our study, the average number of sculpin movements per trial increased with decreasing light intensity (until $3.05\times10^9$ photons m$^{-2}$ s$^{-1}$ where after remaining constant). Additionally, the greatest increase in sculpin movement occurred from $6.0\times10^9$ to

$3.05 \times 10^9$ photons m$^{-2}$ s$^{-1}$, the same light intensity transition where siscowet reaction distance and prey capture both show a greater decline. In contrast to sculpin movement, sculpin reaction distance to siscowet was affected by substrate type in addition to light intensity. Sculpin reaction distance showed a parabolic trend with increasing light intensity characterized by suppressed reaction distances in the dark, peaking at mid-range light intensities (between $3.05 \times 10^9$ and $6.0 \times 10^9$ photons m$^{-2}$ s$^{-1}$) and declining again at upper tested light intensities. Reaction distances to siscowet were greater on gravel, the substrate for which sculpin showed a preference when compared to sand and black fabric.

While sculpin movement increased with decreasing light intensity at all tested light levels, the greatest increase in movement was observed from the transition between $6.0 \times 10^9$ photons m$^{-2}$ s$^{-1}$ to $3.05 \times 10^9$. Interestingly, this light intensity transition is also where a significant decline in both siscowet reaction distance and prey capture was observed in siscowet foraging trials (Keyler et al., in prep). The correlation is evidence of a threshold for siscowet vision at $6.0 \times 10^9$ photons m$^{-2}$ s$^{-1}$ for benthic prey, and may indicate selection against movement above $6.0 \times 10^9$ photons m$^{-2}$ s$^{-1}$ as sculpin would be more susceptible to predation. Below the critical light intensity of $6.0 \times 10^9$ photons m$^{-2}$ s$^{-1}$, sculpin increase activity. This behavior may be associated with a) impaired siscowet visual foraging below the critical light level, b) siscowet moving higher in the water column through the expression of DVM during this period (Hrabik et al., 2006; Gorman et al., 2012a), and/or c) an increase in *Mysis* activity which may initiate foraging behavior in sculpin. It is common behavior for forage fish to shift peak activity to times when predators are less active or absent (Milinski, 1985; Reebs et al., 1995; Reebs, 2008) and

light intensities below $6.0 \times 10^9$ photons m$^{-2}$ s$^{-1}$ may be associated with night when siscowet are generally absent from the profundal zone (Stockwell, 2010).

Unlike siscowet that react upon initial detection of prey, lower sculpin reaction distances at upper light intensities may not indicate a lack of predator perception. Sculpin appear to change their predator avoidance behavior depending on light intensity and substrate; the lower reaction distances for sculpin at upper light intensities may be explained by the tendency to remain still longer to remain cryptic, which is dependent upon restricting movements (Donelly, et al., 1984). Crypsis is a known morphological and behavioral adaption to avoid predator detection (Ellis et al., 1997; Ruxton et al., 2004; Stevens & Cuthill, 2006) and sculpin may avoid movement in the presence of predators (Broom & Ruxton, 2005; Eilam, 2005) at the upper light intensities where siscowet vision is unhindered.

Characteristic of cryptic animals (Hailman, 1977; Donelly et al., 1984), the sculpin in our trials darted short distances upon siscowet detection, and then remained still. Similar behavior is observed in tidepool sculpins, which reduce movement by up to 65% (making only small fleeting movements) on substrates that offer camouflage (Houtman & Dill, 1994). At our lowest tested light levels, the sculpin reaction distances began to decrease incrementally with decreasing light levels as both species' visual capabilities were reduced. It is possible that sculpin detect siscowet first at all tested light levels, given that sculpin have a greater sensitivity to light when compared to siscowet (Harrington el al., 2015) and the sculpin's eyes are oriented upward, allowing them to silhouette potential predators from their benthic position. Ultimately, the sculpin

response to siscowet (to remain still or flee), appears to be dependent upon both the light intensity and the substrate.

The mottled, brown coloration of the sculpin (Scott & Crossman, 1973) provided the greatest camouflage on the gravel substrate as demonstrated by the fewest sculpin captures by siscowet (14%, 30%, and 26% capture rates sculpin on gravel, sand, and black fabric, respectively; Keyler et al., in prep).  Interestingly, while low contrast may have hindered foraging success (Muntz 1990; De Robertis et al., 2003) at upper light intensities, sculpin reaction distances to siscowet were higher for gravel compared to other tested substrates.  This is seemingly counterintuitive as fishes typically hold their position longer on substrates that minimize visibility (Donelly et al., 1984).  However, it is possible that under the perceived safety provided by the matching surroundings, sculpin on gravel initiated flight sooner (greater reaction distance) than substrates where less camouflage was provided.  For example, a study with brook trout (*S. fontinalis*) showed that individuals would initiate flight earlier in response to a predator, if nearby cover was provided (Grant & Noakes, 1987). Sculpin, therefore, may react sooner to siscowet on gravel, when compared to black fabric, since suitable cover/camouflage is readily available.

Future behavioral studies that investigate prey response to siscowet should compare pelagic prey to the benthic data presented here. The kiyi comprises 20-39% of the siscowet diet in Lake Superior (Gamble et al., 2011; Sitar et al., 2008); however, due to excessive barotrauma associated with deepwater collection, the use of kiyi as prey in foraging trials has been impractical.  Successful decompression of deepwater fishes to alleviate barotrauma (Gorman & Keyler, 2016) or the use of hatchery coregonines may

allow for future pelagic prey response trials in an effort to create a more comprehensive understanding of predator-prey interactions within the offshore food web.

**Acknowledgements**
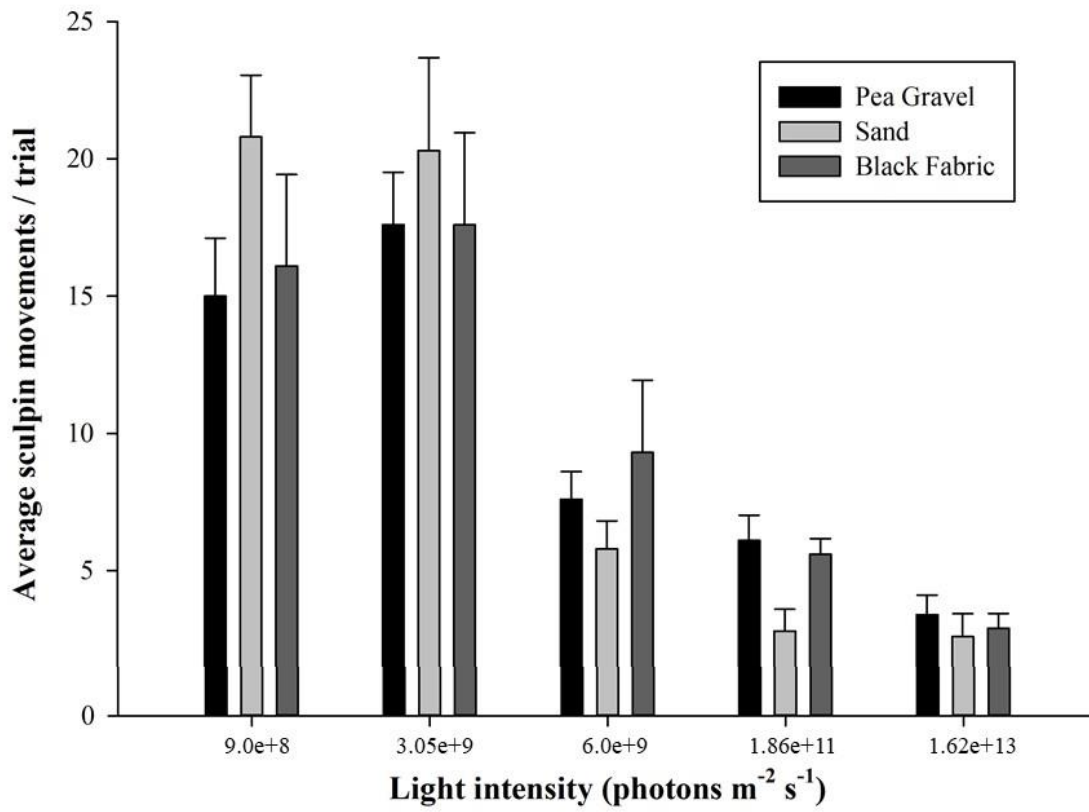
**Figure 1**: Average number of deepwater sculpin movements per 10 min trial at varying

light intensity. Error bars are ± 1 SE.
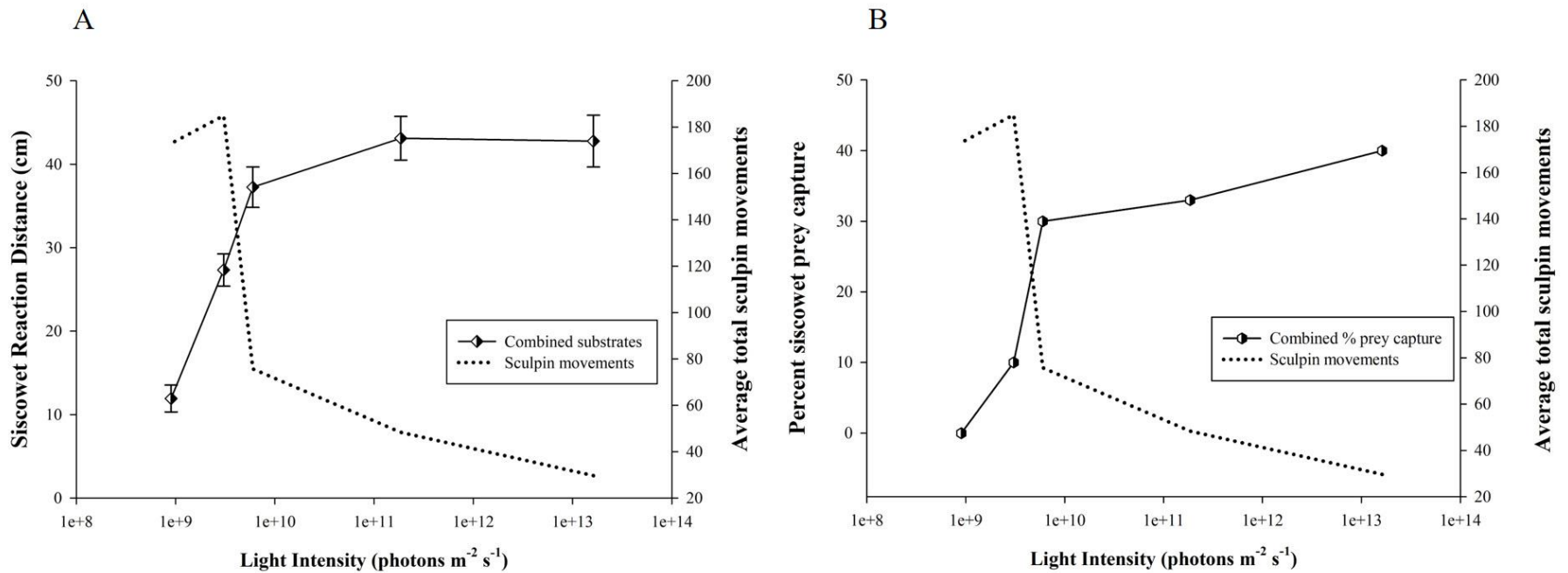
1

2

3  **Figure 2**: (A) Average siscowet reaction distance for combined substrates (◆) plotted against average combined sculpin movements

4  per trial (dotted line). Error bars are ± 1 SE. (B) Total siscowet prey capture for combined substrates (◑) plotted against average

5  combined sculpin movements per trial (dotted line).
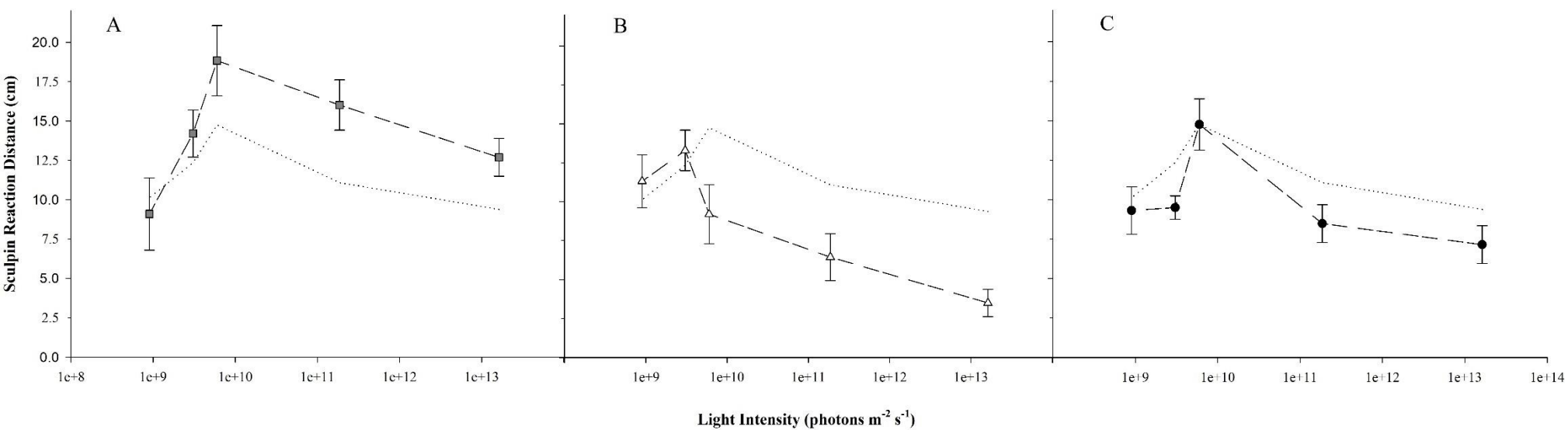
**Figure 3**:   Average reaction distance (cm) of deepwater sculpin in response to moving siscowet (*Salvelinus namaycush siscowet*) at varying light intensity on (A) pea gravel, (B) sand, and (C) black fabric substrates.  The dotted line in each panel indicates the average reaction distance for the combined substrates at each light intensity. Error bars are ± 1 SE.

**Chapter 5: Delineating Siscowet Lake Trout (*Salvelinus namaycush siscowet*) Visual Foraging Habitat Using Daily and Seasonal Light Cycles**

**Synopsis**

Light-mediated diel foraging patterns in fishes are often correlated to depths or times of equal light intensities, representative of a preferred range of light. Using siscowet lake trout (*Salvelinus namaycush siscowet*) as a case study, we use daily and seasonal solar/lunar patterns to describe a model capable of predicting how visual foraging habitat changes: i) daily based on solar and lunar intensity values, ii) seasonally with changes in maximum solar and lunar altitude, and iii) with increased turbidity that may occur with climate warming. Our model predicts a larger foraging window during the day for summer when compared to the winter season (open water, no ice cover) based on solar altitude. The greatest nighttime foraging window was predicted during the winter season when compared to summer. Foraging volumes were inversely related to solar/lunar altitudes, therefore daytime foraging volumes were largest in winter, least in summer and the converse was predicted for lunar values. Finally, with increases in turbidity that may accompany climate change events and the associated increase in light attenuation, foraging depths were reduced to 65% and 80% (when compared to normal lake attenuation values). Our model is useful for predicting when and where organisms feed and is applicable to any aquatic environment that undergoes changes in daily and seasonal solar/lunar intensities.

**Introduction**

Many behavioral and biological processes in fish, including foraging behavior, predator avoidance, and activity levels are influenced by daily and seasonal light cycles (Eggers, 1978; Clark & Levy, 1988; Fraser & Metcalfe, 1997). The impact of light on predator-prey interactions is broadly accepted (Eggers, 1977; O'Brien, 1987; Beauchamp et al., 1999) and light often influences the time of foraging, detection distance, and foraging success of visually-mediated predators (Munz & McFarland, 1977; Eggers, 1978; Boscarino et al., 2010; Keyler et al., 2015). Additionally, the visual capabilities of predatory fishes are typically highly correlated to the light environment of their preferred habitat and temporal niche (Guthrie et al., 1993). Therefore, light-mediated diel foraging patterns are often correlated to depths or times of equal light intensities (Clarke & Backus, 1964; Blaxter, 1975; Huse & Holm, 1993; Staby & Aksnes, 2011).

Visual foraging arenas can be delineated if the visual sensitivity and light intensity preference of that species is known (Melnikov et al., 1981) and if other limiting abiotic factors (e.g. oxygen, temperature) and biotic factors (e.g. prey/predator density) are considered (McFarland, 1986; De Robertis, 2002; Boscarino et al., 2009). Here we are defining foraging arena as a combination of the spatial foraging locations and temporal foraging patterns that describe when and where individuals feed. For instance, the distributions of fishes may be a product of the available habitat for visual foraging (Loew & McFarland, 1990) that have been shown to be closely associated with both solar and lunar light fluctuations (Munz & McFarland, 1977; Helfman, 1981; Gliwicz, 1986). These light cycles can lead to diel migration (DM) patterns in which the spatial foraging

locations are coupled with light intensities or isolumes (Brierley, 2014), as has been observed in freshwater species including lean lake trout (*Salvelinus namaycush namaycush*), siscowet (*S. n. siscowet*), and lake whitefish (*Coregonus clupeaformis*; Gorman et al., 2012a, Hrabik et al., 2006; Stockwell et al., 2010) as well as in marine species including walleye pollock (*Theragra chalcogramma*) and polar cod (*Boreogadus saida*; Adams et al., 2009; Benoit et al., 2010).

Common hypotheses for DMs are the following of prey, optimizing growth rate, and predator avoidance due to light-related mortality (Eggers, 1978; Gabriel & Thomas, 1988; Lampert, 1989; Ahrenstorff, 2011; Hrabik, 2014). Additionally, some pelagic species have threshold light intensities (Widder & Frank, 2001; Brierley, 2014) and DMs could allow organisms to maximize the time spent foraging by following their foraging habitat over a 24-hr period (Narver, 1970; Levy 1990b). DMs are generally categorized into 1) diel vertical migrations (DVM) in which organisms migrate vertically in the water column; and 2) diel bank migrations (DBM), a benthic form of DVM where daily depth transitions are closely associated with the bottom. In both instances, organisms generally move to shallower depths at night and occupy deeper water during the day. DM patterns are often correlated to solar and lunar cycles, and are therefore subject to seasonal variations associated with changing light intensities associated with solar/lunar altitude.

Seasonal changes in light intensity occurring within aquatic systems are reported to affect DMs in fish (Brawn, 1960; Levy, 1990a; Ahrenstorff et al., 2011). Benoit et al. (2010) reported the DVM patterns of small polar cod were precisely synchronized to the light/dark cycle over lengthening and shortening photoperiods throughout the year.

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Similarly, walleye pollock DVM patterns were reported to be influenced by light intensity (Adams et al., 2009) and the DVM patterns of the fontane cisco (*C. fontanae*) and vendace (*C. albula*) were synchronized to light intensities at depth and not dependent upon other conditions (Mehner et al., 2007). Within Lake Superior, the predatory siscowet and their prey, kiyi (*C. kiyi*) migrate concurrently from spring until fall, but spring migrations are less extensive (Ahrenstorff et al., 2011). While seasonal DM patterns are well-characterized during open-water seasons, the understanding of how DMs may change during winter months is much less understood.

The difficulty of studying seasonal DM patterns in fish from temperate and polar climates creates a knowledge gap in the understanding of how DM patterns can vary over an entire year. Given the correlation between light intensity and a species' potential foraging arena (i.e., Clarke & Backus, 1964; Blaxter, 1975; Huse & Holm, 1993), seasonal solar and lunar patterns can be used to predict how DMs change through time. Thus, our objective was to predict the expected depths at a given diel period and season for an organism that displays a high correlation between light intensity and depth patterns. We did this using siscowet as a case study because they are a visually foraging apex predator (Isaac et al., 2012) that exhibit DVM patterns consistent with a light-dependent response to prey distribution (Hrabik et al., 2006). Using previously determined siscowet foraging data from Keyler et al. (2015) and Keyler unpublished data (this thesis), we describe a model for predicting how the siscowet's isolume changes: i) daily based on solar and lunar intensity values and ii) seasonally via changes in maximum solar and lunar altitude.

**Materials and Methods**

  *Lake Superior and the Offshore Community*: Lake Superior, the largest of the

North American Great Lakes, is the largest freshwater lake by surface area (82,103 km$^2$)

and third largest freshwater lake by volume (12,100 km$^3$) in the world (Habermann et al.,

2012). The lake is 560 km long and 260 km wide with 2,938 km of shoreline shared by

Ontario, Minnesota, Wisconsin and Michigan's Upper Peninsula. The average depth is

147 m and the maximum depth is 406 m (Wright, 2006). Lake Superior is a glacial lake

formed approximately 10,000 years ago, characterized by low productivity (oligotrophic),

containing 34 species of native fish (Henson et al., 2010). Surface temperature varies

seasonally, however below the thermocline, temperature remains near 4°C annually

(NOAA, 2012). Additionally, as a dimictic lake, temperature is a uniform 4°C throughout

the water column post-turnover twice a year (MN Sea Grant, 2014).

  The offshore waters (>80m) of Lake Superior represent 80% of the lake by area

(Horns et al., 2003; Stockwell et al., 2006). The community is comprised of a modest

number of native species adapted to the cold, deep water environment (Gamble et al.,

2011). Siscowet are the apex predator within the offshore food web and are the dominant

predator for pelagic planktivorous coregonines, kiyi and cisco (*C. artedi*), and benthic

planktivores, predominantly deepwater sculpin (*Myoxocephalus thmpsonii*; Harvey et al.,

2003; Isaac et al., 2012). These planktivores consume zooplankton including *Mysis

relicta*, found throughout the water column, cladocerans and copepods, found

predominantly in the upper water column, and benthic amphipod *Diporeia spp.*

(Anderson & Smith, 1971; Auer et al., 2013; Oliver et al., 2014). Siscowet are known

consumers of *Mysis* as well, especially as juveniles (Isaac et al., 2012). DVM between

siscowet, the coregonine species, and *Mysis* is tightly correlated (Ahrenstorff et al., 2011;

Hrabik et al., 2006, 2014; Stockwell et al., 2010).  The migration behavior is

characterized by *Mysis* moving shallower in the water column at night to consume

smaller plankton under the safety of darkness, which are followed by the coregonines,

and are in turn followed by the siscowet (Gorman et al., 2012a; Hrabik et al., 2006;

Jensen et al., 2006; Stockwell et al., 2010).  Upon transition to day, *Mysis* retreat to

deeper, darker waters followed by both the coregonines and siscowet, where siscowet

may continue to prey upon coregonines or switch to benthic deepwater sculpin

(Ahrenstorff et al., 2011; Gamble et al., 2011; Gorman et al., 2012a; Hrabik et al., 2014;

Isaac et al., 2012).

Sources of *Data:* Surface solar irradiance intensities $E_{o,s=1,t}$ at time *t* were

obtained from the National Renewable Energy Laboratory's National Solar Radiation

Database (NSRD; https://nsrdb.nrel.gov) for the Western Arm of Lake Superior (46.77N,

-92.02W) from January 1, 2015 to December 31, 2015. We used direct normal irradiance

at time *t*, in quanta units (watts/m$^2$; $E_{q,t}$) and converted to photons/m$^2$/s at time *t* for a

wavelength of 510 nm via

$$E_{o,s=1,t} = E_{q,t} * PAR_{510} * 5.05 \times 10^{15} * 510 \qquad (1)$$

where $PAR_{510}$ is the proportion of total solar radiation allocated to a wavelength of 510

nm, which is equal 0.169.  The wavelength of 510 nm was used since it is the deepest

penetrating within the clear offshore waters of Laker Superior (Jerome et al., 1983).

Direct normal irradiance is the amount of solar radiation from the direction of the sun.

For simplicity, we ignored diffuse radiation because the direction of photon travel is highly randomized. On clear days, direct radiation is the predominant source of light, while diffuse radiation is only predominant on cloudy days. Given that cloud cover can cause up to 70% of solar radiation to be absorbed or scattered (Zaimes & Emanuel, 2006), clouds would effectively decrease siscowet foraging depths.

Estimates of lunar radiation were unavailable for this location. Therefore, we used a combination of lunar characteristics for Duluth, MN (from the US Naval Office; http://aa.usno.navy.mil/data/docs/AltAz.php), lunar radiation at 97% illumination (from Cramer et al., 2013), and the relative lunar brightness at various moon phases (from Nowinszky et al., 1979) to estimate the seasonal patterns of lunar radiation. This process was necessary because relatively few studies have estimated lunar radiation and none to our knowledge have estimated seasonal and/or diel patterns in lunar radiation in photons/m$^2$/s.

Lunar radiation for a full moon $l_{full}$ was calculated using the Cramer et al. (2013) estimate of lunar radiation divided by the relative brightness of a moon with 97% illumination $l_{97}$

$$l_{full} = l_{97}\beta_{5.4}^{-1} \tag{2}$$

where $\beta_{5.4}$ is the relative lunar brightness associated with 97% lunar illumination, which corresponds to a phase angle of 5.4 degrees. Relative lunar brightness at various moon phases were obtained from Nowinszky et al. (1979) to determine the proportion of photons that reach the surface of the earth relative to a full moon. Nowinszky et al. (1979) recorded lunar brightness approximately one day apart (about 12 degree

differences in phase angles). Linear interpolation was used to calculate relative lunar brightness for observed phase angles $\rho_t$ at time $t$. Relative brightness data were then used to calculate the number of photons reflected off of the moon ($s = 2$) that reach the surface of Lake Superior $E_{o,s=2,t}$ at time $t$

$$E_{o,s=2,t} = l_{full}\beta_{\rho_t}^{-1} \tag{3}$$

where $\beta_{\rho_t}$ was the relative brightness associate with a phase angle of $\rho_t$ at time $t$. A wavelength of 500 nm was chosen because 510 nm was not reported in Cramer et al. (2013) and it was close to 510 nm, which was used for solar calculations.

*Siscowet Foraging Dynamics:* Foraging success of siscowet was measured by Keyler et al. (2015) during laboratory trials under various light intensities. Briefly, siscowet foraging trials were conducted under light intensities ranging from 9.00E8 to 1.06E14 photons/m$^2$/s (four replicates at each of six light levels with five siscowet representing a total of 120 trials). These trials were used to quantify foraging characteristics, including the proportion of prey captured at each light level. The probability of foraging success at a given light intensity was estimated using a binomial GLM which was used to describe the predicted siscowet isolume range and mean isolume. Here we define the isolume range as the light intensities between the 10 and 90% prey capture probabilities and the mean isolume as the light level associated with the 50% prey capture probability. The GLM and all following analyses were conducted in program R version 3.4.0 (R Core Team, 2017).

*Model Formulation:* Using the solar and lunar data on light radiation at the surface of Lake Superior and solar/lunar altitude, we were able to estimate the isolume

depth for solar ($s = 1$) and lunar ($s = 2$) irradiance at each time $t$. For consistency, we define the foraging depth as the depth which corresponds to the mean isolume and the foraging window as the depths associated with the isolume range. Foraging volume is the volume of Lake Superior adequately illuminated for visual foraging determined by the size/width of the foraging window in each season.

Depths were estimated using light reflection, Beer's Law, Snell's Law, and basic geometry (Figure 1). When a photon strikes the surface of the water, it will either get reflected or it will travel into the water column. The proportion of photons that reflect off of the water's surface $R_{s,t}$ at time $t$ was calculated using the relationship

$$R_{s,t} = \min\left(1, aA_{s,t}^b\right) \tag{4}$$

where $a$ and $b$ are constants having values of 1.18 and -0.77, respectively (Anderson, 1954) and $A_{s,t}$ is the altitude of the sun/moon at time $t$. At low solar/lunar altitudes (i.e., $A_{s,t} < 1.24$), Anderson's (1954) equation will predict greater than 100% reflection and was therefore capped at one.

Beer's Law can be used to calculate how many photons reach a specified distance $z_{s,t}$ in the water column $E_{z,s}$ for each light source $s$ at time $t$

$$E_{z,s} = E_{o,s,t}(1 - R_t)e^{-kz_{s,t}} \tag{5}$$

where $E_{o,s,t}$ is the surface solar irradiance intensity at time $t$, $k$ is the spectral irradiance coefficient and $z_{s,t}$ is attenuation distance. The parameter $k$ determines how light attenuates through the water column. Low values of $k$ indicate greater attenuation distances. For Lake Superior, $k$ ranges from about 0.085 m$^{-1}$ under normal offshore conditions to 0.280 m$^{-1}$ during turnover and can reach values of 0.43 m$^{-1}$ in the

Duluth/Superior harbor (Jerome et al., 1983; Harrington et al., 2015). We were interested how far light attenuates to reach a critical number of photons $E_{z\_crit}$ (i.e., mean isolume and isolume range). Thus, Beer's Law was rearranged to calculate $z_{s,t}$

$$z_{s,t} = \ln\left(\frac{E_{z_{crit}}}{E_{0,s,t} * (1 - R_t)}\right) k^{-1} \tag{6}$$

given mean isolume and isolume range light levels $E_{z\_crit}$.

Foraging depth characteristics associated with the isolume characteristics ($x_{s,t}$; i.e., expected foraging depth and foraging window) at time $t$ were calculated using a combination of Snell's Law to account for refraction and geometry. Snell's Law incorporates solar/lunar altitude ($\theta_{1.s,t} = 90 - A_{s,t}$) and refractive indices to determine the angle of refraction $\theta_{1,s,t}$

$$\theta_{2,s,t} = \text{asin}\left(\frac{\sin(90 - \theta_{1,s,t})}{1.33}\right) \tag{7}$$

where 1.33 is the refractive index of light traveling from air to water. Finally, foraging depth characteristics were calculated using

$$x_{s,t} = z_{s,t} * \cos(\theta_{2,s,t}) \tag{8}$$

for both solar and lunar light intensities at time $t$. For simplicity, we ignored the effects of waves.

To predict seasonal variation in expected foraging depth and the foraging windows, we selected four periods associated with the 2015 solstices (June 21 and December 21) and equinoxes (March 20 and September 23). Because the presence of clouds interfered with direct normal irradiance, seasonal solar foraging depths were determined using the maximum foraging depth +/- 15 days from the solstice or equinox.

This was done to standardize foraging depths and foraging windows to clear, cloudless days. The maximum solar altitude was likewise determined for each season. Seasonal lunar foraging depths were determined using the calculated lunar intensity from the full moon closest to the solstice or equinox of the respective season and was within the same period used for determining the seasonal solar maximum depth. Due to the different resources used to determine solar and lunar radiations, lunar maxima were not an average of values, but are representative of a single night associated with the full moon in that season.

**Results**

Out of the 120 siscowet foraging trials, 44% ended with the successful capture of prey. The probability of capturing prey decreased with light intensity (i.e., the slope was -7.29 and the p-value was $< 0.001$ and the intercept was 0.27 and the p-value was $< 0.001$). The mean isolume was 3.49E11 photons/m$^2$/sec (i.e., the light level that corresponded with a 50% prey capture probability). The isolume range was between 1.16E8 and 1.05E15 photons/m$^2$/sec, which represented the 10 and 90% probability of prey capture, respectively.

The expected mean siscowet daytime foraging depths varied annually by about 60 m. The deepest foraging depths were predicted in summer (232.9 m), followed by spring/fall (212.2 m and 209.6 m), and winter (172.4 m; Fig. 2). The seasonal differences in the foraging depths were associated with differences in the maximum solar altitudes (65° – 67° in summer, 37° – 49° in fall/spring, and 20° – 21°in winter). Additionally, differences in the solar/lunar altitude both daily and seasonally drove differences in the

size/width of the foraging window. When low on the horizon (i.e., sunrise/sunset) the foraging window sizes were consistently around 124.0 m and increased as the sun moved higher in the sky. This was primarily a function of reflection (which decreases as solar altitude increases), geometry (trajectory angle of the photon decreased as the solar altitude increased), and to a lesser extent, the number of photons reaching the lake surface (the number of photons increased with increasing solar altitudes). Therefore, the winter foraging window size was the smallest at 134.0 m, was then intermediate in the spring/fall (163.7 m), and largest in the summer (179.7 m; Fig.3).

The size/width of the foraging window (when solar/lunar altitude was highest) in each season correlated to the volume of Lake Superior adequately illuminated for visual foraging (hereafter, foraging volume). Daytime foraging volume varied annually by 15% and the deeper summer foraging window corresponded to the smallest foraging volume of the seasons (23%) due to the general morphology of lakes narrowing with depth. Winter, with the shallowest foraging window, had the greatest foraging volume (38%), followed by spring/fall (28%). Greater foraging volumes equate to lower siscowet densities provided the larger volume over which they can distribute when foraging. Additionally, we determined the percent bottom illumination for Lake Superior provided by the foraging window at the height of the day, which corresponds to the 10 and 90% prey capture probabilities. Percentages varied by 3.9 percent annually and were similar for all seasons with 57.2% in spring, followed by 53.6%, 57.5% and 55.7% for summer, fall and winter, respectively. Finally, due to the lengthening and shortening of days throughout the seasons, the duration of time in which we expect siscowet to forage deep

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in the water column varied seasonally (Fig. 3). Around the summer solstice, siscowet are predicted to spend 15 hours deeper in the water column, followed by 12 hours around the spring/fall equinox, and 8 hours around the winter solstice.

Expected mean siscowet nighttime foraging depths under lunar radiation varied annually by 7.5 m. The deepest foraging depths were predicted in winter (32.1 m), followed by spring/fall (29.0 m), and summer (24.6 m; Fig 4). Variation in seasonal depths was a product of lunar altitude (24° in summer, 45° in fall/spring, and 61°in winter). Likewise, the predicted siscowet foraging window was greatest during the winter season (120.0 m), followed by spring/fall (108.6 m) and summer (93.3 m; Fig 2). Nighttime foraging volume varied 13% annually, with the greatest volume predicted in winter (67%), followed by spring/fall (62%), and summer (54%). The percent bottom illumination when lunar altitude was highest in each season, were again similar for all seasons with 33.5% in spring, followed by 29.0%, 33.5% and 37.2% for summer, fall and winter, respectively. Because moonrise can occur at any time during a 24-hour period, there were some days in which there was minimal to no lunar illumination at night and others where there was up to about 12 hours of lunar illumination.

Under typical lake water clarity within the offshore waters of Lake Superior ($k = 0.085$ m$^{-1}$; Fig.5), the maximum daily solar foraging depth ranges from about 170 to 230 m annually and lunar foraging depth values range from around 25 to 32 m. With an increase in $k$ associated with lake turnover ($k= 0.245$ m$^{-1}$), there is a 65% decrease in maximum foraging depth for both solar and lunar radiation compared to normal offshore conditions. If $k$ further increases to levels representative of the Duluth/Superior harbor

($k$= 0.430 m$^{-1}$), there is an 80% decrease in foraging depth compared to the initial

offshore conditions.  With an increase in attenuation values ($k$) associated with turbidity,

the daily/seasonal trends for predicted siscowet DMs remain the same, but the maximum

depths change.

**Discussion**

Our approach demonstrates the possibility of estimating visual foraging habitat

provided 1) that an organism shows a high correlation between light intensity and depth

inhabited, and 2) the light intensity preference of that organism is known.  Our model can

be used to predict the spatial and temporal foraging patterns that describe when and

where organisms feed and is applicable to any aquatic environment that undergoes

changes in daily and seasonal solar/lunar intensities.  Ultimately, this information can be

used to fill a knowledge gap of how DMs vary seasonally, specifically during winter

months where northern temperate climates can make sampling difficult.  The collective

predictions related to where/when fish forage are important for creating foraging models,

where time of day or season, may dictate the available prey species to a predator due to

DM behavior.  Siscowet, for example, may consume benthic deepwater sculpin during

day time hours and switch to feeding on kiyi when higher in the water column at night.

Similarly, there may be implications for management where information related to a

species' distribution may inform fisheries management.  Reducing bycatch of non-target

species, for instance, may be achieved by observing daily and seasonal depth

distributions.

For our siscowet case study, diel and seasonal changes in foraging depths, foraging windows, and foraging volumes were dependent upon solar/lunar altitudes and light intensities. While, seasonal DM patterns are well-characterized for a number of species, it is less understood how DMs may change during winter months. Our model allows for foraging habitat predictions for all seasons and predicts a larger foraging window during the day for summer compared to winter based on solar altitude. Conversely, higher lunar altitude in winter, provides a larger foraging window at night when compared to summer, assuming no ice cover. Foraging volumes were inversely related to solar/lunar altitudes, therefore daytime foraging volumes were largest in winter, least in summer and the converse for lunar values. Finally, our model allows us to predict how foraging depths may change with climate change and the anticipated increase in extreme precipitation events which may increase turbidity. With increases in turbidity, and therefore attenuation values ($k$), foraging depths were reduced to 65% and 80% (when compared to normal lake attenuation values).

Siscowet within Lake Superior perform extensive vertical migrations (Hrabik et al., 2006; Stockwell et al., 2010) where light appears to be the key determinant in the timing of these movements (Ahrenstorrf et al., 2011). Our model predicts how siscowet foraging windows change on a diel and seasonal scale, depending on solar/lunar altitude, and the associated light intensity. Higher solar altitude during the summer season allowed for deeper light penetration and thus, the largest foraging window. Observations of winter DVM patterns in siscowet are unavailable, but our model predicts that Siscowet are higher in the water column during a winter's day with a smaller foraging window

compared to the other seasons. Comparatively, polar cod likewise exhibited shallower DVMs of decreased magnitude in mid-winter that increased in both depth and vertical amplitude with the progression of spring (Benoit et al., 2010). Additionally, just as the duration of time in which we expect siscowet to forage deep in the water column increased with increasing day length, the duration of polar cod DVM likewise followed the lengthening photoperiod from winter to spring.

Our findings are consistent with Ahrenstorff et al. (2011) who showed siscowet migrations from near the bottom during the day (about 130 m, or 80-100% proportion of max. depth) to 30 m of surface at night during the summer season (July). While the reported max. depth of daily migrations did not change throughout seasons as with our model predictions, it is worth noting that the max. depth Ahrenstorff et al. (2011) sampled was approximately 150 m. Sitar et al. (2008) reported that siscowet typically occupy the demersal zone from 150 m to bottom depths > 400 m during the day. Provided the opportunity, siscowet may have occupied greater depths as reported in Hrabik et al. (2014) that showed deeper siscowet DVM in the summer season when compared to fall, which is consistent with our model predictions. Even given these limitations, the predicted upper depth of our foraging window was 143 m, and is close to reported empirical observations.

For lunar illumination, Ahrenstorff et al. (2011) reported siscowet at greater depths (45 m) in the spring (May) and fall (October) and shallower (30 m) during the summer season, also in agreement with our model predictions. Additionally, they report similar durations for which we expect siscowet to forage deep in the water column.

Although our model predicts a longer duration in summer (15 vs 12 hours) and shorter

duration in fall (8 vs 12 hrs), the trend for greater time at depth in summer, moderate time

in spring/fall, and shorter time at depth in winter is consistent with our predictions.  The

minor variations in siscowet foraging depth ranges and foraging times between the

empirical data and our model predictions are likely due to additional factors that may

affect species distributions.  Factors may include temperature (energetic optimization),

time to change location, and prey distributions, in addition to light intensity preference

(Magnuson et al. 1979; Mason and Patrick, 1993).

Turbidity can also play a large role in visual foraging.  Turbidity greatly effects

detection of prey by piscivores (Miner & Stein, 1996; Beauchamp et al., 1999; Hansen et

al., 2013), prey capture (Petersen and Gadomski 1994; De Robertis et al. 2003; Mazur

and Beauchamp 2003), and has been shown to significantly decrease foraging success in

lake trout (Vogel & Beauchamp, 1999).  Turbidity temporarily increases with lake

turnover, and during this period we would expect to observe shallower siscowet DVMs

due to decreased light penetration. These effects are expected to be the greatest for the

nearer-shore extent of the siscowet's distribution, where currents and turbidity are

generally higher.  Our model predicts a 65% and 80% decrease in siscowet solar/lunar

foraging depths with increases in $k$ associated with turbidity.  Similar effects are

predicted with climate change, which is expected to cause warmer temperatures, a rise in

sea-level, and an increase in extreme hydrologic events (National Research Council,

2011; Melillo et al., 2014; Stocker, 2014). Extreme precipitation events are associated

with increased surface water runoff and erosion which increase water turbidity (greater $k$

values) effectively decreasing subsurface light intensities (Schindler, 2001; Nevers &

Whitman, 2005). Within the Great Lakes Basin of North America, both average and

extreme precipitation events have increased (Alexander et al., 2006; Mekis & Vincent,

2011) and are projected to continue with continued warming temperatures (Diffenbaugh

et al., 2005; Tebaldi et al., 2006; Kharin et al., 2007, d'Orgeville et al., 2014). With an

increase in turbidity, the depth at which fish can effectively forage is limited (De Robertis

et al., 2003) and fish will move into shallower waters to compensate for the decreased

illumination (Kaartvedt et al., 1996; Eiane et al., 1999). For example, mesopelagic fishes

in the Norwegian Sea were reported to ascend ~100 m with an increase in turbid water,

while demersal fishes left the benthic zone entirely (Kaartvedt et al., 1996).  Similarly,

our model predicts both shallower daytime and nighttime depths with an increase in

turbidity based on the siscowet mean isolume.

DMs in fishes are closely related to the light intensity change over a 24-hr period

(Gal et al., 1999; Van Gool & Ringelberg, 2003, Ahrenstorff et al., 2011) and may be a

product of visual predators attempting to optimize their foraging (Narver, 1970; Levy,

1990b).  Our predictions suggest siscowet should spend more time deeper in the water

column provided longer periods of daylight, which is likely an attempt to gain the most

energy (prey) for the least expenditure of time and energy (Werner & Hall, 1974).

DVM's allow for foraging optimization by allowing siscowet to prey upon coregonines

(Harvey et al., 2003; Isaac et al., 2012) when higher in the water column at night, and

then continuing to feed on coregonines and sculpins near the bottom during the day

(Conner et al., 1993).  While the deepwater pelagic environment may offer challenges for

pelagic piscivores which rely predominantly on visual foraging (Ali, 1959; Loew &

McFarland, 1990), the absence of prey in the upper water column during the day likely

drives siscowet to deeper waters where sculpin and kiyi densities are higher (Ahrenstorff

et al., 2011).  Sculpin are likely the most vulnerable to siscowet predation given they are

solitary and do not form schools as do kiyi (Gorman, U.S. Geological Survey, 2018,

personal communication) which can deter predation (Pitcher, 1983).  Even with reduced

capture rates at lower light intensities, fishes may forage in suboptimal conditions if prey

densities are high (Crowder & Cooper, 1982), which compensates for increased search

time (Ware, 1973).  Siscowet additionally show enhanced visual sensitivity for successful

foraging of prey at very low light intensities (Harrington et al., 2015; Keyler et al., 2015)

effectively allowing for productive foraging over a 24-hr period.

Given the discrepancies between model predictions and observations from

Ahrenstorff et al. (2011; i.e. siscowet foraging depth ranges and foraging times), it is

important to address some of the model assumptions. Our model predictions are based on

direct solar/lunar light patterns since siscowet display DVM patterns consistent with a

light-dependent response to prey distribution (Hrabik et al., 2006).  However, the

influence of diffuse light and the distribution of prey should not be ignored.  For instance,

the siscowet's transition from shallow to deepwater during DVM observed by

Ahrenstorff et al. (2011) occurred over a longer period than our model predicts.  The

minor discrepancy is likely due to the use of direct light only (negates cloud cover or

diffuse radiation).  Had our model accounted for diffuse light effects, we expect the

predominant horizontal solar rays at sunrise and sunset would allow for a more gradual

light transition and predicted DVM patterns. Moreover, siscowet DVM may be driven by prey distribution (Hrabik et al., 2006). The slower transition of kiyi through the water column with changing light intensities may further explain the more gradual DMs observed in siscowet, which wait for prey to undergo DVM (Mehner, 2012). Given these assumption, we feel that it is important to reiterate that this model describes temporal patterns for the preferred siscowet light habitat, or isolume, and does not account for the spatial and temporal preferences of their prey.

Additionally, we used the plane parallel assumption, which assumes a perfectly flat lake surface. This is common for modelling light attenuation over large areas of open water (Zaneveld et al., 2001). Work by Schenck (1957), indicates that there are certain wave characteristics and sun/lunar angles that can cause light focusing, which could result in increased light penetration, effectively increasing siscowet foraging depth. At low sun/lunar angles and/or with large waves where only part of the wave is illuminated, light penetration will be reduced because the entire wave surface is not receiving direct sunlight (Dera & Stramski, 1986; Stramski, 1986a, 1986b). Nevertheless, the predicted foraging patterns reported here are supported by empirical data and demonstrate the effectiveness of applying daily and seasonal solar/lunar data to delineate visual foraging habitat.

DMs are a wide-spread phenomenon occurring within both freshwater and marine environments (Ringelberg, 1995). Our model allows us to predict how solar/lunar patterns influence siscowet visual foraging habitats as well as predict the impacts of changes in water clarity that may occur with climate warming and extreme weather

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events. Future studies should investigate additional factors that can alter light penetration in lakes including wave action (Schenck, 1957), and ice cover (Roulet & Adams, 1986). Given the light preference of an organism, models like this can be used in both freshwater and marine environments to determine when and where a species forages. This knowledge is useful not only for predicting how DMs may change in winter months, but is also useful for foraging models, where time of day or season may dictate the available prey species to a predator due to DM behavior.

**Acknowledgements**
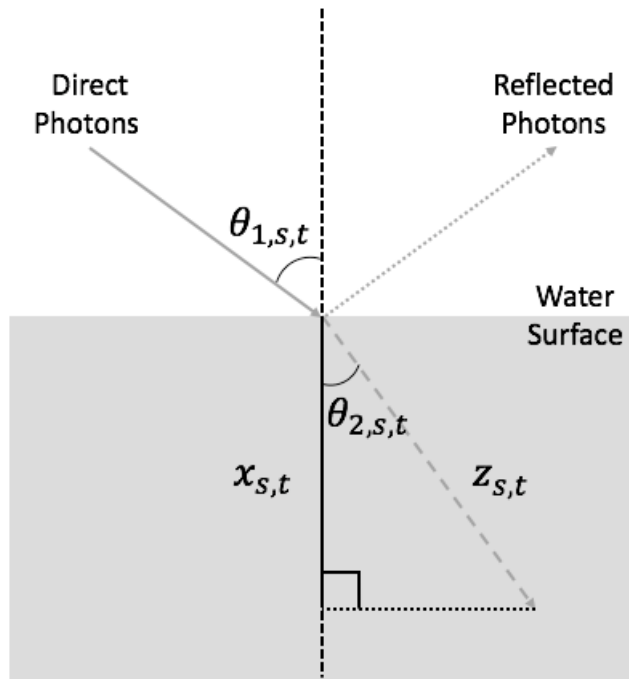
**Figure 1**: Path of photon and penetration depth. Direct photons from solar/lunar

radiation may be reflected at the water's surface or enter the water. Upon entering the

water, photons are refracted and travel the distance $z_{s,t}$, where geometry is used to solve

for the photon penetration depth, $x_{s,t}$.

**Figure 2**: Expected maximum daytime siscowet foraging depths across Lake Superior (left) and a cross-section at 47.5 degrees latitude (right) for spring, summer, fall and winter (top to bottom). Darker shading represents deeper foraging depths.
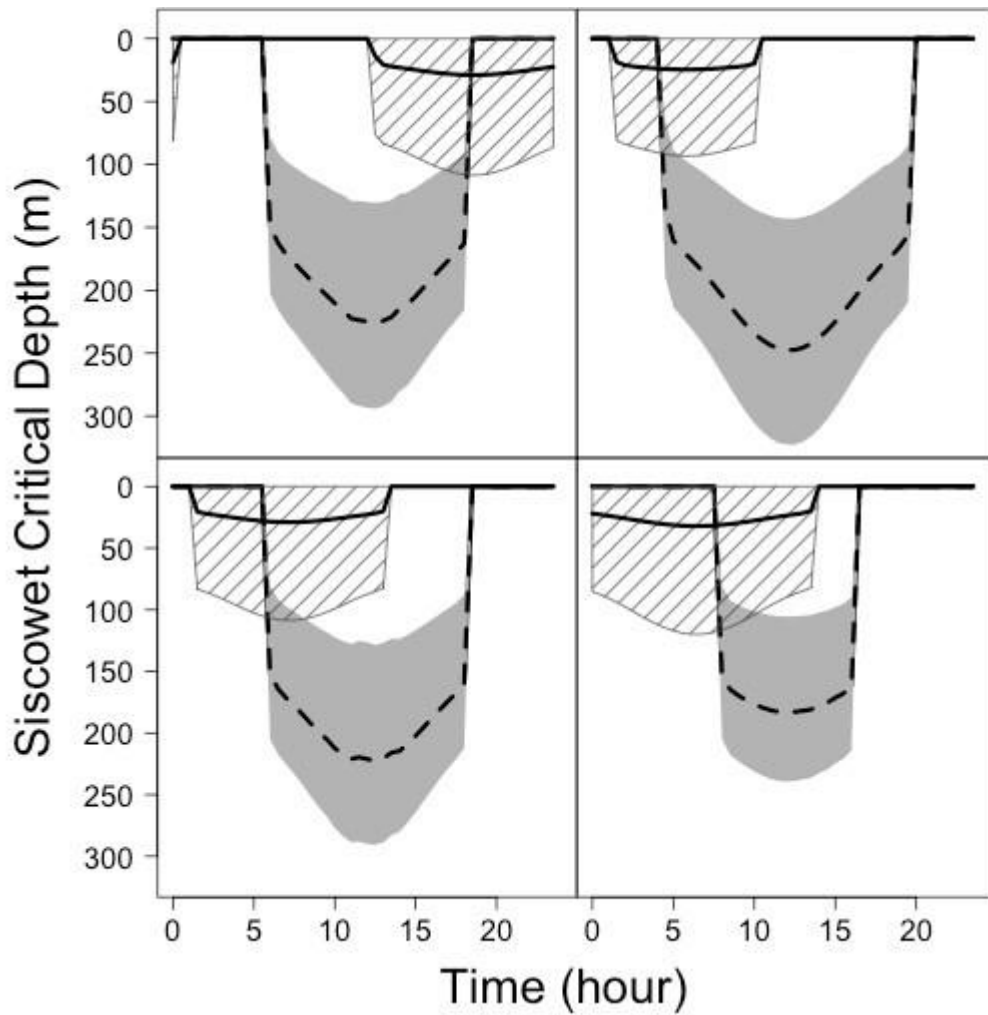
**Figure 3**: Seasonal solar (dashed black lines) and lunar (solid black lines) expected siscowet foraging depths and foraging windows over a 24-hr period. Solid grey and thatched grey shaded regions represent the 80% confidence intervals associated with the 10% and 90% prey capture probability for solar and lunar illumination respectively, in the spring (top left), summer (top right), fall (bottom left) and winter (bottom right).

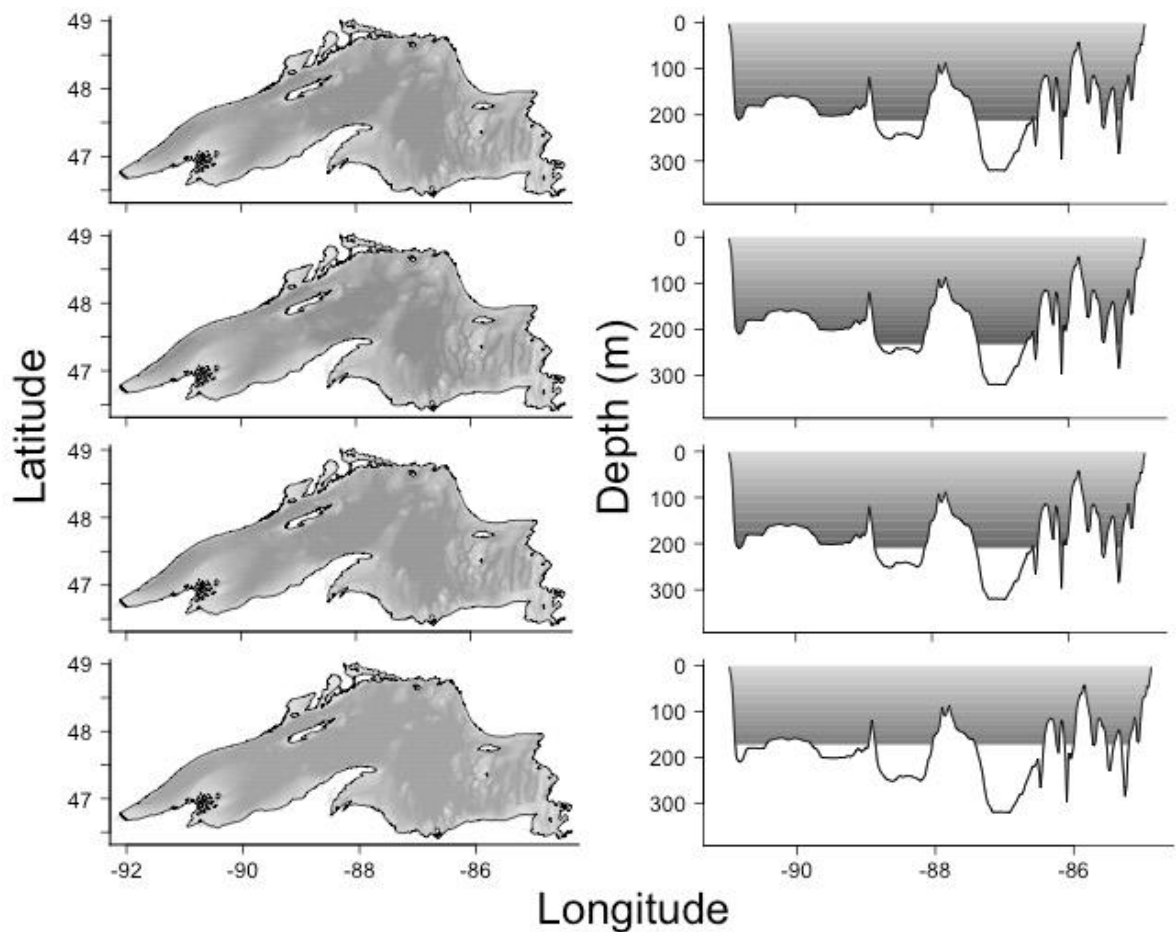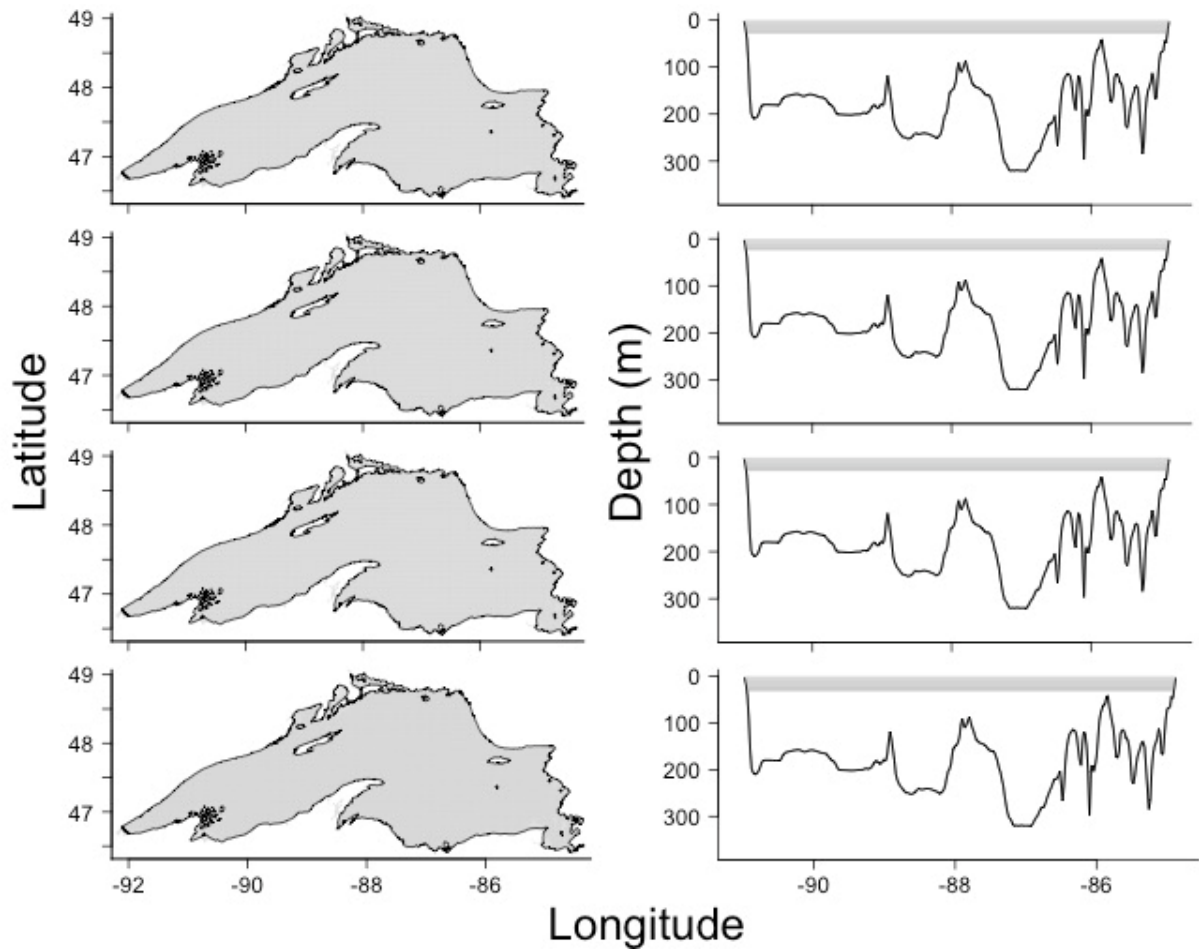**Figure 4**: Expected maximum nighttime siscowet foraging depths across Lake Superior (left) and a cross-section at 47.5 degrees latitude (right) for spring, summer, fall and winter (top to bottom). Darker shading represents deeper foraging depths.
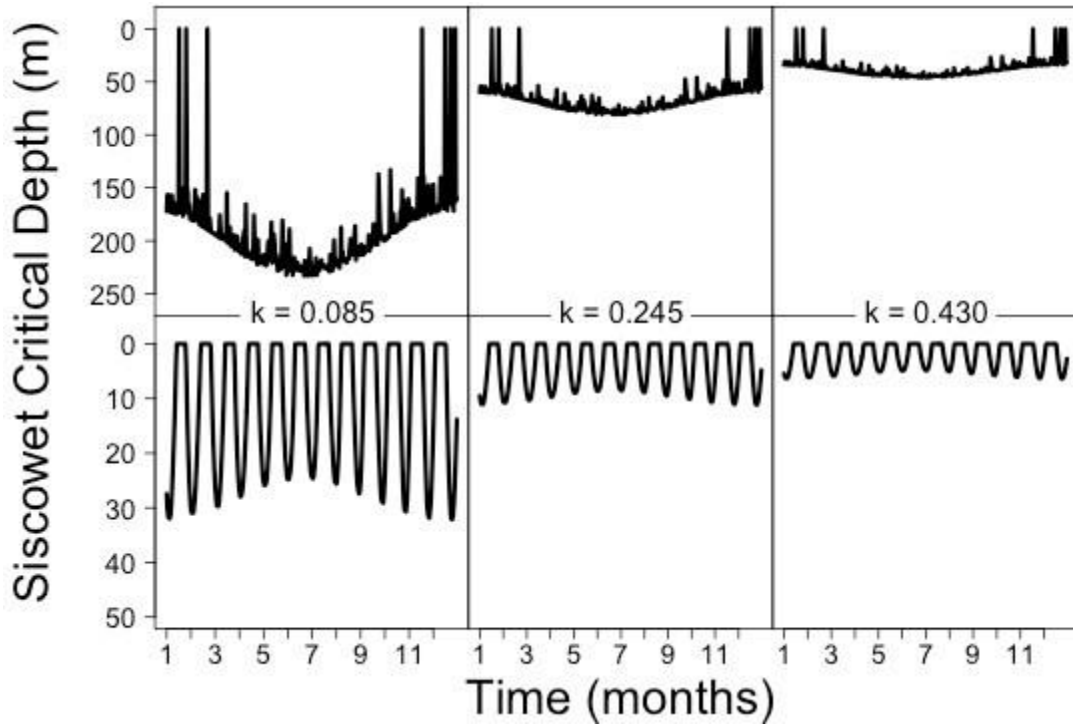
**Figure 5**: Annual siscowet foraging depths based on daily maximum solar (top) and lunar (bottom) radiation under normal conditions ($k = 0.085$ m$^{-1}$), at lake turnover ($k= 0.245$ m$^{-1}$) and values associated with the Duluth/Superior harbor ($k= 0.430$ m$^{-1}$). The inconsistency in daily foraging depth values (vertical black bars on solar plots) are due to days where cloud cover obscured direct sunlight.

**Chapter 6: Conclusions and recommendations**

We have successfully used both physiological and behavioral techniques to address the visual capabilities of three low-light foraging species, the walleye, siscowet lake trout and deepwater sculpin. The findings of these visual studies allow for the improvement of foraging models as well as defining foraging habitat that describes when and where fish forage. Collectively, we have shown that visual physiology studies can reveal the specific wavelengths fish have adapted to detect at low light intensities, as well as the minimal light intensities they are able to perceive which may reveal habitat characteristics important to individual species. Additionally, *in situ* behavioral foraging trials that vary abiotic factors such as light and substrate reveal the dynamics of foraging characteristics pertaining to the threshold of visual detection which are useful when delineating fish visual habitat on spatial and temporal scales.

Our visual physiology research employed electroretinography to determine the scotopic spectral sensitivity of the dark-adapted retina in walleye. The findings support the visual pigment sensitivity hypothesis as walleye show corresponding visual adaptation to their light environment, displaying significantly higher sensitivity to the prevailing downwelling light within typical mesotrophic freshwater environments (Jerlov 1968). Additionally, we determined a visual response to respective depths of at least 77.5 m ($k_{PAR} = 0.3$) and 12.8 m ($k_{PAR} = 1.2$), which are likely more than adequate given that walleye are found at shallow to moderate depths during the day (Kitchell *et al*., 1977; Leach *et al*., 1977).

Behavioral trials can likewise investigate the limits of visual detection through examining predator-prey interactions at varying light levels. Siscowet lake trout and deepwater sculpin consistently occupy a low-light environment that presents challenges for other visually foraging fishes. Our foraging trials highlight how the abiotic environment can alter both prey detection and the prey response. Siscowet lake trout showed adaptation for low-light foraging and reaction distance to deepwater sculpin increased with increasing light intensity up to $6.0 \times 10^9$ photons m$^{-2}$ s$^{-1}$, after which reaction distance remained constant with additional increases in light intensity. Lastly, we observed a strong positive correlation between overall probability of deepwater sculpin capture and siscowet lake trout reaction distance at each light intensity.

Deepwater sculpin behavior was also dependent upon light intensity within our foraging trials. Deepwater sculpin displayed both suppressed activity and reaction distances to siscowet lake trout at the upper tested light intensities, typical of cryptic species (Broom & Ruxton, 2005; Eilam, 2005). Reducing activity to avoid predator detection is a common tactic for many fishes (Dill, 1983; Dill & Fraser, 1984; Godin, 1986; Sih, 1986; Prejs 1987), and deepwater sculpin likely restricted movements to avoid detection by siscowet lake trout at greater light intensities. While neither siscowet lake trout reaction distance, nor deepwater sculpin activity were affected by substrate type in our trials, deepwater sculpin reaction distance to siscowet laketrout was influenced by substrate type. Counterintuitively, deepwater sculpin showed higher reaction distances in response to siscowet lake trout on gravel, the substrate that offered the greatest

camouflage. It is possible that deepwater sculpin on gravel initiated flight sooner (greater reaction distance) under the perception of safety offered by blending in with the substrate.

Foraging characteristics pertaining to the limits of visual detection, such as those determined in the previous study, are useful when delineating fish visual habitat on spatial and temporal scales. Applying the siscowet lake trout's visual foraging parameters, we developed a model to predict siscowet lake trout visual foraging habitat based upon daily and seasonal solar/lunar intensities. Our model predicts a deeper foraging depth during the day for summer compared to winter based on solar altitude. Conversely, higher lunar altitude in winter, provides a deeper foraging depth at night when compared to summer. These predictions are useful for defining how DVM may change seasonally, especially where winter data was previously limited. Additionally, foraging models may benefit from info pertaining to when and where a species forages, which may determine the prey species available (i.e., benthic vs. pelagic prey).

Future work should investigate additional abiotic factors that may affect visual detection within aquatic systems. For example, waves can both increase and decrease the amount of light at depth dependent upon wave characteristics such as wave height and period (Schenck, 1957). Similarly, turbidity has been shown to decrease visual detection (Mazur and Beauchamp, 2003; Vogel and Beauchamp, 1999). A thorough investigation of the combined effects of factors that may alter the light environment can provide a more comprehensive understanding of predator prey interactions in the natural environment. Finally, the role that other sensory modalities play in mediating predator-prey interactions should be clarified. While this dissertation focuses on vision, it is likely

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that mechanosensory and chemosensory detection additionally mediate perception and

the extent to which each sense is used should be characterized.

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