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PLANKTIVORE PREY SELECTION: THE REACTIVE FIELD VOLUME MODEL VS. THE APPARENT SIZE MODEL[1]

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Abstract. Two models proposed to explain prey selection by visually foraging planktivorous fish, the reactive field volume model (RFVM) and the apparent size model (ASM), have been found to yield similar dietary predictions in many situations. However, we found earlier formulations of the ASM to be incorrect. The correct predictions of these two models were compared. Published empirical data from an earlier fish foraging study were reanalyzed and found to fit both models quite well. Interpretation of data from an unpublished study, performed under conditions that should have allowed discrimination between the two models, was somewhat ambiguous. When we performed a similar study the results were consistent with the predictions of the ASM, but differed very significantly from those of the RFVM.

Key words: apparent size model; Culaea inconstans; Daphnia; *foraging behavior;* Gasterosteus aculeatus; *planktivory; prey selection; reactive field volume model; size selection; sticklebacks; zooplankton.*

INTRODUCTION

The relative proportions of zooplankton species found in the diets of planktivorous fish often differ dramatically from the proportions found in the foraging environment of the fish. Specifically, an overrepresentation of larger forms in the diets has been widely noted. Recently, much work has been devoted to examining the nature of this "size-selective" predation (see O'-Brien 1979 for review). Two models that have been proposed to explain the observed selectivity of visually foraging fish are the reactive field volume model (RFVM) and the apparent size model (ASM). The RFVM has been used to model passive selectivity: a fish simply taking each prey type in direct proportion to the number occurring within its field of vision (taking prey "as encountered"; Werner and Hall 1974, Eggers 1982). Because, in general, large prey can be seen at greater distances than small prey, large prey would be encountered, and therefore taken, more frequently than small. In the ASM, fish actively select prey, always choosing to pursue whichever prey item appears largest at the initiation of search (O'Brien et al. 1976).

The dietary predictions of the RFVM and the ASM have been found to be very similar in many circumstances, making these models difficult to distinguish empirically (O'Brien et al. 1976, Gibson 1980, Eggers 1982). Since under most field conditions these two models yield very similar predictions, perhaps either model would serve equally well as a baseline against which to compare observed selection. However, for a greater understanding of the process of prey selection, we believe that the mode of prey choice should be determined. In this paper we compare and contrast the dietary predictions of these two models under various conditions. We then examine the empirical data from fish foraging studies, both those performed under conditions in which the two models yield very similar predictions, and those performed under conditions in which they may be distinguished.

The models

Using computer simulation, Eggers (1982) compared the predictions of the RFVM and the ASM assuming that a fish's reactive distance (RD_i) to an item of prey i is directly proportional to the prey's length (L_i), and modelling fish as selecting prey from a set of stationary spherical reactive volumes with radius RD_i (see Fig. 1). (For additional assumptions of the models see Appendix I.) He found that under conditions of low prey densities with few, widely spaced size categories of prey, the ASM predictions were very similar to those calculated using the RFVM. In situations with high prey densities and/or a large number of closely spaced size categories of prey, the predictions of these two models showed great divergence. We have found, however, that under Eggers' assumptions the two models are mathematically identical and yield identical predictions under all conditions (see Appendix II). As Eggers

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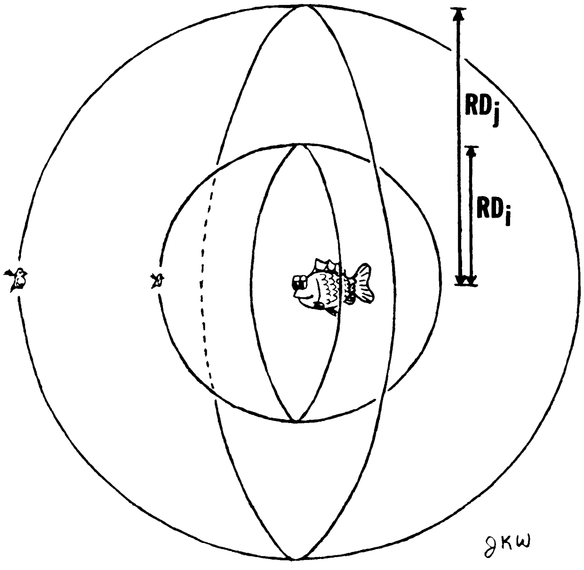

FIG. 1. Diagrammatic representation of a model in which a fish chooses prey from spherical reactive fields. RD_i and RD_j (RD = reactive distance) are the maximum distances at which prey of type i and j, respectively, may be detected. An example of equal truncation of reactive spheres may be visualized by considering this fish as choosing prey only from the forward hemispheres.

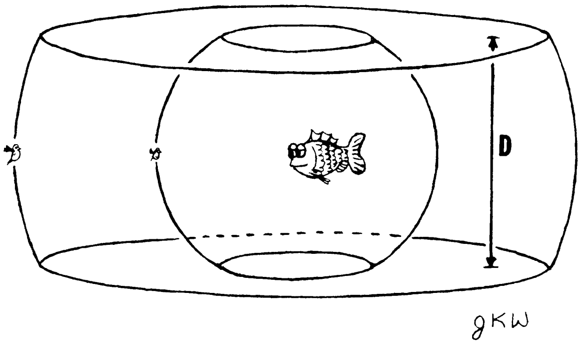

FIG. 2. Diagrammatic representation of a model in which a fish chooses prey from reactive fields based on spheres, but truncated by two parallel planes, simulating foraging in shallow water of depth D. Note that the larger reactive field shows proportionally greater diminution by this truncation.

himself suspected, the differences in predictions he found were simply artifacts of the use of a discrete rather than a continuous function in calculating prey distribution probabilities in the ASM computer simulation of O'Brien et al. (1976). This error in prediction always favors selection of larger prey. The error is insignificant under the conditions for which Eggers found close agreement between the ASM and the RFVM, and is greatest under those conditions for which Eggers found great divergence between the models.

The ASM in its simplest, restricted form (i.e., with Eggers' assumptions) predicts that the fraction (F_i) of prey i of length L_i in a fish's diet will be:

$$F_i = L_i^3 N_i \Big/ \sum_j L_j^3 N_j, \tag{1}$$

where N_j = the density of prey j (see Appendix II). Note that this equation is identical to Eggers' simplified equation for the predictions of the RFVM (Eggers 1982: 390, Eq. 10). This means that, in this restricted case, the diets predicted by the ASM, like those of the RFVM, do not change with changes in absolute prey densities, as long as the relative densities of prey remain constant. Under certain conditions that violate Eggers' assumptions, however, the predictions of these two models do differ. Two examples, explored in this paper, are (1) when reactive distances are not directly proportional to prey length, or (2) when the spherical reactive volumes are truncated in such a way that the volumes for each prey type are not diminished proportionally (e.g., truncation by two parallel planes, simulating shallow water; Werner and Hall 1974; see Fig. 2).

In earlier laboratory studies examining fish foraging on single prey species in clear water, reactive distances to prey items have been found to be approximately proportional to the prey item's length (Werner and Hall 1974, Confer and Blades 1975, Gibson 1980, Wright and O'Brien 1982). However, many studies have shown that factors such as differences in prey shape, coloration, and behavior can affect relative reactive distances to prey, resulting in complicated relationships between length and reactive distance (Zaret and Kerfoot 1975, Confer and Blades 1975, O'Brien et al. 1979, Wright and O'Brien 1982). For example, Wright and O'Brien (1984) found that fish could locate moving diaptomid copepods at three times the distance at which they could locate equivalent-sized nonmoving individuals. Most diaptomids are motionless much of the time, moving only intermittently. This behavior helps make these zooplankton much less vulnerable to visual detection by planktivorous fish than are equivalent-sized *Daphnia,* which exhibit constant movement. (However, some large diaptomids [*Diaptomus kenai, D. nevadensis*] that occur in fishless lakes do exhibit constant movement; R. Crittenden, *personal communication.*) If reactive distance is not proportional to prey length, the spherical RFVM predicts that:

$$F_i = RD_i^3 N_i \Big/ \sum_j RD_j^3 N_j. \tag{2}$$

(This equation reduces to Eq. 1 when $RD_j \propto L_j$.) Under conditions of such nonproportionality, the predictions of the ASM, however, are not so simply derived (see Appendix III), and vary with absolute prey densities (Table 1; see below for an intuitive explanation). At very high prey densities, the predictions of the ASM are insensitive to changes in relative reactive distances, and even extreme deviations from direct proportionality between L_j and RD_j do not alter the predictions of the ASM from those calculated using Eq. 1. At low

TABLE 1. Selectivity for 1-mm prey (β_1) predicted by the reactive field volume model (RFVM) and the apparent size model (ASM) under conditions when reactive distance (*RD*) is not proportional to prey length, 1- and 2-mm prey are supplied in equal densities, and water depth is assumed to be infinite. (See Appendix IV for a description of β.) Most laboratory studies have been conducted at prey densities of >0.1 individual/L for each prey type.

RD_1 (cm)	RD_2 (cm)	RFVM, all densities	ASM Prey density (no. of each prey type/L) .001	.01	.1	1	10	100
		Predicted selectivity for 1-mm prey (β_1)						
8	8	.500	.500	.495	.454	.179	.111	.111
	12	.229	.228	.224	.187	.111	.111	.111
	14	.157	.157	.154	.134	.111	.111	.111
	16	.111	.111	.111	.111	.111	.111	.111
	18	.081	.081	.084	.102	.111	.111	.111
	20	.060	.061	.065	.098	.111	.111	.111
	24	.036	.036	.043	.095	.111	.111	.111
16	16	.500	.496	.463	.215	.111	.111	.111
	24	.229	.225	.194	.112	.111	.111	.111
	28	.157	.155	.137	.111	.111	.111	.111
	32	.111	.111	.111	.111	.111	.111	.111
	36	.081	.083	.099	.111	.111	.111	.111
	40	.060	.064	.093	.111	.111	.111	.111
	48	.036	.042	.088	.111	.111	.111	.111

prey densities, however, the predictions of the ASM become sensitive to changes in relative reactive distances, and converge to those predicted by the RFVM (Eq. 2). The same degree of deviation from proportionality has a greater effect on the predictions of the ASM at shorter reactive distances. Halving all reactive distances has the same effect as lowering all prey densities by a factor of eight (Table 1). This is because the "effective density," the average number of prey items from which the fish chooses, is lowered by a factor of eight.

Several foraging studies have also used truncated versions of these models to simulate foraging in shallow waters, small enclosures, or other nonspherical reactive fields (Werner and Hall 1974, O'Brien et al. 1976, Gibson 1980). Under situations of truncation of the spherical reactive fields, the RFVM predicts that:

$$F_i = Q_i RD_i^3 N_i \Big/ \sum_j Q_j RD_j^3 N_j, \tag{3}$$

where Q_j = the fraction by volume of the original reactive sphere for prey *j* remaining after truncation. The predictions of the truncated RFVM differ from those of the untruncated RFVM only when truncation results in a change in the relative volumes of the reactive fields of different prey types. For example, in Werner and Hall (1974), truncation by two parallel planes (simulating the shallow conditions in their wading pools) resulted in the diminution of the reactive volume of the largest prey (size-class I) by 60%, but diminished the reactive volumes of the smaller prey (size-classes II, III, and IV) by 51, 44, and 24%, respectively. In this situation, $Q_{\mathrm{I}} = 0.40$, $Q_{\mathrm{II}} = 0.49$, $Q_{\mathrm{III}} = 0.56$, and $Q_{\mathrm{IV}} = 0.76$. (A single constant such as *a* as used by Eggers (1982:390 Eq. 9) cannot adequately correct for differently shaped reactive volumes. In fact, as Eggers (1982:382) points out, *a* cancels out of his Eq. 9.) Truncation of the reactive spheres into hemispheres, wedges, cones, etc. reduces all volumes in a proportionately equal way (e.g., for a hemisphere, the reactive volumes for all prey are reduced by 50%; see Fig. 1). Such uniform truncation does not alter the predictions of the RFVM, and affects the predictions of the ASM only under conditions of nonproportionality, in which case reduction of all reactive volumes by 50% would have the same effect as halving all prey densities (see Table 1). Examples of the effects of one form of unequal

TABLE 2. Selectivity for 1-mm prey (β_1) predicted by the reactive field volume model (RFVM) and the apparent size model (ASM) under conditions of truncation of the visual field by two parallel planes, simulating shallow water; 1- and 2-mm prey are supplied in equal densities. Water depth (*WD*) varies as indicated, and fish are assumed to be located at middepth. *RD* = reactive distance.

RD_1 (cm)	RD_2 (cm)	*WD* (cm)	RFVM all densities	ASM Prey density (no. of each prey type/L) .001	.01	.1	1	10	100
				Predicted selectivity for 1-mm prey (β_1)					
8	16	40	.111	.111	.111	.111	.111	.111	.111
		30	.112	.111	.111	.111	.111	.111	.111
		20	.133	.133	.132	.125	.111	.111	.111
		15	.160	.160	.159	.148	.113	.111	.111
		10	.184	.183	.183	.177	.131	.111	.111
		5	.196	.196	.195	.195	.183	.126	.111
		2.5	.199	.199	.199	.199	.197	.179	.122
16	32	80	.111	.111	.111	.111	.111	.111	.111
		60	.112	.111	.111	.111	.111	.111	.111
		40	.133	.132	.126	.111	.111	.111	.111
		30	.160	.159	.151	.115	.111	.111	.111
		20	.184	.183	.178	.137	.111	.111	.111
		10	.196	.196	.195	.186	.131	.111	.111
		5	.199	.199	.199	.198	.183	.126	.111

TABLE 3. Observed diets of sticklebacks feeding on large (L = 2.4 mm) and small (S = 1.4 mm) size-classes of *Daphnia* (data from Gibson 1980) compared to the predictions of the reactive field volume model (RFVM) and the apparent size model (ASM). (Data from all replicates are combined.) The two highest density experiments (200 L + 200 S per litre; 200 L + 800 S per litre) were conducted in a 10-L aquarium (base 43.5 × 43.5 cm; water depth 5.3 cm). All other trials were run in a 100-L aquarium (base 88 × 64.5 cm; water depth 17.5 cm). Reactive distances: RD_L = 14.1 cm; RD_S = 7.6 cm.

Initial densities (no./L)		Diets observed (no. prey)		Diets expected (no. prey)					
				RFVM			ASM		
L	S	L	S	L	S	χ^2	L	S	χ^2
0.2	0.2	53	22	59.1	15.9	3.0	58.6	16.4	2.4
1	1	128	26	121.2	32.8	1.8	120.3	33.7	2.3
5	5	260	55	251.8	63.2	1.3	250.6	64.4	1.7
200	200	257	61	245.6	72.4	2.3	262.8	55.2	0.7
0.2	0.8	64	54	57.4	60.6	1.5	56.0	62.0	2.2
1	4	143	134	130.1	146.9	2.4	128.9	148.1	2.9
5	20	149	152	158.8	142.2	1.3	156.9	144.1	0.8
200	800	173	143	146.4	169.6	9.0*†	173.3	142.7	0.0

*† $P < .005$, chi-square analysis, df = 1. All other differences between observed and predicted diets were nonsignificant ($P > .01$).

truncation, truncation by two parallel planes, are given in Table 2. As in the case of nonproportionality, the predictions of the ASM are accurately calculated using Eq. 1 at high prey densities, but converge with those of the RFVM (Eq. 2) at low prey densities. Unequal truncation also has a proportionally greater effect at shorter reactive distances due to the lower effective prey densities (Table 2).

A simplified interpretation of the complexities of the two foraging models may be summarized as follows. The dietary predictions of the RFVM depend only on the relative abundances of prey contained within the fish's reactive field. These can be calculated using the relative prey densities and the relative sizes of the reactive fields for the various prey. The predictions are thus not affected by changes in absolute prey densities that leave relative densities unchanged, or by changes in the size or shape of the reactive fields that leave relative sizes unchanged. The predictions of the ASM, however, are dependent on the size and shape of the reactive fields and on the relative and absolute prey densities in a somewhat complex manner. At high prey densities, the apparently largest item is usually found quite close to the fish, so the ASM predictions are relatively insensitive to parameter changes that alter the visibility of only those prey located at the periphery of the reactive field (e.g., slight truncation or changes in reactive distances), and predictions can be accurately calculated using Eq. 1. At very low prey densities, the apparently largest prey item is often the only prey item visible. In such a case, the predictions of the ASM coincide with those of the RFVM (i.e., Eq. 3).

Analysis of previous empirical foraging studies

In many field and laboratory studies the numerical predictions of the ASM and the RFVM are quite similar and therefore difficult to separate. Such a situation is found in a study by Gibson (1980). Gibson examined the diets of three-spined sticklebacks (*Gasterosteus aculeatus*) feeding on two size-classes of *Daphnia magna* at prey densities ranging from 0.4 individuals/L to 1000 individuals/L. Reevaluating his data, we found that the fish's diets were well predicted by the ASM in all trials, and differed significantly from the predictions of the RFVM in only one trial (Table 3). Gibson had concluded that these data fit only the RFVM, due to his reliance on the faulty predictions of the ASM computer simulation of O'Brien et al. (1976). In an additional experiment mentioned by Gibson (1980:303), the selectivity of sticklebacks foraging on high densities of *Daphnia* in a small (500-mL) container was examined. Under these conditions of extreme truncation of the fish's visual field, the dietary predictions of the RFVM and the ASM diverge greatly. In the small foraging arena, the fish could theoretically see all prey between it and the wall of the container in any direction. In such a situation, choosing prey randomly from those visible (as in the RFVM) would result in taking prey in direct proportion to ambient densities. The prey densities in these experiments were extremely high, so that the predictions of the ASM were unaffected by the truncation of the visual field, and could be accurately generated using Eq. 1. While the data from these high truncation experiments are more consistent with the predictions of the ASM than with those of the RFVM, the results are still somewhat ambiguous (Table 4). The fish consistently took large prey in greater than ambient proportions, but usually ate more small prey than predicted by the ASM. In 15 of the 18 trials, the observed diets of the sticklebacks were intermediate between those predicted by the ASM and those of the RFVM.

In attempting to explain these results, we considered the possibility that the fish were, in fact, pursuing prey according to apparent size, but that other factors that violate the assumptions of our model (see Appendix

TABLE 4. Observed diets of individual sticklebacks feeding on large (L = 2.4 mm) and small (S = 1.4 mm) size-classes of *Daphnia* under conditions of extreme truncation of the visual field (a 500-mL container), compared to the predictions of the reactive field volume model (RFVM) and the apparent size model (ASM). (Data supplied by R. Gibson, *personal communication.*)

Initial densities no./L		Diets observed (no. prey)		Diets expected (no. prey)					
				RFVM			ASM		
L	S	L	S	L	S	χ^2	L	S	χ^2
200	200	9	4	6.5	6.5	1.9	10.8	2.2	1.8
		20	7	13.5	13.5	6.3	22.2	4.8	1.2
		18	15	16.5	16.5	0.2	27.0	6.0	16.5*†
		20	5	12.5	12.5	9.0*†	20.5	4.5	0.1
		23	7	15.0	15.0	8.5*†	24.6	5.4	0.5
		18	5	11.5	11.5	7.4**	18.9	4.1	0.2
		21	9	15.0	15.0	4.8	24.6	5.4	2.9
		22	9	15.5	15.5	5.5	25.4	5.6	2.5
		17	10	13.5	13.5	1.8	22.2	4.8	6.9**
200	800	11	11	4.4	17.6	12.4*†	12.0	10.0	0.2
		17	15	6.4	25.6	22.0*†	17.2	14.8	0.0
		21	7	5.6	22.4	52.9*†	15.2	12.8	4.8
		22	14	7.2	28.8	38.0*†	19.3	16.7	0.8
		11	22	6.6	26.4	3.7	17.8	15.2	5.6
		20	13	6.6	26.4	34.0*†	17.8	15.2	0.6
		16	16	6.4	25.6	18.0*†	17.2	14.8	0.2
		7	20	5.4	21.6	0.6	14.6	12.4	8.6*†
		10	19	5.8	23.2	3.8	15.7	13.3	4.5

** $P < .01$, *† $P < .005$, chi-square analysis, df = 1. All other differences between observed and predicted diets were nonsignificant ($P > .01$).

I) were causing the observed diets to deviate from those expected. Two factors we considered were multiple prey capture and local prey depletion. Multiple prey capture, the taking of more than one prey in a single strike, may be quite common at extremely high prey densities, particularly with a prey species, such as *Daphnia,* that tends to clump. Local prey depletion, the successive taking of more than one prey item from the same local area, may be common with fish foraging in very small containers, where the fish is afforded little room to swim about freely. The occurrence of either or both of these behaviors would tend to result in an increased proportion of the less preferred (small) prey in the diet. We therefore "repeated" Gibson's high truncation experiments, attempting to minimize the occurrence of multiple prey capture and local prey depletion.

MATERIALS AND METHODS

Foraging trials were performed in a small clear plexiglass tube (9.4 cm diameter) fitted with a removable fine-mesh screen bottom and with an air bubbler in the side wall 2.5 cm from the base. The tube was placed on top of a brick inside a 115-L aquarium filled to a depth such that the tube held 800 mL of water (11.5 cm deep within the tube).

Seven brook sticklebacks (*Culaea inconstans*) (5.1 ± 0.5 cm standard length) were seined from Sewage Treatment Pond Number 1 on the Michigan State University campus, East Lansing, Michigan. The fish were maintained in the same 115-L aquarium that housed the experimental tube, and were fed *Daphnia pulex* several times daily. Brook sticklebacks were chosen for these experiments because Gibson's (1980) experiments had indicated that sticklebacks show a consistent pattern of prey selection over a wide range of prey densities. In contrast, bluegill sunfish (*Lepomis macrochirus*) exhibit a shift in selectivity with changes in prey density (J. K. Wetterer, *personal observation*; reanalysis of Werner and Hall 1974). While choosing prey in proportions similar to those observed for sticklebacks at low prey densities, at high prey densities bluegills shift toward greater specialization on larger prey.

Daphnia pulex were cultured in large (≈600-L) laundry tubs and sorted into two distinct size-classes using standard brass soil sieves. Fifty individuals of each size-class were measured under a dissecting microscope for each set of runs. The average length of the *Daphnia* varied somewhat from day to day. (Large individuals ranged from 1.79 to 1.84 mm mean length, not including the caudal spine; small from 1.15 to 1.23 mm.) This variation between runs was taken into account when calculating the predictions of the ASM.

Experiments were performed at two starting densities, 50 large/100 small prey per litre and 100 large/200 small prey per litre. The prey were added to the tube, and the bubbler set them churning. After ≈2 min, one stickleback was moved from the larger tank to the tube, and the air flow was reduced to a slow trickle. After every one or two prey items taken by the fish, the air was given a short blast to remix the prey. Foraging was terminated after at least 20 attacks were

TABLE 5. Observed diets of individual sticklebacks feeding on large (L ≈ 1.8 mm) and small (S ≈ 1.2 mm) size-classes of *Daphnia* under conditions of extreme truncation of the visual field and remixing of prey to prevent local depletion, compared to the predictions of the reactive field volume model (RFVM) and the apparent size model (ASM).

Initial densities (no./L)		Diets observed (no. prey)		Diets expected (no. prey)					
				RFVM			ASM		
L	S	L	S	L	S	χ^2	L	S	χ^2
50	100	17	5	7.3	14.7	19.3*†	13.1	8.9	2.9
		16	12	9.3	18.7	13.6*†	16.2	11.8	0.0
		15	14	9.7	19.3	13.7*†	16.8	12.2	0.5
		16	10	8.7	17.3	12.8*†	15.2	10.8	0.1
		14	7	7.0	14.0	10.5*†	12.4	8.6	0.5
100	200	28	17	15.0	30.0	16.9*†	26.7	18.3	0.2
		24	15	13.0	26.0	14.0*†	23.4	15.6	0.0
		19	15	11.3	22.7	7.8**	20.5	13.5	0.3
		24	10	11.3	22.7	21.3*†	20.5	13.5	1.5
		20	18	12.7	25.3	6.3	24.5	13.5	2.3

** $P < .01$, *† $P < .005$, chi-square analysis, df = 1. All other differences between observed and predicted diets were nonsignificant ($P > .01$).

observed at the lower density or at least 30 attacks at the higher density. Several times the fish refused to eat or ceased feeding before the prescribed number of attacks, usually as a result of being frightened by a blast of air; data from these trials were not included in the analysis.

At termination of a trial, the tube was removed from the aquarium and the fish was poured into a small bowl. The bowl was checked to determine if any prey had been inadvertently transferred with the fish. These, with the uneaten *Daphnia* in the tube, were washed down into the screen and from the screen into a small jar. They were then killed in formaldehyde solution and counted under a dissecting microscope.

RESULTS

The diets of the fish were consistent with the predictions of the apparent size model in all trials; in contrast, in 9 of 10 trials a significant difference was found between the diets of the fish and those predicted by the reactive field volume model (Table 5).

In addition to differences in the dietary predictions of the RFVM and the ASM, there are also important differences in the behavioral patterns suggested by each model. The behavioral interpretation of the RFVM is that the fish randomly chooses prey items from those within its field of vision. Each prey item seen, regardless of its size or distance from the fish, has an equal probability of being pursued. In contrast, a fish foraging by apparent size at high prey densities would be seen to pursue only nearby prey. In casual observation of the sticklebacks feeding during the trials, the fish were observed to pursue only nearby prey, never striking at a prey item more than 2.5 cm distant. The fish clearly were not pursuing prey randomly within the tube.

DISCUSSION

The observed diets of the fish in these experiments provide strong evidence against the reactive field volume model of foraging. R. M. Gibson (*personal communication*) has agreed that multiple prey capture and local prey depletion may have been significant factors in his high truncation experiments (Gibson 1980). If so, it appears that our method of prey "randomization" alleviated these problems.

While the results of the experiments presented here are consistent with the apparent size model of foraging, they are also consistent with another closely related model of foraging: feeding by "greatest stimulus," that is, always pursuing the prey item that affords the greatest visual stimulus. Such selection is, in fact, more consistent with the results of several earlier studies (Zaret 1972, Mellors 1975, Zaret and Kerfoot 1975). For example, Zaret (1972) found that *Ceriodaphnia* that were pigmented from having ingested india ink were chosen selectively over less pigmented individuals. If the relative reactive distances for different prey types may be taken as approximations of the relative visual stimuli offered by the prey at any given distance, then a new model of prey selection may be defined, the greatest stimulus model (GSM). When $RD_j \propto L_j$, then this model yields predictions identical to those of the ASM under all conditions. When reactive distances to prey are not proportional to prey length, predictions of the spherical GSM can be calculated using Eq. 2. Truncation affects the predictions of the GSM in ways analogous to its effect on the predictions of the ASM. Unfortunately, the reactive distances to various prey types under different field conditions are not as readily available, nor as simple to measure, as prey lengths. Analyses will be complicated by such factors as variability in behavior and pigmentation both within and between prey species (Zaret and Kerfoot 1975, Zaret 1980). Well-controlled experimental work is needed to clarify the role of prey conspicuousness in prey selection by visually foraging planktivorous fish.

In conclusion, data from earlier fish foraging studies (e.g., Werner and Hall 1974, Gardner 1981) must be reevaluated with respect to the correct predictions of the ASM, as opposed to the inaccurate predictions from the ASM computer simulations of O'Brien et al. (1976). When the RFVM yields predictions very similar to those of the ASM at high prey densities, consistency with these predictions might be more properly interpreted as prey selection by apparent size, or at least some form of active prey selection. Fish, such as bluegills, that can specialize on larger prey to an extent greater than predicted by the ASM appear to be capable of discriminating the actual sizes of prey items from their apparent sizes. The nature of this ability, and the economics of the observed shift toward specialization at high prey densities (i.e., costs and constraints of size discrimination vs. benefits of specialization) should be topics of future investigation. For such analyses and further studies of the behavioral bases of prey selection by planktivorous fish, direct observation of foraging behavior will be essential.

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APPENDIX I

ASSUMPTIONS OF THE MODELS

The major assumptions for the models are: (1) a Poisson distribution of prey items throughout the foraging bouts (no prey clumping or local depletion), (2) definitive reactive distances (i.e., all prey i closer than RD_i from the fish are seen, all prey i beyond RD_i are not seen), (3) the fish is considered a point origin, (4) prey are captured individually and with equal success, (5) all prey are the same shape, and (6) zero variance in prey size and variability (within a size-class). The restricted models further assume that reactive fields are spherical, and that reactive distances are directly proportional to prey length. These restrictions are dropped in the models allowing truncation and nonproportionality, although the reactive fields in these models are still based on concentric spheres. In the examples of truncation by two parallel planes, the models assume that the fish is located at midwater depth, with no truncation of the visual field due to the walls. In simulating the extreme visual truncation experiments, the models assume that the fish is located at the center of the foraging arena. The effects of relaxing or altering some of the assumptions of these foraging models are under investigation.

APPENDIX II

A MATHEMATICAL PROOF

Given the above assumptions for the foraging models, the predictions of the ASM and the RFVM in Eggers' restricted case can be shown to be identical. In a system with two prey types, a and b, at densities N_a and N_b respectively, define random variables y and z as:

y = volume of the smallest sphere centered at the origin containing an item of prey type a
= $(4/3)\pi d^3$, where d is the distance (from the origin) of the closest type a prey; and
z = the same as y, but for prey type b.

Let $r = L_b/L_a$, and $RV_a = (4/3)\pi RD_a^3$,
P_1 = the probability that at least one prey item is visible, and that the apparently largest item is of type a
= $P(0 \le y \le RV_a \text{ and } z \ge r^3 y)$

and P_2 = the probability that at least one prey item is visible

$$= P(y \le RV_a \text{ or } z \le r^3RV_a)$$
$$= 1 - P(y \ge RV_a)\cdot P(z \ge r^3RV_a).$$

Then at any given moment when at least one prey item is visible, the probability that a prey item of type a is the apparently largest prey item $= (F_a) = P_1/P_2$. Under a Poisson distribution, the probability that at least one prey item i is found in volume V is $\int_0^V N_i e^{-N_i x}\,dx$. Thus we can compute:

$$P_1 = \int_0^{RV} \int_{r^3y}^{\infty} N_a N_b \exp(-N_a y)\exp(-N_b z)\,dz\,dy$$
$$= [N_a/(N_a + r^3N_b)][1 - \exp(-N_a + r^3N_b)RV_a]$$

and

$$P_2 = 1 - \left[\int_{RV_a}^{\infty} N_a \exp(-N_a y)\,dy\right]\left[\int_{r^3RV_a}^{\infty} N_b \exp(-N_b z)\,dz\right]$$
$$= 1 - \exp(-N_a + r^3N_b)RV_a.$$

Hence $P_1/P_2 = N_a/(N_a + r^3N_b) = L_a^3N_a/(L_a^3N_a + L_b^3N_b)$, which is the same prediction given by the RFVM (Eq. 1).

APPENDIX III

The Apparent Size Model: a More General Case

The computations for the more general ASM which allows reactive distances to prey to be independent of prey length, and the reactive spheres to be truncated by two parallel planes each at distance m from the center, may be set up as follows. Let $RV_a = v(RD_a)$ and $RV_b = v(RD_b)$, where $v(d) = (4/3)\pi d^3$ for $d < m$, and $v(d) = 2\pi m(d^2 - m^2/3)$ for $d > m$. Reasoning as in the previous case (Appendix II),

$$P_2 = P(y \le RV_a \text{ or } z \le RV_b)$$
$$= 1 - \exp(-N_aRV_a - N_bRV_b)$$

and

$$P_1 = P(y \le RV_a \text{ and } z \ge RV_b) + P\{y \le RV_a \text{ and } z \le RV_b \text{ and } z > v[rv^{-1}(y)]\}$$
$$= [1 - \exp(-N_aRV_a)]\exp(-N_bRV_b) + \int_0^c \int_{v[rv^{-1}(y)]}^{RV_b} N_aN_b\exp(-N_ayN_bz)\,dz\,dy,$$

where $c = \min[RV_a, v(RD_b/r)]$. The above integral may simplified to:

$$N_a \int_0^c \exp(-N_ay - N_bv[rv^{-1}(y)]\,dy - \exp(N_aRV_b)[1 - \exp(-N_ac)],$$

where $v[rv^{-1}(y)] =$

$$\begin{cases} r^3y & \text{for } y < v(m),\ y < v(m/r) \\ 2\pi m[r^2(4\pi/3)^{-2/3}y^{2/3} - m^2/3] & \text{for } y < v(m),\ y > v(m/r) \\ (4\pi r^3/3)(y/2\pi m + m^2/3)^{3/2} & \text{for } y > v(m),\ y < v(m/r) \\ r^2y + (r^2 - 1)(2\pi m^3/3) & \text{for } y > v(m),\ y > v(m/r). \end{cases}$$

With the required parameters (L_a, L_b, N_a, N_b, RD_a, RD_b, and m), a short BASIC program was used to calculate F_a, numerically estimating the remaining integral using Simpson's Rule with 100 increments. This was found to give at least three-place accuracy in the calculated selectivity for the range of parameters that we examined.

APPENDIX IV

Manly's Selectivity Index ($\hat{\beta}$)

The selectivity index formulated by Manly (1974) may be calculated for prey i as:

$$\hat{\beta}_i = \log(r_i/A_i)/\sum_j \log(r_j/A_j), \qquad \text{(IV.1)}$$

where A_i = the number of prey i at the start of the experiment, and r_i = the number of prey i remaining at the end of the experiment. $\hat{\beta}_i$ may be thought of as an estimation of the fraction of prey i that would have occurred in the predator's diet (F_i) had all prey been offered in equal densities and had there been no depletion. Under conditions of constant selection throughout a foraging bout (i.e., RFVM selectivity, or ASM selectivity at high prey densities where predictions are unaffected by truncation and nonproportionality), the expected selectivity (β) is independent of prey densities or depletion levels (the ASM predicts $\beta_i = L_i^3/\sum_j L_j^3$ and the RFVM predicts $\beta_i = RD_i^3/\sum_j RD_j^3$). In situations with two prey types, the expected number of each prey type taken for each model may be calculated deterministically by plugging the values of A_1, A_2, and the appropriate β_1 (replacing $\hat{\beta}_i$) into Eq. IV.1, and solving for r_1 and r_2 using reiterative estimation. When prey are offered at low densities under conditions of truncation or nonproportionality, however, the predicted selectivity of the ASM may change somewhat during the course of the foraging bout due to prey depletion. For example, for Gibson's (1980) lowest density run (0.2 individuals/L for each prey type), the ASM predicts that the selectivity for the small prey (β_s) at the start of the bout will be 0.170. By the end of the runs, however, the mean density of small prey remaining had dropped to 0.156 individuals/L, and of large prey to 0.094 individuals/L. For these values the ASM predicts a β_s of 0.168. In Gibson's (1980) three lowest density trials, where β_s changed by >0.0005 within a bout (all changes were <0.003), a deterministic depletion model that updated selectivity after every 0.2 *Daphnia* taken was used to calculate the diets predicted by the ASM.