Foraging mechanisms of siscowet lake trout (*Salvelinus namaycush siscowet*) on pelagic prey

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ARTICLE INFO

ABSTRACT

The reaction distance, angle of attack, and foraging success were determined for siscowet lake trout (*Salvelinus namaycush siscowet*) during laboratory trials under lighting conditions that approximated downwelling spectral irradiance and intensity (9.00×10^8–1.06×10^{14} photons m^{-2} s^{-1}) at daytime depths. Siscowet reaction distance in response to golden shiners (*Notemigonus crysoleucas*) was directly correlated with increasing light intensity until saturation at 1.86×10^{11} photons m^{-2} s^{-1}, above which reaction distance was constant within the range of tested light intensities. At the lowest tested light intensity, sensory detection was sufficient to locate prey at 25 ± 2 cm, while increasing light intensities increased reaction distance up to 59 ± 2 cm at 1.06×10^{14} photons m^{-2} s^{-1}. Larger prey elicited higher reaction distances than smaller prey at all light intensities while moving prey elicited higher reaction distances than stationary prey at the higher light intensities (6.00×10^9 to 1.06×10^{14} photons m^{-2} s^{-1}). The capture and consumption of prey similarly increased with increasing light intensity while time to capture decreased with increasing light intensity. The majority of orientations toward prey occurred within 120° of the longitudinal axis of the siscowet's eyes, although reaction distances among 30° increments along the entire axis were not significantly different. The developed predictive model will help determine reaction distances for siscowet in various photic environments and will help identify the mechanisms and behavior that allow for low light intensity foraging within freshwater systems.

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Introduction

The offshore community of Lake Superior is comprised of a relatively small number of native species that have evolved to use the resources of a cold, deep water environment (Gamble et al., 2011). Offshore waters (>80 m depth) represent 80% of Lake Superior by area (Horns et al., 2003; Stockwell et al., 2006) and the aquatic organisms in this zone are glacial relicts and remnants from arctic seas during the Pleistocene Era (Dadswell, 1974). The simplicity of the offshore food web makes it an ideal system to study food web dynamics and predator prey relationships. Apex predators, burbot (*Lota lota*) and siscowet lake trout (*Salvelinus namaycush siscowet*) (hereafter siscowet) occupy the top trophic level, and prey on subsequent trophic level occupants including deepwater sculpin (*Moxocephalus thompsonii*) and the coregonines, kiyi (*Coregonus kiyi*) and cisco (*C. artedi*) (Harvey et al., 2003; Isaac et al., 2012). These planktivorous fish in turn consume zooplankton, including *Mysis relicta*, cladocerans, *Diporeia* and copepods (Anderson and Smith, 1971; Auer et al., 2013).

Four morphotypes of lake trout are currently identified in Lake Superior including the lean lake trout, siscowet, humper and redfin (Bronte and Moore, 2007; Muir et al., 2014). The siscowet is a deepwater morphotype occupying offshore waters. Siscowet, the most abundant piscivore in the lake (Gorman et al., 2012a,b), vastly outnumber the other morphotypes by approximately 10 to 1 (Bronte et al., 2003; Ebener, 1995) and siscowet biomass is $22\times$ greater than lean lake trout biomass within Lake Superior (Gorman et al., 2012b). Siscowet generally occupy the offshore waters from 80 m (Harvey et al., 2003) to bottom depths > 400 m during the day (Sitar et al., 2008) and move higher in the water column at night expressing diel vertical migration (DVM) (Jensen et al., 2006; Hrabik et al., 2006; Stockwell et al., 2010; Gorman et al., 2012a). Genetic differences between the morphotypes (Goetz et al., 2010) result in higher lipid production in siscowets, resulting in 30–70% body fat composition compared to 20% in lean lake trout (Eschmeyer and Phillips, 1965; Wang et al., 1990). Greater lipid levels may be adaptive for regulation of buoyancy in the deeper water and may facilitate DVM (Eshenroder and Burnham-Curtis, 1999; Goetz et al., 2013). Nitrogen is more soluble in fatty tissues than lean tissues, and greater lipid content may allow for quicker vertical migrations (changes in pressure) without

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associated barotrauma as a result of nitrogen escaping leaner tissues (Shilling, 1976).

Siscowet perform DVM by moving shallower in the water column at night to consume kiyi which are in turn following migrating mysid shrimp (Gorman et al., 2012a; Hrabik et al., 2006; Jensen et al., 2006; Stockwell et al., 2010;). During the day, siscowet follow kiyi that are likewise exhibiting DVM to deep waters (>140 m) where they prey on both kiyi and deepwater sculpin (Ahrenstorff et al., 2011; Gamble et al., 2011; Gorman et al., 2012a; Hrabik et al., 2014; Isaac et al., 2012). The siscowet diet is primarily comprised of deepwater sculpin and coregonines, with kiyi being the most vulnerable coregonine (Gamble et al., 2011; Gorman et al., 2012a; Hrabik et al., 2006; Sitar et al., 2008; Stockwell et al., 2006, 2010; Yule et al., 2009). Kiyi, which are found between 325 m (day) and 30 m (night) (Hrabik et al., 2006), are numerically Lake Superior's most abundant deep water pelagic prey species (Gorman et al., 2012b) although cisco are the most abundant pelagic prey species. They are a more energy dense food source than the deepwater sculpin (Negus et al., 2008), and DVM between siscowet and kiyi are tightly correlated (Ahrenstorff et al., 2011; Hrabik et al., 2006, 2014; Stockwell et al., 2010). Due to both diurnal migration behavior, and the depths of water inhabited, siscowet spend much of their lives in low light environments.

Recent visual studies in marine fish show that predatory fish have visual sensitivity correlating to the light intensity at which they forage; and similarly benthic fish have greater sensitivity to low light (Horodysky et al., 2010). Within Lake Superior, 500 nm is the deepest penetrating wavelength in spring and summer which shifts to 550 nm in late fall due to seasonal turbidity (Jerome et al., 1983). Electroretinography studies have shown peak wavelength sensitivity for adult siscowet at approximately 525 nm, which overlaps with the downwelling light spectrum (below 35 m) within Lake Superior for these seasons (Harrington et al., 2015; Holbrook et al., 2013).

Foraging mechanisms for siscowet under ecologically relevant light intensities are unknown and until recently, little work has been done on fish that occupy depths greater than 100 m in Lake Superior (Negus et al., 2008). Previous work on adult lean lake trout has shown that reaction distance in response to prey increases with light intensity to an upper threshold and then remains constant. However, this upper threshold value may differ for siscowet and lean lake trout due to differences in physiology and the wavelengths of light available at depth (>80 m). Additional studies have shown a reduction in reaction distance at light intensities below 18 lx (~1.98×10^{15} photons m^{-2} s^{-1}) in adult lean lake trout (Vogel and Beauchamp, 1999; Mazur and Beauchamp, 2003) and below 0.9 lx (~1.60×10^{13} photons m^{-2} s^{-1}) in age-0 lean lake trout (Confer et al., 1978). However, recent studies using spectrally matched lighting (440–550 nm) show effective foraging at lower intensities (0.4 lx or ~9.58×10^{12} photons m^{-2} s^{-1}) for age-0 lean lake trout (Holbrook et al., 2013).

A thorough examination of predator prey interactions is needed to understand how predation may influence future ecological interactions in the Lake Superior offshore system. Development of a foraging model applying visual specificity and light threshold effects on visual predation will aid in these objectives (Boeuf and Le Bail, 1999; Horodysky et al., 2010). The association between behavior and habitat used when modeling is unknown for most species (Roth et al., 2008), and current model simulations of predator prey interaction intensity without accurate prey detection and foraging models may be flawed.

The objectives of this study were to determine foraging characteristics of siscowet under ecologically relevant light intensities, 9×10^8 to 1×10^{14} photons m^{-2} s^{-1}, including reaction distance, angle of attack and foraging success. Additionally, the association between light intensity and reaction distance was used to develop a predictive prey detection model.

Materials and methods

Fish collection and culture

Siscowet were collected by the research vessel *Kiyi,* under operation of the United States Geological Survey (Ashland, WI) via daytime bottom trawls on 24 June 2013 and 29 October 2013. Ten minute trawls (12 m Yankee bottom trawl) at a depth between 115 and 120 m were conducted east of Stockton Island in the Apostle Islands of Lake Superior (Latitude: 46° 54.751 Longitude: 90° 30.611).

Collected fish were treated for 2 min in a tank (570 L) consisting of a solution of chilled lake water (4–6 °C) aerated with compressed O$_2$, 0.026% Stresscoat® (Mars Fishcare North America Inc., Chalfont, PA), 0.002% MS-222, tricaine methanesulfonate (Sigma Chemical Co., St. Louis, MO) and 0.5% Instant Ocean® (Aquarium Systems Inc., Mentor, OH) to reduce osmotic stress. Gas bladders were then vented using sterile 14 gauge veterinary needles (QC Supply, Schuyler, NE) and insertion sites were cleansed post injection with betadine (Purdue Products L.P., Stamford, CT) before fish were placed back in the solution for 5 additional minutes. Fish were then transferred to a transport tank (285 L) aerated with compressed O$_2$ consisting of a 0.5% Instant Ocean®, 0.026% Stresscoat®, and 0.0002% MS-222 lake water solution.

Fish were housed at the University of Minnesota Duluth (Duluth, MN) in mechanically and chemically filtered (Penn-Plax Cascade™) 1900 L recirculating systems. Tanks were maintained in a cold room at 5.5 °C and were subjected to a 14 h light:10 h dark photoperiod with a light intensity of 3.05×10^9 photons m^{-2} s^{-1} for the diurnal segment. Doors were lined with foil and the entrance to the cold room was baffled with suspended black plastic to prevent ambient light from entering. Prior to siscowet introduction, tanks were aerated with compressed O$_2$ (16 ppm) for three days and tank salinity (Instant Ocean®) was maintained at 0.5% (isotonic to fish).

Upon siscowet introduction, tanks were treated with Stresscoat® (0.026% overall solution) and carbon filtration was suspended. Seven days post-introduction, oxygenation was discontinued, carbon filtration was resumed and feeding was initiated.

Siscowet were fed white suckers (*Catostomus commersonii)* twice weekly until foraging trials were initiated. Upon initiation of testing, siscowet were sustained by golden shiners (*Notemigonus crysoleucas*) captured during foraging trials. If siscowet were unsuccessful in capturing prey during their weekly trial, one white sucker was fed to supplement their diet. This allowed siscowet to maintain a state that ensured foraging behavior but maintained proper fish sustenance and health.

Temperature, pH, nitrite, ammonia and oxygen concentration were recorded twice daily for the initial two weeks and then daily thereafter. Tank maintenance, fish selection and feeding were done under low intensity red lighting (Sunbeam 40 W, 630–700 nm, ~1.62×10^{13} photons m^{-2} s^{-1}). All experiments, including the use of golden shiners, conformed to the University of Minnesota animal care protocols (Protocol Number: 1208A19622) and were approved by the Institutional Animal Care and Use Committee.

Prey

Kiyi comprise a large portion (20–39%) of the siscowet diet in Lake Superior (Gamble et al., 2011; Sitar et al., 2008), and diel vertical movements between the two species are tightly correlated (Hrabik et al., 2006, 2014; Ahrenstorff et al., 2011; Stockwell et al., 2010). Due to excessive barotrauma during collection, husbandry of kiyi has proven unsuccessful (Gorman and Keyler, unpublished data). The golden shiner, another non-benthic species, was substituted as a surrogate for kiyi in the experiments as they are of similar size, body shape (deep, compressed) and color.

Golden shiners were obtained from Chalstrom's sport shop (Duluth, MN) and hand selected to meet size criteria. Shiners (n = 120) were housed in mechanically and chemically filtered 113 L aquaria

(~10 animals/tank) and subjected to the same 14 h light:10 h dark photoperiod as the siscowet. All fish were acclimated to 5.5 °C for 24 h prior to trials and were used in experiments within three days of acquirement. Two size classes of shiners were used in trials and separated by mass and length (Mean ± S.E.). Large shiners ranged from 123 to 176 mm in total length (L_T) and averaged 142 ± 2 mm and ranged in mass from 20 to 37 g with a mean mass of 30 ± 1 g, while the small shiner size class was 63–113 mm L_T, 94 ± 1 mm and 2.8–12 g, 7 ± 0 g, respectively. Careful ethical consideration was used when selecting the golden shiner for our trials, and live prey was necessary to model siscowet reaction distance, which was previously unknown. Trials were limited to 10 min to reduce the stress on prey and no shiner was used more than once. Injured prey were quickly euthanized via 0.01% MS-222, tricaine methanesulfonate in accordance to the Institutional Animal Care and Use Committee, Protocol Number: 1208A19622.

Foraging arena

The foraging arena consisted of an 1892 L rectangular (2.28 m × 0.81 m) fiberglass tank (Hydro Composites LLC, Stockdale, TX). The interior sides of the arena were lined with black landscaping cloth to create a matte black surface. Acrylic inserts (Northern Acrylics, Duluth, MN) were gridded with 12.7 mm red striping tape (3 M, St. Paul, MN) in a 200 × 200 mm grid pattern and affixed to the bottom and sides of the tank to aid in digital analysis of predator/prey movement. Water temperature was maintained at 5.5 °C, water depth was a constant 0.4 m and water in the foraging arena was mechanically and chemically filtered by two Penn-Plax 1500 Cascade™ filters, which were inactivated during testing (Fig. 1). The tank was partitioned by an opaque lift gate to separate siscowet and shiner prior to the trial and black fabric enclosed the tank to eliminate observer interference.

Cyan light emitting diode (LED) lights (Cree XLamp XR Series, Durham, NC) with a spectral range of 500–510 nm were used to match the approximate predominant downwelling light in Lake Superior (Jerome et al., 1983). Eight light engines with six LEDs were positioned 1.3 m above the surface of the water and arranged in two rows (0.27 m apart) to the long axis of the tank with 0.6 m between each light engine. White light diffusing paper (Savage, Universal, Chandler, AZ) exhibiting 66% light transmittance was suspended 20 cm below light sources to prevent glare on the water surface. Light intensity was controlled via a driver (IRIS LED driver dimmer, Power Vector, Waterloo, ON) and a DMX 6 channel controller (Elation SCD-6 DMX Controller, Los Angeles,

CA). For light intensities below 1.62×10^{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 (6×10^9–9×10^8 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 intensity was measured in both radiometric and photometric units at the water's surface using the International Light Technologies ILT1700 Research Radiometer (Peabody, MA) where a SED033/F/HMR/W broadband silicon detector was used to measure light intensity in watts cm^{-2} s^{-1} and a SUD033 broadband underwater silicon detector was used to measure light intensity in lux.

Four infrared LED sources (CMVision, Houston, TX) were mounted to the sides of the tanks to provide adequate illumination for cameras. The infrared LEDs produce an 850 nm peak wavelength, which has been proven to be outside the range of visual sensitivity for teleost fishes (Dartnall, 1975; Douglas and Hawryshyn, 1990). Additionally, Mazur and Beauchamp (2003) found no significant effect of infrared lighting on reaction distance for lake trout. Foraging trials were recorded using six infrared capable Vantage (model LBC7081) night vision, wide-angle cameras (30 frames/s) and an ECO2 series (LH130) DVR, Lorex Technologies, Markham, ON. Three cameras were suspended above the tank and three cameras were mounted on the side of the tank to record predator and prey movements.

Light intensity

Experiments were conducted at 9.00×10^8, 3.05×10^9, 6.00×10^9, 1.86×10^{11}, 1.62×10^{13}, and 1.06×10^{14} photons m^{-2} s^{-1} equivalent to approximately 0.0001, 0.0005, 0.001, 0.01, 1, and 10 lx. Here, 9.00×10^8 photons m^{-2} s^{-1} indicates total darkness as these readings were taken in a sealed cold room with no light source. Light intensities are reported in radiometric units opposed to photometric lux units, which are calculated in regards to human vision and not suitable for fish visual studies (Johnsen, 2012). While light intensity readings were collected in both photons m^{-2} s^{-1} and lux, approximate lux values are reported only as a reference for previous studies. Solar/lunar irradiance at depth and conversion of measurements in watts cm^{-2} s^{-1} and μ einsteins m^{-2} s^{-1} to photons m^{-2} s^{-1} were calculated using the methods of Harrington et al. (2015). Additionally, light intensity at depth (x) was calculated using the Beer-Lambert equation (Hutchinson, 1957):
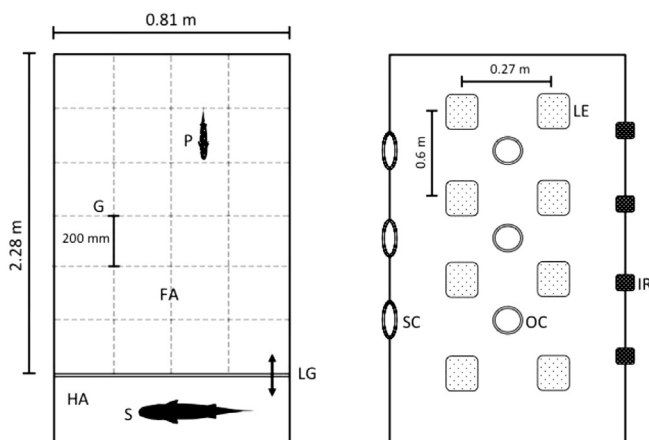
$$I_x = I_o e^{-kx} \tag{1}$$

Where surface irradiance, $I_o = 450 \pm 87$ μ einsteins m^{-2} s^{-1} (Mean ± S.E.) was determined as the average of daily solar surface intensities in summer (Fahnenstiel et al., 1984) and $k = 0.115$ was used for the vertical attenuation coefficient (Sterner, 2010). Lunar surface irradiance (waning gibbous 2 days post-full) reported by Cramer et al. (2013) was used to calculate light intensity at depth during the night. Light intensities for solar and lunar values correlated to depth at which siscowet may effectively use visually mediated foraging behavior are shown in Table 1. It should be noted that the average daytime surface irradiance is less for other seasons and the reported summer

Fig. 1. Schematic drawing of foraging arena viewed from above (left) and light and camera placement for experimental trials (right). After light intensity acclimation, the siscowet (S) was released from the holding area (HA) by raising the lift gate (LG) whereupon the siscowet entered the gridded (G) foraging arena (FA) to interact with the prey (P) (Left). Eight light engines (LE) were evenly spaced around the tank while three suspended overhead cameras (OC) and three side cameras (SC) recorded fish movements. Four external infra-red lights (IR) were mounted on the side of the tank (Right).

Table 1
Solar and lunar light intensities values correlated to depth at which siscowet may effectively use visually mediated foraging behavior.

Photons m^{-2} s^{-1}	Lux (approx.)	Solar depth (meters)	Lunar depth (meters)
9.00×10^8	0.0001	213.8	62.3
3.05×10^9	0.0005	203.2	51.7
6.00×10^9	0.001	197.3	45.8
1.86×10^{11}	0.01	167.4	15.9
1.62×10^{13}	1	128.6	–
1.06×10^{14}	10	112.2	–

surface irradiance values represent near maxima for optimal foraging conditions.

Foraging parameters

All foraging trials were conducted between January 1, 2014 and June 6, 2014. Siscowet ($n = 5$) ranging from 340 to 500 mm L_T were fasted for 48 h prior to testing. At the beginning of a trial, the siscowet and prey were separated by a lift gate within the experimental tank. The siscowet was placed within the holding area while the prey was released into the foraging arena. Both siscowet and prey were acclimated to the experimental light intensity for a minimum of 30 min. Trials initiated when the lift gate was manually raised via a rope and pulley system allowing the tester to remain on the outside of the shrouded arena. Trials were conducted for 10 min or until prey was consumed; to ensure prey was outside of the maximum reaction distance at the beginning of the trial, the gate was only raised once prey was a minimum of 100 cm away, which is the determined maximum reaction distance for lean lake trout (Vogel and Beauchamp, 1999). This minimum prey distance criteria minimized the constraint of the holding area once the lift gate was raised and allowed the siscowet a full range of movement at the start of the trial; this prevented the prey from consistently being perpendicular to the siscowet when foraging commenced.

Data analysis

Foraging trials were reviewed using Windows Media Player (Microsoft, v. 12) and Snagit (TechSmith, v. 12) was used to capture video images. Images from the suspended cameras were then analyzed for 2 dimensional fish movement using ImageJ software (NIH, v. 1.48) to determine reaction distance and angle of attack, which were measured at the moment the fish located and oriented toward the prey according to the methods of Holbrook et al. (2013). Reaction distance was measured as the distance between midpoint of the prey and the midpoint of the siscowet's eyes. Angle of attack was calculated as the angle of the prey off axis from the longitudinal axis of the siscowet from midpoint of predator eyes to midpoint of prey body just prior to locating and orientating toward prey. Prey location is defined as siscowet orientation toward prey indicated by turning of the head. The distribution of orientations toward prey were compared between 60° increments to determine the effect of prey position in front, alongside and behind siscowet.

Foraging success was also calculated for all trials as the probability of a fish successfully locating (orientating to), pursuing, attacking and retaining the prey. Using the methods of Richmond et al. (2004), location was defined as the proportion of orientations toward prey; pursuit as actively chasing prey; attack as hitting the prey with an open mouth; and retention as consuming prey. The amount of time to capture prey and whether the prey was stationary or moving prior to siscowet orientation was also recorded.

Modeling

A Michaelis–Menten saturation function (O'Neill et al., 1989) was used to show the relationship between light intensity (L_i, photons m^{-2} s^{-1}) and reaction distance (R_d cm).

The model is represented by:

$$R_d = \frac{R_{max}L_i}{\alpha + L_i} \qquad (2)$$

Where R_{max} is equal to the maximum reaction distance (cm) and α is equal to the half saturation constant (photons m^{-2} s^{-1}). This model has previously been applied to demonstrate the relationship between light intensity and reaction distance in juvenile lake trout (Holbrook et al., 2013) and yellow perch (Perca flavescens) (Richmond et al., 2004).

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 $\alpha = 0.05$. Unless noted otherwise, prey size classes were pooled for analysis.

Results

Reaction distance

There was a significant effect of light intensity on siscowet reaction distance (Fig. 2a; ANOVA, $F_{5,367} = 26.83$, $p > 0.0001$). Reaction distance increased with light intensity from 9.00×10^8 to 1.86×10^{11} photons m^{-2} s^{-1} thereafter remaining constant. The reaction distance at each light intensity was compared and from 6.00×10^9 to 1.86×10^{11} photons m^{-2} s^{-1} there was a significant increase in reaction distance (Tukey's HSD, $p < 0.01$) and a significant difference between the two lowest light intensities, 3.05×10^8 and 9.00×10^8 photons m^{-2} s^{-1} (Tukey's HSD, $p < 0.0001$). The maximum average reaction distance (59 ± 2 cm) was recorded at 1.06×10^{14} photons m^{-2} s^{-1} and the minimum average reaction distance (25 ± 2 cm) at 9.00×10^8 photons m^{-2} s^{-1}.
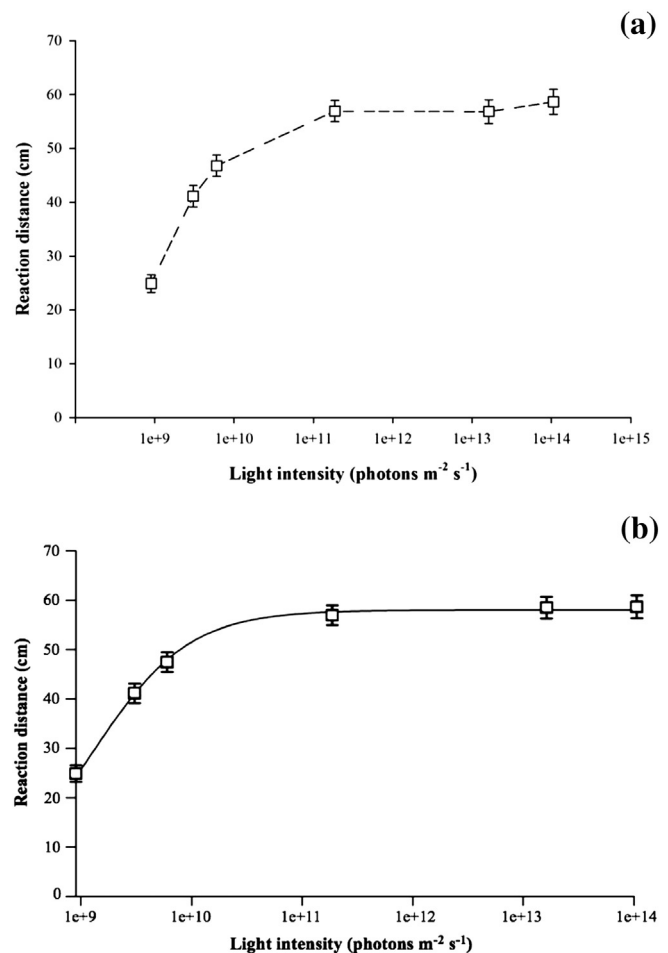

Fig. 2. (a) Average reaction distance (cm) of siscowet lake trout in response to Notemigonus crysoleucas at varying light intensity. (b) A Michaelis–Menten function was used to fit the data where $R_{max} = 57.5$ and $\alpha = 1.24 \times 10^9$ ($R^2 = 0.98$). Error bars for both panels are ± 1 SE.

Foraging model

A Michaelis–Menten saturation function (Fig. 2b) was used to estimate the relationship between light intensity (L_i, photons m^{-2} s^{-1}) and reaction distance (R_d, cm). The estimates of the parameters in the model were $R_{max} = 57.5$ and $\alpha = 1.24 \times 10^9$ (SS$_{total} = 20.6$). The model accounted for 98% of the variability in reaction distance at light intensities between 9.00×10^8 and 1.06×10^{14} photons m^{-2} s^{-1} (non-linear regression, R$^2 = 0.98$).

Prey movement

Prey movement and light intensity influenced reaction distance of siscowet (Fig. 3a; Two way ANOVA, $F_{5,249} = 11.46$, p < 0.0001). As in earlier results, reaction distance increased with light intensity up to 1.86×10^{11} photons m^{-2} s^{-1} (Light intensity effect, $F_{11,249} = 11.46$, p < 0.0001). There was an overall trend for higher reaction distances for moving prey (48 ± 1 cm) than stationary prey (43 ± 4 cm), but this effect was only marginally significant (Prey movement effect, $F_{1,249} = 2.62$, p = 0.11). There was little difference in mean reaction distance between moving and stationary prey at lower light intensities, but greater differences were observed at the four highest light intensities. However, the difference was not significant, possibly due to low sample size (Interaction effect, $F_{5,249} = 0.34$, p = 0.89). For all light intensities the majority of prey continually swam along the perimeter of

the foraging arena and only remained motionless periodically if stopped before resuming swimming. From 9.00×10^8 to 1.62×10^{13} photons m^{-2} s^{-1}, prey remained motionless for at least 10% (11.4–20.8%) of the 10 minute trial on average (Table 2). At 1.06×10^{14} photons m^{-2} s^{-1}, prey were slightly less inclined to remain motionless and were stationary for approximately 6% of the trial.

Prey size

Prey size and light intensity influenced reaction distance of siscowet (Fig. 3b; Two way ANOVA, $F_{11,361} = 14.64$, p < 0.0001). As with the pooled data, reaction distance increased with light intensity up to 1.86×10^{11} photons m^{-2} s^{-1} (Light intensity effect, $F_{5,361} = 22.50$, p < 0.0001), after which reaction distance did not change with increasing light intensity. At all light intensities, there was a significantly greater reaction distance for larger prey (142 ± 2 mm, 30 ± 1 g) than for smaller prey (94 ± 1 mm, 7 ± 0 g) (Prey size effect, $F_{1,361} = 13.56$, p = 0.0003; Interaction effect, $F_{5,361} = 1.19$, p = 0.31). Thus, siscowet responded to larger prey at greater distances than smaller prey.

Orientations

Orientations toward prey were not equally distributed among 60° increments (Fig. 4; $\chi2 = 61.54$, d.f. = 2, P < 0.0001). Significantly more orientations toward prey occurred between ±0 and 60° (forward sector) (N = 101) from the longitudinal axis of the siscowet than between ±60 and 120° (lateral sector) (N = 62) and ±120–180° (rear sector) (N = 15). However, there was not a significant difference for reaction distance between the 60° increments and values remained relatively constant (ANOVA, $F_{2,175} = 0.13$, p = 0.88).

Foraging success

Siscowet had an overall foraging success of 41% among feeding trials at the various light intensities totaling 53 prey captures. There was an increase in foraging success with increasing light intensity from 5% (1 capture) at 9.00×10^8 photons m^{-2} s^{-1} (Fig. 5a) to 80% success (16 captures) at 1.06×10^{14} photons m^{-2} s^{-1}. Additionally, there was only a 50% probability of siscowet orienting toward prey at 9.00×10^8 photons m^{-2} s^{-1}, while at the second lowest light intensity (3.05×10^9 photons m^{-2} s^{-1}) there was an increase to 83% prey location probability. Prey location probabilities remained within the 80th percentile from 3.05×10^9 - 1.62×10^{13} photons m^{-2} s^{-1} until 1.06×10^{14} photons m^{-2} s^{-1} where a 98% probability of orientation was obtained. Similarly, prey retention steadily increased with increasing light intensity from 10% at 9.00×10^8 photons m^{-2} s^{-1} to 41% at 1.06×10^{14} photons m^{-2} s^{-1} (Table 3).

The range of individual reaction distances was consistent from 6.00×10^9 to 1.06×10^{14} photons m^{-2} s^{-1} with six or more reactions greater than 80 cm at each light intensity (Fig. 6a). The range decreased at 3.05×10^9 photons m^{-2} s^{-1} with only one reaction greater than 80 cm (Fig. 6b). Similarly, the range of angle of attack was consistent from 3.05×10^9 to 1.06×10^{14} photons m^{-2} s^{-1} with eight or more
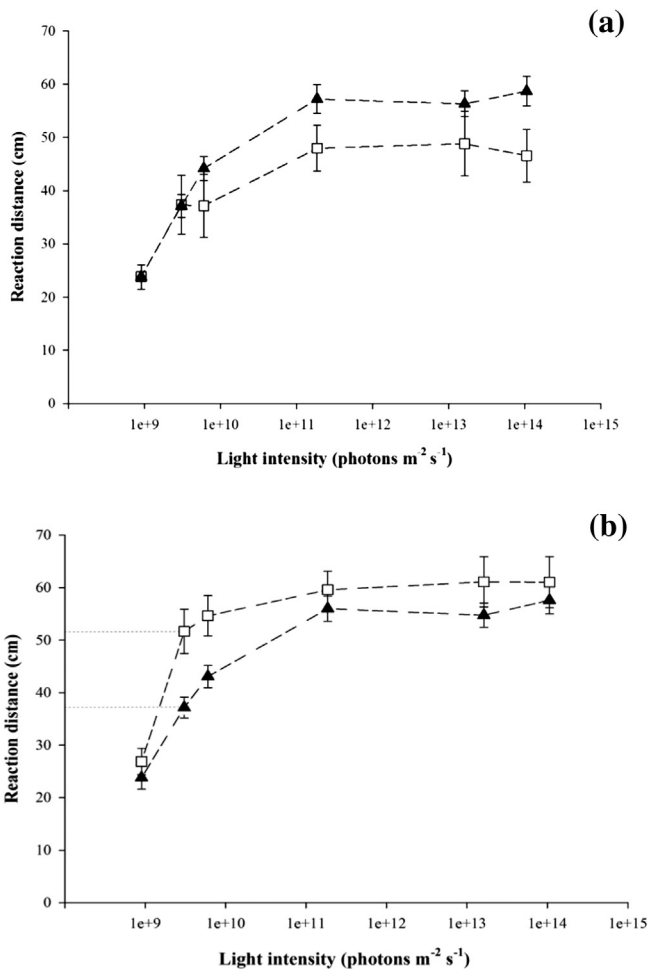

Fig. 3. Average reaction distance (cm) of siscowet lake trout in response to: (a) moving (▲) and stationary (□) prey at varying light intensity and (b) two prey size classes (▲ < 12 g and □ >20 g) at varying light intensity where horizontal dashed lines at 37 and 51 cm indicate increased window of vulnerability for larger prey. Error bars for both panels are ± 1 SE.

Table 2
Average time in seconds and percent of 10 minute trial time that prey were stationary at varying light intensity.

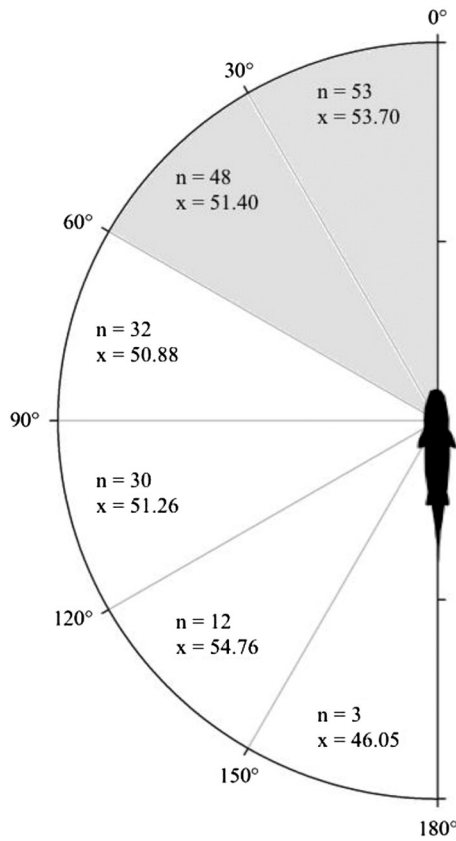| Photons m^{-2} s^{-1}	Stationary (s)	% of trial
9.00×10^8	68.6	11.4
3.05×10^9	101.6	16.9
6.00×10^9	101.4	16.9
1.86×10^{11}	80.0	13.3
1.62×10^{13}	124.8	20.8
1.06×10^{14}	38.9	6.4
Mean	**85.9**	**14.3**

Means are shown in bold.

Fig. 4. Average reaction distance (x) and total number of orientations (n) plotted within 30° increments for combined light intensities. The solid fish figure in the middle represents the orientation of the fish relative to degrees off axis of prey. The majority (54%) of orientations are within the first 60°.

orientations toward prey greater than 100° at each light intensity with only one orientation greater than 100° occurring at 9.00×10^8 photons $m^{-2} s^{-1}$ (Fig. 6c).

The time to capture prey decreased with increasing light intensity (Fig. 5b; Kruskal-Wallis, $F_{2,50} = 5.21$, $p = 0.009$). From 9.00×10^8 - 3.05×10^9 photons $m^{-2} s^{-1}$, the average time to capture prey was 400 s. The time to capture decreased to ~200 s for the midrange light intensities (6.00×10^9 - 1.86×10^{11} photons $m^{-2} s^{-1}$), and then

Table 3
Average probability of prey location, pursuit, attack, and retention for siscowet lake trout during foraging trial events (n = 381) at varying light intensities. The total column is the product of the average probability of prey location, pursuit, attack, and retention.

Photons $m^{-2} s^{-1}$	Location	Pursuit	Attack	Retention	Total Probability	N
9.00×10^8	0.50	0.55	0.59	0.10	0.01	**39**
3.05×10^9	0.83	0.88	0.49	0.12	0.04	**77**
6.00×10^9	0.89	0.93	0.44	0.26	0.09	**75**
1.86×10^{11}	0.84	0.93	0.45	0.30	0.11	**72**
1.62×10^{13}	0.87	0.98	0.65	0.43	0.18	**55**
1.06×10^{14}	0.98	0.95	0.65	0.41	0.25	**63**
Mean	**0.82**	**0.87**	**0.54**	**0.27**	**0.11**	

Means are shown in bold.

decreased below 200 s for the highest light intensities (1.62×10^{13} - 1.06×10^{14} photons $m^{-2} s^{-1}$). As prey becomes more difficult to detect, the time to capture prey increases significantly.

Discussion

Results of this study indicate siscowet have evolved visual sensitivity that allows for successful foraging under very low intensity light and may use mechanosensory detection when light is absent. While pelagic fish in oceanic waters are estimated to detect light as deep as 1000 m due to adaptation and water clarity (Clarke and Denton, 1962), visually mediated foraging below 100 m is rare in freshwater systems due to greater light attenuation (Guthrie et al., 1993). Siscowet are unique in that visually mediated foraging may be possible as deep as 200 m within Lake Superior as siscowet reaction distance increases with increasing light intensity up to 1.86×10^{11} photons $m^{-2} s^{-1}$, where after reaction distance remains constant as predicted by the Michaelis–Menten saturation function. Time to capture prey showed a negative correlation and decreased with increasing light levels, while amount of prey captured increased with greater light intensities at all levels. Prey mass was a significant factor with larger prey eliciting higher reaction distances at all light intensities. Similarly, there were greater reaction distances for moving prey than stationary prey at the four highest light intensities tested. Finally, the majority of orientations toward prey occurred within the first 60° of the siscowet's midline (forward visual sector) and reaction distances between lateral and rear visual sectors (60° and 180°) were not significantly different.

Foraging behavior of native fishes is important to the Lake Superior ecosystem because it affects population dynamics and species
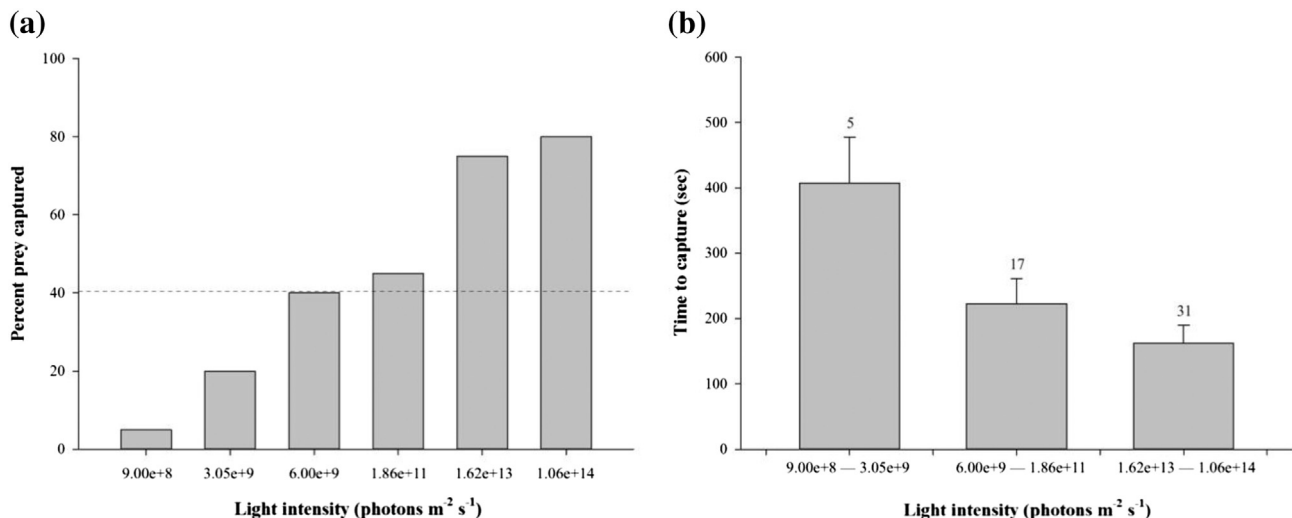
(a)

(b)

Fig. 5. (a) Percentage of prey captured by siscowet lake trout at varying light intensity. Horizontal dashed line indicates average number of prey captured for all trials. (b) Average time to capture prey (sec) for siscowet lake trout at varying light intensity. Numbers above error bars indicate number of prey captured at corresponding light level. Error bars are ± 1 SE.
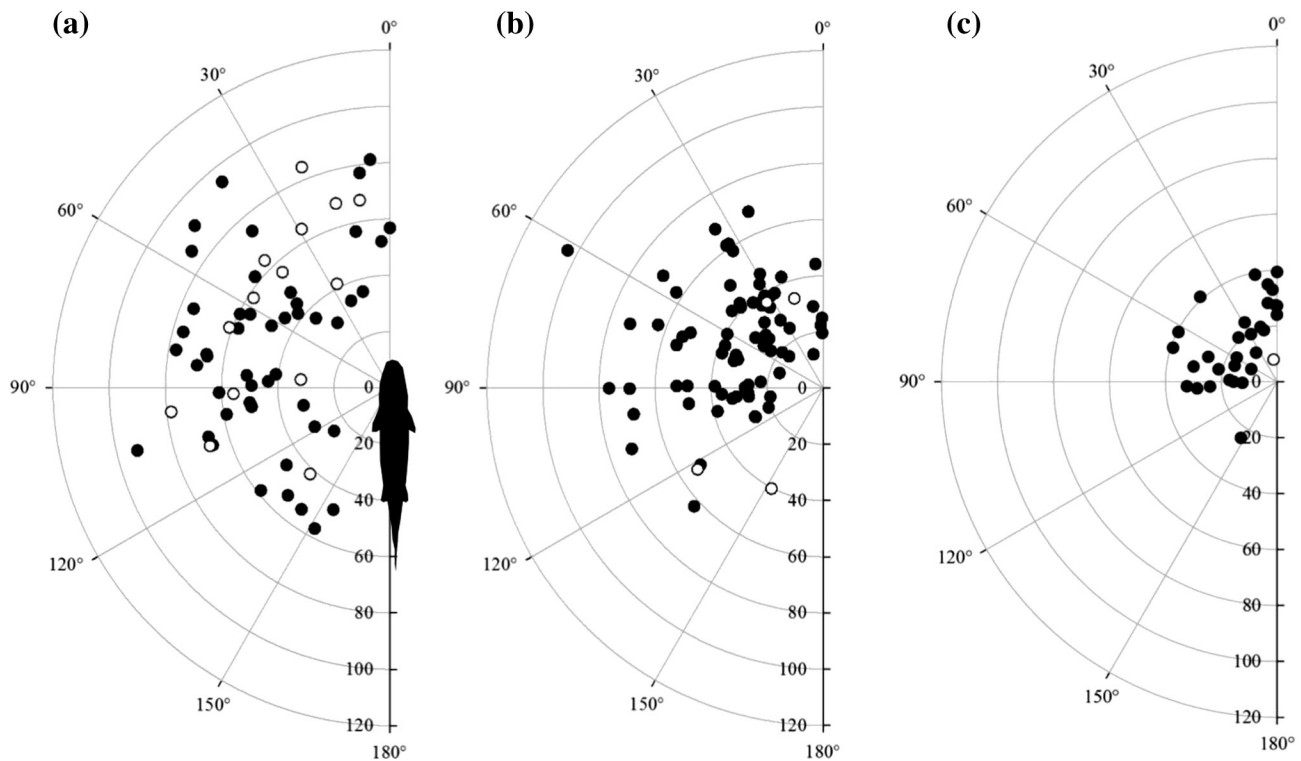
Fig. 6. Polar plot representation of reaction distance and angle of attack for siscowet lake trout in response to prey at three light intensities ranging from high to low (a) 1.62×10^{13} (b) 3.05×10^9 and (c) 9.00×10^8 photons m^{-2} s^{-1}. Solid circles represent orientation toward prey and open circles represent a capture. Each concentric circle represents a distance of 20 cm.

interactions, thereby influencing ecosystem structure and function. However, the physical environment in which siscowet forage poses challenges (i.e. light limitation). Based on the findings, the challenges with visual foraging may be offset by, but not limited to: i) adaptive foraging at night using lunar light, ii) spectral sensitivity matched to downwelling light, iii) detection of both prey movement and larger prey to improve foraging efficiency, and iv) mechanosensory detection in inadequate light environments.

Successful siscowet foraging occurred at all tested light intensities with a 15% increase in prey capture from total darkness to the second lowest light intensity, 3.05×10^9 photons m^{-2} s^{-1}. Using the Beer-Lambert equation it was determined a light intensity of 3.05×10^9 photons m^{-2} s^{-1} is equivalent to light at a depth of approximately 200 m within Lake Superior on a clear summer day at noon. Siscowet and kiyi both occupy the demersal zone >150 m during the day (Stockwell et al., 2006), and results indicate that siscowet would need to be at most 200 m depth or above to successfully capture 20% of prey or more. Interestingly, although reaction distance saturated with increasing light intensity, percent of prey captured did not. Between the 1.86×10^{11} and 1.62×10^{13} photons m^{-2} s^{-1} light intensity trials, there was an approximate 50% increase in prey capture while average reaction distance remained the same. This is notable because visual encounter rate models that are based solely on reaction distance may grossly underestimate foraging success between these two light intervals.

At night, both kiyi and siscowet vertically migrate higher in the water column. Siscowet are reported to migrate to within 30 m of the surface on average during the summer and fall months (Ahrenstorff et al., 2011). However, terrestrial insects found during stomach analysis of siscowets from a range of lake depths indicate migration to the lake surface (Sitar et al., 2008). Similarly, kiyi perform 100–175 m vertical migrations from the demersal zone up to shallower waters as they track *Mysis* at night (Ahrenstorff et al., 2011; Hrabik et al., 2006; Stockwell et al., 2010). In general, pelagic fishes prefer light levels less

than 0.001 lx (6.00×10^9 photons m^{-2} s^{-1}) during the evening (Yule et al., 2007). Ahrenstorff et al. (2011) reported kiyi at nighttime depths ~40 m during summer and fall, while Hrabik et al. (2006) reported consistently netting kiyi during 30 m depth trawls. Peak moonlight intensity values produce 3.05×10^9 photons m^{-2} s^{-1} (~0.0005 lx) at ~50 m, a light intensity where feeding was observed in the lab. DVM behavior may therefore help offset the challenge of light limited foraging as moonlight offers adequate illumination for successful capture of kiyi at depth during summer and fall within Lake Superior. Due to the concurrent vertical movements of kiyi and siscowet (Ahrenstorff et al., 2011; Gamble et al., 2011; Gorman et al., 2012a,b; Hrabik et al., 2014; Isaac et al., 2012), the preference of kiyi as high nutritional food source (Rottiers and Tucker, 1982; Vondracek et al., 1996) and the capability of foraging under moonlight at shallower depths, it is likely a substantial portion of the foraging for pelagic fish occurs at night.

Results indicate a disparity for threshold light intensities between the lake trout morphotypes. The threshold is represented by the light intensity where reaction distances decrease below the threshold light intensity value, but remain constant above this value. A threshold light intensity of 1.86×10^{11} photons m^{-2} s^{-1} (~0.01 lx) was determined for siscowet while Vogel and Beauchamp (1999) and Mazur and Beauchamp (2003) reported a threshold value of 17.8 lx (~1.98×10^{15} photons m^{-2} s^{-1}) for lean lake trout. Studies in juvenile lake lean trout by Confer et al. (1978) found a threshold of 50 lx (~1.47×10^{15} photons m^{-2} s^{-1}). These disparities have likely developed in part due to the different environments and associated diets of the lake trout morphotypes. Lean lake trout display crepuscular feeding behavior and diel bank migration (DBM) occupying higher light intensity shallower waters (0–80 m) (Gorman et al., 2012a) and consuming shallow water coregonines, rainbow smelt (*Osmerus mordax*) and benthic fish (Gamble et al., 2011; Harvey et al., 2003).

While some earlier studies used broad spectrum lighting, which may increase trout sensitivity to motion and contrast (Lythgoe, 1984; White et al., 2005; Krauss and Neumeyer, 2003), recent studies by Holbrook

et al. (2013) employed spectrally matched blue green LED lighting (450–550 nm) representative of downwelling light in deep, oligotrophic lakes (Boscarino et al., 2010). The authors determined a peak spectral sensitivity of 500 nm in age-0 lean lake trout, the midrange of wavelength at depth and ultimately determined a threshold for vision of 1.9 lx (~3.48×10^{13} photons $m^{-2} s^{-1}$) in age-0 lean lake trout. This upper vision threshold in age-0 lean lake trout correlates to the shallow water habitat with higher ambient light levels occupied by younger fish. Harrington et al. (2015) likewise determined peak sensitivity of 525 nm for the siscowet morphotype, which is midway between spring and fall downwelling light conditions in Lake Superior. In clearer, spring waters, 500 nm penetrates deepest in the water column while increased particulates in the fall allow green shifted 550 nm wavelengths to penetrate deepest. This optimization of spectral sensitivity to match the light environment at depth could be one adaptation for reduced light pelagic foraging.

Moving prey elicited higher reaction distances for siscowet than did stationary prey at the four higher light intensities (6.00×10^{9} - 1.06×10^{14} photons $m^{-2} s^{-1}$) indicating that moving prey assist in foraging at light environments of 6.00×10^{9} photons $m^{-2} s^{-1}$ and above. Other freshwater species, such as largemouth bass (*Micropterus salmoides*) have likewise shown an increase in reaction distance with prey motion and are more likely to pursue moving prey over stationary prey (Howick et al., 1983). Similarly, some marine predatory species have shown that visually detected prey movements are the most important factor for eliciting attacks at higher light intensities (Fouts and Nelson, 1999) and are the most important factor when compared to shape and anatomical features of prey (Holmes and Gibson, 1986). Prey movement may also be more important for clear water foraging such as in oligotrophic Lake Superior where planktivore reaction distance has been shown to increase with prey movement (Wright and O'Brien, 1984). Similarly, Holbrook et al. (2013) reported greater reaction distances for planktivorous age-0 lean lake trout when foraging for moving versus stationary mysid shrimp.

Prey size had the second most significant effect (following light intensity) on siscowet reaction distance in the study and the effect was greatest at the near lowest light levels (6.00×10^{9} and 3.05×10^{9} photons $m^{-2} s^{-1}$). While studies in age-0 lean lake trout reported higher reaction distances for larger *Mysis* over smaller prey (Holbrook et al., 2013), studies in adult lean lake trout by Vogel and Beauchamp (1999) did not see this trend. Detection distance for prey generally decreases with light intensity and varies proportionally with the size of the prey (Chesney, 1989; De Robertis et al., 2003; Dill, 1974), and studies with freshwater largemouth bass reported the trend of increasing reaction distance with increasing prey size with varying light intensity (Howick et al., 1983). Again, the use of spectrally matched lighting in this study as well as a black lining in the tank may have allowed for greater contrast between prey and background, which is more important for pelagic species detecting prey at depth where visual acuity becomes marginalized (Cerri, 1983). Additionally, larger prey offer a greater nutritional value per meal and less time may be spent foraging in order to consume an equivalent amount of smaller prey (Rottiers and Tucker, 1982).

At the lowest tested light intensity (9.00×10^{8} photons $m^{-2} s^{-1}$), average reaction distance (24.9 cm) was approximately 1/2 the body length of siscowet, which is consistent with reported findings for other dark tested species (Palmer et al., 2005; Price and Mensinger, 1999). It is probable that foraging at 9.00×10^{8} photons $m^{-2} s^{-1}$ (5% forage success) was mediated by mechanosensory detection and not olfaction as continuous mixing of water by predator and prey movements should have eliminated an odor point source, a condition of the testing tank, but not the natural environment (Bergstrom and Mensinger, 2009). At 9.00×10^{8} photons $m^{-2} s^{-1}$, siscowet were likely detecting water motion and pressure gradients created by prey movement via neuromast cells along the lateral line or head of the fish (Bleckmann and Zelick, 2009). In other freshwater species, the lateral line has been shown to facilitate low light foraging and may act in the place of vision

in the dark (Liang, 1998; Richmond et al., 2004). Siscowet may similarly employ mechanosensory means at low light intensities when visually mediated foraging is not feasible.

Average reaction distance for all light intensities combined was 49 cm while the maximum reaction distance (non averaged) observed during an experimental trial was 125 cm (1.06×10^{14} photons $m^{-2} s^{-1}$). While the maximum dimension of the foraging arena (220 cm) did not limit reaction distance, the minimum dimension (81 cm) may have been a limiting factor at the highest tested light intensities. However, it is unlikely that captivity altered reaction distances for siscowet as Vogel and Beauchamp (1999) reported a maximum reaction distance of ~1 m for lean lake trout both during their experimental trials as well as in the field. Additionally, tank effects on predation rates were inevitable with this type of *in situ* experiment (Tang and Boisclair, 1993), and the use of golden shiners as a surrogate for kiyi may have further confounded prey consumption data. However the study objectives were not dependent upon, and did not aim to suggest, natural intake rates for siscowet (Speare et al., 1995). As a natural forage fish for siscowet, kiyi may be more capable of avoiding predation due to their similar visual sensitivity to downwelling light spectra and intensities (Harrington et al., 2015). It is not likely though that the detection of prey, angle of attack, and reaction distance of siscowet would be affected by predator avoidance as these parameters are indicative of when the siscowet first detects and reacts to prey.

These findings in part owe to proper care and the testing of healthy fish. Other examples of successful adult siscowet husbandry are unknown or unreported and the techniques may be applicable to optimize care of other freshwater fishes. There was 100% survival for siscowets from day of collection until the end of trials, and study fish were still thriving and displaying foraging behavior as of November, 2014, more than a year later. Initial survival of siscowets is likely due to their increased lipid content allowing for reduced barotrauma during collection, while proper husbandry techniques and daily monitoring assured extended survival. During collection, precautions were taken to limit siscowet exposure to light intensities greater than 1.06×10^{14} photons $m^{-2} s^{-1}$ (10 lx) as mid-water fish may experience retina damage when exposed to daytime surface irradiations (Frank et al., 2012). While fish were briefly exposed to mid-day intensities during collection, Harrington et al. (2015) demonstrated that siscowet from the same trawls had intact retinal components, displayed strong electroretinograms, and showed spectral sensitivity curves similar to other pelagic species. Additionally, all siscowet displayed active foraging behavior exhibited by swimming around the foraging arena during trials demonstrating successful visual location of prey down to very low light intensities. This is indicative of healthy fish as foraging behavior is atypical for visually impaired fish (Robinson et al., 2013).

Future studies should focus on determining reaction distances for additional species under varying light intensities to create a comprehensive understanding of foraging within the pelagic food web in Lake Superior, as well as determine which species have a low light intensity advantage. Turbidity may also affect reaction distance and while turbidity is generally low in open water portions of Lake Superior, it has been shown to significantly decrease reaction distance in lean lake trout (Mazur and Beauchamp, 2003; Vogel and Beauchamp, 1999). Turbidity effects may similarly affect siscowet reaction distance, particularly in the late fall, post lake turnover (Jerome et al., 1983). Finally, the role of the lateral line in siscowet should be examined further to determine the extent of use under zero light intensity foraging. Collectively, these future studies would provide for a more integrated understanding of significance of vision in fish predator/prey relationships of fresh, deep-water lake ecosystems.

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