APPARENT SIZE AS THE DETERMINANT OF PREY SELECTION BY BLUEGILL SUNFISH (*LEPOMIS MACROCHIRUS*)[1]

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Abstract. Although it is known that visual predation by planktivorous fish tends to be size selective, the mechanism by which fish select their prey has not previously been described. Experiments in which bluegill sunfish (*Lepomis macrochirus*) were given a binary choice between prey of different sizes presented at different distances showed the fish selected the prey that appeared largest, either because of its actual size or its proximity to the fish. This paper incorporates this mechanism of prey selection by apparent size into a model of bluegill predation. According to the model, bluegill, in choosing the apparently largest prey under all conditions, alter their diet composition depending upon the abundance of prey. When prey are abundant, bluegill predominantly select prey of the largest size class available because these have the greatest probability of appearing largest; as large prey become scarce and smaller prey have a greater chance of appearing large, the fish tend to eat more prey from smaller size classes. When the model is tested against data from published fish-feeding experiments, the predicted size ratios of prey eaten correlate accurately with the observed ratios and numbers of prey eaten.

Key words: Daphnia; *fish foraging; food selection;* Lepomis; *model; plankton; predation; predator tactics; size selection.*

INTRODUCTION

Much recent attention has focused on the study of the feeding patterns of freshwater planktivorous fish. It has been clearly shown that many species of planktivorous fish feed on the larger species of zooplankton out of proportion to the density of these prey in the environment (cf, Hrbacek et al. 1961, Brooks and Dodson 1965, Brooks 1968, Hall et al. 1970, Nilsson and Pejler 1973, O'Brien 1975). This fact has served as the impetus for considerable speculation concerning the theoretical implications of size-selective predation.

Most notably, two recent models have been proposed to explain the foraging strategy of planktivorous fish. One, that of Confer and Blades (1975), accurately describes the feeding of *Lepomis gibbosus* on *Daphnia* under situations of very low prey densities using the hypothesis that encounter frequency is the prime determinant of prey selection. The other, put forth by Werner and Hall (1974), also proposes the mechanism of encounter frequency, but enlarges the concept to suggest that bluegill eat prey of different sizes depending upon the densities of those sizes in the perceptual sphere of the fish; that is, the ratio of prey size classes within the fish's reactive volume will be reproduced in the fish's gut. Werner and Hall conclude from their analyses that

this foraging strategy optimizes the fishes' energy and time allocation.

Neither of these papers provides a statement of the physiological mechanism of planktivore prey selection. When prey densities are very low, as in the situation described by Confer and Blades, no mechanism is necessary; a fish eats whatever prey it can find and tends to eat more large prey, or more prey offering greater contrast with the surrounding environment (Zaret and Kerfoot 1975), because it can see them over greater distances. When prey densities are increased, however, fish can locate more than one prey and must make a choice; the means by which they make that choice becomes important to an understanding of foraging patterns. Under these conditions, simply stating that fish eat prey as they are encountered is not a satisfactory explanation for bluegill's arriving at what Werner and Hall (1974) term an "optimal diet breadth." Furthermore, Werner and Hall's analysis claims that this optimal breadth of diet alters with an alteration in prey densities, yet they offer no obvious mechanism for the fishes' selection of prey and instead explain the prevalence of large prey in the diet as resulting simply from the fishes' ability to see more of them.

Our hypothesis is that bluegill select the prey that, either by virtue of absolute size or proximity to the fish, appears to be largest at the instant the fish initiates its search for food. This paper presents experimental evidence for this hypothesis and incorporates the idea of selection based on apparent size into a model whose predictions correspond very
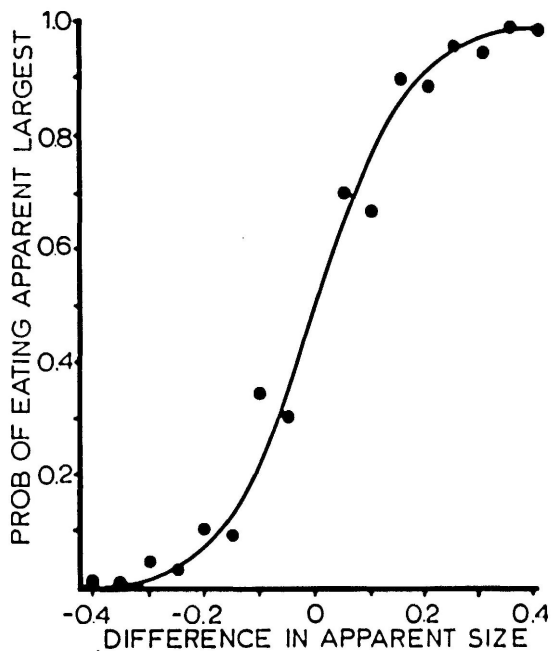
FIG. 1. Plot of binary choice experiments showing probability of eating the apparently larger prey as a function of the apparent size. The line is a hyperbolic tangent function fit to the data. The line and data below 0.5 are the inverse of those above.

TABLE 1. Bluegill sunfish choice of prey according to difference in apparent size

Difference in apparent size of prey (arctan)	No. of times chosen	
	Apparently larger	Apparently smaller
0.01°–0.10°	61	35
0.11°–0.20°	39	5
0.21°–0.30°	29	2
0.31°–0.40°	13	0
0.41°–0.50°	9	3
0.51°–0.60°	6	0
0.61°–0.70°	3	0
0.71°–0.80°	4	1
0.81°–0.90°	2	0
0.91°–1.00°	2	0
1.01°–1.10°	2	0
1.11°–1.20°	1	0
1.21°+	3	0

closely with the experimental fish feeding data reported by Werner and Hall (1974). We believe the quantification of this explanatory mechanism produces a mathematical expression of bluegill predation that is more accurate over a wider range of prey densities than any previously proposed.

PREY SELECTION EXPERIMENTS

A series of more than 300 experiments was performed to elucidate the mechanism by which sunfish make a selection between different sized prey.

Method

Prey selection experiments were performed in a long Plexiglas® aquarium (2.5 m × 20 cm × 15 cm deep, illuminated by two 40-W fluorescent tubes suspended 42 cm above the water surface). One bluegill at a time was offered a choice between two different sized *Daphnia magna* with each individual prey at variable distances from the fish. With the fish behind a screen, two *D. magna* individuals of known size, varying from 1 mm to 3.5 mm, were introduced at distances from the fish of 6 cm to 48 cm, always within the reactive distance of the particular prey size. The fish was then allowed to swim through a small opening in the screen. At the moment the fish began its pursuit, both the prey chosen and the distance between the fish and both

prey were recorded. To determine which prey appeared larger to the fish, the apparent size of each of the two prey was calculated by dividing the height of each prey by its distance from the fish and taking the arc tangent of the result. Thus, if a prey 1 mm in size was 10 cm from the fish and another prey 2 mm in size was 20 cm from the fish, the arc tangents of both prey would be 0.57° and there would be no difference in apparent size. If, on the other hand, the 1 mm prey was presented at 7 cm from the fish, its arc tangent would be 0.82° and the fish would see it as larger than the 2 mm prey 20 cm away.

Results

Bluegill sunfish offered a choice between two prey differing in apparent size by an arc tangent of at least 0.2° overwhelmingly selected that prey that appeared larger (Fig. 1 and Table 1). Where the difference in apparent size was smaller, there was greater variability. When the apparently smaller prey was selected, chi-square tests reveal no selection for either absolutely larger or smaller prey ($\chi^2 = 0.95$; df = 1). Likewise, the choices of the apparently larger were not predominantly situations in which that prey was also the absolutely larger ($\chi^2 = 0.03$; df = 1). Instead, the fish chose consistently on the basis of apparent size with variability occurring when the differences in apparent size were small. At no time during these experiments did a fish begin pursuit of one prey and then change toward another.

THE MODEL

The model is based on the hypothesis that bluegill sunfish, when faced with an array of otherwise similar prey of different sizes, select that prey that appears largest at the moment the fish decides to feed. To express the consequences of this hypothesis mathematically, one must calculate the various prob-

abilities of prey of given sizes appearing largest to a sunfish at different prey densities. In doing so, we made several assumptions: (1) The prey are distributed randomly; thus, the number of prey in random samples of any specified volume follows a binomial distribution. (2) The size classes of prey are independently distributed so that the probability of mutual occurrence (or absence) is the product of the separate probabilities of occurrence or absence for each prey size. (3) The fish is exposed to the average conditions in the entire environment without consideration of local deviations in density of certain prey sizes. (4) In accordance with the assumption of Werner and Hall (1974) we developed the model on the basis of a spherical visual field; however, simulations were also run assuming a hemispherical field, which we believe to be a more accurate representation. (5) For the purposes of comparison to the data of Werner and Hall (1974), the "fish" was assumed to be at the mid-depth of the pool and located such that its largest perceptual volume was not intersected by the side of the pool.

To determine the probability of a fish's eating a member of a given prey size class, the probability of at least one individual of that size class occurring at a given distance from the predator must first be calculated. This is then multiplied by the probability of no prey of any other size class occurring close enough to the predator so as to appear larger than the prey being considered. The resulting product is then integrated over all distances from zero to the upper limit of reactive distance for that prey size. The integrals for each size class are then converted to probabilities by summing integrals for all size classes and dividing each by the sum. This yields an estimate of the probability of a prey of a specific size class being eaten. This probability is compared to a random number between 0 and 1 drawn from a uniform distribution. The larger the probability the greater the chance of a prey's being selected and removed from that size class. The entire process is then repeated at the new densities and size class distributions. We developed a computer program to carry out these calculations using data reported in Werner and Hall (1974) and ancillary data made available to us by the authors.

For our simulations we assumed a pool depth of 14 cm and radius of 65 cm for experiments using 25 and 50 individuals per each of four size classes and a pool depth of 28 cm and radius of 85 cm for all other experiments (D. J. Hall, *personal communication*). We then used the initial prey densities of the various prey sizes and computed the probabilities of each size class being eaten. The probability of at least one prey (equals one minus the probability of zero prey) of the ith size class oc-
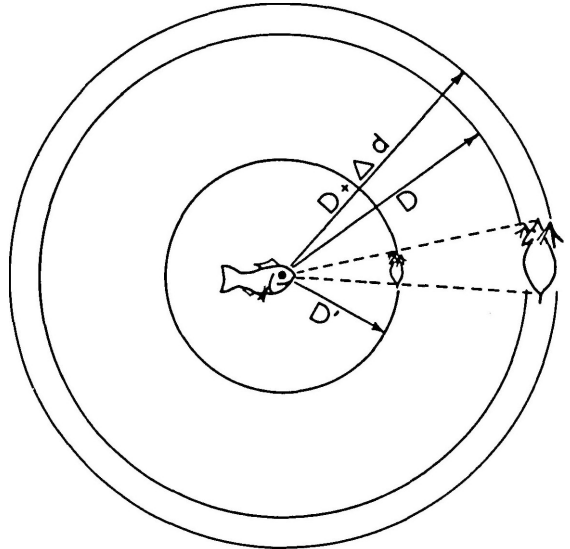

FIG. 2. Illustration of the parameters considered in the model. Probability of occurrence of one or more prey of a given size class within a shell of width Δd is first computed, then probability of no prey of any other size class appearing larger is computed based on the distance D'. D' is determined for each of the other prey size classes as the distance at which their apparent size becomes larger. These probabilities are then multiplied and the product integrated over distances from zero to the upper limit of the reactive distance for that prey size. The integrals are then converted to an estimate of the probability of eating a prey of the given size by summing integrals for each of the size classes and dividing by the sum.

curring at a particular distance was calculated by computing the probability of this prey's occurring within a shell of width Δd (1.0 cm) at an average distance of $D + \Delta d/2$ from the predator according to the equations given below (see Fig. 2 for diagram of distances):

The volume of the shell of width Δd was found by

$$V = V_L - V_S \qquad (1)$$

where

$$V_S = \tfrac{1}{3}\pi D^3 \qquad \text{if } D \leqslant \text{pool mid-depth, or} \qquad (2)$$

$$V_S = 2\pi M(D^2 - M^2/3) \qquad \text{if } D > \text{pool mid-depth}, \qquad (3)$$

and V_L was calculated by substituting $(D + \Delta d)$ for D in Eq. (2) or (3). M is the mid-depth of the pool. The probability of a specific prey of the ith size class, λ_i, occurring in this volume was calculated by

$$\lambda_i = V/(2\pi R^2 M) \qquad (4)$$

where R is the radius of the pool and all other terms are as previously defined. The probability of

no prey from the ith size class in this volume, $p(0)_i$, assuming a binomial distribution, was calculated as

$$p(0)_i = (1 - \lambda_i)^{N_i} \qquad (5)$$

and the probability of at least one prey, $p(1)$, was equal to $1 - p(0)_i$. The probability of no members of another size class, j, being close enough to appear larger than a member of size class i at mean distance $D + \Delta d/2$ was calculated by finding the distance D'_j by

$$D'_j = (D + \Delta d)H_i/H_j \qquad (6)$$

if $D'_j \leqslant$ reactive distance for j^{th} size class. Otherwise, $D'_j =$ reactive distance of jth size class where H_i and H_j are the heights of the ith and j^{th} size classes.

The appropriate volume, V, is found by applying Eq. (2) or (3) with D'_j substituted for D. If the fish is assumed to search hemispheres rather than spheres, $V/2$ was substituted for V. λ_j can then be found by Eq. (4), and substituting N_j for N_i, the probability of no individual of the jth size class occurring in this volume is then $(1 - \lambda_j)^{N_j}$ by Eq. (5).

A value proportional to the probability of a prey of the ith size class being eaten is then found by summing $p(1)\prod_{i,j}p(0)_j$ over all D from zero to the reactive distance reported by Werner and Hall (1974). These sums are then converted to probabilities, E_i, and a uniform random number between 0 and 1 is selected. The ith prey class is decremented by one member if it is the first size class for which $\sum_{j=1}^{i}E_j$ exceeds the random number selected. The numbers of each size class are recomputed and the whole cycle repeated for any specific number of iterations, each representing the ingestion of a single prey item. Since the selection of a prey from any specific size class array is a stochastic process, a series of 10 simulations were run and averaged for comparison to Werner and Hall's results.

Comparison of model to observed feeding ratios

In considering tests of the model's accuracy, we determined that adequate experimental fish-feeding data were already available in the literature. Therefore, we compared the results of the model with the experimental data reported by Werner and Hall (1974) and found generally very good agreement. The model predicts that the ratio in which the fish select prey of different size changes noticeably as the feeding of the fish changes the prey densities and size class distributions (Fig. 3). At the initiation of feeding, prey of the largest size class, which are most likely to appear largest to the fish, are selected almost exclusively. As the large prey become scarce, however, there is a greater chance for prey of smaller
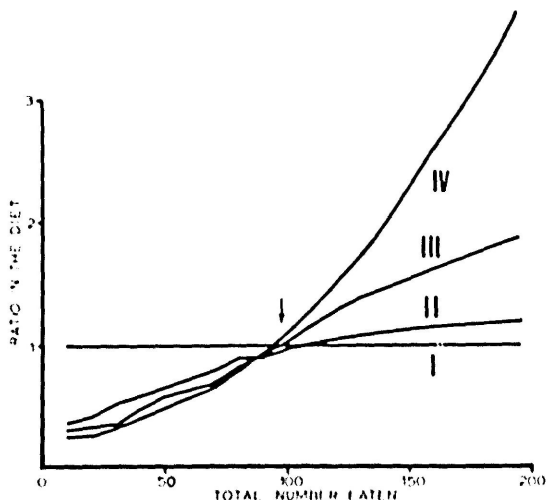

FIG. 3. Plot of average of 10 simulations showing the change of proportions of different size classes of prey eaten (relative to Class 1) by the model as prey are consumed. This plot is based on a simulation using a "uniform effective density" based on 25 Class 1 prey. Prey size classes used in simulations involving data from Werner and Hall (1974) are: I = 3.6 mm, II = 2.5 mm, III = 1.9 mm, and IV = 1.4 mm.

absolute size to appear larger, and the fish consume them in greater numbers. Thus, the model produces a changing series of ratios of size classes eaten.

The jaggedness of the lines at the beginning of the simulation show the stochastic nature of the model. Even though the graph shows the results of the average of 10 runs of the model there is still some random variation. Of course, this almost disappears towards the end of the simulation when a number of prey have been eaten.

A least squares procedure was used to select the ratio for a given experiment that had the lowest sum of squared deviations from the observed. These ratios are presented in Table 2. The fit of the ratios generated by the model to the experimental data is striking, but because the model ratios were chosen for best fit, no statistical analysis of the fit can be made. A more easily testable method of analyzing the model's results in terms of their comparability to observed feeding of bluegills is to look at the predicted ratios generated by the model at the number of prey eaten in the experiments of Werner and Hall (1974). Before obtaining the data on numbers eaten from E. Werner and D. Hall (*personal communication*), we first employed the model to predict them. We found the prediction to be surprisingly accurate, as Table 2 shows. While the ratios at the actual number eaten (also shown in Table 2) may not be as close as those selected by least squares, with one exception they are highly unlikely to have occurred by chance as shown by a chi-square test

TABLE 2. Predicted total number of zooplankton prey eaten and ratios of particular size classes eaten during feeding experiments as compared with observations of actual feeding of bluegill sunfish

Initial density per size class[a] I : II : III : IV	Predicted ratios eaten I : II : III : IV	Predicted no. eaten	Observed ratios eaten[a] I : II : III : IV	Observed no. eaten[b]	Predicted ratios at observed no. eaten[c] I : II : III : IV	x^2
25:25: 25:25	S[d] 1:0.79:0.46:0.28	60	1:0.80:0.51:0.18	61	1:0.78:0.48:0.31	1.38
	H[c]1:0.77:0.47:0.30	60				
50:50: 50:50	S 1:0.87:0.63:0.31	137	1:0.87:0.57:0.37	128	1:0.79:0.46:0.29	1.14
	H 1:0.86:0.62:0.33	137				
25:30: 46:93	S 1:0.98:1.0 :1.0	97	1:0.86:0.96:1.05	95	1:0.95:0.97:1.02	0.21
	H 1:0.93:0.96:1.01	94				
20:28: :74	S 1:0.99: :0.81	52	1:0.90: :0.90	33	1:0.82: :0.58	1.19
	H 1:0.95: :0.88	52				
50:50: :50	S 1:0.59: :0.13	73	1:0.60: :0.07	64	1:0.55: :0.10	0.50
	H 1:0.60: :0.14	72				
75:75: :75	S 1:0.42: :0.06	76	1:0.42: :0.06[e]	68	1:0.42: :0.06	0.00
	H 1:0.42: :0.06	70				
200:200: :200	S 1:0.60: :0.10	315	1:0.62: :0.01	177	1:0.33: :0.05	22.21
	H 1:0.60: :0.11	309				
300:300: :300[f]	S 1:0.23: :0.04	153	1:0.23: :0.05	154	1:0.23: :0.04	0.29
	H 1:0.23: :0.04	147				

[a] Data from Werner and Hall (1974).
[b] Data provided by E. Werner and D. Hall.
[c] Data generated from simulation assuming a hemispherical reactive volume.
[d] Data generated from simulation assuming a spherical reactive volume.
[e] Ratios include feeding of three fish that ate only Class I and thus were excluded by Werner and Hall (1974).
[f] Data representing an average of experiments using initial densities of either 300 or 350 individuals per size class.

(Table 2). The one exception is the experiment using 200 D. *magna* in size classes I, II, and IV, an experiment which was not replicated.

DISCUSSION

We believe the model developed here is what Holling (1968) termed tactical, as opposed to strategic. That is, it quantifies one of the actual day-to-day criteria by which sunfish select their prey when faced with an array of different sized prey: choice of that prey that appears largest. It is interesting to note that the results of this tactic are in accord with those predicted by current theories concerning foraging strategies. For example, many foraging theories suggest that the breadth of a predator's diet increases with decreasing prey density (Schoener 1971). Table 2 and Fig. 3 show that our model yields exactly such a result. In selecting the apparently largest prey in all situations, the fish's diet will vary depending upon the prey size concentrations in the environment. Thus, at high initial prey densities the model "fish" predominantly choose large prey because they appear largest most frequently. As prey numbers are reduced, greater numbers of smaller prey appear largest and are therefore eaten. Only if the prey are very rare does encounter frequency control diet composition; as prey become

more abundant the active selection process dictates a higher and higher proportion of large prey in the diet. This process of narrowing dietary breadth is continuous rather than saltatory as implied by Werner and Hall (1974), and involves no change in the tactical selection mechanism. Further, as any given simulation proceeds and the number of large prey declines, the fish choose more and more smaller prey. Hence the "fish" simulated by our model exhibit "prey switching" (Murdoch 1969; Oaten and Murdoch 1975) although the process is a gradual change rather than an abrupt switch. An observer recording only the frequency of prey eaten might also interpret the simulated results as the formation of search images by the fish since feeding tends to be concentrated on particular but changing size classes as the simulation proceeds (Fig. 3).

It also appears that the tactic we propose of choosing the apparently largest prey could maximize the energy obtained *versus* that expended in pursuit. In taking a small prey which appears large due to its proximity, the fish expends little energy, whereas in taking larger prey at greater distances the fish receives greater energy yield. However, until the energy expenditures in a given pursuit distance and the energy gained from a specific prey size can be precisely assessed, it is not possible to ascertain

energy balances. Neither we nor any other workers can determine energy efficiencies from given search, pursuit, and capture patterns without such information. However, we contend that choosing the apparently largest prey might work to lower energy expenditure.

A major point of difference between the analyses involved in the model proposed here and those previously published (Werner and Hall 1974, Confer and Blades 1975) is that we propose active prey selection by apparent size at all but the most sparse prey densities or shortest reactive distances rather than diet composition based on encounter frequency. Confer and Blades (1975) state that when the probability of simultaneously encountering two prey is small, prey should be chosen in proportion to the square of the reactive distance times the density of a given prey size. Our model will also generate such a process in situations of very short reactive distances and/or very low prey densities. However, according to our simulations, these densities would have to be extremely low. For example, with reactive distances of 4, 3, 2, and 1 cm for the size classes given, the density necessary for a feeding ratio in complete agreement with the ratio of perceptual volume is ~ 4.0 × 10⁻¹ prey/liter, which is an extremely low density of zooplankton. At greater reactive distances, the density would have to be even lower.

In all experiments performed by Werner and Hall the fish could see many more than one prey at a time. In the small pools used for the low density experiments the reactive volume for the largest prey was 126 liters, or about 63% of the total pool volume. At the lowest density used, 25 prey per size class, the fish would, at the beginning of an experiment, see an average of 16 individuals of prey size I. While fish would perceive fewer of the other size classes, they would average 37 prey in the visual field at the beginning of an experiment. Some selection on the part of the fish must therefore occur. No selection at these prey densities would imply that the fish simply took the closest prey available; such a mechanism would yield a composition in the gut proportional to overall density, not proportional to density within the reactive volume, as proposed by Werner and Hall. A process that would result in a diet composition proportional to reactive volume density is random selection of prey. But such a mechanism is hardly a strategy to minimize pursuit time (or optimize net energy gain) as the fish would be just as likely to go to the extreme of the reactive distance of size class I as to take a prey only a few centimetres away.

A number of the assumptions on which the model is based were particularly appropriate to the experiments of Werner and Hall (1974) and should be modified for application to other conditions. In the experimental situation the prey were physically mixed, and therefore the assumptions of random and independent distributions of size classes of prey seem valid. It is known that zooplankton in nature tend to be distributed in a patchy fashion under some conditions (Wiebe 1971, Stavn 1971, George and Edwards 1973), and this should be considered in application of the model to the field.

More important to the actual fit to the model might be assumptions about the visual or reactive field of the fish. Werner and Hall assumed the fish search a spherical visual field, but the model fits the data better under the assumption of a hemispherical visual or reactive field, which also accords better with our observations. In some feeding experiments reported in Vinyard and O'Brien (1975) we never observed sunfish turning 180° to take a prey. However, the difference between assuming a spherical or hemispherical visual field is slight in changing the fit of our model to the data.

A variable that might potentially affect the model's performance is the reactive distance of the fish to various-sized prey. However, we found that reduction of reactive distance by more than half had virtually no impact on the predicted pattern of prey selection. This result occurred because at even the lowest prey densities simulated a fish only rarely would pursue a prey near the edge of its perceptual volume; rather, there are almost always other apparently larger prey closer to the fish.

Another important factor that affects the model is the size and depth of the pool used in various experiments. We have in all cases used the pool sizes suggested by E. Werner and D. Hall (*personal communication*); small pools were used in the 25 and 50 prey per four size class experiments and large pools were used for all other experiments.

Of course, there may be other factors important in determining planktivorous fish diet composition under different circumstances. Confer and Blades (1975) show that escape behavior is an important factor with fish feeding on copepods. They show that capture success varies with copepod species and through time but arrive at an average value of 80% capture success for copepods. They find that *Lepomis gibbosus* has a 100% capture success for *Daphnia*, and we find the same is true of *L. macrochirus*. Thus, escape behavior is of little concern in the experiments of Werner and Hall (1974) and likely not of concern with *Daphnia* as prey in natural situations.

Differences in contrast may alter the reactive distance of the fish to the prey. Zaret (1972) and Zaret and Kerfoot (1975) have clearly shown that in some cases the determining factor in planktivorous fish prey selection appears to be eyespot size.

Whether the demonstrated increase in predation on individuals with large eyespots is a function of fish selecting the largest apparent-sized eye or of increased reactive distance cannot be determined from the published results. Vinyard and O'Brien (1975), using both gut-pigmented *Daphnia* and *Daphnia* greatly pigmented with rich amounts of hemoglobin, show that sunfish exhibit no greater preference (as estimated using change in dorsal tilt) for these pigmented forms but do tend to feed on them to a greater extent than the clearer forms. This is interpreted as showing that increased contrast may increase reactive distance (accessibility) but in these two cases did not alter preference.

Prey motion is another potentially important factor that could influence the choice of prey by planktivorous predators. Little work has been done with this factor in other studies of zooplankton predation. We have noticed during various feeding experiments that bluegill show no interest in motionless *Daphnia*, and during choice experiments will always choose a moving prey over one held motionless. In preliminary work using the tilt box apparatus (Vinyard and O'Brien 1975) no increased response has been found with increasing motion. Thus, it appears that, with *Daphnia* and bluegill sunfish at least, some motion, even sinking, is necessary for the fish to consider the particle as prey, but the extent of motion does not affect prey selection.

In summary, we feel that there is compelling evidence that bluegill sunfish, when faced with high enough prey densities so that they often see more than one prey, base their selection of prey on apparent size. Only at very low prey densities and/or short reactive distances for certain prey will the probability of encounter alone be important in prey selection. Under these latter conditions the models proposed here and in Werner and Hall (1974) and Confer and Blades (1975) are all very similar. At greater prey densities, however, we feel our model provides a more satisfactory explanation of the existing data.

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