Scotopic Visual Sensitivity of Lean Lake Trout (*Salvelinus namaycush*) and Siscowet Lake Trout (*Salvelinus namaycush siscowet*): A Morphotype Comparison

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Abstract

The Lean Lake Trout (*Salvelinus namaycush*) is an apex predator within the littoral zone of Lake Superior. These fish exhibit diel bank migration in contrast to the pelagic Siscowet Lake Trout (*Salvelinus namaycush siscowet*) which perform diel vertical migration. Diel migration in both planktivorous and piscivorous fishes is triggered by changing light levels and temperatures which allow for an increase in foraging opportunities and the avoidance of predators. The intensity of light that Lean Lake Trout can perceive depends on the amount of light available at the surface, the depth that light can penetrate through the water column, and the visual sensitivity of their photoreceptors. Lean Lake Trout scotopic spectral sensitivity was determined via electroretinography (ERG) and compared to the scotopic spectral sensitivity data of the pelagic Siscowet Lake Trout obtained from Harrington *et al*. (2015). The peak spectral sensitivity for Lean Lake Trout was found to be 550 nm while Siscowet had a spectral sensitivity peak of 525 nm. Both peak spectral sensitivities are correlated to the down-welling light within the littoral and pelagic zones of Lake Superior. The results support the Sensitivity Hypothesis which states that a fish's spectral sensitivity will match the light available in its environment. Lean Lake Trout spectral sensitivity was found to be green-shifted compared to the blue-shifted Siscowet Lake Trout which could be explained by Lean Lake Trout's shallower position in the water column as well as the exposure to a broader spectrum of light. Somewhat surprisingly, both morphotypes had similar absolute visual sensitivity despite different photic environments.

INTRODUCTION

Siscowet, lean, humper and redfin lake trout are the four morphotypes of lake trout that occupy Lake Superior. The two most common morphotypes are the lean and siscowet lake trout (Muir *et al.*, 2014).

Lean and siscowet lake trout are crepuscular fish foraging most during dawn and dusk via diel migration. It is believed that diel migration is triggered by predator avoidance of species throughout all trophic levels (Zaret and Suffern, 1976; Wright *et al.*, 1980; Gliwicz, 1986; Bollens and Frost, 1989; Lampert, 1989; Ohman *et al.*, 1983; Scheurell and Schindler, 2003; Gorman *et al.*, 2012). Diel migration in Lake Superior is triggered by zooplankton which causes a “cascading migration of organisms” (Bollens *et al.*, 2011, Gorman *et al.*, 2012). Lake Trout forage mainly upon the piscivorous deep-water Cisco the Kiyi (*Coregonus kiyi*) which migrate through the water column to prey upon the zooplanktivorous Opossum Shrimp (*Mysis duluviana*) (Hrabik *et al.*, 2006; Jensen *et al.*, 2006; Ahrenstorff *et al.*, 2011; Gorman *et al.*, 2012). Lean lake trout (hereafter lean) will exhibit diel bank migration (DBM) moving from depths of less than 100 m (day) to the surface (night). In comparison to the siscowet lake trout (hereafter siscowet) which will exhibit diel vertical migration (DVM) moving up the water column from depths up to 405 m (day) to the surface (night) (Figure 1) (Goetz *et al.*, 2010; Borden *et al.*, 2010; Gorman *et al.,* 2012; Sitar *et al.*, 2008).

In close range conditions fish will rely on their mechanosensory lateral line and visual inputs for cues of their surrounding area (Dijkgraaf, 1963; Pitcher, 1993)

Very little is known about the morphotype difference in scotopic visual properties of lean and siscowet lake trout. The Sensitivity Hypothesis states that a species’ spectral sensitivity will match the spectrum of light available in its environment (Munz and McFarland, 1973). Figure 2 illustrates how light attenuates through the water column in a clear freshwater system.

MATERIALS AND METHODS

In this study all surgical procedures were conducted under controlled anesthesia to minimize stress. The study followed the recommendations detailed in the Guide for the Care and Use of Laboratory Animals of the Nation Institutes of Health and was approved by the Institutional Animal Care and Use Committee of the University of Minnesota Protocol ID: 1504-32496A.

Fish Collection and Culture

All lake trout were collected via gillnetting with the Minnesota Department of Natural Resources. Leans for electroretinography were collected along the Duluth, MN Lake Superior shoreline (Lat: 46.791 Long: 92.084) on October 21, 2015 and October 29, 2015 at depths of 8.75 m and 11.37 m respectively. Once removed from the gillnets, lake trout were submerged in a 200 L holding tank filled with 6 ± 1°C circulating lake water. Before being transported to the University of Minnesota Duluth, 0.026% Stresscoat (Mars Fishcare North America Inc., Chalfont, PA) was added to the holding tank to minimize stress. During transport the holding tank was aerated via 13 mm Deluxe Bubble Disks (Penn Plax, Hauppauge, NY).

At the University of Minnesota Duluth, lake trout were held in two 575 L stock tanks (Miller Manufacturing, Eagan, MN) whiche were housed in a refrigerated, 6 ± 2°C, dark room. Stock tanks were equipped with Penn-Plax Cascade 1500 canister filters (Penn Plax, Hauppauge, NY).

Electroretinogram (ERG) Experimental Set-Up

Electroretinography (hereafter, ERG) was used to determine the spectral sensitivity of leans (n=5) ranging from 64-70 cm (L_T). All ERG procedures were conducted under indirect red lighting (Sunbeam 40W red light). Before beginning ERGs, leans were moved to a 50 L holding tank filled with recirculating 6 ± 2°C d_iH_2O solution consisting of a phosphate buffered solution and 0.002% MS-222. Complete anesthetization of leans was achieved by administering an intramuscular injection (0.1% bodyweight) of pancuronium bromide dissolved in 0.9% NaCl. Leans were then immersed to the ventral border of their eyes in an experimental tank (64 x 26 x 18 cm) (Southern Patio Deck Box, Atlanta, Georgia), which was housed inside a solid metal faraday cage (77 x 67 x 96 cm). Leans received artificial ventilation throughout the experiment from the same chilled d_iH_20 solution they were subject to in the 50 L holding tank. Once finished with the ERG, the gills were flushed with 6 ± 2°C freshwater until re-equilibrating.

ERG Procedure

All ERG procedures adhered to the ERG procedures conducted by Harrington *et al.* (2015). A 100 W quartz tungsten-halogen lamp (Newport model 6333, Stratford, CT) powered by a constant current power supply (Newport model 68938) provided the light stimulus. An Oriel Electronic Shutter (model 76994) and Controller (model 76995) regulated the stimulus duration by producing square wave light pulses, 3.0 ms delay, 3.0 ms rise time and 5.0 ms fall time respectively. The light pulse produced was then passed through a monochromator (Newport model 77250). Light intensity was measured using a radiant power energy meter (Ophir model 70260) and probe (Ophir model 70268) which was regulated via neutral density filters (0.1-3.0). Light intensity calculations were determined respective to Harrington *et al.* (2015), see paper for further details. Light was then delivered to the eye through a fiber optic light pipe (Newport model 77632). A 0.20 mm diameter Ag-Ag Cl recording electrode was inserted through an incision in the limbus and implanted into the vitreous portion of the eye while a reference electrode was placed in the nare of leans. Amplification of ERGs was done using a World Precision Instrument, Inc. amplifier (1000×, 1 Hz low pass, 3 kHz high pass, model DAM50; Sarasota, FL), filtered using a 60 Hz notch filter, recorded via PowerLab 4SP (AD Instruments, Castle Hill, Australia) and stored on a portable computer using Lab Chart 7 (AD Instruments, Castle Hill, Australia).

After electrode insertion, leans were dark-adapted for at least 30 mins before beginning testing. A 200 ms flash of monochromatic light with wavelengths ranging from 400 to 700 nm were presented in random 25 nm increment order to elicit the ERG (figure 3). Stimulus intervals were determined for leans by presenting consecutive flashes to a control fish to determine the delay, 65 s, required to produce the same response amplitude to minimize photobleaching.

The response criterion of the ERG determined by the b-wave amplitude following Harrington *et al.* (2015), was set at 5μV at 400 nm. This amplitude insured that at least a 5 μV response was attainable throughout the wavelengths tested. Wavelengths were reduced in intensity by neutral density filters until the b-wave amplitude equaled 5 μV for each wavelength tested. The corresponding irradiance to achieve the criterion response at each wavelength was used to generate spectral sensitivity curves for both species.

RESULTS

Visual Spectral Sensitivity

Visual spectral sensitivity curves for dark-adapted leans and siscowets (manipulated from Harrington *et al.*, 2015) were constructed using ERG responses to monochromatic light of varying incremental wavelengths. Leans displayed a peak spectral sensitivity at 550 nm (green) while siscowets had a more blue-shifted peak spectral sensitivity occurring at 525 nm (blue-green) (Figure 4).

Visual Depth Profiles

Visual depth profiles were created for both species to determine the maximum depth under solar and lunar conditions at which sufficient irradiance was available to elicit the criterion ERG response to approximate the depth at which light can be detected. Under solar and lunar Lake Superior conditions siscowets elicited less ERG sensitivity indicating maximum visual depths occur shallower then leans. Under solar conditions it was found that siscowets could detect light at depths of 325 m during summer (k_{PAR}= 0.1) and 76 m during the fall (k_{PAR} = 0.3) while leans could detect light at depths of 336 m during the summer (k_{PAR} = 0.1) and 82 m during the fall (k_{PAR} = 0.3) (Figure 5). Under lunar conditions during the summer (k_{PAR} = 0.1) siscowets could detect light at depths of 31 m and 7 m during the fall (k_{PAR} = 0.3), whereas leans during summer (k_{PAR} = 0.1) could detect light at depths of 42 m and during fall (k_{PAR} = 0.3) at 13 m (Figure 6).

DISCUSSION

Lean spectral sensitivity was green-shifted in comparison to the blue-shifted siscowet. This may allow for optimal sensitivity for siscowet in deep clear water environments where blue is the predominant downwelling wavelength. Leans would have a visual advantage in shallower waters where more green light is still available or in more turbid waters which allow for green wavelengths to penetrate deepest.

Somewhat surprisingly, both morphotypes had similar absolute visual sensitivity despite different photic habitats.

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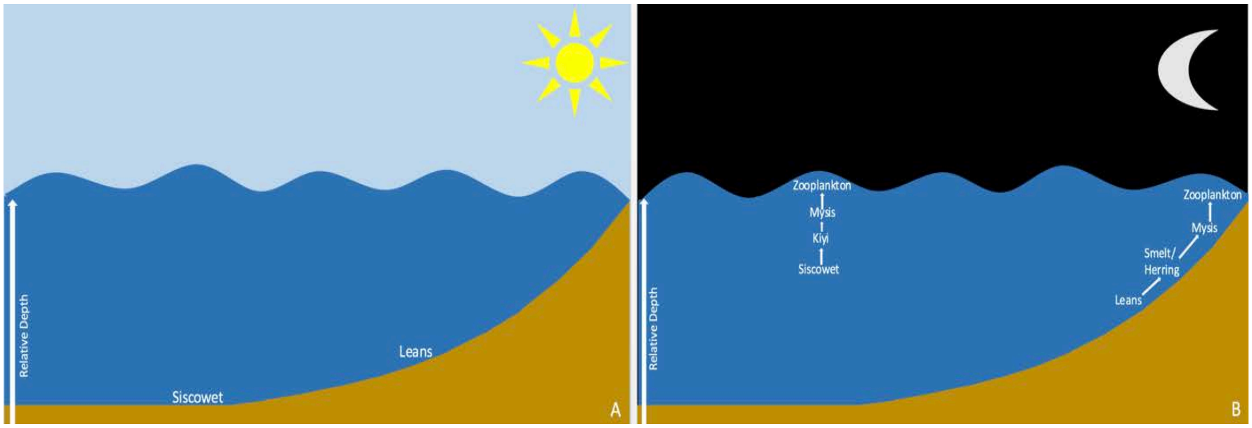


Figure 1: During day (A) lean and siscowet lake trout remain near the bottom of Lake Superior. During normal feeding times of dawn and dusk (B) lean lake trout will exhibit diel bank migration and siscowet lake trout will exhibit diel vertical migration in search of food.

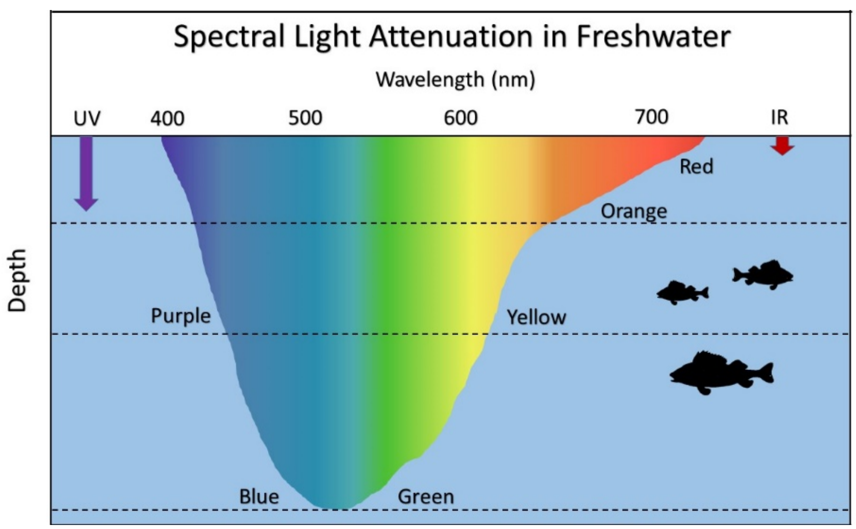
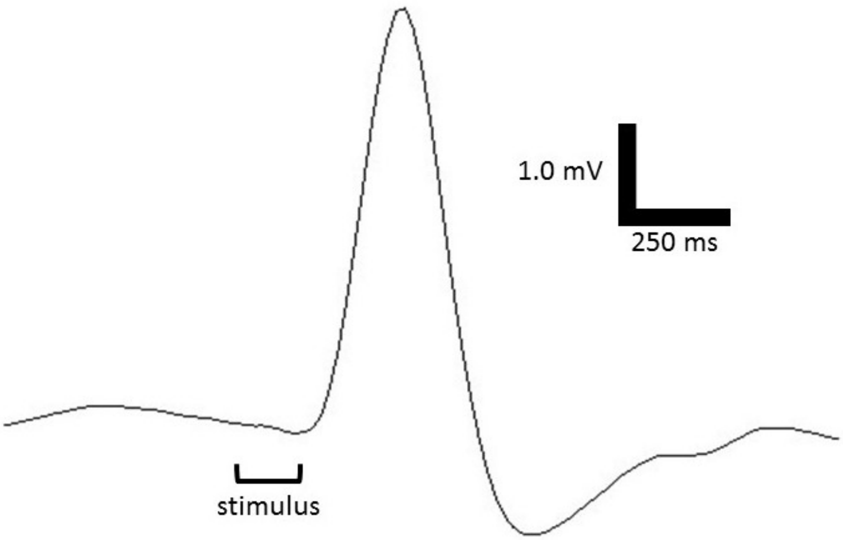


Figure 2: Spectral attenuation of light in a clear freshwater system.



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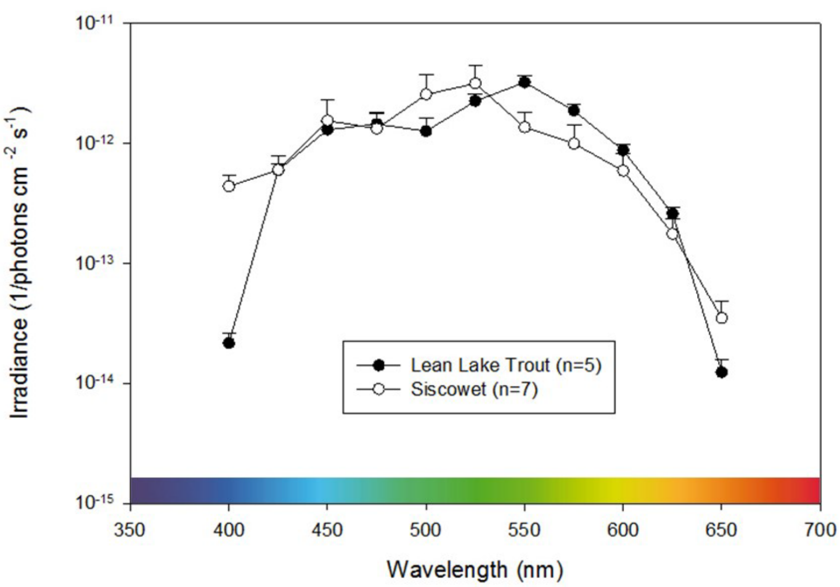

Figure 4: The average irradiance (1/photons cm^{-2} s^{-1}) needed to invoke the criterion response vs. wavelength (nm) for lean (black circles) and siscowet lake trout (open circles). Siscowet data manipulated from Harrington *et al.* (2015).

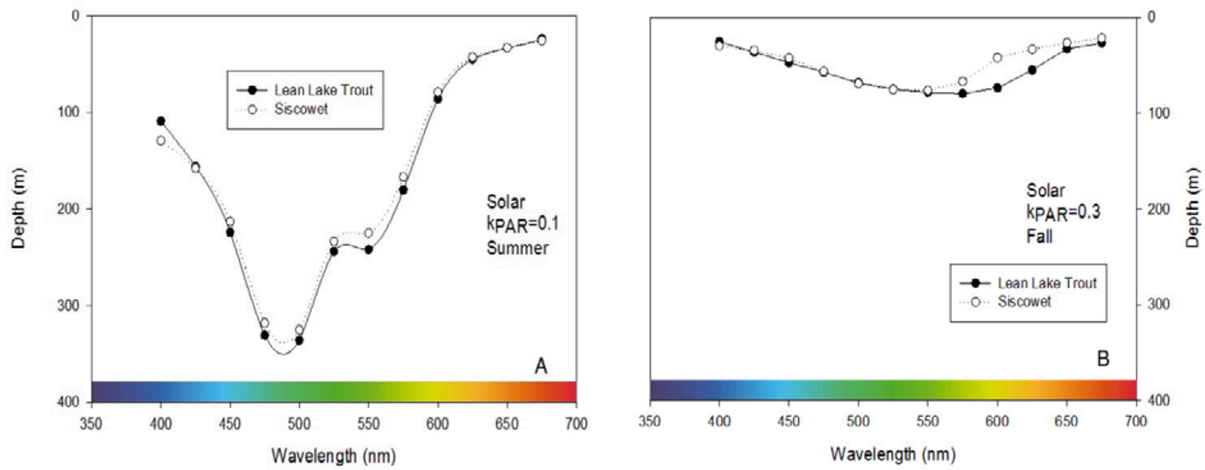

Figure 5: The maximum depth under solar conditions at which sufficient downwelling irradiance is available to elicit an ERG response plotted against depth (m) for lean (black circles) and siscowet lake trout (open circles) for (A) summer (k_{PAR} = 0.1) and (B) fall (k_{PAR} = 0.3) for clearwater conditions in Lake Superior. Siscowet data manipulated from Harrington *et al.* (2015).

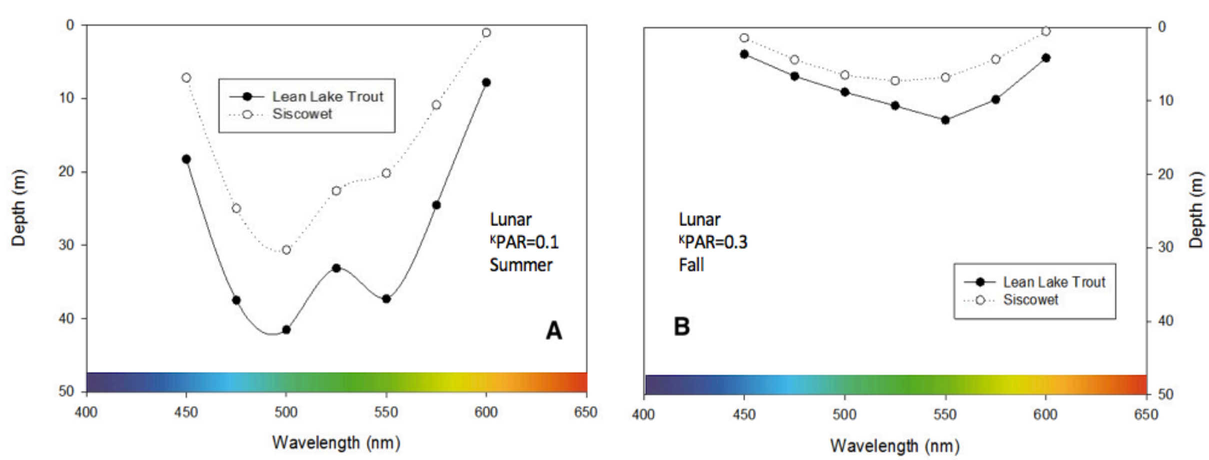

Figure 6: The maximum depth under lunar conditions at which sufficient downwelling irradiance is available to elicit an ERG response plotted against depth (m) for lean (black circles) and siscowet lake trout (open circles) for (A) summer (k_{PAR} = 0.1) and (B) fall (k_{PAR} = 0.3) for clearwater conditions in Lake Superior. Siscowet data manipulated from Harrington *et al.* (2015).

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