

Effects of light, prey size, and turbidity on reaction distances of lake trout (*Salvelinus namaycush*) to salmonid prey

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Abstract: Most studies on visual foraging by fish have focused on reaction distances to invertebrate prey; however, these acuity-based results considerably overestimate reaction distances of piscivores to prey fish. In laboratory experiments, we quantified reaction distance of adult lake trout (*Salvelinus namaycush*) to rainbow trout (*Oncorhynchus mykiss*) and cutthroat trout (*Oncorhynchus clarki*) as a function of light (0.17–261 lx), prey size (55, 75, and 139 mm), and turbidity (0.09, 3.18, and 7.40 NTU). Reaction distances increased rapidly with increasing light from <25 cm at 0.17 lx to about 100 cm at a light threshold of 17.8 lx. Reaction distance declined as a decaying power function of turbidity. By constructing equations that describe the combined effects of light and turbidity on reaction distances, we can begin to model prey detection capabilities of piscivores at any depth at any time of day in natural environments.

Résumé : La plupart des études sur le rôle de la vision dans la recherche de nourriture par les poissons se sont concentrées sur les distances de réaction à l'égard des proies invertébrées; cependant, ces études fondées sur l'acuité visuelle surestiment considérablement les distances de réaction des piscivores à l'égard des poissons proies. Dans des expériences en laboratoire, nous avons quantifié la distance de réaction de touladis (*Salvelinus namaycush*) adultes à l'égard de truites arc-en-ciel (*Oncorhynchus mykiss*) et de truites fardées (*O. clarki*) en fonction de l'éclairage (0,17–261 lux), de la taille des proies (55, 75, 139 mm) et de la turbidité (0,09, 3,18 et 7,40 NTU). Les distances de réaction ont augmenté rapidement avec l'accroissement de l'éclairage, passant de <25 cm, à 0,17 lux, à environ 100 cm, à partir de 17,8 lux. La distance de réaction a diminué avec l'accroissement de la turbidité suivant une fonction exponentielle décroissante. En établissant des équations qui décrivent les effets combinés de la lumière et de la turbidité sur les distances de réaction, nous pouvons commencer à modéliser les capacités de détection des proies des piscivores à n'importe quelle profondeur et n'importe quel moment de la journée dans les milieux naturels.

[Traduit par la Rédaction]

Introduction

Although the influence of predation on the structure and dynamics of aquatic communities has been well documented (Carpenter et al. 1985; Kerfoot and Sih 1987; Northcote 1988; Carpenter and Kitchell 1993), little is known about how pelagic piscivores detect prey. Except in turbid systems, visual foraging is effective in limnetic systems because vision provides greater search volume and offers more precise orientation to prey than other sensory systems (Guthrie and Muntz 1993). Numerous studies have examined visual feeding by zooplanktivores (e.g., Vinyard and O'Brien 1976; Confer et al. 1978; Wright and O'Brien 1984; Henderson and Northcote 1985), but only three studies have measured

visual responses of piscivores to prey fish (Cerri 1983; Howick and O'Brien 1983; Miner and Stein 1996), and none of these examined the combined effects of light, turbidity, and prey size. By studying the combined effects of these three factors simultaneously, we can determine the relative importance of each and include interactions that would not be apparent from one- or two-factor experiments.

Visual foraging models depend on improved parameterization of the prey encounter and selection process to predict feeding rates (Eggers 1977; Wright and O'Brien 1984; Aksnes and Giske 1993; Beauchamp et al. 1999). Such models generally estimate a search volume approximated by a cylinder with radius equal to the reaction distance and length equal to the distance traveled during the foraging period (Eggers 1977). Since estimates of search volume will vary in proportion to the square of reaction distance, visual foraging models will be quite sensitive to errors in reaction distance estimates. Thus, estimates of reaction distance as a function of light, turbidity, and prey size can be incorporated into a general pelagic piscivore foraging model. Such a model would improve our understanding of how physical and biotic processes constrain prey detection in time and space. This approach would simulate how predators perceive availability of different prey types and thus should lend insight into why the magnitude of piscivory varies among systems (Beauchamp et al. 1999).

Fish use different visual systems to detect large prey like

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fish versus smaller invertebrate prey. Breck (1993) demonstrated that an acuity-based model for zooplanktivores grossly overestimated reaction distances by piscivores to prey fish. In pelagic systems where piscivory involves relatively large prey under generally low light conditions, visual acuity should be less important than detecting the contrast between prey and its background (Eggers 1977; Cerri 1983; Breck 1993). Contrast will be affected by available light, turbidity, and the backscattering of light between predator and prey (Loew and McFarland 1990; Aksnes and Giske 1993; Breck 1993). In contrast-limited systems, reaction distances to prey are expected to be independent of or minimally dependent on prey size at large distances (Eggers 1977; Breck 1993). Thus, a visual foraging model for piscivores should be constructed from measurements of piscivores reacting to prey fishes rather than extrapolating from zooplanktivore foraging models.

Salmonids are top predators in many northern cold-water lakes and reservoirs; however, little is known about the relationship between their feeding behavior and the temporal and spatial distribution of prey. Lake trout (*Salvelinus namaycush*) have been introduced both legally and illegally into many lakes in western North America and potentially threaten the ecological integrity of existing salmoniform-dominated communities in the region like Yellowstone Lake (Varley and Schullery 1995), Bear Lake (Ruzycski and Wurtsbaugh 1995), and Flathead Lake (McIntyre 1998). In this study, reaction distances of lake trout to prey-sized rainbow trout (*Oncorhynchus mykiss*) and cutthroat trout (*Oncorhynchus clarki*) were measured experimentally as a function of light intensity, turbidity, and prey size in a laboratory tank. By examining the prey detection capabilities of lake trout, we hope to gain insight into how the role of this potential predator and competitor might differ among waters of different optical characteristics, morphometry, and species assemblage.

Methods

Fish exhibit characteristic or stereotypic behaviors when reacting to prey. Upon detection, fish orient head-on to prey (Confer and Blades 1975). This suggests that fish are better able to monitor the prey's position using binocular vision in the frontal field, as has been observed in cichlids (Ingle 1968) and sunfish (Confer and Blades 1975). Reaction distance was determined by measuring the distance from where the fish first orients toward the prey (Vinyard and O'Brien 1976; Howick and O'Brien 1983). This definition can be used for the predator's reaction to prey or, conversely, for the reaction of prey to the predator (Howick and O'Brien 1983; Savitz and Bardygula 1989; Miner and Stein 1996).

Reaction distances were measured for lake trout (330–456 mm total length, $N = 19$) taken from first-generation offspring of wild brood stock. For 1–4 months prior to the experiments, these predators were conditioned to feed on live prey similar to those used in experiments. Prey fish (acquired from several hatcheries in the area) were either rainbow or cutthroat trout depending on the availability of each size-class (mean \pm SE total length: 55 \pm 1 mm, 75 \pm 2 mm, and 139 \pm 2 mm). The prey fish at these sizes (55–139 mm) had the same basic morphometric characters and coloration (dark with parr marks). Since the two prey species were not visually different in appearance, both prey species were utilized. Small prey fish (55 mm) were used for the clear-water treatment but were not available for other treatments. Subsequently, only 75- and 139-mm prey fish were available for measuring reaction distances across all

combinations of light and turbidity. The fish-holding facility was indoors, and fish experienced 11 h of daylight and 13 h of darkness (building hours 07:00–1800). Fish were held in rectangular and circular tanks supplied with river water maintained at 9–11°C.

To determine how light level, turbidity, and prey size influenced the reaction distances of lake trout to juvenile rainbow and cutthroat trout, reaction distances were measured in a rectangular tank (4.5 m long \times 1 m wide \times 1 m high). The experimental arena was lined inside with semirigid opaque gray plastic sheets; bottom sheets were etched and painted with a white grid (10 \times 25 cm rectangles) on the bottom to aid in measuring reaction distances. The experimental tank, overhead lights, and camera frame were shrouded in two layers of black plastic to exclude any external sources of light. Light levels were generated from four fluorescent lights with two light tubes per fixture (50-W fluorescent tubes) hung end-to-end about 1 m above the water. Light intensities were controlled by adding multiple layers of fiberglass window screen over the lights until the desirable light condition was achieved (Neverman and Wurtsbaugh 1992). Light intensity declined exponentially ($r^2 = 0.998$, $df = 11$, $P < 0.001$) as layers of window screen were added:

$$(1) \quad lx = 273.1e^{-0.504s}$$

where s is the number of layers of screen. Light intensities ranged from 0.17 to 261 lx measured to the nearest 0.1 lx at the water surface with a Spur Scientific (model 840006C) light meter.

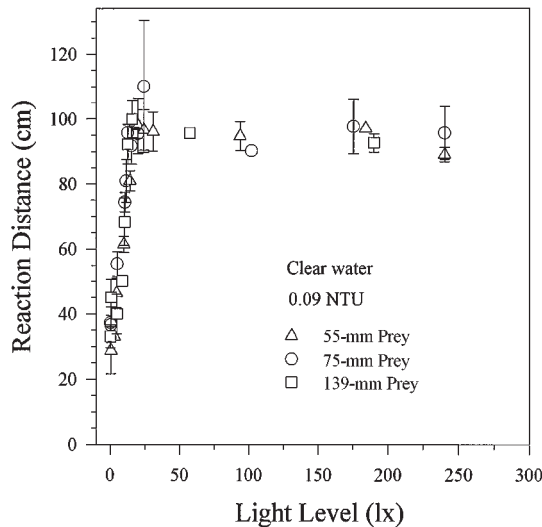
Turbidities were controlled by adding various amounts of bentonite clay to achieve three turbidity levels of 0.09, 3.18, and 7.40 nephelometric turbidity units (NTU) measured with a LaMotte (model 2008) turbidity meter. The bentonite clay remained in suspension without circulators during each 4-h experiment.

We used one lake trout and one to three rainbow or cutthroat trout prey in each trial. Before the experiments, lake trout were deprived of food for at least 48 h and were held in the experimental arena for at least 1 h at experimental light intensities and turbidities (Vinyard and O'Brien 1976) with water temperatures between 9 and 11°C. Four to 11 predators were tested individually at each combination of light, turbidity, and prey size.

Predators were placed at one end of the tank behind an opaque sliding door with prey at the opposite end in a 38-L glass aquarium (50.8 cm long \times 25.4 cm wide \times 30.5 cm deep) inside the large experimental tank to eliminate all but visual stimuli. Inside the prey's aquarium, a piece of rigid gray plastic sheeting was used to confine the prey fish to a smaller region (50.8 cm long \times 5 cm wide \times 30.5 cm deep) to keep them oriented generally perpendicular to the predator, yet allowed the prey fish to swim freely in this space. Some preliminary experiments (55-mm prey size and 0.09 NTU level at 17.8 and 184 lx) showed no significant differences between mean reaction distances to tethered prey outside the aquarium and those to prey in the aquarium ($F_{3,37} = 0.9$, $P = 0.445$). Consequently, we used the fish inside the aquarium for all subsequent experiments, since this eliminated all but visual stimuli and simplified the measurements of reaction distance. The predator was released and allowed to swim freely in the tank for 1–4 h. Periodically, prey fish and predators were allowed to swim freely in the arena to prevent predators from becoming conditioned to a specific prey location.

Reaction distances of lake trout to prey were recorded using two Polaris CCD black and white surveillance cameras (model VT-90D) with two, four-head Magnavox videocassette recorders (model VRT 242) (with 8-h videotapes), and tapes were replayed later for analysis. When light levels were outside the range of the video cameras (i.e., <0.6 lx), reaction distances were measured directly. Two observers were stationed at the end of the tank and recorded measurements for a specified period of time, with both observers coming to a consensus after a reaction distance behavior was observed. Cameras could record at light levels down to 0.6 lx

Fig. 1. Reaction distances of lake trout (330–456 mm total length) to 55-, 75-, and 139-mm prey as a function of light (0.17–240 lx) in clear water (0.09 NTU). Data points represent the means \pm 2 SE of individual average reaction distances for 4–11 lake trout at each combination of light and prey size.



in the low-turbidity treatment but were only effective in light levels to ≥ 4 lx in higher turbidity treatments.

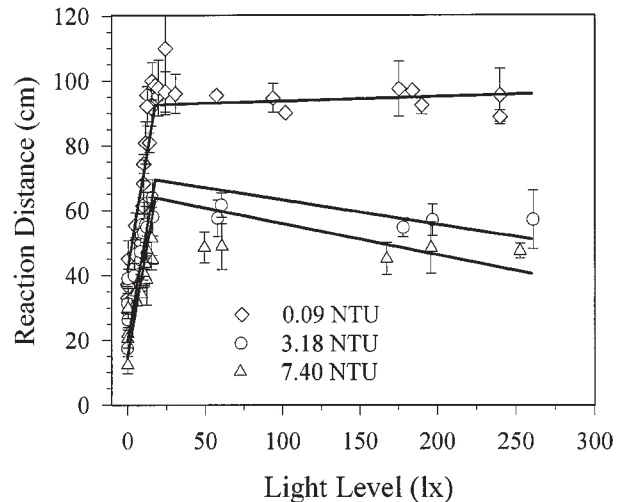
Reaction distances were measured from video recordings using two methods, depending on the angle at which a predator approached the prey fish. When the predator reacted in a direct line perpendicular to the prey and continued this line up to a specific prey in the aquarium, this point was marked by pausing the videocassette recorder at the beginning of the behavior. The distance was then determined by counting the rectangles between the fish and prey item. However, if the predator swam at some angle to the prey, again following this line up to a specific prey in the aquarium, the lateral and longitudinal distances were recorded and a reaction distance was calculated using the Pythagorean theorem.

Reaction distances of lake trout were measured for three prey sizes (55, 75, and 139 mm) in clear water (0.09 NTU) and for two prey sizes (75 and 139 mm) at 3.18 and 7.40 NTU. Reaction distance was analyzed as a linear function of prey size, a piecewise linear function of light level, and a linear function of \log_e -transformed turbidity. Turbidities were \log_e transformed to capture the exponential decline in reaction distance reported in other studies (Vinyard and O'Brien 1976; Wright and O'Brien 1984; Miner and Stein 1996). Interaction among light, prey size, and turbidity was included. Regressions were performed on the mean reaction distances calculated individually for each predator ($N = 4$ –11) within each combination of light, turbidity, and prey size. All piecewise linear regression models were fit using PROC NLIN in SAS release 6.12 (SAS Institute Inc. 1996); this procedure iteratively estimated the intercept, breakpoint, and slope parameters. Significance levels for regression parameter estimates (i.e., nonzero slopes, difference between slopes) were obtained from t tests. The R^2 values were computed as (regression SS/uncorrected total SS). An F -test for significance of the entire regression was computed (Zar 1984).

Results

Reaction distances were not affected by prey size (Fig. 1). Over all light levels (0.17–240 lx), the slopes of reaction distances to different prey fish sizes were not significantly different in clear water (0.09 NTU; $t = 0.570$, $df = 27$, $P = 0.574$), at 3.18 NTU ($t = 1.36$, $df = 14$, $P = 0.195$), or at 7.40 NTU ($t = 1.92$, $df = 15$, $P = 0.074$).

Fig. 2. Unified model of lake trout reaction distances as a function of light (0.17–261 lx) and turbidity (0.09, 3.18, and 7.4 NTU) pooled over the three prey sizes. Data points represent the means \pm 2 SE of individual average reaction distances for 4–11 lake trout at each combination of light and turbidity.



Reaction distances (RD) were highly correlated with light and turbidity ($R^2 = 0.984$, breakpoint = 17.83 lx, $P < 0.001$) (Fig. 2):

- (2) Increasing limb: $RD = 26.84 + 2.81(lx) - 6.09 \ln(\text{turbidity}) - 0.025 \ln(\text{turbidity})(lx)$
- (3) Level limb: $RD = 77.79 - 0.046(lx) - 6.09 \ln(\text{turbidity}) - 0.025 \ln(\text{turbidity})(lx)$.

Reaction distances increased rapidly from the lowest light level (0.17 lx) to a threshold or breakpoint at 17.83 lx (termed the saturation intensity threshold (SIT) by Henderson and Northcote 1985). Above SIT, reaction distance declined gradually with a small, but significantly negative slope (-0.046) for the effect of light ($t = 2.24$, $df = 68$, $P = 0.028$). Reaction distances declined with increasing turbidity, and there was a significant interaction between light and turbidity ($t = 3.75$, $df = 68$, $P < 0.001$). As light or turbidity increased, the interaction term $-0.025 \ln(\text{turbidity})(lx)$ gradually reduced the reaction distance, suggesting that both factors increased backscattering between piscivore and prey fish.

Discussion

By examining the combined effects of light, turbidity, and prey size on reaction distances of piscivorous fish, we gained new insights into the prey detection capabilities of piscivores under different optical conditions expected over a diel cycle and throughout the water column in many salmonid lakes. In this study, reaction distances increased rapidly to a plateau at light ≥ 17.8 lx, declined with increasing turbidity, but showed no effect of prey size. This threshold effect is significant because it sets an upper limit on reaction distances to prey. Thus, as predators or prey ascend above the SIT depth, increasing light contributes no further advantage for prey detection and no further risk to prey. In fact, prey fish appear to have the advantage over predators at

higher light levels in terms of greater reaction distances (Howick and O'Brien 1983) and more effective predator evasion (Savitz and Bardygula 1989; Petersen and Gadomski 1994). Previous studies have also reported different light thresholds for maximum reaction distances of different fishes to both zooplankton and fish prey; however, these thresholds have rarely been measured precisely: 50–180 lx for lake trout reacting to zooplankton (Confer et al. 1978), 3 lx for Dolly Varden (*Salvelinus malma*) and 5–56 lx for cutthroat trout reacting to zooplankton (Henderson and Northcote 1985), ≥ 10 lx for bluegill (*Lepomis macrochirus*) reacting to zooplankton (Vinyard and O'Brien 1976), and 5.59 lx for largemouth bass (*Micropterus salmoides*) reacting to bluegill (Howick and O'Brien 1983). This variability in reaction distances among species and the differences in reaction distances to zooplankton versus prey fish represent a fertile area for continued research to define differences in foraging potential among species and under different environmental conditions. Species-specific differences in prey detection capabilities under different optical conditions could have important implications for predatory or competitive advantages of some species over others. Valuable insights can be gained by examining the role of temporal–spatial changes in the visual environment in habitat partitioning, competitive advantage, foraging–predation risk trade-offs, and other interactions.

Maximum reaction distances were achieved at relatively low light intensities that corresponded to ambient midday light intensities at 10–40 m depths in mesotrophic to meso-oligotrophic lakes. Thus, piscivores enjoy nearly maximum turbidity-specific reaction distances to prey fish through a range of depths where light is at or above SIT. During crepuscular periods, reaction distances decline rapidly with depth and change rapidly over short time scales. At night, reaction distances will be extremely low, even at the surface. The interaction term between light and turbidity suggests that, above SIT, reaction distances should decline gradually as light increases because increased backscattering reduces the contrast between prey and its background (Cerri 1983; Loew and McFarland 1990; Guthrie and Muntz 1993). This decline becomes more pronounced with higher turbidity. Thus, prey detection could be inhibited near the surface in bright sunlight and improve with depth until ambient light drops below SIT.

Our reaction distances for lake trout differed somewhat from those of Howick and O'Brien (1983) for largemouth bass. Prey size was not a significant factor affecting the reaction distance of lake trout to salmonid prey (55–139 mm) in our experiments, and maximum reaction distances were about 1 m. In contrast, Howick and O'Brien (1983) determined that reaction distances of largemouth bass increased with increasing prey size in clear water over a wide range of light levels (0.195–3340 lx), and maximum reaction distances were about 2 m. Prey size may presumably become important for reaction distances by lake trout at some smaller (<55 mm) prey size, but the shift from a contrast- to an acuity-based prey detection system may only become relevant when feeding on small translucent larval prey fishes. Prey detection might also depend more on the cross-sectional area rather than on the length of prey (Eggers 1977; Aksnes and Giske 1993). If so, then reaction distances

should be greater for deep-bodied prey (e.g., bluegill) than for fusiform prey (e.g., cyprinids and salmonids). Interestingly, Howick and O'Brien (1983) found that reaction distances of largemouth bass were actually greater with fusiform redbfin shiner (*Lythrurus umbratilis*, previously *Notropis umbratilis*) than with bluegill. These differences could also result from interspecific differences in foraging mode, different neurophysiological prey detection capabilities, or differences in experimental methods. Largemouth bass are predominantly sit-and-wait predators, whereas salmonids tend to be cruising predators. Prey movement increased reaction distances in clear-water situations for planktivores (Wright and O'Brien 1984) and for largemouth bass responding to smaller prey fish (Howick and O'Brien 1983). In our experiments, prey fish were allowed to swim in a confined area, so movement might have influenced reaction distance. For cruising salmonids, even motionless prey would appear to move through the visual field. Although the implications of these different feeding modes on prey detection are currently unknown, it is important to identify these as potentially important factors for determining reaction distance.

We used a neutral gray background, whereas Howick and O'Brien (1983) used a "clear" back to their experimental arena without describing the background color that resulted from this arrangement. Consequently, we cannot determine whether a difference in background coloration might explain the difference in reaction distances measured in this study compared with Howick and O'Brien (1983). Given the natural variability in background colors in lakes, we decided that gray offered the best reproducible compromise in background coloration.

Turbidity was a significant factor in reducing the reaction distances of lake trout. Miner and Stein (1996) examined turbidity effects on reaction distances between prey fish and piscivores over a much larger range (0.3–91.0 NTU) than in this study, but >80% of the observed decline in reaction distance occurred over 0–5 NTU. Moreover, the turbidities used in our experiments reflected the natural range expected in cold-water salmonid systems (except for some glacial lakes: 5–120 NTU; Koenings et al. 1990). Other experiments have focused largely on planktivorous centrarchids, which often experience turbidity levels around 20 NTU in midwestern and southern lakes and reservoirs (Vinyard and O'Brien 1976).

The experimental conditions under which reaction distances were estimated in this study should be considered before applying the reaction distance functions to natural systems. Light levels in this study were indicative of light levels in natural systems from midday (20–200 lx) at depths of 25–40 m through midcrepuscular periods (0.17 lx) at depths of 0–10 m (Henderson and Northcote 1985). We conducted these experiments in a shallow rectangular arena that was essentially a two-dimensional system and cannot duplicate the scale or complexities of lakes. Depth should be considered in future refinements of this approach. Coho salmon (*Oncorhynchus kisutch*) showed longer reaction distances to zooplankton above the horizontal visual plane (Dunbrack and Dill 1984), and Confer et al. (1978) obtained similar results with lake trout. Results from our study suggest that similar reaction distance measurements should be feasible in

larger three-dimensional arenas because the predators react to prey at much shorter distances than the visual detection range of humans or video equipment. Maximum reaction distances by predators were only 1 m in clear water under relatively high light intensity in our experiments. In natural conditions, we have observed lake trout attacking tui chub (*Gila bicolor*) at reaction distances of about 1 m at a depth of 20 m during early dusk in Lake Tahoe (NTU = 0.01, 360 lx).

Visual foraging models for top predators show considerable potential for enhancing our understanding of how piscivores influence the structure and function of limnetic communities (Beauchamp et al. 1999). The results of this study provide key parameters for estimating visual detection capabilities of a piscivore over a range of optical conditions. The resulting reaction distance functions simplify the modeling process, since only light and turbidity are required for a common size range of fusiform prey fishes (for prey 55–139 mm) encountered by salmonids in limnetic systems. To apply this model to specific lakes, basin-specific data (turbidity, light extinction coefficient, temporal changes in incident light levels, and diel prey distribution) can be collected quickly, and relatively inexpensively, thus making it a potentially powerful management tool.

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