FORAGING MECHANISMS OF SISCOWET LAKE TROUT (*SALVELINUS NAMAYCUSH SISCOWET*) ON PELAGIC PREY

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Dedication

This thesis is dedicated to my wife, Brigitta as well as my parents and sister, Dan, Cheryl and Courtney.

Abstract

Little is known about the foraging mechanisms of siscowet (*Salvelinus namaycush siscowet*), the most abundant piscivore within Lake Superior because they occupy light-limited environments as a result of diel vertical migration. The reaction distance, angle of attack, and foraging success were determined for siscowet during laboratory trials under lighting conditions that approximated downwelling spectral irradiance and intensity (0-10 lx) at daytime depths. Siscowet reaction distance in response to golden shiners (*Notemigonus crysoleucas*) was directly correlated with increasing light intensity until saturation at 0.01 lx, and afterwards the relationship was asymptotic within our range of tested light intensities. In total darkness, lateral line sensory detection was sufficient to locate prey at 24.9 ± 1.7 cm, while increasing light intensities increased reaction distance up to 58.6 ± 2.3 cm at 10 lx. 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 (0.001-10 lx). 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 axis were not significantly different. Our 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 pelagic 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). Pelagic waters (> 80 m depth) represent 80% of Lake Superior (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 this 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*) (siscowet) occupy the top trophic level, and prey on second trophic level occupants including deepwater sculpin (*Moxocephalus thompsonii*) and the coregonines, kiyi (*Coregonus kiyi*) and cisco (*Coregonus artedi*) (Harvey et al. 2003; Isaac et al., 2012). These planktivorous fish in turn consume zooplankton, including mysis (*Mysis relicta*), cladocerans, diporeia and copepods (Anderson and Smith 1971; Auer et al., 2013).

Four morphotypes of lake trout are currently identified in the lake including the lean lake trout, siscowet, humper and redfin (Bronte et al., 2007; Muir et al., 2014). The siscowet is a deepwater morphotype of lake trout occupying the pelagic waters of Lake Superior. Siscowet, the most abundant piscivore in the lake (Gorman et al., 2012a, 2012b), vastly outnumber the other morphotypes by approximately 10 to 1 (Bronte et al., 2003; Ebener et al., 1995) and siscowet biomass is 22x greater than lean lake trout biomass within Lake Superior (Gorman et al., 2012b). Siscowet occupy the pelagic zone 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 Philips, 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 associated barotrauma as a result of nitrogen escaping leaner tissues (Shilling et al., 1976).

Siscowet perform DVM by moving shallower in the water column at night to consume kiyi (*Coregonus kiyi*), which are in turn following migrating mysis shrimp (*Mysis relicta*) (Jensen et al. 2006; Hrabik et al. 2006; Stockwell et al. 2010; Gorman et al. 2012a). During the day, siscowet follow kiyi to deep waters (>140 m) where they prey on both kiyi and deepwater sculpin (*Moxocephalus thompsonii*) (Ahrenstorff et al., 2011; Gamble et al., 2011; Gorman et al., 2012a; Isaac et al., 2012; Hrabik et al., 2014). Due to both diurnal migration behavior, and the depths of water inhabited, siscowet spend much of their lives in light-limited 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 that 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 and shifts to 550 nm

in late fall due to turbidity. Electroretinography studies have shown peak wavelength

sensitivity for siscowet at approximately 525 nm, which overlaps with the down-welling

light spectrum (below 35 m) within Lake Superior for these seasons. (Harrington et al., in

review; Holbrook et al. 2013).

However, foraging mechanisms for siscowet lake trout 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., 2007). Previous

work on adult lean lake trout has shown reaction distance in lake trout increases with

light intensity to an upper threshold and then remains constant. Additional studies have

shown a reduction in reaction distance at light intensities below 18 lx in adult lake trout

(Vogel and Beauchamp, 1999; Mazur and Beauchamp, 2003) and below 0.9 lx in age-0

lake trout (Confer et al., 1978). However, these previous studies employed broad

spectrum lighting, which differs from the *in situ* light environment, potentially reducing

ecological relevance of their inferences (Boscarino et al., 2010). More recent studies

using spectrally matched lighting (440-550 nm) show effective foraging at lower

intensities (0.4 lx) for age-0 lake trout (Holbrook et al., 2013).

Pelagic salmonids are predominantly visual feeders (Ali, 1959) and the ultra

oligotrophic pelagic waters of Lake Superior offer greater light penetration when

compared to more eutrophic lakes and may allow for more effective visual predation at

greater depth. The siscowet diet is primarily comprised of deepwater sculpin and

coregonines, with kiyi being the most vulnerable coregonine owing to a smaller size

(Gamble et al., 2011; Gorman et al., 2012a; Hrabik et al., 2006; Sitar et al., 2008;

Stockwell et al., 2006; Stockwell et al., 2010, Yule et al. 2009). Kiyi, which are found

between 325 m (day) and 30 m (night) (Hrabik et al., 2006), are numerically the most

abundant pelagic prey species (Gorman et al. 2012b). They are a more energy dense food

source than the deepwater sculpin (Negus, 2008) and diel vertical movements between

siscowet and kiyi are tightly correlated (Hrabik et al., 2006, 2014; Ahrenstorff et al.,

2011; Stockwell et al., 2010). However, due to the difficulty of *in situ* observational

studies, the mechanisms of interactions between the predator and prey are unknown.

Predation is a key determinant of the structure of pelagic communities (Paine,

1966; Carpenter et al., 1985; Carpenter and Kitchell, 1993), and overconsumption of prey

by siscowet may potentially alter the current Lake Superior ecosystem. Recent data

suggests the siscowet population is near carrying capacity, consuming 80% of the kiyi

population annually and over consuming deepwater sculpin (Hrabik, personal

communication; Yule et al., 2008 and Kitchell et al., 2000). Both kiyi and deepwater

sculpin are major links in the offshore trophic system and a population decline could alter

food web interactions.

A thorough examination of the mechanisms of predator-prey interactions is

needed to understand how predation may define future population trends in the Lake

Superior pelagic system. Determining movements and habitat use of fish are critical

when modeling population trends (Hayes et al., 2009; Rose, 2000) and development of a

foraging model applying visual specificity and light threshold effects on visual predation

will aid in these objectives (Boeuf and Bail, 1999; Horodysky et al., 2010). The

association between behavior and habitat used when modeling is unknown for most

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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 parameters of siscowet lake trout under ecologically relevant light intensities 0-10 lux, 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 lake trout (*Salvelinus namaycush siscowet*) were collected by the research vessel *Kiyi,* under operation of the United States Geological Survey (Ashland, WI) via daytime bottom trawls on June 24, 2013 and October 29, 2013. Ten-minute trawls (12 m Yankee bottom trawl) at a depth between 115-120 m were conducted east of Stockton Island in the Apostle Islands of Lake Superior (Latitude: 6° 54.751 Longitude: 90° 30.611).

Collected fish were treated for two minutes 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[TM]) 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 0.0005 lux for the illuminated portion. Cold room doors were lined with foil and the entrance to the cold room was protected by 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 (white suckers, *Catostomus commersonii,* twice weekly). 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, ~3 lx). All experiments

conformed to the University of Minnesota animal care protocols and were approved by the Institutional Animal Care and Use Committee.

Prey

Kiyi (*Coregonus 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 (*Notemigonus crysoleucas*), another non-benthic species, was substituted as a surrogate for kiyi in our 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 per tank) and subjected to the same photoperiod (see above). All fish were acclimated to 5.5°C for 24 hrs prior to trials and all fish were used in experiments within three days acquirement. Two size classes of shiners were used in trials and separated by mass and length (Mean ± S.E.). Large shiners ranged from 123-176 mm in total length (TL) and averaged 141.8 ±1.9 mm and ranged in mass from 20-37 g with a mean mass of 29.8 ± 1.2 g, while the small shiner class was 63-113 mm TL, 93.7 ±1.1 mm and 2.8-12 g, 7.2 ± 0.2 g, respectively.

Foraging Experiments

Foraging Arena

The foraging arena consisted of an 1892 L rectangular (2.28 m x 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 (3M, St. Paul, MN) in a 200 x 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 and water depth was a constant 400 mm. 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. Water in the foraging arena was mechanically and chemically filtered by two Penn-Plax 1500 Cascade^{TM} filters, which were inactivated during testing (Figure 1).

Cyan light-emitting diode (LED) lights (Cree XLamp XR Series, Durham, NC) with a spectral range of 450-560 nm were used to match the approximate predominant down-welling light in Lake Superior. 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 lx, a 0.3 neutral density filter (FOTGA, Hong Kong, CH) was

placed over the light source. To reach the lowest light intensities tested (0.001 and 0.0005

lx), 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 appropriate levels. Light intensity was measured in lux using

the International Light Technologies ILT1700 Research Radiometer and a SUD033

broadband underwater silicon detector, Peabody, MA.

Four infra-red 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 & Hawryshyn, 1990). Additionally,

Mazur and Beauchamp (2003) found no significant effect of infra-red 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/sec) 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 0, 0.0005, 0.001, 0.01, 1 and 10 lux, equivalent to

0.0000052, 0.00001, 0.001, 0.01, and 0.1 μE/m2/s, with 1 μE/m2/s equivalent to 95 lx.

These light intensities correlate to the light present at depths of approximately 160, 150, 140, 120, 80 and 60 m respectively, on a midsummer day at noon at which siscowet may effectively use visually mediated foraging behavior. 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, $I_o = 10,000$ lux (Mason and Patrick, 1993) and $k = 0.115$ for the vertical attenuation coefficient (Sterner, 2010).

Foraging Parameters

All foraging trials were conducted between January 1, 2014 and June 6, 2014. Siscowet lake trout ($n=5$) ranging from 340-500 mm TL were fasted for 48 hr 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 began 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 lasted 10-minutes 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).

Data analysis

Foraging Trials

Foraging trials were reviewed using Windows Media Player (Microsoft, v. 12) and Snagit (TechSmith, v. 12) was used to capture video images. Video images 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 towards 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 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.   Time to capture prey and whether the prey was stationary

or moving prior to siscowet orientation was also calculated as part of the above

parameters.

Modeling

A Michaelis–Menten saturation function (O'Neill et al., 1989) was used to show

the relationship between light intensity (L_i, lux) and reaction distance (R_d cm).

The model is represented by:

$$R_{d\ =}\ R_{max}L_i(\alpha\ +\ L_{i.})^{-1} \tag{2}$$

Where R_{max} is equal to the maximum reaction distance (cm) and α is equal to the half-

saturation constant (lux). 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 perch (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

Foraging Parameters

Siscowet length

There was no significant difference of trout length on reaction distance ($R^2 =$ 0.002, y =0.1x + 45.2, P = 0.36). Trout were separated into two size classes (>40 and <40 cm) for further analysis. Again, while trout length and light intensity together had a significant effect on reaction distance (Figure 2; Two-way ANOVA, $F_{11,361}$=12.59, p<0.0001), the difference was attributed to light intensity (Light intensity effect, $F_{5,361}$= 25.94, p<0.0001), and not trout length (Trout length effect, $F_{1,361}$=0.02, p=0.89) or the interaction between light intensity and trout length (Interaction effect, $F_{1,361}$=1.33, p=0.25). For the size range of siscowet we tested, trout were seeing prey similarly during our trials independent of trout size. Due to the lack of significance of trout length on reaction distance, all following results are reported using pooled lengths for siscowet.

Reaction Distance

There was a significant effect of light intensity on siscowet reaction distance (Figure 3; ANOVA, $F_{5,367}$= 26.83, p>0.0001). Reaction distance increased with light intensity from 0 to 0.01 lx, where after the relationship became asymptotic. From 0.001 to 0.01 lx, there was a significant increase in reaction distance (Tukey's HSD, p<0.01) and a significant difference between the two lowest light intensities, 0.0005 and 0 lx

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(Tukey's HSD, p<0.0001). The maximum average reaction distance (58.6 ± 2.3 cm) was recorded at 10 lx and the minimum average reaction distance (24.9 ± 1.7 cm) at 0 lx.

Foraging model

A Michaelis–Menten saturation function (Figure 4) was used to estimate the relationship between light intensity (L_i, lux) and reaction distance (R_d, cm). The estimates of the parameters in the model were R_{max} = 57.5 and α = 0.0001 (SS_{total} = 20.6). The model accounted for 98% of the variability for reaction distance at light intensities between 0-10 lx (non-linear regression, R^2 = 0.98)

Prey size

Prey size and light intensity influenced reaction distance of siscowet (Figure 5; Two-way ANOVA, $F_{11,361}$=14.64, p<0.0001). As with the pooled data, reaction distance increased with light intensity up to 0.01 lx (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 (141.8 ±1.9 mm, 29.8 ± 1.2 g) than for smaller prey (93.7 ±1.1 mm, 7.2 ± 0.2 g) (Prey size effect, $F_{1,361}$=13.56, p=0.0003; Interaction effect, $F_{5,361}$=1.19, p=0.31). Thus, siscowet are able to see larger prey at greater distances than smaller prey.

Prey movement

Prey movement and light intensity affected reaction distance of siscowet (Figure 6; Two-way ANOVA, $F_{5,249}$=11.46, p<0.0001). As in earlier results, reaction distance increased with light intensity up to 0.01 lx (Light intensity effect, $F_{11,249}$ = 11.46, p<0.0001). There was an overall trend for higher reaction distances for moving prey (47.64 ± 1.08 cm) than stationary prey (43.07 ± 3.5 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 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 0-1 lx, prey remained motionless for at least 10% of the 10-minute trial on average (Table 2). At 10 lx, prey were slightly less inclined to remain motionless and were stationary for approximately 6% of the trial.

Orientations

Orientations toward prey were not equally distributed among 60° increments. Significantly more orientations toward prey occurred between ±0–60° (forward sector) (N = 101) from the longitudinal axis of the siscowet than between ±60–120° (lateral sector) (N = 62) and ±120–180° (rear sector) (N = 15) (Figure 7 (see alternate figs) ; $\chi2$ =

61.54, *d.f.* = 2, *P* < 0.0001). 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 lake trout 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 0 lx (Figure 8) to 80% success (16 captures) at 10 lx. Additionally, there was only a 50 % probability of siscowet orienting toward prey at 0 lx, while at the second lowest light intensity (0.0005 lx) there was an increase to a 83% location probability. Location probabilities remained within the 80th percentile from 0.0005-1 lx until 10 lx where a 98% probability of orientation was obtained. Similarly, prey retention steadily increased with increasing light intensity from
10% at 0 lx to 41% at 10 lx (Table 1).

The range of individual non-averaged reaction distances was consistent from 0.001- 10 lx with six or more reactions greater than 80 cm at each light intensity (Figure 9). The range decreased at 0.0005 lx with only one reaction greater than 80 cm. Similarly, the range of angle of attack was consistent from 10-0.0005 lx with eight or more orientations toward prey greater than 100° at each light intensity with only one orientation greater than 100° occurring at 0 lx.

The time to capture prey decreased with increasing light intensity (Figure 10; Kruskal-Wallis, $F_{2,50}$ = 5.21, p=0.009). From 0-0.0005 lx, the average time to capture prey was 400 s, decreased to ~200 s for the midrange light intensities (0.001-0.1 lx) and then decreased below 200 s for the highest light intensities (1-10 lx). As prey becomes more difficult to see, the time to capture prey increases significantly.

Discussion

Results of our study suggest siscowet lake trout have evolved visual sensitivity that allows for successful foraging under low intensity light. 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 caused by particulates (Guthrie and Muntz, 1993). Siscowet are unique in that visually mediated foraging may be possible as deep as 150 m within Lake Superior. We have found that siscowet reaction distance increases with increasing light intensity up to 0.01 lx, where after the relationship is asymptotic 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. Although siscowet length had no effect on reaction distance, prey mass was a significant factor with larger prey eliciting higher reaction distances at all light intensities. Similarly, there

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were greater reaction distances for moving prey, than stationary prey at the four highest light intensities tested. Finally, we saw that 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.

Our 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 our techniques may be applicable to optimize care of other fresh water 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 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. (in review) 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).

Foraging behavior of native fishes is important to the Lake Superior ecosystem because it effects population dynamics and species interactions, thereby influencing ecosystem structure and function. However, the physical environment in which siscowet forage poses challenges (i.e. light-limitation at depth). Based on our findings, the challenges with visual foraging may be offset by, but not limited to: 1) adaptive foraging at night in a better light environment, 2) spectral sensitivity matched to downwelling light, 3) movement of prey to improve foraging efficiency, 4) larger prey owing to easier capture and higher energy content, 5) mechanosensory detection in inadequate light environments.

Siscowet foraging occurred at light intensities as low as 0.0005 lx where 20% of prey was captured, and reaction distances remained 70% of maximum values. Using the Beer-Lambert equation we determined a light intensity of 0.0005 lx is equivalent to light at a depth of approximately 150 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), however our results indicate that siscowet would need to be at most 150 m depth or above to successfully capture 20% of prey or more.

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 (Ahresnstorff 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 the metalimnion as they track mysis at night

(Ahresnstorff et al., 2011; Hrabik et al., 2006; Stockwell et al., 2010). In general, pelagic

fishes prefer light levels less than 0.001 lx during the evening (Yule et al., 2007) and

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 trawls.   For

northern latitude lakes, a full moon during summer produces 0.1 lx at the lakes surface

(Janiczcek and DeYoung, 1987) producing 0.0005 lx at approximately ~45 m depth.

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., 2012; 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 visually

mediated foraging with moonlight at shallower depths, it is likely the majority of foraging

for pelagic fish may occur at night.

Our results indicate a disparity for threshold light intensies 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 asymptotic above

this value. We determined a threshold light intensity of 0.01 lx (0.0001 $\mu E/m2/s$) for

siscowet while Vogel and Beauchamp (1999) and Mazur and Beauchamp (2003) reported

a threshold value of 17.8 lx (0.2 $\mu E/m2/s$) for lean lake trout and studies in juvenile lake

trout by Confer et al. (1978) found a threshold of 50 lx (0.53 μE/m2/s). 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 (Harvey et al., 2003; Gamble et al., 2011).

However, these previously determined reaction distances for lean lake trout may also be inflated due to the use of broad-spectrum lighting which can 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. Additionally, Holbrook 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 (0.02 μE/m2/s) in age-0 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. (in review) 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 (0.001-10 lx) suggesting moving prey assist in

visual foraging at light environments of 0.001 lx and above. Other freshwater species,

such as largemouth bass have likewise shown an increase in reaction distance with prey

motion and are more likely to pursue moving prey over stationary prey (Howick and

O'brien, 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 ultra-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 lake trout when foraging for moving

versus stationary mysid shrimp.

Prey size had the most significant effect on siscowet reaction distance in our study

and the effect was greatest at the two lowest non-zero light levels (0.001 and 0.0005 lx).

While studies in age-0 lake trout reported higher reaction distances for larger mysid prey

over smaller prey (Holbrook et al., 2013), studies in adult lake trout by Vogel and

Beauchamp (1999) did not see this trend. Detection distance for prey generally decreases

with light intensity and varies proportionately with the size of the prey (Chesney, 1989;

De Robertis et al., 2003; Dill, 1974) and the freshwater largemouth bass reported the

trend of increasing reaction distance with increasing prey size with varying light intensity

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(Howick and O'Brien, 1983). Again, the use of spectrally matched lighting in our study as well as a black lining in our 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 0 lx light intensity, average reaction distance (24.9 cm) was approximately ½ 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 0 lux 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 0 lux, 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 et al., 1998; Richmond et al., 2004). Siscowet may similarly employ mechanosensory means at depths where 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 (10 lux). 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), however our objectives were not dependent upon, and did not aim to suggest, natural intake rates for siscowet lake trout (Speare, 1995).

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 predator fish/prey relationships of fresh deep-water lake ecosystems.

Tables

Table 1: The average probability of prey location, pursuit, attack and retention for siscowet lake trout during foraging trial events (n=381) at varying light intensity.

Light (lx)	Location	Pursuit	Attack	Retention	Total	N
0	0.50	0.55	0.59	0.10	0.01	39
0.0005	0.83	0.88	0.49	0.12	0.04	77
0.001	0.89	0.93	0.44	0.26	0.09	75
0.01	0.84	0.93	0.45	0.30	0.11	72
1	0.87	0.98	0.65	0.43	0.18	55
10	0.98	0.95	0.65	0.41	0.25	63
Mean	0.82	0.87	0.54	0.27	0.11	

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

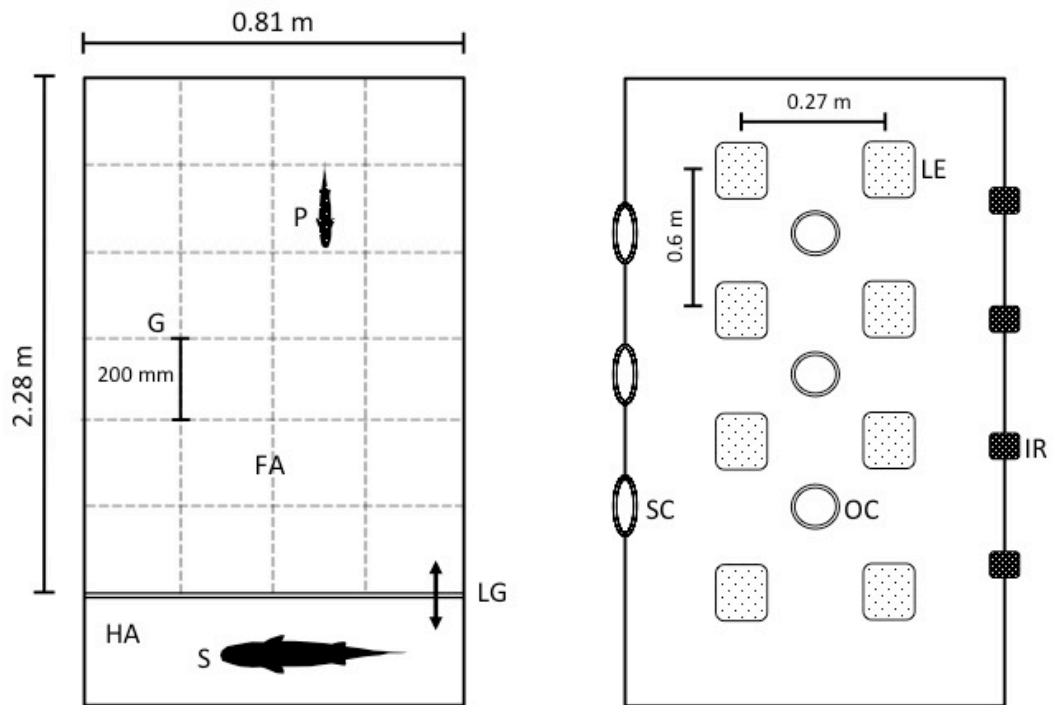| Light (lx)	Time stationary (sec)	% of Trial
0	68.6	11.4
0.0005	101.6	16.9
0.001	101.4	16.9
0.01	80.0	13.3
1	124.8	20.8
10	38.9	6.4
Mean	85.9	14.3

Figures

Figure 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).
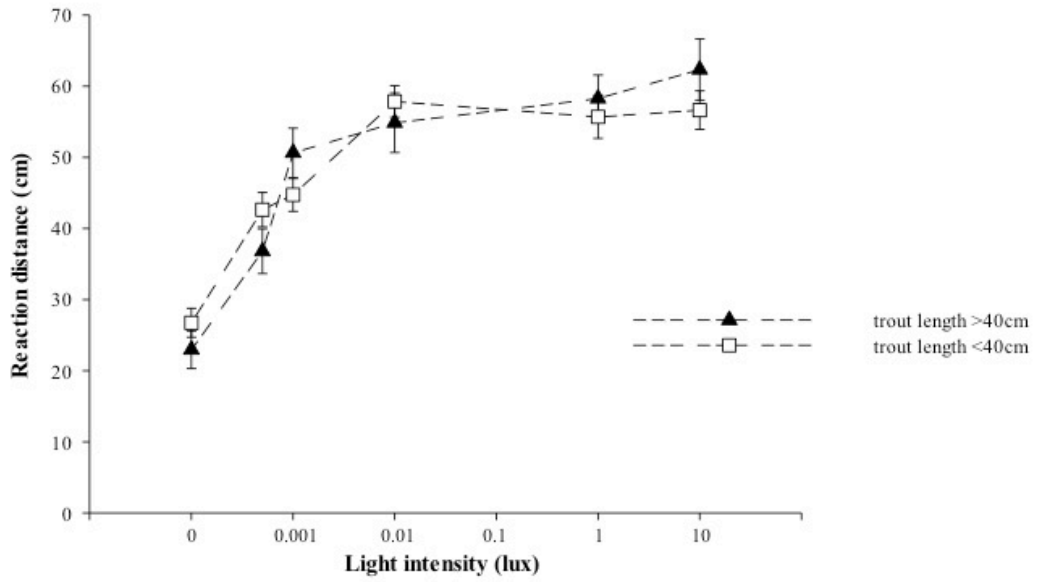
Figure 2: Average reaction distance (cm) for two different size classes of siscowet lake trout (<40 cm and >40 cm) in response to prey at varying light intensity. Error bars are ± 1 SE.
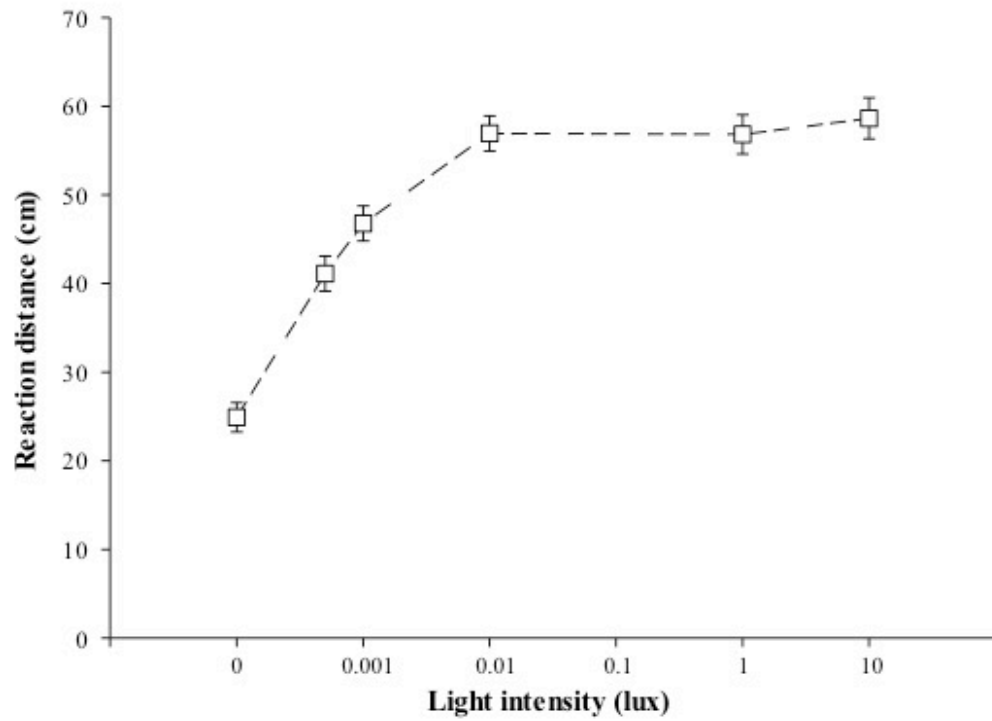
Figure 3: Average reaction distance (cm) of siscowet lake trout in response to *Notemigonus crysoleucas* at varying light intensity. Error bars are ± 1 SE.
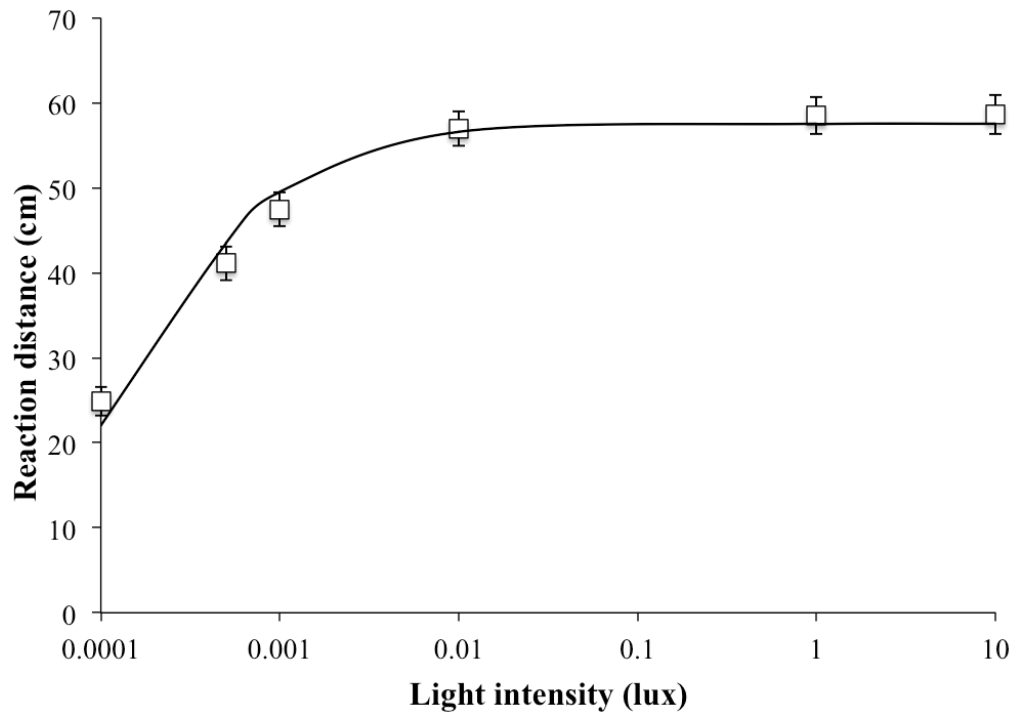
Figure 4: Average reaction distance (cm) of siscowet lake trout in response to *Notemigonus crysoleucas* at varying light intensity. A Michaelis–Menten function was used to fit the data (R^2 = 0.98). Error bars are ± 1 SE
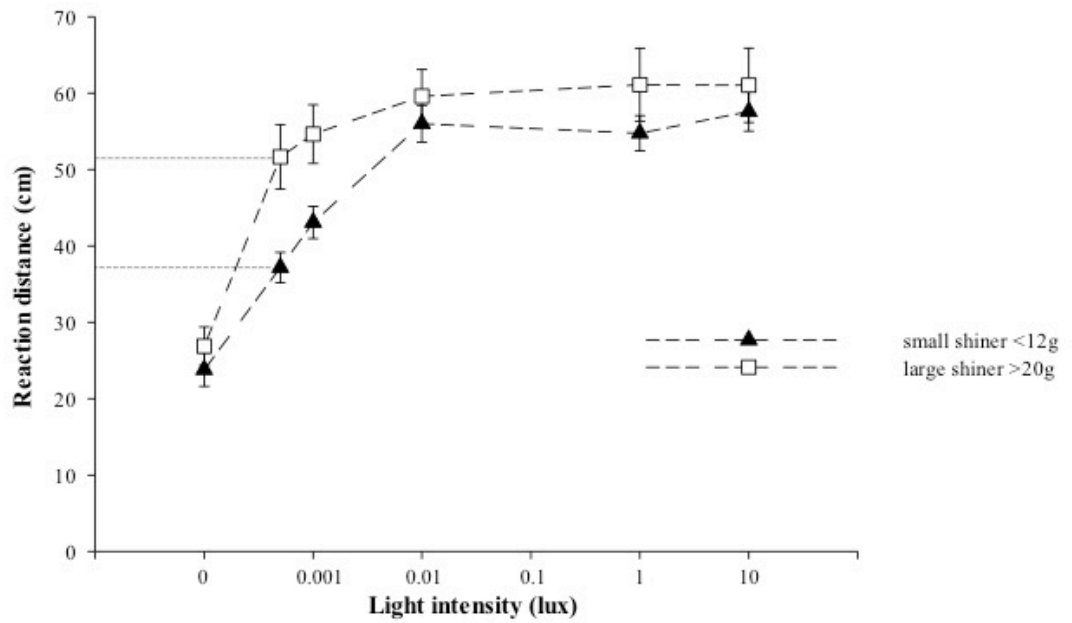
Figure 5: Average reaction distance (cm) of siscowet lake trout in response to two prey size classes (<12 g and >20 g) at varying light intensity. Horizontal dashed lines at 37 and 51 cm indicates increased window of vulnerability for larger prey. Error bars are ± 1 SE.
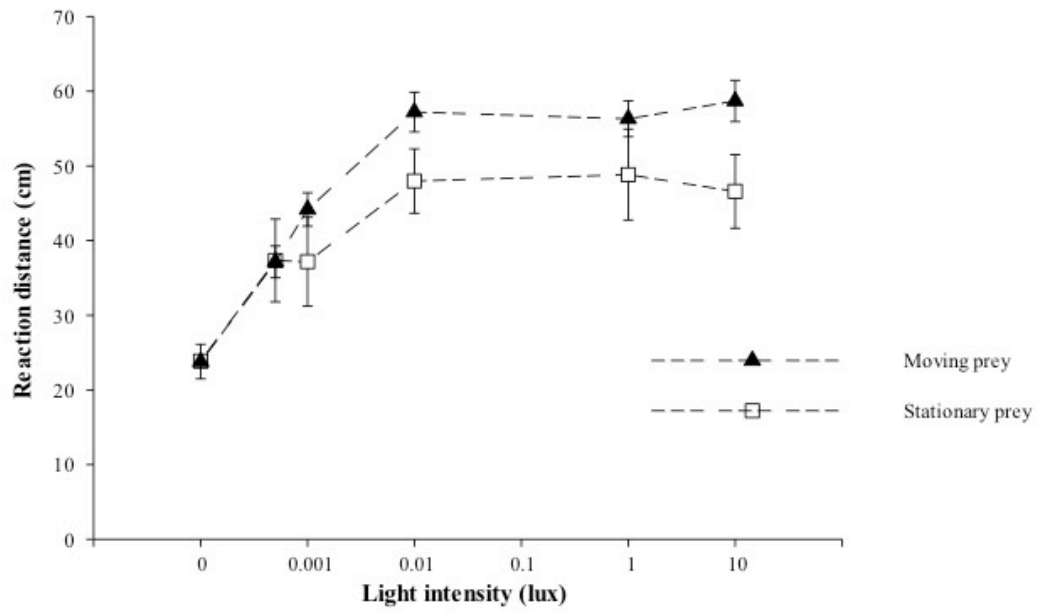
Figure 6: Average reaction distance (cm) of siscowet lake trout in response to moving
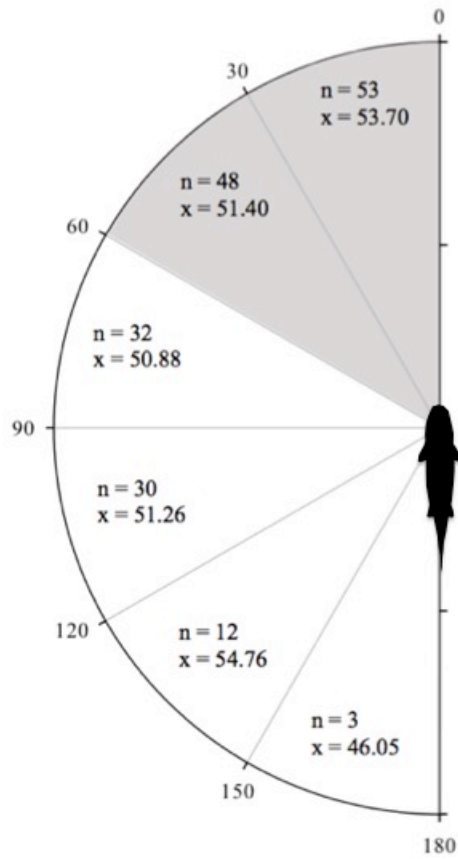and stationary prey at varying light intensity. Error bars are ± 1 SE.

Figure 7: 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°.
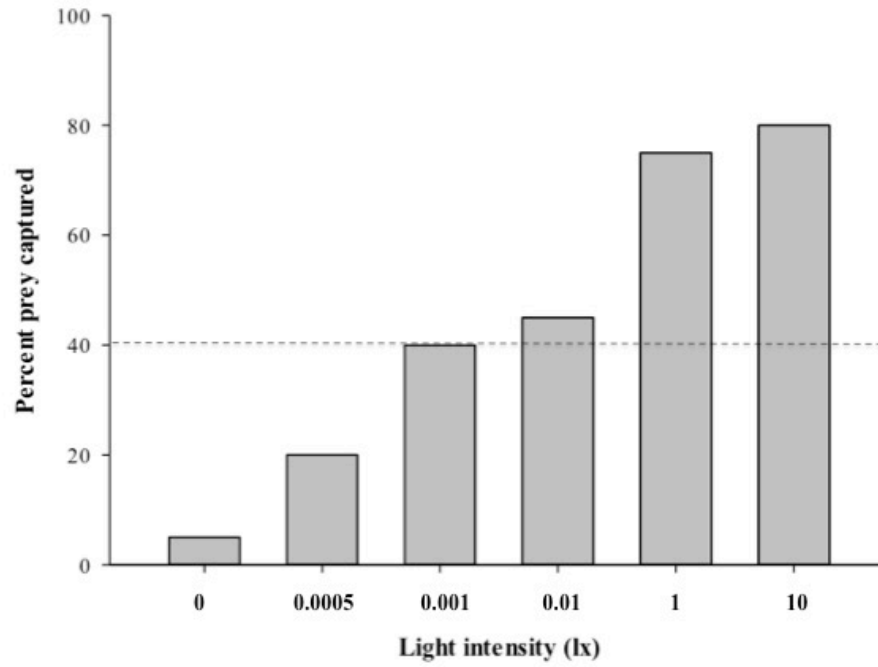
Figure 8: Percentage of prey captured by siscowet lake trout at varying light intensity. Horizontal dashed line indicates average number of prey captured for all trials.
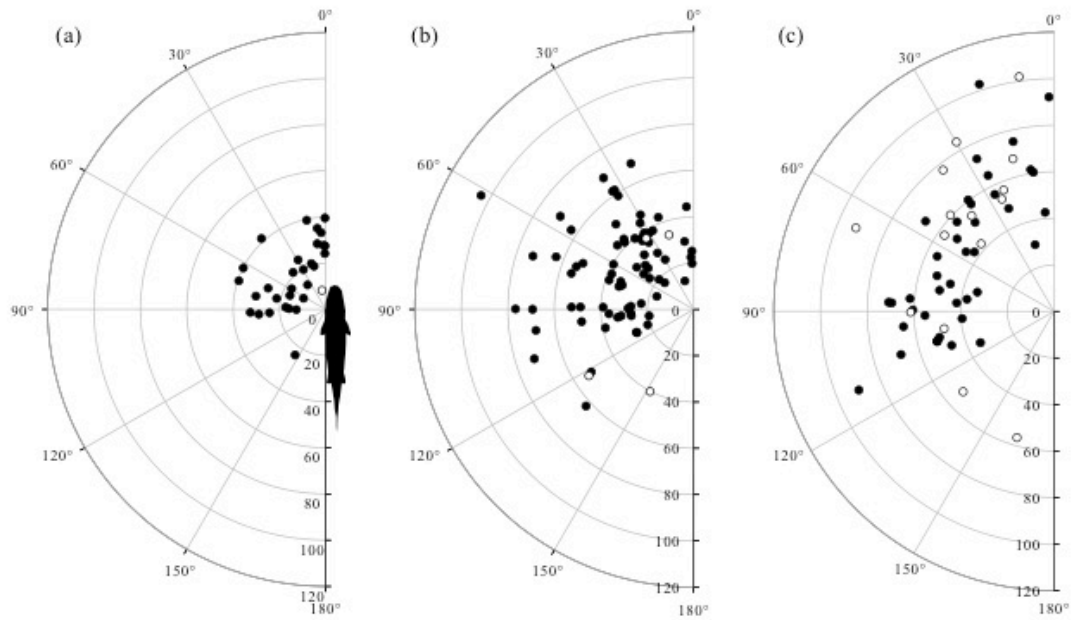
Figure 9: Polar plot representation of reaction distance and angle of attack for siscowet lake trout in response to prey at three light intensities representing high variation (a) 0, (b) 0.0005 and (c) 1 lux. Solid circles represent orientation toward prey and open circles represent a capture. Each concentric circle represents a distance of 20 cm.
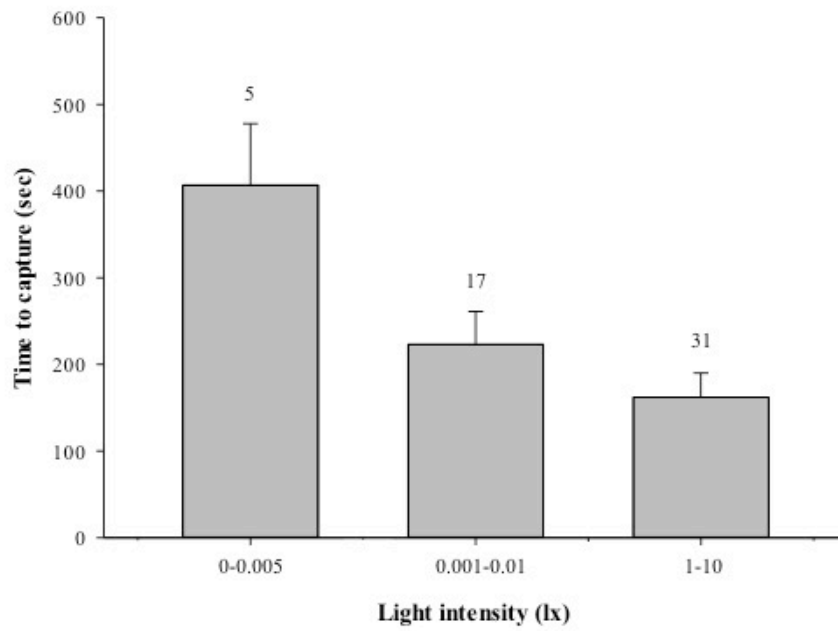
Figure 10: Average time to capture prey (sec) for siscowet lake trout at varying light intensity. Numbers above error bars indicate number of prey captured at corresponding light level. Error bars are ± 1 SE.

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