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Foraging success of largemouth bass at different light intensities: implications for time and depth of feeding

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Laboratory feeding trials were conducted to determine how light intensity affects foraging success by the visual piscivore, the largemouth bass (*Micropterus salmoides*). Foraging success was greater than 95% at light levels ranging from low intensity daylight ($2{\cdot}43 \times 10^{2}$ lx) to moonlight (3×10^{-3} lx), but declined significantly to 62% at starlight (2×10^{-4} lx) and near 0% in total darkness. Over a range of low to high water clarities (0·5, 2·0, and 4·0 m Secchi depth), estimated depth limits for feeding during the day ranged between 5·5 to 44 m and from 1·6 to 13 m at night during a full moon. At starlight, light intensity rapidly attenuated to a level below the feeding threshold within 0·5 m of the surface at all water clarities. The depth of the water column available for feeding in low clarity water (0·5 m Secchi) was 67 and 75% less than at moderate (2·0 m Secchi) and high (4·0 m Secchi) water clarities. The findings illustrate how differences in the light environment can have important ramifications for predator–prey interactions.

Key words: *Micropterus*; largemouth bass; foraging; light intensity.

INTRODUCTION

Light is an important abiotic factor influencing predator–prey interactions in aquatic communities. Diel movements, habitat use, and feeding patterns of predators and prey are governed strongly by the relative foraging success and predation risk associated with different light intensities (e.g. Hobson, 1979; Cerri, 1983; Beers & Culp, 1990). Light influences foraging success of visual foragers by affecting prey encounter rates and search volumes (Vinyard & O'Brien, 1976; Beers & Culp, 1990), as well as the diel duration and depth to which prey can be captured (Dabrowski & Jewson, 1984).

One of the most widely distributed visual piscivores in fresh waters of North America is the largemouth bass (*Micropterus salmoides* L.). A number of studies have described its food habits (e.g. see references in Howick & O'Brien, 1983), but information describing its prey capture ability at different light levels is limited. Most studies indicate that feeding peaks at twilight (e.g. Olmsted, 1974), but other studies have found that feeding occurs mostly during daylight (Zweiacker & Summerfelt, 1974). Angling reports indicate that largemouth bass can also capture prey at night (Manns & Hope, 1992), but other evidence is suggestive of reduced foraging success at chronically low light intensities associated with high turbidity (Buck, 1956).

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Foraging ability of largemouth bass at different light levels has been inferred mostly from studies of gut contents (Olmsted, 1974; Zweiacker & Summerfelt, 1974) or of angling success relative to time of day (Manns & Hope, 1992). However, such analyses are limited in the information they provide about light conditions present at the time and depth of prey capture. The visual acuity of bass has been profitably explored in laboratory studies of reaction distance to bluegill (*Lepomis macrochirus* Rafinesque) (Howick & O'Brien, 1983) and crayfish (*Procambarus acutus* Girard) (Crowl, 1989) prey at different light levels. However, the relationship between reaction distance and actual prey capture is uncertain since reaction distance is only the first of four steps (detection, pursuit, attack, capture; Nyberg, 1971) necessary for success. Moreover, how laboratory light intensities compare to those encountered by largemouth bass in nature has not been established in previous studies.

In this study, the foraging success of largemouth bass was determined over a range of nighttime to daytime light intensities in the laboratory. These data were combined with (1) light intensities measured in the field over a diel cycle and (2) different light attenuation values, to estimate the relative foraging habitat available to largemouth bass in waters having differing light environments.

MATERIALS AND METHODS

FIELD LIGHT INTENSITIES

Ambient light intensity was measured with an underwater light meter (Holanov, 1980) sensitive over the range of starlight to daylight. The meter was fitted with a Wratten 106 gel filter to shift its peak spectral sensitivity (350 to 450 nm; range 300 to 650 nm) to more closely match that of the centrarchid eye (*c*. 525 nm; Bridges, 1964). Measurements were made at a position 2·5 cm below the water surface with the sensor pointing upward. The change in light intensity from sunlight to full moonlight was measured on 15 December 1983 under calm, cloud-free conditions at Pena Blanca Lake, a turbid (0·4 m Secchi depth) reservoir in Arizona, U.S.A. Starlight measurements were made during clear, moonless nights at Parker Canyon Lake and Alamo Lake, Arizona, during summer 1983. Measured light levels were converted from amps to lux following the method of Holanov (1980).

LABORATORY FEEDING EXPERIMENTS

Largemouth bass (270 to 330 mm total length, T.L.) were collected from local ponds. Fish were held separately in 300-l indoor tanks under a natural photoperiod for at least 1 month prior to experiments and conditioned to feed on mosquitofish (*Gambusia affinis* Baird and Girard). Feeding experiments were conducted under controlled light conditions in a circular pool, 1·7 m in diameter and 0·7 m deep, having a water depth of 42·5 cm. The pool was painted a light green colour to mimic the background of clear water. Since largemouth bass are 'ambush' predators (Helfman, 1981*a*), an opaque plexiglass sheet (38 × 46 cm) was positioned 19 cm off the bottom to provide overhead cover. The pool was enclosed with double layers of black plastic sheeting to eliminate outside light. When light was sufficient, fish were observed during experiments through a slit in a curtain surrounding the pool. Light intensity was varied by placing plexiglass filters of differing opacity into a slot on the lower side of a wooden box housing two 40 W 'Daylight' fluorescent bulbs suspended 1·2 m above the water surface. Light intensities were measured with the same underwater light meter used in the field at 2·5 cm below the

water surface and at the pool bottom (sensor pointing up). Bottom light measurements were *c.* 20% lower than surface measurements. Pool light intensity was obtained by averaging the measurements.

Foraging success of largemouth bass was examined at eight levels of light intensity ranging from low intensity daylight to total darkness. Each successive light intensity was *c.* an order of magnitude lower than the previous one (312, 28, 2·2, $2{\cdot}1 \times 10^{-1}$, $2{\cdot}6 \times 10^{-2}$, 3×10^{-3}, $2{\cdot}6 \times 10^{-4}$, and total darkness, 0 lx). Water temperatures of 22 to 25° C and a simulated natural photoperiod were maintained during experiments. Individual bass were acclimated to the test pool for 72 h before the start of feeding trials. During acclimation, test fish were held under a simulated natural photoperiod and fed mosquitofish daily via a 2·5 cm dia. plastic tube positioned 5 cm below the water surface. Those fish (two of 12 tested) that failed to acclimate to test conditions (i.e. failed to eat all prey within 5 min) were eliminated from further testing.

An experiment began by adjusting the light level for 4 h to allow light adaptation of the eyes. Ten mosquitofish (27 to 37 mm T.L.) were then added to the pool from outside the enclosure by carefully pouring prey and water from a 25 ml beaker into the feeding tube. The feeding tube was located at the opposite end of the tank from the overhead cover. Prey were added to the test pool when bass were positioned beneath the overhead cover and out of sight of the feeding tube. Bass position could be determined at light levels of 3×10^{-3} lx and above. The distance between the feeding tube and overhead cover (175 cm) was greater than the detection distance of bass (<100 cm) for the prey sizes and light intensities used in our experiments (Howick & O'Brien, 1983). Foraging success was measured by counting the number of prey eaten after 15 min; at 0 lx, an additional trial was run for 1 h. A bright light was turned on at the end of a trial and the pool area entered to stop bass from feeding and to count and remove remaining prey. Light filters were then removed to restore the normal day : night light cycle. For each fish, nine feeding trials were run in a sequence of progressively lower light levels over the course of a 15 to 18 day period. A 24 to 72 h lapse occurred between each trial. The same sequence of changes in light levels was used for each fish rather than randomly selecting light levels and fish for each trial in order to limit potential effects on feeding associated with repetitive handling. To test the possibility that disturbance, appetite, or other factors might have influenced feeding success over the course of a set of trials, an additional trial was conducted at ' daytime ' light intensities (312 lx) with five of the test fish the day following the final trial run at 0 lx. In all cases, bass ate 100% of prey offered, suggesting that foraging ability was not affected by the experimental protocol. A total of 10 series of feeding trials were run using naive bass.

The threshold for visual feeding was defined as the light intensity where 50% of the prey were eaten (see also Dabrowski, 1982). Previous studies of feeding success in visual fishes have generally shown a sigmoidal response with declining light, with feeding success sharply increasing or decreasing at light intensities above or below the inflection point of the curve (Holanov & Tash, 1978; Dabrowski, 1982).

INFLUENCE OF WATER CLARITY ON DEPTH OF WATER COLUMN AVAILABLE FOR FORAGING

The depth of the feeding threshold during a diel light cycle was determined using the Lambert–Beer light attenuation equation (Weinberg, 1976):

$$d = \log_e(I_o/I_d)/-k;$$

where d = depth of feeding threshold; I_o = ambient light intensity just below surface; I_d = light intensity of feeding threshold; and k = the light attenuation coefficient of the water. The threshold depth for feeding by largemouth bass in waters of different light attenuation properties was compared by using Secchi depths (D_{sd}) representative of a range of low to high water clarities (0·5, 2·0, and 4·0 m Secchi depth). Secchi depths were

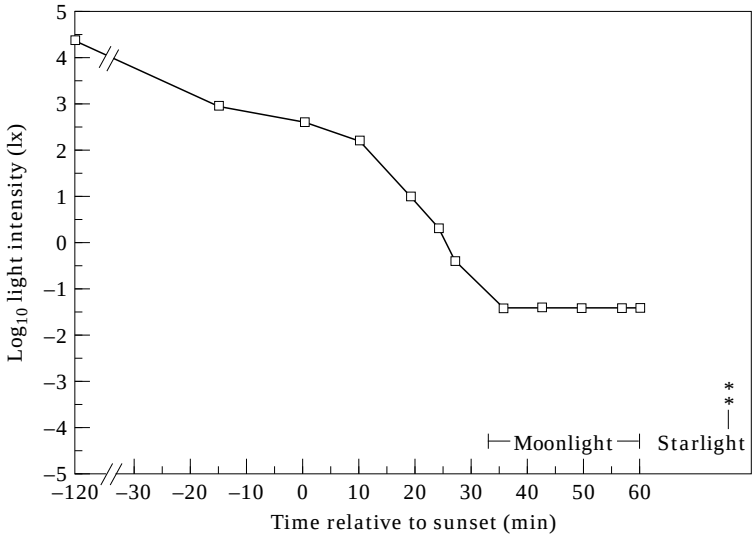

FIG. 1. Changes in light intensity during the transition from sunlight to full moonlight, Pena Blanca Lake, Arizona, U.S.A. Light intensity shown as time relative to sunset at 17.23 hours. Starlight light intensity (*) was measured at Parker Canyon and Alamo lakes, Arizona.

used as a convenient way to approximate light attenuation. Secchi depths were converted to light attenuation coefficients by the equation (Idso & Gilbert, 1974):

$$k = 1{\cdot}7/D_{sd}.$$

RESULTS

Subsurface light intensity in the field declined from $2{\cdot}5 \times 10^{4}$ lx at 2 h before sunset, to 4×10^{-2} lx at 1 h after sunset during a full moon, to 2×10^{-4} lx at starlight (Fig. 1).

Foraging success by largemouth bass in laboratory feeding trials averaged between 95 and 100% at light intensities ranging from low intensity daylight (312 lx) to full moonlight (3×10^{-3} lx) (Fig. 2). At these light levels, bass emerged from cover soon after prey were introduced and most prey were consumed within 1 to 2 min. Mean foraging success declined significantly to 62% (Tukey's $P<0{\cdot}001$), and was more variable, at starlight ($2{\cdot}6 \times 10^{-4}$ lx). Bass could not be observed at this light level, but the sounds of feeding noises (' popping ' at water surface, colliding with tank sides) occurring throughout the test period suggested a higher failure of pursuit and attack behaviours. No prey were captured, and no feeding noises heard, at 0 lx during 15 min feeding trials, but half of the fish tested consumed one prey each (2·5% mean foraging success) when the feeding trial was extended to 1 h. The threshold for visual feeding by bass (light intensity at 50% prey capture success) was estimated as $1{\cdot}6 \times 10^{-4}$ lx (Fig. 2).

Water clarity had a pronounced effect on the estimated depth of the water column available for feeding (Fig. 3). The maximum feeding depth ranged from 44 m at high (4 m Secchi depth) to 5·5 m at low (0·5 m Secchi depth) water clarity

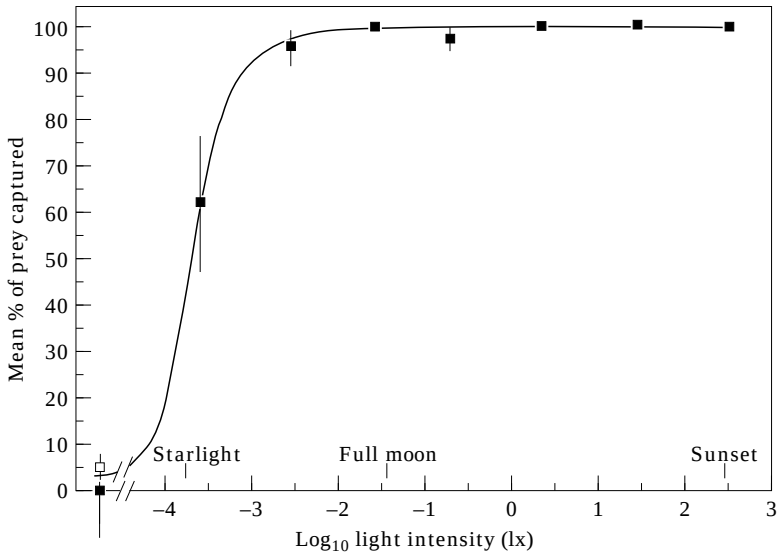

FIG. 2. Mean percentage of prey captured by largemouth bass in relation to light intensity. ■, 15 minute test periods; □, 1 h. Vertical bars represent ± 2 S.E. Curve fitted by eye. Approximate light intensities of starlight, full moon, and sunset are also indicated.

during daylight and from 13 m to 1·6 m during moonlight. Light intensity during starlight rapidly attenuated to a level below the feeding threshold within 0·5 m of the surface at all water clarities.

The average depth of the water column available for feeding by largemouth bass over a diel period under different water clarities was estimated by averaging hourly feeding depth thresholds for each Secchi depth. In this calculation, 15 m was considered as the maximum depth of feeding since largemouth bass are rarely found below this depth (Wanjala *et al.*, 1986). The average diel feeding depth at 0·5 m Secchi depth (3·8 m) averaged 67 and 75% less than that at Secchi depths of 2·0 (11·1 m) and 4·0 m (14·1 m).

DISCUSSION

In our experiments, foraging success of largemouth bass was undiminished at light intensities ranging from low intensity daylight to moonlight. Significant declines in foraging success occurred at light intensities equivalent to starlight and below. In contrast, Howick & O'Brien (1983) found that the detection distance of largemouth bass to bluegill prey declined significantly at twilight light intensities (1·49 lx) when tested over the range of $3{\cdot}3 \times 10^{3}$ to $1{\cdot}95 \times 10^{-1}$ lx. For comparison, using 1·49 lx as the prey detection threshold would result in a *c.* 50% reduction in the estimated foraging habitat available (Fig. 3). Large differences in the light intensity threshold for detection and for capture of prey have also been noted for other fishes (Blaxter, 1970; Confer *et al.*, 1978). We suggest that the two thresholds likely frame a range of light intensities that limit foraging ability by largemouth bass: the upper threshold where detection distance is first reduced, and the lower threshold where it becomes so small that pursuit and attack behaviours often fail.

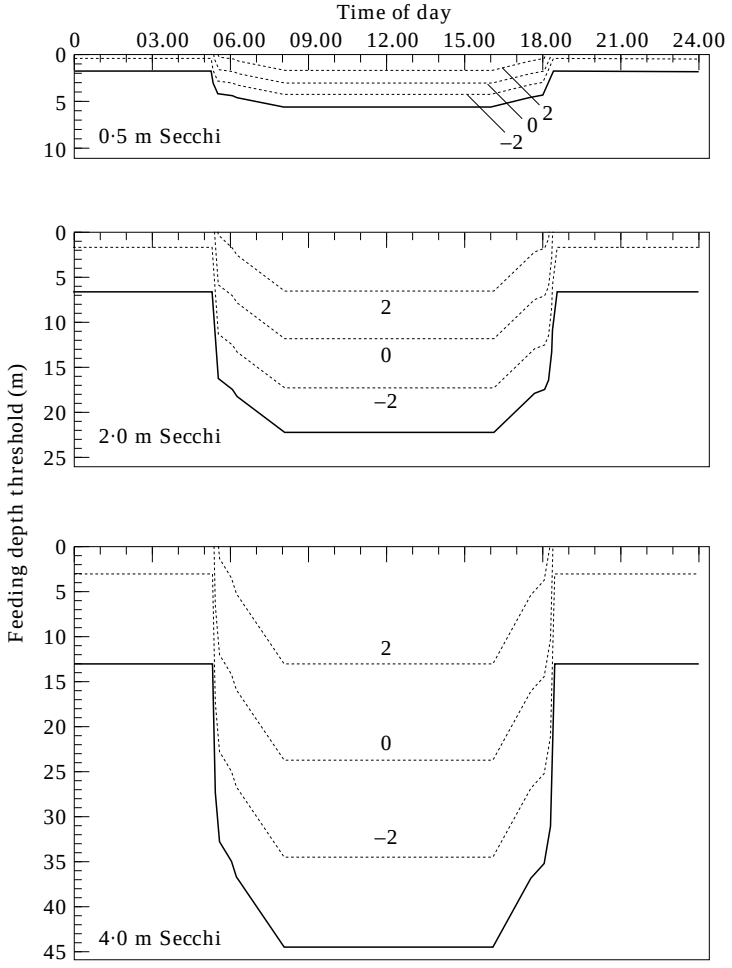

FIG. 3. Estimated maximum feeding depths (solid lines) for largemouth bass over a diel cycle (12 h light : 12 h dark; sunrise, 06.00 hours; sunset, 18.00 hours) during a full moon at water clarities of 0·5, 2·0, and 4·0 m Secchi depths. Isolumes ($\log_{10}$ lx) are shown as dashed lines.

A comparison of the foraging abilities of largemouth bass with other visual piscivores cannot be made due to a lack of similar data from other fishes. However, their ability to feed at starlight light levels in the laboratory was surprising given that they do not possess a tapetum as do walleye (*Stizostedion vitreum* Mitchill), a piscivore well known for its adaptations to foraging in dim light (Ryder, 1977). The ability of largemouth bass to capture prey in total darkness (this study) and in the absence of vision (Janzow, 1978), although limited, does suggest that non-visual senses may aid in detecting prey in low light.

Although we found that bass are able to feed over a wide range of light intensities in the laboratory, feeding in nature usually peaks during twilight (Olmsted, 1974), despite the rapid decline in the maximum depth for feeding (Fig. 3) and the reduction in reaction distance (Howick & O'Brien, 1983) that

occurs at this light level. A likely explanation for this phenomenon is that at twilight light intensities largemouth bass can detect prey before prey can detect them, while the advantage is reversed at higher light intensities (Howick & O'Brien, 1983). At twilight, predators gain a further visual advantage over their prey by attacking from below, a behaviour observed in many piscivores (Hobson, 1979), including largemouth bass (Wanjala *et al.*, 1986). Diel movements of largemouth bass in lakes appear to follow isolumes that would prolong the duration of this visual advantage (Wanjala *et al.*, 1986).

Reduced foraging at high light intensities has been commonly observed in fishes (e.g. Hobson, 1979; Cerri, 1983; Beers & Culp, 1990). This response is thought to be the result of more effective predator avoidance by prey (Cerri, 1983) and higher predation risk associated with higher light intensities (Beers & Culp, 1990). During the day, largemouth bass are typically found near cover (Helfman, 1981*a*; Wanjala *et al.*, 1986) which shields them from high light intensities and provides a concealed vantage point for occasionally ambushing prey (Helfman, 1981*b*). The absence of a decline in foraging by bass at higher light intensities in our study was probably due to our test pool design (lack of prey cover) and experimental protocol (introduction of prey via the feeding tube) which limited normal predator avoidance behaviour of prey.

The more twilight-like light intensities near the surface of waters having low water clarity (Fig. 3) would seem to provide optimal conditions for largemouth bass foraging. However, any visual advantage is probably offset by a reduction in the visual contrast of prey from increased backscattering of light and by a diminished difference in downwelling and upwelling light intensity in more turbid waters (Hemmings, 1966). Previous studies have shown that even small decreases in water clarity can affect foraging success of fish by reducing prey abundance (Lloyd *et al.*, 1987) and individual search volumes (Confer *et al.*, 1978; Crowl, 1989). Our results suggest that water clarities less than 0·5 m Secchi depth could reduce bass foraging success by sharply curtailing the area of the water column available for prey search.

Our results were obtained in laboratory conditions favouring prey capture by largemouth bass. Differences in prey species and size, cover availability, predation risk, and spectral composition of light have also been shown to affect foraging success in the laboratory (Cerri, 1983; Howick & O'Brien, 1983; Dabrowski & Jewson, 1984; Crowl, 1989) and would undoubtedly alter the results presented here. Nonetheless, the findings illustrate how differences in water clarity can significantly modify the amount of foraging habitat available to visual piscivores such as largemouth bass. Similarly, Dabrowski & Jewson (1984) showed that changes in light penetration could potentially influence survival and growth of the planktivore *Coregonus pollan* Thompson [now *Coregonus autumnalis* (Pallas)] by affecting the time and depth available for feeding. These findings illustrate how differences in the light environment can have important ramifications for predator–prey interactions.

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