Effects of crayfish size, orientation, and movement on the reactive distance of largemouth bass foraging in clear and turbid water

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Abstract

Laboratory experiments were performed in clear and turbid water to determine the effects of prey size, orientation, and movement on the reactive distance of largemouth bass *(Micropterus salmoides)* when feeding on crayfish *(Procambarus acutus)*. In clear water, the reactive distance increased linearly with an increase in prey size, and prey movement resulted in a significant increase in the reactive distance. Prey orientation (head-on versus perpendicular) did not change the reactive distances. In moderately turbid water, the reactive distance did not increase with increased prey size, and prey movement did not result in any changes in the reactive distance. The absence of any effects of prey orientation in clear water or prey movement in turbid water is inconsistent with results from studies using different species (primarily planktivorous fish). I propose that largemouth bass change their foraging tactics as prey visibility changes. When prey are highly visible (low turbidity), predators attack (react) only after prey recognition, which is based on multiple cues such as prey size (length, width) and movement. When prey are less visible (high turbidity), predators attack immediately upon initial prey sighting, which does not depend on prey size or movement.

Introduction

Reactive distance is defined as the greatest distance at which a predator can locate a prey (Holling, 1959). This distance and its relationship to prey encounter rates have been used as a measure of prey accessibility and have been useful in explaining the size-selective nature of predation (Ware, 1971; Ware, 1973; Werner & Hall, 1974; Vinyard & O'Brien, 1976; Gerritsen & Strickler, 1977; Eggers, 1977; O'Brien & Vinyard, 1978; Howick & O'Brien, 1983). This approach has been especially useful in studies that involve planktivorous fish feeding on zooplankton (Con-fer & Blades, 1975; see references in O'Brien, 1987), as well as for benthivores and piscivores (Ware, 1973; Moore & Moore, 1976; Howick & O'Brien, 1983; Holmes & Gibson, 1986).

The reactive distance of fish increases linearly with prey size in situations of high visibility – low turbidity and high light (Werner & Hall, 1974; Confer & Blades, 1975; Howick & O'Brien, 1983). Prey movement results in a significantly higher reactive distance in clear water (Moore & Moore, 1976; Wright & O'Brien, 1982; Howick & O'Brien, 1983). In turbid water (or low light), the reactive distance becomes independent of prey size (Moore & Moore, 1976; Vinyard & O'Brien,

1976). All of these results have been explained using the theory of contrast perception initiated by Ware (1971) and expanded by Eggers (1977), in which the encounter rate of prey depends on mechanical constraints associated with visual predators (Ware, 1973). That is, when the inherent contrast of prey is high (high light or low turbidity), the distance at which prey are sighted is proportional to the size and activity of the prey. When inherent prey contrast is low (low light or high turbidity), the reactive distance is independent of prey size (but still depends on prey activity).

In this paper, I present an analyis of the relationship between a visual predator, the largemouth bass, and a relatively large, benthic (bottom-dwelling) prey, the crayfish. The effects of prey size, orientation, and movement, as well as turbidity levels, on predator recognition of prey are investigated.

Materials and methods

Largemouth bass (280–300 mm total length) were collected in August and September of 1982 by electroshocking in two Oklahoma reservoirs – Draper Lake (a turbid reservoir; 19 JTU) and Arbuckle Lake (a clear reservoir; 3 JTU). Fish were kept in large holding tanks at 25 C and conditioned to feed in the laboratory for several weeks. Feeding experiments were conducted in rectangular experimental tanks (5 m × 0.75 m). Fish were placed individually in compartments at the ends of the experimental tanks which were equipped with opaque sliding doors. Fish were then trained to leave the compartment when the door was opened and search for crayfish prey.

Crayfish, collected from small ponds, were held in large tanks and fed lettuce and small fish. Standard morphometric measurements (carapace length, total length, and chelae length) were recorded for all crayfish immediately prior to the beginning of experiments.

The reactive distance of largemouth bass to crayfish was determined by placing an individual crayfish in the tank, releasing a fish that had been starved for 24 h from a compartment, and noting

a change in bass swimming speed, orientation, or eye fixation on the prey (Howick, 1981). The size of the crayfish used for any particular trial was chosen randomly; crayfish ranged from 16.6 to 28.5 mm (carapace length, to the nearest 0.1 mm). As a control for reaction behaviors, some trials (also chosen randomly) were run without a crayfish being placed into the tanks. To insure that the fish did not sight the crayfish from different heights (i.e. looking down versus looking straight across at the crayfish), the water level in the tank was maintained at 8 cm, a height which insured that all of the fish were swimming in contact with the tank bottom.

To determine the effects of prey size on the reactive distance, crayfish were immobilized in an ice bath and placed in the tanks with their bodies oriented perpendicular to the line of sight of the bass. In a second series of experiments, immobilized crayfish were placed into the tank at a head-on orientation to the approach path of the fish. Finally, crayfish were placed into the tanks and allowed to move freely. When the crayfish had moved 10 cm in any direction, the compartment door was opened to release a bass and the reactive distance determined. Comparison of these distances with those observed using immobilized crayfish elucidated the effects of crayfish movement on the reactive distance of largemouth bass.

For each fish, at least 25 feeding trials were run for each treatment combination. In all trials, crayfish were immediately consumed by the fish following a pursuit. In all cases, light and temperature were maintained at 200 lux and 25 C, respectively. All of these experiments were performed first in clear water (1–3 JTU), and then repeated in turbid water (17–19 JTU). Turbidity was induced by suspending fine particles of bentonite clay in the water. In the first experiment (stationary crayfish, clear water), seven fish were used. Because there were no differences between fish (see results), only four of these fish were used in the additional trials.

Finally, to determine the effects turbidity had on prey recognition, 40 feeding trials were run (in clear and turbid water) with a rectangular stone

(roughly 'crayfish shaped') offered as the prey. The number of trials that a fish reacted to the stone was recorded in both clear and turbid water. These trials were randomly interspersed with trials in which a crayfish was offered as the prey.

Statistical analyses were performed using the SAS statistical package (SAS Institute Inc., 1982). Because prey sizes were not grouped into discrete prey sizes, all comparisons of Y-intercepts and slopes between lines were performed using analysis of covariance.

Results

The effect of prey size on reactive distance was determined individually for seven largemouth bass using nonmoving crayfish at perpendicular orientation in clear water. For all fish, regression analyses indicated a significant, positive linear relationship between the reactive distance and crayfish size (Fig. 1). Because there were no significant differences among regression lines for any of the fish (ANCOVA; $F = 0.84$, $P = 0.54$), data from all fish were pooled; the resulting equation of the line was $Y = 35.3 + 3.24X$ (Table 1) where Y is reactive distance and X is crayfish carapace length. As measured by analysis of covariance, reactive distances did not change as a result of time $(P = 0.45)$. Fish did not increase their reactive distances as a result of experience. In trials run without a crayfish in the tank, fish did not exhibit any reaction behaviors. Thus, the behaviors used to measure a reaction were entirely due to a fish seeing and reacting to a prey item. Additional controls run in the dark, with luminescent tags on the fish, also showed that olfaction was not an influence in reactive distance. To determine the precision of the measurements, 41 trials were run in clear water with two observers simultaneously determining the reactive distance. The average difference between the observers was 3.4 cm. Thus, measurement error had no effect on the interpretation of the data. The relationship between prey size and reactive distance for prey at a head-on orientation was determined for four fish and as above, all fish showed significant, positive relationships between reactive distance and prey size (Table 1). There were no significant differences among the fish (ANCOVA; $F = 0.02$, $P = 0.99$) and data were pooled (Table 1). To test the effect of prey orientation on reactive distance, an analysis of covariance was performed on the pooled data for crayfish at perpendicular and head-on orientations. No significant differences in Y-intercepts or slopes between perpendicular versus head-on orientation were found (Table 2). Thus, prey orientation had no effect on the relationship between reactive distance and crayfish size in clear water. The combined body width and chelae width accounted for only 40% of the total body length of crayfish. This, this does not explain the lack of difference of reactive distances exhibited

Table 1. Regression analyses of reactive distance on carapace length for pooled data (all fish within a treatment, pooled).

Treatment	N	P-value	R^2	Equation
Clear water				
Stationary crayfish				
Perpendicular	554	0.0001	0.43	$35.3 + 3.24X$
Head on	198	0.0001	0.41	$34.7 + 3.22X$
Moving crayfish	174	0.0001	0.25	$81.5 + 4.75X$
Turbid water				
Stationary crayfish				
Perpendicular	125	0.5791	0.00	$29.0 + 0.06X$
Moving crayfish	83	0.7481	0.00	$29.5 + 0.07X$

Table 2. ANCOVAs of pooled data comparing slopes and Y-intercepts between treatments.

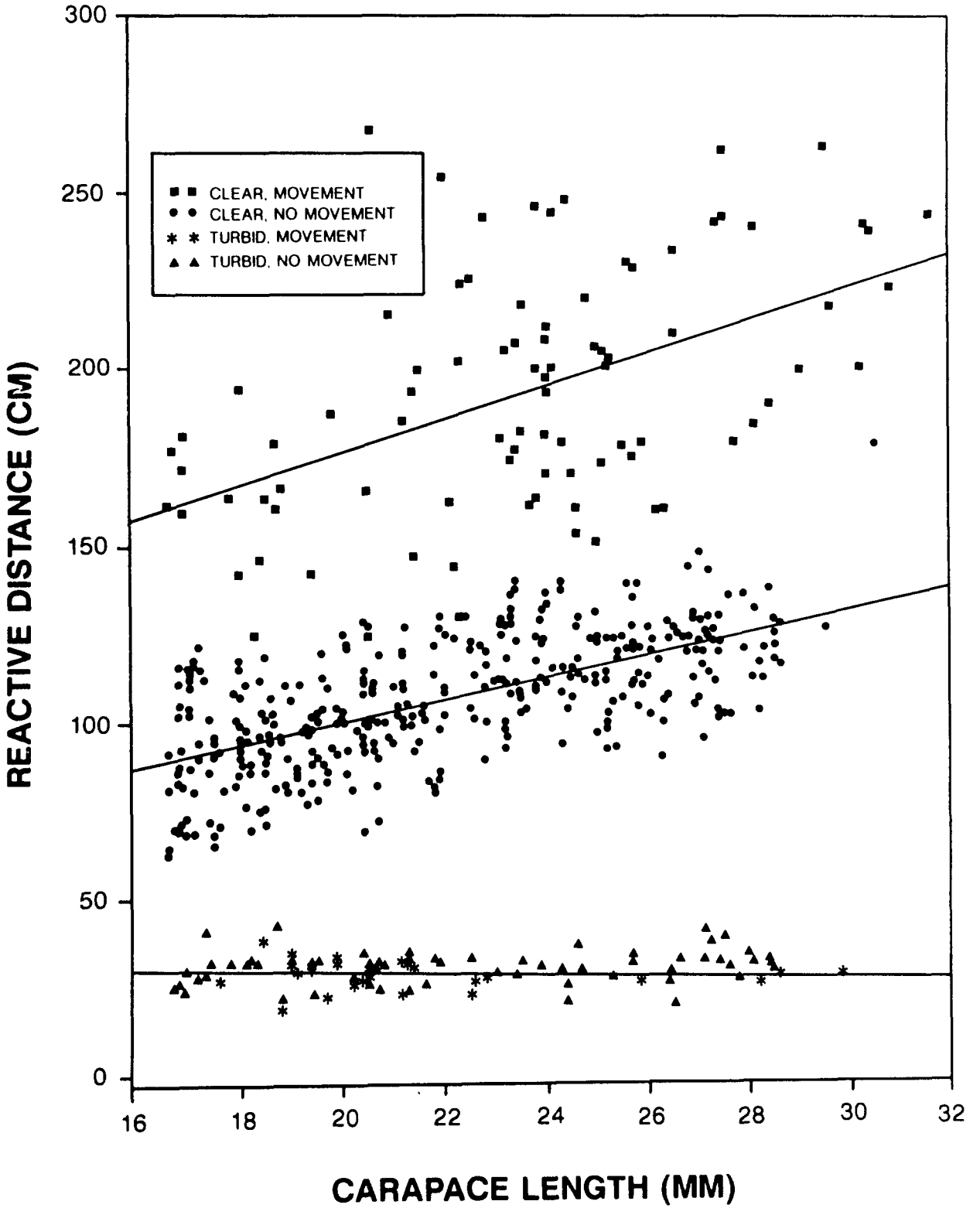| Treatments being compared	F-value	P-value
Clear water		
stationary crayfish		
perpendicular vs head-on	0.02	0.9452
stationary vs moving	13.02	0.0003
Turbid water		
stationary vs moving	1.82	0.1564
Clear stationary vs		
turbid stationary	90.14	0.0001
Clear moving vs		
turbid moving	107.86	0.0001

Fig. 1. Association of reactive distance and crayfish size with: crayfish moving and nonmoving in clear and turbid water. Each line represents pooled data for that treatment.

for head-on versus perpendicular oriented crayfish. Additionally, reactive distance trials were run with crayfish which had only one or no chelae. In all cases, the reactive distances exhibited for these crayfish did not differ from those exhibited for crayfish with both chelae.

Four fish were used to determine the relationship between reactive distance and prey size for moving crayfish. All fish exhibited the same positive, linear relationship to prey size and were not significantly different from each other. The comparison between moving and nonmoving prey in clear water did, however, reveal significant differences (Fig. 1). Both the Y-intercept ($P < 0.001$) and the slope ($P < 0.001$) differed, with both being higher for moving prey (Table 2). The equation of the line describing the relationship between reactive distance and crayfish size (with crayfish moving) is $Y = 81.47 + 4.75X$.

Four fish were used to determine the relationship between reactive distance and prey size in turbid water (17–19 JTU). Regression analyses on all fish resulted in a nonsignificant relationship between reactive distance and prey size with the reactive distance remaining at 30 cm irrespective of prey size (Fig. 1). All data were pooled (Table 1) and the equation of the regression line was determined ($Y = 29.03 + 0.06X$). There was a significant difference ($P < 0.001$) between the regression lines for nonmoving prey in clear versus turbid water (Table 2; Fig. 1).

Four fish were used to determine the effects of high turbidity on the reactive distance for moving prey. Regression analyses resulted in nonsignificant linear relationships between prey size and reactive distance for all fish ($P > 0.5$ in all cases). There were no significant differences between any of the fish (ANCOVA; $F = 1.82$, $P = 0.16$) and comparisons of moving and nonmoving prey in turbid water (Fig. 1) resulted in nonsignificant differences in Y-intercepts or slopes of regression lines for pooled data (Table 2).

Turbidity had a marked effect on prey recognition. In turbid water, 38 out of 40 trials resulted in fish reacting to a stone placed into the tank as prey. In most cases, fish attacked and actually grabbed the stone. In clear water, fish never attacked the stone.

Discussion

Largemouth bass react to crayfish in a linearly-dependent fashion in clear water: As crayfish size increases, so does the reactive distance. These results are consistent with those obtained in previous studies with planktivores (Werner & Hall, 1974; Vinyard & O'Brien, 1976; Confer et al., 1978; Kettle & O'Brien, 1978; Howick & O'Brien, 1983) and have been explained using the theory of contrast perception (Ware, 1971; Eggers, 1977). This theory suggests that if the inherent contrast of the object is high (as in clear water) the reactive distance is proportional to the length of the prey object (Eggers, 1977), because the predator can see larger prey from a greater distance.

The relationship between the reactive distance and prey size will only remain proportional if the shape of the object is constant (Eggers, 1977). Fish are expected to discriminate between prey objects on the basis of prey orientation, as well as size and shape (Ingle, 1971). Supporting evidence for this discrimination has been provided by Wright and O'Brien (1982) who found that the relationship between the reactive distance of white crappie *(Pomoxis annularis)* and phantom midge larvae *(Chaoborus)* was altered by the orientation of *Chaoborus* and by Holmes and Gibson (1986) for juvenile turbot *(Scophthalmus maximus)* feeding on small crustaceans. For largemouth bass feeding on benthic prey items such as crayfish, one would expect this same alteration in the relationship between the reactive distance and prey size to occur with different prey orientations. My results, however, suggest that the relationship between the reactive distance and prey size is independent of prey orientation. This independence may occur because of the effect of perceptual constancy (Thouless, 1972) in which the orientation of an object may be changed with the perceived image remaining relatively constant. For largemouth bass preying on large, opaque crayfish, prey orientation may not affect the perceived prey size resulting in no effect on reactive distances. The difference between a planktivorous fish and a fish that eats relatively large, opaque

prey items may be due to the types of cues used by the different predators for prey detection. Planktivores must rely on high-contrast structures of their zooplankton prey (such as eye pigments or egg yolk pigments for females) due to the relative invisibility of most zooplankton (Zaret, 1975; Tucker & Woolpy, 1984). These pigmented structures become visible to different degrees depending on the orientation of the prey item. Fish that feed on relatively large, opaque prey items can rely on many cues such as prey length and height, as well as more complex cues, such as chelae, legs, and antennae (for crayfish). The relative visibility of these kinds of cues is independent of prey orientation.

Additionally, because of their morphology, even when a largemouth bass is in contact with the substrate, its eyes may be 25 mm above the substrate. This may allow the fish some vertical reference. Furthermore, because largemouth bass are not restricted to the substrate when searching for prey, their typical encounter with benthic prey (e.g. crayfish) will generally be from a 'looking down' perspective, that will eliminate any orientation effect of the prey.

Prey movement resulted in a significant increase in the reactive distance of the fish to crayfish in clear water. This finding is consistent with other empirical data (Ware, 1973; Wright & O'Brien, 1982; Howick & O'Brien, 1983) and can be explained on the basis of the area of retinal stimulation (Eggers, 1977). My results are different with respect to the manner in which the reactive distance increases. Ware (1973) postulated that prey movement was both an additive and constant effect to reactive distances recorded with nonmoving prey. The slopes of the two lines are not expectedto be different. My findings show that the slopes of regression lines for moving versus nonmoving prey are significantly different (Fig. 1), with prey movement being progressively more important as prey size increases. Wright & O'Brien (1982) also found that the slope of the reactive distance line for moving prey was significantly greater than the slope of the line for the nonmoving prey for white crappie preying on *Chaoborus*. Their explanation that large

zooplankton swim proportionately faster than smaller zooplankton works equally well for crayfish. That is, larger crayfish move at a faster rate than do smaller crayfish.

At increased turbidity levels (17–19 JTU), largemouth bass reactive distances are independent of crayfish size (carapace length). These results are consistent with predictions made by Ware (1971) and Eggers (1977). When turbidity levels are high (or light levels low) the inherent contrast of the prey object is low and the reactive or sighting distances are independent of prey size or shape. Contrary to theoretical predictions, prey movement did not result in an increase in the contrast threshold (Eggers, 1977) as it did in clear water; the Y-intercept did not increase. The lack of difference in the reactive distance due to prey movement (in turbid water) or prey orientation (in clear water) represents inconsistencies with previous findings and theoretical predictions.

Visual predators, such as largemouth bass, which consume few, relatively large prey, may alter their foraging strategy depending on the relative visibility (reactive distance) of prey. In clear water, reactive distance may reflect the distance at which the predator 'recognizes' the prey rather than the maximum sighting distance of a prey as has been commonly assumed (Ware, 1972; Werner & Hall, 1974; Confer & Blades, 1975). This recognition distance increases as a function of prey size. Prey movement in clear water may not increase the reactive distance because of an increase in the retinal area stimulated but because movement is used as a cue that the object is a possible prey item. When a predator is searching for prey items, detected movement acts as a recognition stimulus and elicits an immediate response from the predator. The finding that fish did not react to a rectangular stone when offered as a prey item in clear water is consistent with this explanation.

Conversely, poor visibility (due to high turbidity or low light) may trigger an immediate reaction by predators at the first sighting of any prey item. In this study, fish almost always attacked a stone, offered as a prey in turbid water. Such a foraging tactic would result in reactive distances being

independent of prey size or movement and may be adaptive in situations where visual encounter of prey items is greatly reduced. In these situations, predators can increase the number of possible prey captures by reacting to any initial prey sighting. This kind of tactic is not necessary under conditions of high prey visibility because prey capture opportunities will be much higher due to increased encounter rates. In these high-encounter situations, reacting at the time of initial prey recognition and not at first sighting would be more efficient energetically.

This switching tactic as a function of water clarity differs from predators which must encounter and consume large numbers of small prey (such as planktivorous fish). In these situations, predators must rely on maximum sighting distances alone to insure a high enough encounter rate to sustain their biomass, independent of water clarity. Evidence for this was provided by Gardner (1981), who found no difference in selectivity for *Daphnia* by bluegill between clear and turbid water. Turbidity did not alter the feeding tactics of planktivorous bluegill. For predators which feed on relatively few, large prey items, initiating an attack only after recognition in conditions of high visibility (hence high encounter rates) may decrease their own risk to other predators while increasing prey capture efficiencies. Alternatively, in conditions of low prey encounter rates (high turbidity, low light), initiating an attack upon initial sighting may be required to insure sufficient prey encounters.

The results discussed here were obtained under controlled, simplified laboratory conditions and the relevance to the predation cycle under field conditions cannot be known. The information is relevant to our understanding of the roles of prey complex cues in predator-prey interactions and how these interactions are modified by turbidity. Finally, the results presented here have suggested a number of question that need to be answered if we are to understand how predators feeding on relatively large, complex prey obtain their diets.

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