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

Beth V. Holbrook *, Thomas R. Hrabik, Donn K. Branstrator, Allen F. Mensinger

Department of Biology, University of Minnesota Duluth, 207 SSB, 1035 Kirby Drive Duluth, Minnesota, 55812, USA

**A R T I C L E   I N F O**

Article history:
Received 29 June 2012
Accepted 3 December 2012
Available online 5 January 2013
Communicated by Ellen Marsden

Index words: Lake trout
Reaction distance
Foraging
Intake rate

**A B S T R A C T**

Reaction distances under various light intensities (0–19 μE/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 diluviensis) 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 μE/m²/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–Menten equation and that even under low mysid densities (3 individuals/m²), age-0 lake trout could quickly satisfy their energetic demands in a benthic setting.

© 2012 International Association for Great Lakes Research. Published by Elsevier B.V. All rights reserved.

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...
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 (Lumbricillus 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.

Mysis 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. Mysis 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. Mysis 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 microeinstein, μE/m²/s) was measured with a LI-COR 1400 PAR sensor and datalogger, Lincoln, NE while lux (lx) was measured with a Spek Scientific Ltd. 840020, Scottsdale, AZ. With the lighting used in this study, 1 μE/m²/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 μE/m²/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 0.007, 0.02, 0.09, 0.6, 4.0, and 19.2 μE/m²/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 μE/m²/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
total lengths of the prey, reaction distances, and angles of attack. The reaction distance and angle of attack were measured at the moment the fish oriented towards a prey. The reaction distance was measured between the midpoint of the eyes of the fish and the midpoint of the body of the prey. The angle of attack was calculated as the location of the prey off-axis, with the axis being oriented longitudinally along the head of the fish. DLTdataviewer2 (Hedrick, 2008) was used in MATLAB (v. 7.4.0.287, Mathworks Inc., Natick, MA) to estimate the swimming speed of the lake trout and their prey prior to the moment at which the fish oriented towards its prey. The burst attack speed of lake trout and the burst escape speed of mysids were also measured as the speeds achieved during pursuit (lake trout) and avoidance (mysids) after a fish oriented towards its prey.

Intake rate experiments (see below) also were analyzed for reaction distances, angles of attack and swimming speeds if mysid densities were less than 9/m², because this density corresponded with 3 mysids per the large foraging arena, which was a manageable number to track simultaneously.

Due to time-constraints, a subset of randomly-selected data representing 40% of all amphipod and mysid foraging trials was used to estimate average foraging success. Foraging success was defined as the individual probabilities of a fish successfully locating, pursuing, attacking, and retaining amphipods and mysids that were encountered during trials. These probabilities were calculated using methods described in Richmond et al. (2004), where: 1) location was the proportion of encounters where the fish oriented towards the prey; 2) pursuit was the proportion of locations where the fish chased the prey; 3) attack was the proportion of pursuits where the prey was captured; and 4) retention was the proportion of attacks where the prey was successfully consumed. Similar to Richmond et al. (2004), trials in which fish attacked previously rejected or escaped prey were counted as non-retentions. Additionally, because age-0 lake trout appeared sensitive to prey movement during foraging trials, a subset of randomly-selected data representing 25% of all amphipod and mysid foraging trials was used to estimate the amount of time that mysids and amphipods actively moved around the foraging arena compared to the amount of time that prey remained stationary.

**Intake rate**

Prey intake rate (number/min) for lake trout was evaluated at a subset of light levels (0.007, 0.02, 0.09, and 4.0 μE/m²/s) using various prey densities (3, 6, 9, 15, 45, 157, and 392/m² for amphipods; 3, 6, 9, 24, and 157/m² for mysids). Mysid prey densities corresponded to densities (individuals/m²) observed near a lake trout spawning shoal in Lake Superior (B. Holbrook, unpublished data). The size of the foraging arena used was dependent on prey density. Trials were conducted for 10 min. Prey that was consumed was replaced so total prey density remained constant during a trial. Data were imported digitally (see Foraging behaviors above). ImageJ software was used to measure the total length (cm) of lake trout in each trial. Numeric intake rates (number/min) were converted to a biomass intake rate (mg/min) using an average dry weight (mg) estimate for each prey species (see Intake rate above). The maximum reaction distance (cm) and α is the half-saturation constant (μE/m²/s).)

Modeling

A Michaelis–Menten function was used to represent the relationship between light intensity (I, μE/m²/s) and reaction distance in response to D. magna (Rd, cm):

\[
R_d = \frac{R_{\text{max}}}{\alpha + I}
\]

where \(R_{\text{max}}\) is the maximum reaction distance (cm) and \(\alpha\) is the half-saturation constant (μE/m²/s).

We also compared lake trout measured intake rate with two models, a Michaelis–Menten function and a foraging rate model. The Michaelis–Menten function took the form:

\[
I = \frac{I_{\text{max}}N_p}{\alpha + N_p}
\]

where \(I\) is the predicted intake rate (number/min or mg/min), \(I_{\text{max}}\) is the maximum intake rate (number/min or mg/min) when prey density is unlimited, \(\alpha\) is the half-saturation constant (number/min or mg/min), and \(N_p\) is prey density (number/m² or mg/m²). The parameters \(I_{\text{max}}\) and \(\alpha\) were estimated using Gauss–Newton nonlinear least-squares methods (nls) in the Rcmdr package within the R environment.
The foraging model was calculated using an encounter rate model of the volume of water searched \((Z)\) developed by Gerritsen and Strickler (1977):

\[
Z = \left( \frac{nR_d^2}{3} \right) \left( \frac{3v^2 + u^2}{v} \right) N_p
\]  
(3)

where \(R_d\) is the reaction distance of the lake trout (cm), \(v\) is the swimming speed of the lake trout (cm/s), \(u\) is the swimming speed of the prey (cm/s), and \(N_p\) is the prey density (number/cm\(^3\)). The encounter rate model assumes that fish use a conical search area when foraging for prey and was developed for use at a prey density scale of approximately 1 cm\(^3\) (Gerritsen and Strickler, 1977). Because the reaction distance of lake trout in response to amphipods and mysids was often greater than the depth of our foraging arenas (7 cm), it was unknown whether it would be more appropriate to calculate \(N_p\) using the actual depth in the arena or to assume that measured areal prey density (number/m\(^2\)) was equivalent to a three dimensional prey density (number/m\(^3\)), given that amphipods and mysids exhibited primarily benthic behavior at light intensities greater than 0 µE/m²/s, as did lake trout when they were actively searching for prey. Therefore, we calculated \(N_p\) using both methods.

To estimate foraging rates on amphipods and mysids (number/min), \(Z\) was multiplied by the cumulative probability \((C_p)\) that a fish would undergo a series of chronological predation events where a prey item would be located, pursued, attacked, and retained (Wright and O’Brien, 1984). However, we determined that \(R_d\) varied significantly depending on whether prey was mobile or stationary. Therefore we modified Eq. (3) so that the final foraging model \((F,\) number/min) took the form:

\[
F = \left( \frac{R_{d1}^2 P_1 + R_{d2}^2 P_2}{N_p} \right) \left( \frac{3v^2 + u^2}{v} \right) N_p C_p
\]  
(4)

where \(R_{d1}\) was the reaction distance in response to inactive prey, \(P_1\) was the proportion of time prey were inactive, \(R_{d2}\) was the reaction distance in response to moving prey, and \(P_2\) was the proportion of time prey moved.

Results

Foraging parameters

Reaction distances

Foraging trials conducted at 0 µE/m²/s were excluded from statistical analyses because there was only one successful capture of prey, an amphipod, at 0 cm out of 24 trials conducted at this light intensity \((n = 11\) with amphipods and \(n = 13\) with mysids). When controlling for prey type, prey movement, and light intensity, there was no significant effect of arena size (likelihood ratio test, mixed effect models) so data were combined for both foraging arenas. Analyses conducted on the combined dataset indicated that the most appropriate model included the effect of prey type and prey movement, but not the effect of fish length or light intensity (Fig. 1) on lake trout reaction distance (likelihood ratio test, mixed effect models). Post-hoc comparisons indicated that lake trout reaction distance in response to stationary amphipods versus stationary mysids was similar but that there was a significant increase in reaction distance in response to mobile mysids compared to other prey groups (Fig. 2). There was no significant relationship between amphipod length and reaction distance, but there was a significant positive relationship between mysid length and reaction distance (Spearman rank correlation coefficient, \(\rho = 0.16, p < 0.01\)). An analysis of prey movement indicated that amphipods were active on average 55% the duration of a foraging trial while mysids were active on average 30% the duration of a foraging trial.

Reaction distance experiments were also conducted with D. magna to determine the effect of using pelagic prey in conjunction with LED lighting that simulated deepwater downwelling aquatic spectrum. The results of our experiments (Fig. 3) indicated that there was a significant decrease in reaction distance at the light level of 0.007 µE/m²/s compared with all other light levels (mixed effect models, Tukey’s comparisons, \(p < 0.05\)). A Michaelis–Menten function was used to represent the relationship between light intensity \((I)\) µE/m²/s and reaction distance (cm) in response to D. magna \((R_d,\) Fig. 3). The nonlinear least
square estimates of the parameters in the model were $R_{\text{max}} = 15$ and $L_i = 0.004 \mu E/m^2/s$.

**Horizontal angle of attack**

More than half of all events in which lake trout oriented towards prey occurred at angles ±0–60° from the longitudinal axis of the lake trout (64% of located amphipods; 56% of located mysids, Fig. 4). Foraging fish oriented towards few prey located posterior at angles ±150–180° from the longitudinal axis of the lake trout (2% of located amphipods and mysids, Fig. 4).

**Swimming speeds**

The average swimming speed of lake trout was greater than either amphipods or mysids (Fig. 5). There was a significant effect of both prey species and movement on the burst swimming speed of lake trout after fish located prey (likelihood ratio test, mixed effect models). Post-hoc comparisons indicated that lake trout had a significantly greater burst speed in response to mobile prey compared with stationary prey, and in response to mobile mysids compared with mobile amphipods (data not shown). Lake trout burst swimming speeds were positively correlated with the swimming speeds of their prey prior to an attack event (Spearman rank correlation coefficient: amphipods: $\rho = 0.46$, $p < 0.001$; mysids: $\rho = 0.50$, $p < 0.001$). In contrast to amphipods, mysids appeared to attempt to avoid capture by quickly propelling themselves forward when a lake trout approached, which may have been the result of mysids sensing a pressure wave from an approaching lake trout. Mysid escape burst speed was significantly greater than the burst speed of an attacking lake trout (Fig. 5; mixed effect models, Tukey’s comparison, $p < 0.001$).

**Foraging success**

Age-0 lake trout had an overall average foraging success of 42% for amphipods and 25% for mysids. The low foraging success for amphipods was due in part to a 63% retention rate (Fig. 6). Age-0 lake trout often successfully captured the amphipod in their buccal cavity only to reject the prey. The rejected prey was often recaptured multiple times until it was finally retained. In contrast to amphipods, lake trout had a high mysid retention rate (94%, Fig. 6). However, lake trout successfully attacked only 31% of mysids that were encountered, located, and pursued (Fig. 6).

---

**Fig. 3.** Reaction distance of age-0 lake trout in response to *Daphnia magna*. Data were fit with a Michaelis–Menton function (solid line, see text). Error bars are ±2 SE.

**Fig. 4.** Simultaneous representation of attack angle and reaction distance for lake trout in response to amphipods ($n = 338$, left panel) and mysids ($n = 381$, right panel). Closed circles represent moving prey and open circles represent stationary prey. The gray shaded “fish” figure in the middle oriented towards 0° represents the orientation of the fish in each trial. Each concentric circle represents a distance of 20 cm.

**Fig. 5.** Average and burst swimming speeds (cm/s) for lake trout, amphipods, and mysids. Amphipods did not have a burst escape speed. Error bars are ±2 SE.
Intake rate

At the four light levels tested (0.007, 0.02, 0.09, and 4.0 $\mu$E/m$^2$/s), there were no significant effects of light intensity on the intake rate of lake trout that consumed amphipods (ANOVA, $F_{3,73} = 1.8$, $p > 0.05$) or mysids (ANOVA, $F_{3,44} = 0.9$, $p > 0.05$). When the intake rates (number/min) were combined across all light levels for each prey species, there was a significant effect of prey density on intake rates for both amphipods (ANOVA, $F_{6,73} = 13.5$, $p < 0.001$) and mysids (ANOVA, $F_{4,44} = 6.3$, $p < 0.001$, Fig. 7). Corresponding biomass intake rates (mg/min) for both prey species are displayed in Fig. 8. There was no significant relationship between fish length and intake rate for amphipods, but there was a correlation for mysids (Spearman rank correlation coefficient; amphipods: $\rho = 0.07$, $p > 0.05$; mysids: $\rho = 0.62$, $p < 0.001$).

Measured intake rates (number/min, mg/min) were modeled using the Michaelis–Menten function (Eq. (2), Table 1) and the foraging model (Eq. (4), Table 2). Foraging models calculated using a volumetric estimate of prey density based on actual water depth in the foraging arena was the most inaccurate (Figs. 7 and 8). Foraging models calculated using an areal estimate of prey density (assuming that prey density/m$^2$ was equivalent to prey density/m$^3$, see Methods) predicted intake rates similar to measured intake rates at the lowest prey densities. However, foraging models did not include a satiation mechanism to limit consumption at higher prey densities (Figs. 7 and 8). In contrast, Michaelis–Menten functions closely modeled measured intake rates at both low and high prey densities. Results indicated that there was a maximum intake rate beyond which consumption did not increase. Observations indicated that this functional response was likely the result of satiation due to consuming large-bodied prey.

When plotted on the same scale using biomass estimates, lake trout intake rates (mg/min) at the lowest prey densities were similar between both prey species (Fig. 8). However, age-0 lake trout had a higher maximum intake rate of mysids compared with amphipods (Fig. 8).

Daily consumption

The maximum daily consumption on a per weight basis (mg/mg/day wet weight) decreased as the fish grew in weight (Fig. 9). Based on the maximum daily consumption and the modeled intake rate (Fig. 8), age-0 lake trout apparently need very little foraging time to achieve maximum consumption. For example, consider a 1000 mg lake trout that our data indicate would consume a maximum of 113 mg wet weight/day (Fig. 9). At high prey densities, the maximum lake trout intake of mysids was 1.38 mg dry weight/min (Table 1, Fig. 8), or the...
Discussion

Diet studies of age-0 lake trout captured in the field indicate that they have a preference for mysids (Hudson et al., 1995; Roseman et al., 2009), and results from our laboratory study indicate that this predator–prey relationship is highly advantageous for maximizing age-0 lake trout intake rates. Although each individual attack event had a low probability of success, age-0 lake trout encountered mysids often enough even at the lowest prey densities that we tested (3 individuals/m²) that the Michaelis–Menten model predicted they would become satiated within 30 min. Unless mysid densities were fewer than 0.15 individuals/m², we predict that age-0 lake trout could meet their metabolic needs by foraging intermittently throughout the day.

Because age-0 lake trout need to capture so few mysids to reach their daily maximum consumption, our study suggests that foraging during daylight hours alone could maximize age-0 lake trout needs. Nighttime foraging may be a relatively minor component of their overall daily intake for two reasons. First, mysids undergo diel vertical migration at night (Bowers, 1988; Gal et al., 1999), so prey densities become more diffuse. Second, light levels at night are lower than those that we tested and thus may limit foraging success. Even under full-moon conditions, the light intensity at the water’s surface during summer months in northern latitudes is approximately 0.002 μE/m²/s (0.1 lx, Janiczek and DeYoung, 1987), and would be exponentially lower at the depths of 15–40 m at which age-0 lake trout are typically captured (Bronte et al., 1995). Although we were unable to test light levels lower than 0.007 μE/m²/s due to limitations in our equipment, it is likely that a threshold exists below this level that would limit age-0 lake trout visual acuity, given that similar thresholds have been observed in other lake trout foraging experiments (Confer et al., 1978; Mazur and Beauchamp, 2003; Vogel and Beauchamp, 1999).

Our results on threshold light levels differ from previous lake trout foraging studies in that we did not detect such a threshold at light levels analogous to those used in other studies. For example, Vogel and Beauchamp (1999) and Mazur and Beauchamp (2003) observed a reduction in reaction distance for adult lake trout below 18 lx (~0.2 μE/m²/s depending on the spectrum of light being used) and Confer et al. (1978) observed a reduction in reaction distance at 1 lx and 10 lx (~0.01 μE/m²/s and 0.1 μE/m²/s, respectively). It is possible that our use of benthic prey and the shallow depth in the foraging arena reduced the number of escape dimensions for prey.

Another explanation for differences in our results compared to previous foraging studies is that we used blue-green LED lighting that more closely mimics the downwelling spectrum in the lake trout’s underwater habitat. In an attempt to tease apart the effect of using benthic prey versus the effect of using blue-green LED lighting, we conducted experiments using D. magna to determine whether use of a pelagic zooplankton species would result in a response curve more similar to those observed in previous studies. Unlike with amphipods and mysids, we found a significant decrease in reaction distance at 0.007 μE/m²/s. However, we also found that our maximum reaction distance was approximately twice that of our minimum (non-zero light level) reaction distance, which was less than Confer et al. (1978) who found a maximum reaction distance three times the minimum reaction distance even though lengths of age-0 lake trout (~7–9 cm) and D. magna (0.3 cm) were similar in both studies. One potential explanation for differences in our results compared to Confer et al. (1978) may have been the lighting that was used during experimental trials.

Broad spectrum lighting, such as that used by Confer et al. (1978) may actually enhance visual acuity of age-0 lake trout by increasing contrast (Lythgoe, 1984). Several studies have documented that longer wavelengths create greater visual contrast between zooplankton prey and their surroundings (Umé-Palm, 1999; White et al., 2005). Longer wavelengths may also increase a fish’s sensitivity to motion (Krauss and Neumeyer, 2003; Schaer and Neumeyer, 1996). Because age-0 lake trout are sensitive to prey movement, improved perception of motion could cause an increase in reaction
distance when using non-natural lighting. Conversely, using ambient spectrums which align closely with peak spectral sensitivity of age-0 lake trout should enhance visual acuity. Utne-Palm and Bownmaker (2006) demonstrated that using lighting with wavelengths most similar to the maximum spectral sensitivity of photoreceptors in the two-spotted goby (Gobiusculus flavescens) caused maximum reaction distances to increase. In this study, age-0 lake trout may have been highly sensitive to the lighting, which explains why they appeared equally responsive to amphipods and mysids under all non-zero light levels tested. Sensitivity to the experimental light may also explain why age-0 lake trout appeared to reach a maximum reaction distance in response to D. magna at lower light levels than was previously observed for lake trout (Confer et al., 1978; Vogel and Beauchamp, 1999). Therefore, our results, in conjunction with previous research (Downing and Litvak, 2001; Utne-Palm and Bownmaker, 2006; White et al., 2005), suggests that reaction distances and foraging rates may be strongly dependent on the light spectrum used in the experiments.

We selected amphipods for use in trials until we could capture mysids in the field because amphipods are visible, mobile, benthic, and could withstand 8°C temperatures used in the trials. However, there were significant differences between the two prey species, including that age-0 lake trout had an average successful attack percentage of 91% on amphipods compared with 31% on mysids. Mysids had a quick, jerky escape response that reduced age-0 lake trout attack success. A similar escape response has also been observed in Euphausiids (O'Brien, 1987) and marine mysids (O'Brien and Ritz, 1988; Rademacher and Kils, 1996). The maximum mysid escape speeds that we recorded (63 cm/s) were similar to reported maximum escape speeds recorded for the marine mysid Neomysis integer (80 cm/s) which, in that study, resulted in an overall foraging success of 25% for the fifteen-spined stickleback (Spinacia spinachia, Rademacher and Kils, 1996), similar to the foraging success measured in our trials.

Another significant difference between prey species was that the retention rate was 63% for amphipods compared with 94% for mysids. It is unclear why age-0 lake trout rejected amphipods at such a high rate, given that the size of amphipods (~0.3 cm) was less than 10% the total length of the smallest age-0 lake trout used in the study and that age-0 lake trout readily consumed mysids up to 30% their total length. Furthermore, age-0 lake trout continued to have problems successfully retaining amphipods after two months of experimental trials in which fish grew in size and became more experienced in foraging for prey. One possible explanation for the low retention rate may be the presence of dorsal tergite spines on H. azteca. The presence of similar morphological spines on the amphipod Gammarus roeseli was identified as an antipredator defense causing reduced ingestion rates for brown trout (Salmo trutta, Bollache et al., 2006). Although G. roeseli was much larger than the H. azteca that we used in our study, the amphipods in both studies were approximately 10% the total length of the respective fish species. It is also possible that amphipods are an undesirable prey species for age-0 lake trout for other reasons. Diporeia hoyi, a deepwater amphipod that lacks dorsal tergite spines and is common to the Great Lakes (Dermott, 1978; Guiguer and Barton, 2002; Winell and White, 1984), were not found in age-0 lake trout stomachs even when found in slimy sculpin (Cottus cognatus) stomachs at locations where both fish species co-occurred (Hudson et al., 1995).

Despite differences in the behavior of age-0 lake trout in response to amphipods and mysids, the foraging models (Eq. (4), Table 2) predicted similar intake rates for the two prey species when we converted numeric intake rates to dry weight biomass intake rates. Although the areal foraging model was fairly accurate at low prey densities, the linear predictions of the model were inappropriate at higher prey densities. For this model to be useful for estimating age-0 lake trout consumption, it would be important to incorporate a functional response or a satiation mechanism at higher prey densities. Similar to the foraging model predictions, measured biomass intake rates at low biomass prey densities were similar between the two prey species. At high biomass prey densities, however, the measured intake rates were higher for mysids than for amphipods (Fig. 8). This difference in maximum intake rate may have been a result of prey preference for mysids, although results from the daily consumption trials suggest that it may also be an effect of using larger fish on average when conducting trials with mysids. Age-0 lake trout averaged 4.9 cm in length during amphipod intake rate trials and 6.1 cm in length during mysid intake rate trials.

We were unable to eliminate the effect of age-0 lake trout growth while attempting to test multiple combinations of light levels and prey densities. We did not detect a relationship between fish length and amphipod intake rate, but we did detect a relationship between fish length and mysid intake rate. Previous research has indicated that encounter rates increase and prey handling times decrease with increasing fish size (Mittelbach, 1981). Encounter rates can be influenced by reaction distance and swimming speed of the predator (Eq. (3)), but we did not detect a relationship between fish length and reaction distance or between fish length and swimming speed. Although we did not measure handling time, the results of our study suggest that age-0 lake trout may be more similar in their foraging mechanisms to piscivorous fish than to zooplanktivorous fish that are efficient in their daily reliance on a few, large prey, in which case handling time per prey is likely inefficient compared with time involved in gastric evacuation and digestion (Breck, 1993). It is most likely, therefore, that stomach capacity associated with fish length explains differences in maximum intake rate.

Our study highlights the importance of mysids as a forage species on and near lake trout spawning shoals for maximizing age-0 lake trout growth. However, our study also suggests that as long as mysids are present, even in relatively low densities, food availability may not be a primary factor limiting age-0 lake trout survival as long as visual acuity is unimpaired by thiamine deficiencies (Carvalho et al., 2009; Fitzsimons et al., 2009). Eddsall et al. (2003) made similar conclusions after determining that age-0 lake trout were highly resistant to starvation upon hatching and that food shortages were unlikely to be a major cause of mortality. One caveat to these results is that intake rates estimated in the laboratory are likely optimistic and present a “best-case” foraging scenario. In the wild, age-0 lake trout may experience turbidity, vulnerability to predation, competition, and substrate heterogeneity that reduce optimum foraging rates.

Although we simulated oligotrophic lake conditions in this study, lake trout spawning shoals may be subject to localized turbidity, particularly on shallow reefs impacted by re-suspension of feces and pseudofeces from non-native mussels Dreissena spp. (Barbiero and Tuchman, 2004; Roditi et al., 1997). It is likely that turbidity would reduce age-0 lake trout intake rates given that foraging experiments on adult lake trout have found a reduction in reaction distances with increasing turbidity (Mazur and Beauchamp, 2003; Vogel and Beauchamp, 1999). Conversely, in areas where age-0 lake trout are prone to predation, increased turbidity may reduce predation risk for age-0 lake trout because the reaction distance of piscivorous fish may be disproportionately reduced in turbid conditions (De Robertis et al., 2003; Gregory and Leving, 1998). Both intraspecific and interspecific competition could also influence foraging behavior, and both have been found in other studies to reduce intake rates of arctic char (Salvelinus alpinus), a closely related species to lake trout (Amundsen et al., 2007; Guénard et al., 2012). We did not test effects of habitat complexity, but this factor has also been found to influence foraging rates in salmonids (Dahl and Greenberg, 1997), and would likely decrease age-0 lake trout intake rates if benthic prey had more places to hide.

This laboratory study provides a first attempt at quantifying the foraging behavior of age-0 lake trout upon their preferred prey using...
lighting that closely mimics the deepwater downwelling aquatic spectrum. We have demonstrated that this predator–prey relationship is advantageous for maximizing age-0 lake trout consumption with a minimum of foraging effort. Although our laboratory-estimated intake rates may be optimistic given the ecological complexity that age-0 lake trout experience in the wild, these models provide an important baseline for future comparisons. Additionally, the results of this study make it possible to estimate intake rates based on prey densities, which may be useful for determining whether prey abundance is a factor in the heterogenous distributions of age-0 lake trout on and near spawning shoals during their first summer.

Acknowledgments

We thank the Minnesota Department of Natural Resources Lake Superior Area Fisheries, the United States Geological Survey Lake Superior Biological Station, and the Trout Lake Research Station for providing ship time and/or equipment for capturing mysids. Dustin Wing provided assistance setting up lighting and foraging arenas. Ron Regal provided advice regarding data analysis, and John Sandberg provided field assistance capturing mysids. This project was funded in part through a summer grant provided by the University of Minnesota Duluth Visualization and Digital Imaging Lab. This work is the result of research sponsored by the Minnesota Sea Grant College Program supported by the NOAA office of Sea Grant, United States Department of Commerce, under grant No. NA030AR4170048. The U.S. Government is authorized to reproduce and distribute reprints for government purposes, not withstanding any copyright notation that may appear hereon. This paper is journal reprint No. JR 599 of the Minnesota Sea Grant College Program.

References


