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

T.D. Keyler [a,*], T.R. Hrabik [a], C.L. Austin [a], O.T. Gorman [b], A.F. Mensinger [a]

[a] *Biology Department, University of Minnesota Duluth, 1035 Kirby Drive, Duluth, MN 55812, USA*
[b] *U.S. Geological Survey, Lake Superior Biological Station, 2800 Lake Shore Dr. East, Ashland, WI 54806, USA*

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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.

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× 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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[*] Corresponding author. Tel.: +1 218 726 7079.

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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