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Foraging mechanisms of age-0 lake trout (*Salvelinus namaycush*)

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ABSTRACT

Reaction distances under various light intensities (0-19 uE/m2/s), angles of attack, swimming speeds, and percentage of overall foraging success were measured. Extensive efforts have been invested in restoring lean lake trout (*Salvelinus namaycush*) populations in the Laurentian Great Lakes, but successful natural recruitment of lake trout continues to be rare outside of Lake Superior and parts of Lake Huron. There is evidence of high mortality during the first several months after eggs hatch in the spring, but little is known about the foraging mechanisms of this age-0 life stage. We developed a foraging model for age-0 lake trout (*S. namaycush*) in response to amphipods (*Hyalella azteca*) and mysids (*Mysis diluviana*) by simulating underwater environmental conditions in the Great Lakes using a temperature-controlled chamber and spectrally matched lighting. Reaction distances under various light intensities (0–19 uE/m^2/s), angles of attack, swimming speeds, and percentage of overall foraging success were measured. Intake rates under different light intensities and prey densities were also measured. Age-0 lake trout were non-responsive in the dark, but were equally responsive under all light levels tested. Age-0 lake trout also demonstrated a longer reaction distance in response to moving prey, particularly mysids, which had an escape response that reduced overall foraging success. We determined that prey intake rate (numeric or biomass) could be modeled most accurately as a function of prey density using a Michaelis–Menton equation and that even under low mysid densities (3 individuals/m^2), age-0 lake trout could quickly satisfy their energetic demands in a benthic setting.

Introduction

Lake trout (*Salvelinus namaycush*) is a long-lived, slow-growing salmonid predator in oligotrophic northern lakes and reservoirs, and was once an important commercial species in the Laurentian Great Lakes. Annual catches averaged between 3 and 6 million pounds each in Lakes Huron, Michigan, and Superior prior to the 1940s (Smith, 1968). By the 1960s, a combination of sea lamprey predation, overharvesting, and habitat degradation eliminated lake trout from Lakes Michigan, Erie, and Ontario, and severely reduced populations in Lakes Superior and Huron (Christie, 1974; Lawrie and Rahrer, 1972; Smith, 1972). Although restoration efforts have been underway since the 1950s and have been successful in establishing adult lake trout populations throughout the Great Lakes, most populations still rely heavily on introductions of hatchery raised fish (Zimmerman and Krueger, 2009).

Currently, natural recruitment of lake trout is common only in Lake Superior and parts of Lake Huron (Bronte et al., 2003; Morbey et al., 2008; Riley et al., 2007). Despite decades of failure, reestablishing self-sustaining native lake trout populations throughout the Great Lakes remains a management goal (Zimmerman and Krueger, 2009). Mortality during the age-0 life stage has been identified as one of the primary factors impeding rehabilitation of native stocks (Holey et al., 1995; Zimmerman and Krueger, 2009). Early Mortality Syndrome caused by thiamine deficiency and predation upon age-0 lake trout have been two factors identified as significant sources of early life stage mortality (Krueger et al., 1995; Tillitt et al., 2005; Zimmerman and Krueger, 2009). Recent research has indicated that in addition to acute mortality, thiamine deficiency causes reductions in age-0 lake trout visual acuity, prey capture rates, and specific growth rates (Carvalho et al., 2009; Fitzsimons et al., 2009). The influence of these factors on age-0 lake trout survival are not well understood and are difficult to assess without the development of a baseline foraging model.

Modeling prey consumption based on foraging mechanisms observed in a laboratory are important for scaling up individual behaviors to a population level that can then be applied to predict habitat utilization in the field (Mittelbach, 1981). For example, the development of an age-0 lake trout foraging model may be valuable, when combined with temperature and bioenergetics modeling, for assessing factors that influence age-0 lake trout distribution on spawning shoals. Previous research has indicated that age-0 lake trout are often heterogeneously distributed across spawning shoals and "nursery areas", but the controlling factors have not been determined (Bronte et al., 1995). Identifying the most important factors influencing age-0 lake trout distribution may be useful for assessing the rehabilitation potential of spawning shoals throughout the Great Lakes.

In this study, we examined foraging patterns of age-0 lake trout in a laboratory setting. Specifically, our objectives were to: 1) determine

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foraging behaviors, including reaction distances under various light intensities, angles of attack, swimming speeds, and overall foraging success; 2) measure intake rates under various light intensities and prey densities, and model these rates using a Michaelis–Menten function and a foraging model; and 3) quantify daily consumption rates. Each objective was addressed using data collected in foraging arenas in a carefully controlled laboratory setting using artificial lighting that was spectrally matched to ambient downwelling light in their native environment.

Methods

Collection and culture

Age-0 lake trout

Approximately 80 hatchery-raised post-emergent age-0 lake trout averaging 3.0 cm in total length (TL) were received from the Les Voigt Hatchery operated by the Wisconsin Department of Natural Resources (Bayfield, WI) in mid February 2007. Lake trout were housed at the University of Minnesota Duluth (Duluth, MN) in a mechanically and chemically filtered recirculating 150-L system. The fish were maintained in a cold room at a constant 8 °C and on a 14 h light: 10 h dark photoperiod. Age-0 lake trout were fed a mixture of commercial trout pellets replete of thiamine. To acclimate fish to live prey, lake trout were also fed freshwater oligochaetes (*Lumbriculus variegatus*) and amphipods (*Hyalella azteca*) twice daily until satiated. *L. variegatus* and *H. azteca* were received from the Mid-Continental Division of the U.S. Environmental Protection Agency (USEPA, Duluth, MN). All experiments conformed to the University of Minnesota animal care protocols.

Prey

Diet analyses of age-0 lake trout captured from Lakes Superior and Huron have indicated that these fish feed primarily on *Mysis diluviana* (formerly *M. relicta*, Hudson et al., 1995; Roseman et al., 2009). In our experiments, we used amphipods (*H. azteca*) as prey in feeding trials until mysids could be captured in the field. We also used *Daphnia magna* as prey for a subset of trials.

Amphipods were received from the USEPA (see above), maintained at room temperature (~50 animals per 3.25 L aerated tank at 20 °C), and fed a mixture of Yeast, Cereal leaves, and Trout pellets (YCT, 20 mL per 3.25 L tank, three times per week). Amphipods averaged 3.3 (±1.0 SD) mm length and were acclimated to a temperature of 8 °C for a minimum of 24 h prior to use in foraging trials.

Mysids were captured using a Wisconsin net (50-cm diameter opening, 250-μm mesh) from Lake Superior (St. Louis County, MN) on 17 May 2007 and 28 May 2007 and from Greenwood Lake (Cook County, MN) on 2 June 2007 and 17 June 2007. Mysids were maintained in 38 L aerated tanks (approximately 30 animals per tank) in a cold room at 5 °C and consumed zooplankton that were captured concurrently with their collection. Mysids used in foraging trials averaged 14.7 (±2.9 SD) mm length.

D. magna were used for a subset of experiments to determine whether age-0 lake trout foraging patterns differed in response to pelagic prey compared to benthic prey such as amphipods and mysids. *D. magna* were received from Carolina Biological Supply Company (Burlington, NC) and maintained in a 38 L tank at room temperature (20 °C). *D. magna* were fed 250 mL of YCT and 250 mL of green algae three times per week. Daphnids used in foraging trials averaged 3.0 (±0.4 SD) mm length.

Foraging experiments

Experimental set-up

Trials were conducted beginning on 5 March 2007 and ending on 27 July 2007. The three prey species were used at different times: *H. azteca* from early March until early June (lake trout size: 3.5–7.5 cm TL), *M. diluviana* from mid May through early July (lake trout size: 4.5–8.5 cm TL), and *D. magna* from early through late July (lake trout size: 7.0–9.0 cm TL). Two circular arenas (0.29-m and 0.65-m diameter) were used and water depth maintained at 7 cm. This shallow depth was used to minimize vertical movements of the lake trout within the water column so that measurements of distance and swimming speed could be made accurately using an overhead digital video camera. Experiments were conducted in a variable temperature dark room where the temperature was maintained at 8 °C. Additionally, a black fabric enclosure was used around the foraging arena to shield fish from any movement of the observer.

Electroretinograms indicated that age-0 lake trout were most sensitive to wavelengths between 490 and 550 nm with peak sensitivity at 500 nm (B. Holbrook, unpublished data). These wavelengths also comprise the majority of light in deep, clear, oligotrophic lakes inhabited by lake trout. For example, offshore in midsummer in Lake Superior, wavelengths between 490 and 550 nm comprise 80% of light at a depth of 15 m and approximately 95% of light at depths greater than 35 m (S. Green, unpublished data).

We simulated oligotrophic lake conditions in a laboratory setting by using cyan light-emitting diode (LED) lights (Cree XLamp XR Series, Durham, NC) ranging from 450 to 550 nm with peak spectral power at 500 nm. Four light engines with six LEDs each arranged in a pentagonal pattern were mounted 18 cm above the water surface on the corners of the arena and angled to provide diffuse light. The intensities of the LED lights were controlled by using a driver dimmer (IRIS LED driver dimmer, Power Vector, Waterloo, ON) and a DMX controller (Elation SCD-6 DMX Controller, Los Angeles, CA). Black mesh filters were used to further reduce light intensity at the two lowest non-zero light levels. Light flux (as microeinsteins, $\mu E/m^2/s$) was measured with a LI-COR 1400 PAR sensor and datalogger, Lincoln, NE while lux (lx) was measured with a Sper Scientific Ltd. 840020, Scottsdale, AZ. With the lighting used in this study, 1 $\mu E/m^2/s$ was equivalent to 95 lx.

Feeding trials were videotaped using an overhead Sony DCR-TRV250 digital video camera recorder (30 frames/s). The camera had a built-in infrared capacity that was used to record feeding trials conducted at light levels less than 0.02 $\mu E/m^2/s$. Fish used in foraging trials were separated from the main tank and housed in 9-L tanks that were maintained at 8 °C. All food was withheld for a minimum of 24 h before experimental trials. Prior to each trial, fish were acclimated to experimental light conditions for a minimum of 30 min.

Foraging behaviors

Light intensities used in the foraging behavior trials for all three prey species included 0, 0.007, 0.02, 0.09, 0.6, 4.0, and 19.2 $\mu E/m^2/s$, which were selected to simulate a range of light conditions under which age-0 lake trout might forage. These light levels represent light found at depths of approximately 30 m to 100 m at midday in midsummer on a lake trout spawning shoal in Lake Superior (B. Holbrook, unpublished data). Additionally, levels less than 18 lx (~0.2 $uE/m^2/s$ depending on the spectrum of light being used) have been shown to cause a decrease in foraging efficiency of adult lake trout (Vogel and Beauchamp, 1999).

The smaller arena was used for amphipod prey until lake trout grew to approximately 4.5 cm length and then the larger arena was used. The larger arena was also used throughout trials where mysids and *D. magna* were used as prey. A 5-mL pipette was modified to provide a larger opening (8 mm) to insert prey into the foraging arena opposite the orientation of the fish. Prey were replaced sequentially as they were consumed. A trial was terminated after 20 min or once the lake trout consumed 3 prey items.

Video was imported digitally using Windows MovieMaker (Microsoft, v. 5.0). ImageJ software (v. 1.38, National Institute of Health) was used to measure the total lengths of the lake trout, the