This is to certify that the

dissertation entitled

The Foraging Behavior of Largemouth Bass

in Structured Environments

presented by

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has been accepted towards fulfillment
of the requirements for

Ph.D degree in Zoology

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Date 5/23/83

THE FORAGING BEHAVIOR OF LARGEMOUTH BASS

IN STRUCTURED ENVIRONMENTS

By

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A DISSERTATION

Submitted to
Michigan State University
in partial fulfillment of the requirements
for the degree of

DOCTOR OF PHILOSOPHY

Department of Zoology

1983

ABSTRACT

THE FORAGING BEHAVIOR OF LARGEMOUTH BASS
IN STRUCTURED ENVIRONMENTS

By

Owen Anderson

The specific effects of environmental structural complexity on foraging behavior have been poorly understood. A laboratory study using largemouth bass (Micropterous salmoides) and three prey types demonstrated that variation in structural complexity significantly influenced prey encounter rates, handling times, and values, and the ability of predators to learn about prey. Prey encounter rates generally declined with increased structure, but the effect was non-linear, with greater changes occurring between high and intermediate structures than between intermediate and low. In one case, using a schooling prey, encounter rates increased from low to medium structure. Two morphologically similar insect prey types had drastically different encounter rates, and structure modified their encounter rates differently.

Structural complexity and prey handling times were positively related. Mechanisms producing handling time changes, including the relative frequencies of multiple captures and shortened pursuits, were examined. Decrements in overall energy intake associated with longer handling times were larger in less structured environments.

Prey value, traditionally viewed as dependent on physical attributes of predator and prey, declined with increased structure and was also found to be influenced by prey density and distribution. Structure had minimal effects on prey capture success and the energetic costs of handling and searching for prey. I suggest that variation in structural complexity will have substantial effects on predators' breadths of diets and that because of the complexity of the relationship between structure and diet breadth, generalizations relating the two variables will be difficult to make. Evidence from the laboratory and field corroborates these assumptions.

An optimal foraging model was utilized to predict prey selection by largemouth bass in two laboratory environments with identical prey communities but different densities of macrophytes. Patterns of prey selection by the bass corresponded closely with the predictions of the model, with bass in low structure being more specialized.

Finally, growth rates and diet breadths of largemouth bass were examined in stream environments with different levels of macrophytes. In the field, largemouth bass had the greatest final weights and narrowest diets at intermediate levels of structure. Bass in both low structure, where the resource community was impoverished, and high structure, where prey were more effectively shielded by vegetation, had reduced growth rates and broader diets than their medium vegetation counterparts.

ACKNOWLEDGMENTS

I would like to thank my major professor, William Cooper, for his advice, enthusiasm, and support during the course of this research. Don Hall made many valuable contributions both during the planning and implementation of this research. Jack King was a constant source of encouragement and help. Rich Merritt, Earl Werner, Bob Robbins, Craig Osenberg, Jim Wetterer, and Ed Turancik made many valuable comments which contributed to this work. Jack Arthur and his staff at the EPA outdoor laboratory in Monticello, Minnesota, allowed me to use their pole barn for a laboratory. Tom Henry instructed me in the fine art of pumping Mississippi River water into the lab. Scott Cooper, Mike Pease, and Brent Danielson helped develop the inner workings of the laboratory in Minnesota, and Julie Bebak, Scott Cooper, Mike Pease, and Gary and Mike Unger helped with various parts of the field work.

Rangnar Anderson assisted in the building of a laboratory in Michigan. Sue Anderson, Cori Anderson, Elena Ugarte, Amy Outman, Neil Anderson, Craig Anderson, and Oren Anderson helped collect damselflies in the field. Squeaky and Cindy, my two "catfish", helped greatly by staying out of the laboratory aquaria.

This work was supported by a National Science Foundation predoctoral fellowship to the author and by EPA grant CR807555 to Drs. William Cooper and Robert Boling.

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INTRODUCTION

Interactions between predators and their prey are usually not carried out in homogeneous arenas but take place in environments with varying amounts of physical structure. Despite the pervasiveness of physical structure, large gaps have existed in our understanding of the effects of environmental structural complexity on foraging behavior. Although ecologists have been aware that variation in structure can alter prey encounter rates and the energetic costs of searching for and handling prey, little has been known concerning the effects of structure on prey handling times, prey values, the ability of predators to learn about prey, and predator diet breadths. Such effects, if present, should influence the intensity and outcome of predator-prey interactions as well as the extent of diet overlap between potentially competing predator species.

The research described in this dissertation represents a quantitative examination of the foraging behavior of young largemouth bass (*Micropterous salmoides*) in relation to changes in structural complexity. Young bass are active foragers in the well-structured littoral regions of North American lakes and encounter wide variation in structural complexity both within lakes and throughout their natural range.

The research is divided into three separate papers. The first manuscript describes a situation in which bass are free to select prey in environments with identical prey communities but different levels of structure. The predictions of an optimal foraging model are compared with actual prey consumption of the bass. The second paper describes in quantitative terms the changes in bass foraging behavior produced by variation in structure. Both of these studies were carried out in the laboratory. Finally, the third portion of this thesis analyzes the growth rates and diet breadths of bass in stream environments with different levels of macrophytes. The foraging behavior of bass in the field is compared with predictions based on the laboratory studies.

OPTIMAL FORAGING BY LARGEMOUTH BASS IN STRUCTURED ENVIRONMENTS

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INTRODUCTION

Vegetation, rocks, and debris are pervasive features of littoral zone environments, yet the role of such structures in determining the foraging behavior of fish has been poorly understood. Although increased amounts of structure have been correlated with lowered rates of prey capture by fish predators (Glass 1971, Ware 1973, Vince et al. 1976, Stein 1977, Stoner 1982), the effects of structure on prey handling times and on the specific energetic costs of both searching for and handling different prey types have been unknown. Such effects, if present, may be quite important since the actual composition of fish diets has been demonstrated to depend on the relative values of the available prey (Mittelbach 1981, Werner and Mittelbach 1981). Prey value, in turn, incorporates both the time required to handle a prey item and the net energy gained from that prey individual (Charnov 1976).

Increased structure has been shown to have opposite effects on the diet breadths of fish predators. Vince et al. (1976) documented increases in diet breadth at higher levels of structure while Stoner's (1982) work implied narrower diets in highly structured portions of the environment. Greater diet breadth could occur at higher structural levels if encounter rates with prey types declined uniformly and predators became less selective. This negative relationship between prey availability and diet breadth has been documented repeatedly (Ivlev 1961, Werner and Hall 1974, Curio 1976). Conversely, if increased structure influenced the availability of prey types differentially, certain prey might gain almost complete refuge from predation in high structure (Stoner 1982). Other, evasive prey might have high pursuit costs or low capture probabilities in high structure (Glass 1971). These effects could produce an inverse relationship between structure and diet breadth.

Knowledge of the relative importance of such factors is rudimentary. Indeed, there has been only one attempt to predict quantitatively the composition of predators' diets in relation to changes in structural complexity (Mittelbach 1981). However, Mittelbach's experimental manipulations altered both the structural complexity of the foraging environment and the nature of the prey community. In this study I quantify parameters of an optimal foraging model proposed by Charnov (1976) as functions of structural complexity in an attempt to predict diet choice by predators in environments with identical prey communities but different amounts of structure. Optimal foraging theory was employed because of its recent successes in predicting resource utilization by animals in the field (Belovsky 1978, Mittelbach 1981) and laboratory (Werner and Hall 1974, Krebs, Ryan and Charnov 1974, Cowie 1977, Cook and Cockrell 1978.

Small (76 mm TL) largemouth bass (Micropterous salmoides) were used as predators because they are active foragers in the vegetatively structured littoral regions of North American lakes (Heidinger 1975). Furthermore, largemouth bass are distributed widely (MacCrimmon and Robbins 1975) and generally represent a significant portion of the total fish biomass in lakes in which they are found (Heidinger 1975).

METHODS

The tests were carried out using six largemouth bass which were 74–78 mm in total length. The fish were obtained from the Frankfort National Fish Hatchery, Frankfort, Kentucky when they were 30 mm in length and were fed small aquatic invertebrates in the laboratory until they reached the appropriate size. The bass were housed separately in two 110-L aquaria, each of which had been divided into three compartments with the insertion of fiberglass screen dividers mounted on wooden frames. The fish were divided into two groups. Initially, three fish foraged only in an environment with a small amount of structure (vegetation); the other three fish foraged in a highly structured environment. The fish were tested one at a time, and a complete record of the foraging behavior of each bass was carefully maintained.

The low structure environment consisted of a 208-L aquarium with 5 plastic *Elodea* plants (12 stems/plant) spaced uniformly and anchored in a sand substrate. The 208-L high structure tank contained 17 plants. Stem densities were $200/m^2$ in low structure and $670/m^2$ in high. These stem densities are similar to values found commonly in the field (Gerking 1957).

Each 208-L aquarium was divided into two unequal sections with the insertion of a sliding Plexiglas door. The larger 184-L portion contained the vegetation and any experimental prey which had been introduced. The small 24-L section served as an acclimation chamber for each bass prior to a foraging bout.

A specific foraging trial proceeded in this manner: following transfer from the holding tank, an individual bass acclimated for thirty minutes in the 24-L chamber. The Plexiglas door was then raised, allowing the bass to commence searching for prey in the larger volume. From behind a blind, an observer recorded the foraging behavior on a voice tape recorder, categorizing the time spent by the bass as either search or handling time and noting the success or failure of each capture attempt. At the end of each day's six foraging trials, the tape was replayed and a Heuer 410 microsplit digital stopwatch was employed to determine actual search and handling times for each prey item. Handling times which did not end in prey capture were added to the next successful handling time for purposes of determining average handling time per captured prey item.

A bass searched for prey by swimming at a steady rate through the water, frequently changing its direction and adjusting the position of the eyes. Handling behavior, which included the pursuit, capture, and swallowing of a prey item, plus a pause afterward, was easily distinguishable from searching. The beginning of handling time (pursuit) involved an accelerated, unidirectional movement toward a prey item which could usually be seen by the observer. At the end of the handling period for a particular prey individual, a bass was usually stationary, with the gill covers flaring in and out in a pumplike manner.

Search was reinitiated when the bass stopped the pronounced gill cover movement and resumed swimming with a strong thrust of the caudal fin. While many authors have separated pursuit and handling time, the two are combined in this study because together they represent a time investment which must be made by a predator to gain energy from a prey type once it is detected. For purposes of determining an optimal diet, combining pursuit with the rest of handling time is essential (see Equation 3, which follows).

The aquaria were marked horizontally and vertically with 5 cm markings and the third spatial co-ordinate was estimated by the observer based on the known width of an aquarium so that the spatial positions of the bass could be recorded throughout the timed trials. Since the distance traveled by a bass for each search or handle could then be calculated as it moved through a 3-dimensional grid, it was possible to compute average velocities of the bass for each activity. These velocities were then used to determine the costs (in J/s) of searching for and handling prey, using the relationship described by Glass (1971),

$$(1) \qquad Y = RM + bV^c$$

where Y is the oxygen consumption in mg/hour, RM is the rate of oxygen consumption at zero velocity (routine metabolic level or Y_{min}), V is the velocity of the bass in cm/s, and b and c are constants. For 76 mm bass at an ambient temperature of 20°C., the appropriate equation is (Glass 1971),

$$(2) \qquad Y = 2.08 + (.026)(V)^{1.7}$$

In this study water temperatures actually varied from 19-21^{o}C., but this produces only slight changes in oxygen use. Oxygen consumption was then converted to joules expended/second using the relationship established by Elliot and Davison (1975), where 1 mg oxygen consumed equals 13.6 J. Non-swimming handling costs, including the energy required to mouth and swallow prey, are unknown for bass, and no attempt was made to estimate them.

Two prey types were utilized in the experiments - uniform sizes of Coenagrionid damselflies and female guppies (Lebistes reticulatus). In order to determine encounter rates, handling times, and costs of searching for and handling each prey type, guppies or damselflies were initially presented alone in the foraging environments at densities of 30 damselflies (210/m^3) or 4 guppies (28/m^3). Bass in each structural type were allowed to eat either all 4 guppies or eight damselflies during a foraging bout (after 4 guppies or 8 damselflies, 76 mm bass begin to become satiated, and handling times increase). For the optimal foraging experiments, both prey were present, and bass in high and low structure were allotted five minutes total foraging time.

To predict the foraging behavior of the bass when both prey were available, an optimal foraging model similar to that described by Charnov (1976) and utilized by Mittelbach (1981) was employed. In the model, the net rate of energy intake of a predator can be formulated as,

$$(3) \qquad E_n/T = \frac{\sum_{i=1}^{n} B_i E_i - C_s}{1 + \sum_{i=1}^{n} B_i H_i}$$

where E_n = the net energy gained while foraging (J), T = the time spent foraging (s), B_i = the encounter rate with prey type i (# captures/second of search), E_i = the net energetic gain associated with prey type i (J), C_s = the cost of searching (J/s), and H_i = the time required to handle prey type i (s).

Further, E_i, the net energetic gain associated with prey type i, can be defined as,

$$(4) \qquad E_i = Ae_i - C_h H_i$$

where e_i = the actual energetic content of prey type i (J), A = the fraction of the prey's energy content which can be assimilated by the bass, and C_h = the cost of handling prey type i (J/s). The assimilable fraction of energy ingested (A) was assumed to be .7 (Elliot 1976). The e_i's were estimated by drying the guppies and damselflies in a Fisher Isotemp 501 drying oven at 45°C. for 48 hours and then weighing the prey to the nearest .1 mg. Dry masses were then converted to joules by assuming that 1 mg dry mass = 21.3 J for damselflies (Cummins and Wuycheck 1971), and 1 mg = 20.9 J for the guppy prey (Adams 1975). Mean dry masses of damselflies and guppies were

7.6 $\pm$ .3 and 26.1 $\pm$ .7 mg, respectively (n=30 for each prey type). Equations 2 and 4 were used to compute the net energetic gain (E_i) associated with each prey type: 113.3 J for damselflies, 381.8 J for guppies (structure had no significant effect on E_i - see Results).

Encounter rates, handling times, and costs of searching and handling were determined only after the bass had become acclimated to the laboratory environments and had maximized their encounter rates and minimized their handling times for each prey type. This initial process took from 3 to 7 days while the bass foraged for damselflies and three days for the guppy prey. There followed six consecutive days during which the bass foraged for damselflies, then six days with guppies only as prey. Prior to the optimal foraging tests, the two prey were presented on alternating days for six days (each prey type presented three times). Thus 108 total foraging trials were available for analysis and predictive purposes prior to the optimal foraging experiments.

The format for the optimal foraging work was as follows: both damselflies and guppies were available to the bass at the prescribed densities for seven consecutive foraging bouts. During this period the three bass which had been trained only in low structure continued to forage there, and the high structure bass foraged in high structure. Seven days (foraging bouts) has been shown to be an adequate time for fish to maximize their foraging efficiency while learning to forage in a novel situation (Werner et al. 1981). After seven days the two groups of fish were switched, i.e., on the eighth day the original low structure bass foraged in high structure, and vice-versa. This marked the first time that the fish in either group had been exposed to the alternate environment. The bass were then allowed to forage in their new environments for seven consecutive days. This changeover design was utilized so that more fish could be tested in each environment and so that potential residual effects resulting from foraging in the alternately structured environment could be determined.

Bass in high and low structure consumed approximately 1630 net joules per day during the optimal foraging experiments. Since the fish were given no other food, bass in both treatments began their foraging trials in approximately the same motivational state. While foraging, bass in low and high structure acquired energy at much different rates, however. Fish in low structure initially had higher rates of prey capture and then consumed few prey during the latter stages of foraging bouts; fish in high structure captured prey at a slow but fairly steady rate throughout the five minute trials. The result was a similar overall net energy intake per day (foraging trial). 76 mm bass require about 840 J/day for routine metabolism; thus the bass grew slightly during the experiments - about 1 mm per week.

RESULTS OF THE PRELIMINARY EXPERIMENTS

In all cases, increased structural complexity significantly lengthened the time required by the bass to search for and handle prey items (Tables 1 and 2). ANOVA could not be utilized to compare search times for guppies between high and low structure due to heterogeneous variance. Furthermore, in high structure there was a strong dependence of search time on capture order, with the third and fourth guppies taken in a foraging bout requiring much longer search times than the first two (Table 2). Therefore, Welch's solution (Gill 1978) was used to test for search time differences between structures for a given capture number (where 1 is the first guppy taken during a bout and 4 is the fourth and last). For each capture, there is a significant difference in the search time between structures (Table 2).

Structure had an effect on the swimming speed of the bass while searching for damselflies and while handling damselflies and guppies (Table 3). While searching for damselflies, bass swam 1.6 times faster in low structure than in high (6.1 cm/s vs. 3.8 cm/s). The mean search time required to detect a damselfly was 23.1 s in low structure and 37.5 s in high (Table 1). These search times translate into encounter rates (# captures per second of search) of .043/s and .027/s, respectively. Thus, the encounter rate in low structure is .043/.027 = 1.6 times greater than the rate in high and can apparently be directly related to the differences in search velocities between structures.

Handling velocity, the average rate of movement of the bass while handling prey, was elevated in low structure for both prey types (Table 3). Handling velocity consisted of the average rate of movement during the entire handling period and thus incorporated the potentially different velocities of the bass during the various subcomponents of

TABLE 1. Search and handling time relations for two prey of largemouth bass at two structural levels. Mean times per prey item ($\pm$ 1 SE) are given in seconds. Values of F and the probability of type I error are given for each foraging parameter (ANOVA). N = the number of prey captures.

	Low Structure	High Structure	N	F
Damselfly Search Time	23.1 ± 3.1	37.5 ± 4.4	144	7.3**
Damselfly Handling Time	6.6 ± .5	8.9 ± .6	144	14.3***
Guppy Handling Time	5.9 ± .6	7.9 ± .7	120	4.8*

* $P < .05$

** $P < .01$

*** $P < .001$

TABLE 2. Relationship between capture order within foraging trials for guppies and the mean search times (in seconds) required to detect guppies in low and high structures. Welch's t' statistic is given based on comparisons of means for each capture number, with probability of Type I error.

Capture Number	Search Time Low Structure	Search Time High Structure	t'
1	3.8 $\pm$ 1.0	15.8 $\pm$ 2.7	4.2**
2	2.4 $\pm$ .6	17.0 $\pm$ 4.4	3.1*
3	3.2 $\pm$ .9	113.1 $\pm$ 14.7	5.2**
4	12.0 $\pm$ 2.8	134.6 $\pm$ 13.8	6.0**

* $P < .005$

** $P < .0005$

TABLE 3. Mean velocities (± 1 SE) of 76 mm largemouth bass while searching for or handling either damselflies or guppies in two differently structured environments. Velocities are expressed in cm/s. Values of F and the probability of Type I error are given for each comparison between structures (ANOVA).

	Low Structure	High Structure	N	F
Damselfly Search Velocity	6.1 ± .2	3.8 ± .2	144	16.2***
Damselfly Handling Velocity	5.2 ± .4	3.0 ± .2	144	22.4****
Guppy Search Velocity	6.8 ± .6	6.4 ± .6	60	.6*
Guppy Handling Velocity	10.5 ± .9	6.4 ± .6	60	8.4**

* NS
** $P < .05$
*** $P < .025$
**** $P < .001$

handling (pursuing, capturing, swallowing, pausing). An increase in pursuit velocities probably accounted for the higher handling velocities in low structure. In low structure bass can detect prey items at greater distances, and a positive relationship between pursuit velocity and distance from prey at which pursuit is begun has been documented by Nyberg (1971). Actual pursuit velocities were not calculated, however, and it is also possible that average handling velocities were greater in low structure because pursuit represented a larger proportion of total handling time there. Pursuits in high structure were usually initiated at a closer distance to the prey than in low structure. For a complete discussion of the effects of structure on handling time, see Anderson (1983).

The differences in costs incurred by bass in the two environments were small. For example, the bass in low structure swam 1.6 times as fast as their high structure counterparts (6.1 vs. 3.8 cm/s, Table 3) while searching for damselflies yet experienced only a small increment in cost (from Equation 2, .010 J/s vs. .009 J/s). Similarly, despite the fact that bass in low structure increased their average rate of movement while handling guppies from 6.4 to 10.5 cm/s compared to high structure bass, this represented an increase of only .003 J/s, from .010 to .013 J/s. Since the difference in handling time between low and high structure was two seconds (Table 1), this represented a miniscule alteration (.006 J) in the net energetic content (E_i) of the prey.

Structure had little influence on capture success. Greater than 98% of all damselfly and 90% of all guppy capture attempts were successful at each structural level.

Using this preliminary information, it was possible to use Equation 3 to calculate the net energetic returns in each habitat for each foraging mode. In low structure the optimal foraging behavior involved eating guppies until there were none left. This strategy had a predicted E_n/T of 35.6 J/s compared with 31.2 J/s for eating guppies and damselflies as encountered and 3.8 J/s for eating only damselflies. Thus, a bass specializing on guppies could have increased its rate of energy intake by 13% compared to a generalized foraging mode (taking guppies and damselflies as encountered) and 844% compared to specialization on damselflies. The prediction was not so simple in high structure. The strong inverse relationship in high structure between number of guppies already captured and search time required to detect another guppy (Table 2) made it necessary to reapply the optimal foraging model after each guppy capture in order to predict the best pattern of prey selection. The question then could be stated: Was the encounter rate with the more valuable prey type, guppies, ever low enough in high structure so that bass could increase their energy intake rate by including damselflies in the diet? The value (E_i/H_i) of a damselfly in high structure was 113.3 J/8.9 s = 12.7 J/s. Using the optimal foraging model (Equation 3) and the appropriate parameters for guppy prey in high structure (E_i = 381.8 J, H_i = 7.9 s), it can be shown that if the encounter rate with guppies fell to below .045/s, the net rate of energy acquisition (E_n/T) while foraging for guppies would be less than 12.7 J/s and it would be energetically favorable to include damselflies in the diet. Thus the critical guppy search time in high structure was 1/.045 = 22.2 s. If a bass encountered guppies less often than every 22.2 seconds, generalization was predicted. From Table 2 it can be seen that the critical search time was exceeded, on average, for the third and fourth guppies taken during a foraging bout. Thus, the optimal strategy in high structure was to initially specialize, taking two guppies, and then to generalize thereafter, taking any prey item encountered.

It should be noted that the calculated value of E_n/T is quite insensitive to possible variation in energetic costs incurred by the bass while foraging. The lack of sensitivity of E_n/T to changes in cost is important, because, as mentioned, an average handling velocity was utilized to estimate energetic costs of bass while pursuing and capturing prey. Such averaging may underestimate the cost of handling prey, since cost is not linearly related to velocity (Equation 2) and pursuit (at higher than average handling velocity) represented an unknown fraction of handling time. Table 4 summarizes the changes in cost per handled prey item and the resultant changes in E_n/T when pursuit time is allowed to be a varying portion of total handling time. Data is presented for a bass foraging in high structure for the first two guppy prey, with a search time of 16.4 s and handling time = 7.9 s. In case A, the average handling velocity is used to determine handling cost and E_n/T. Case B assumes that pursuit time (P_T) occupied all but one second of total handling time. Case C assumes that pursuit time required only 2 seconds. Note that changes in total cost per handled prey item and E_n/T are small. Similar results are obtained if low structure bass are analyzed. Also, differences in the costs of searching for damselflies vs.

TABLE 4. Calculation of handling cost and E_n/T when pursuit time is a large or small fraction of total handling time or when an average overall handling velocity is used. P_T = pursuit time; H_T = handling time not including pursuit. Y = oxygen or energy consumption.

Case	Time (s)	Velocity (cm/s)	Y (mg/hr)	Y (J/s)	Weighted Average (J/s)	Total Cost $(J/(H_T+P_T))$	E_n/T (J/s)
A: $H_T + P_T$*	7.9	6.4	2.69	.0102	.0102	.0806	15.7035
B: H_T only	1.0	0.0	2.08	.0079	.0103	.0079	15.7035
P_T only	6.9	7.3	2.84	.0108		.0738	
						.0817	
C: H_T only	5.9	0.0	2.08	.0079	.0139	.0466	15.7023
P_T only	2.0	25.3	8.39	.0317		.0634	
						.1100	

*Original

guppies in high structure (Table 3) produce insignificant changes in E_n/T.

RESULTS OF THE OPTIMAL FORAGING EXPERIMENTS

The foraging behaviors exhibited by the bass in low and high structure were markedly different, despite the similarity of the prey communities. In low structure, bass consumed four guppies before eating any damselflies (the optimal predicted pattern) on 32 out of 42 possible foraging trials (Tables 5 and 6). Bass in high structure never captured all guppy prey without eating damselflies and generally consumed many more damselflies and fewer guppies than their counterparts in low structure (Figure 1). Patterns of prey selection by bass in high vegetation agreed less well with optimal foraging predictions; bass in high structure began 23 (out of 42) foraging bouts by eating two fish prey and then capturing damselflies (Tables 5 and 6). Six trials began with consumption of three guppies, 10 with one guppy, and 3 with damselflies as initial prey. However, the most efficient method of foraging in high vegetation, i.e., taking two guppies and then generalizing thereafter (where generalizing would mean that a damselfly was the most probable third prey - its search time was 37 s in high structure vs. 113 s for the third guppy), was much more likely to occur during the latter stages of any fish's exposure to the high structure environment. For example, fishes 4-6 foraged in the optimal manner 8 out of 9 times on

TABLE 5. Patterns of prey selection by largemouth bass in low and high structure for the first seven days of the optimal foraging experiments. L = low structure, H = high structure, F = fish prey, and D = damselfly prey. Prey are represented in the order in which they were captured and eaten during a foraging bout.

	Day 1	Day 2	Day 3	Day 4	Day 5	Day 6	Day 7
Fish 1(L)	FFFDDDF	FFFDF	FFFFDDD	DFDFFFDDD	FFDDFD	FFFFDD	FFDFDDDD
Fish 2(L)	FFFFD	FFFF	FFFF	FFFFD	FFFFDD	FFFFDD	DFDFFFD
Fish 3(L)	FFFF	FFFF	FFFFDDDD	FFFF	FFFF	FFFFD	FFFF
Fish 4(H)	FFFDDDD	FFFDDDDDD	FDDDFDFD	FDFDDDD	FFDDDDDD	FDFDDDFD	FFDDDDFD
Fish 5(H)	FFDDF	FFDDDDDDDD	FDDDDFDDDDD	FDDD	FFDDDDF	FFDDDDDDD	FFDDDDDD
Fish 6(H)	FFFDDF	FDDDF	FDDFDDDD	FFDDDDF	FFDDDFDD	FFDDFDD	FFDDDFDD

TABLE 6. Prey selection by largemouth bass on days 8–14 of the optimal foraging experiments. Fishes 1–3 had been switched to high structure, fishes 4–6 to low structure.

	Day 8	Day 9	Day 10	Day 11	Day 12	Day 13	Day 14
Fish 1(H)	FFFDDDDD	FDFDDDDD	DFFDFDDDD	FDDFDFD	FFDDDFDDDD	FFDDDDDDD	FFDFDDDDDD
Fish 2(H)	FFDDDD	DFFDDDF	FFDDDFDD	FFDDDFD	FFDDFFDDD	FFDDFDD	FFDDDDFD
Fish 3(H)	FD	FF	FFF	FFF	DDFFDD	FFDFD	FFDDDDD
Fish 4(L)	FFFDDDDDD	FFFFDD	FFFFDD	FFFFDD	FFFFDD	FFFFDD	FFFFD
Fish 5(L)	FFDDFF	FFFFDD	FFFDFD	FFFF	FFFFD	FFFFD	FFFFDDD
Fish 6(L)	FFDDFFD	FFFF	FFFFD	FFFFDDD	FFFFDD	FFFFD	FFFFDD

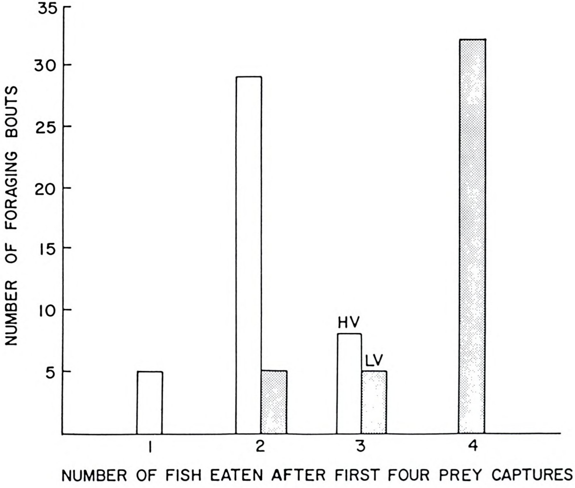

FIGURE 1. Consumption of fish prey by largemouth bass in low (LV) and high (HV) structure during 14-day optimal foraging experiments.

days 5-7 (Table 5) of the optimal foraging experiments, and fishes 1-3 did the same on days 12-14 (their fifth through seventh days of experience with the two prey, high structure experimental regime, see Table 6). The probability of these patterns occurring if the foraging behaviors of the bass were random is extremely low. Since the encounter rate with the first two guppies in high structure was approximately twice the encounter rate with damselflies (.06/s vs. .03/s, see Tables 1 and 2), taking prey at random would mean that the probability of the first prey being a guppy would be 2/3; the probability of a damselfly being the first prey would have been just half that, or 1/3. Thus, the probability of taking two guppies in succession was 4/9, while the probability that the first two prey taken were not both guppies would have been 5/9. From the binomial, the probability of eight of the nine trials beginning with two guppies would then be $(.44)^8(.56)(9!)/(8!) = .007$.

While the bass in high structure tended to begin foraging bouts by eating two (or more) guppies during their first few days in high structure (this happened 5 out of 6 times for fishes 4-6 on days 1-2, Table 5, and 3 out of 6 times for fishes 1-3 on days 8-9, Table 6), they took inordinate amounts of time to capture the third prey. For example, both of the third guppies taken on day 1 (by fish 4 and fish 6) were captured after long searches (greater than 80 s) and the third item eaten by fish 5, a damselfly, was also captured after a long search (120 s), suggesting that the bass were not also searching for damselflies (the optimal pattern) during that time period (on average a damselfly should be encountered every 37 seconds in high structure, Table 1). A similar lengthy time interval between the capture of the second and third prey items was observed for fishes 4 and 5 on day 2. In contrast, on days 5-7, when the optimal behavior was consistently present, there was an immediate upswing in the damselfly capture rate after two guppies were eaten. The implication is that on their first few days in high structure, bass had not yet learned when to stop specializing on guppies.

To illustrate the differential receptivity of bass to damselflies during the optimal foraging experiments in high structure, the search time spent by the bass in high structure was divided into ten second intervals and the number of damselfly captures per ten second search interval were examined. Since the mean search time required to capture the first two guppy prey in high structure was slightly less than forty seconds (Table 2), one can compare the number of damselfly captures per ten second interval for the first forty seconds of search on days 5-7 of the optimal foraging trials with the capture rate for the first forty seconds of the foraging trials on three days immediately prior to the optimal foraging experiments when the bass foraged for damselflies alone. If the bass were actively excluding damselflies from the diet, there should have been a significant downturn in the damselfly capture rate during the first forty seconds of search in the optimal foraging trials, and there was (Figure 2, A vs. B, $P < .00015$). This depression of the damselfly encounter rate was not caused by the fact that the bass were spending foraging time eating guppies instead

FIGURE 2. Number of damselfly captures per ten seconds of search ($\pm$ 1 SE) for bass in high structure at various stages of the foraging experiments. A = damselfly capture rate during the first forty seconds of search when bass foraged for damselflies alone. B = damselfly capture rate during first forty seconds of search on days 5–7 of the optimal foraging experiments (both prey present). C = damselfly capture rate on days 5–7 once two guppies had been eaten.

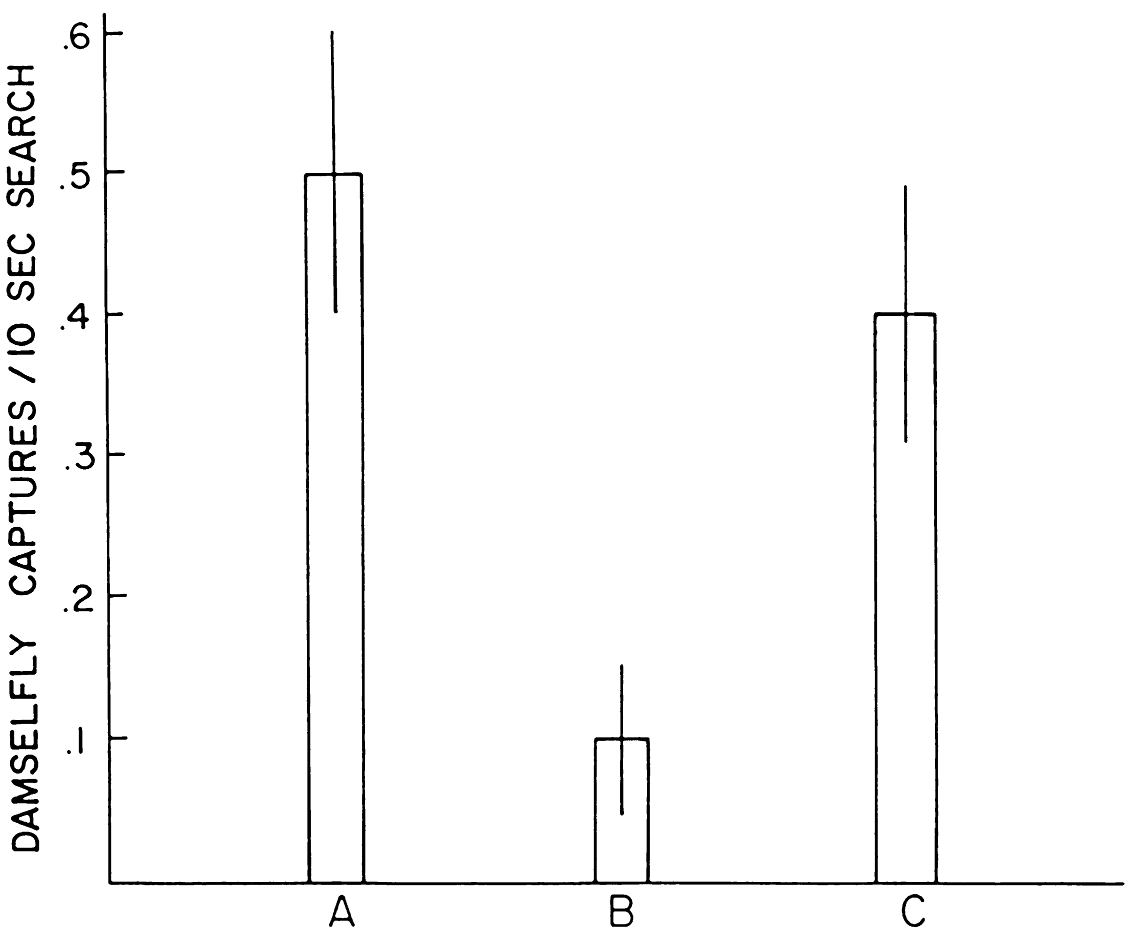

FIGURE 2.

of searching for damselflies, because the damselfly encounter rate is expressed as the number of captures per 10 seconds of search. Thus handling time with guppies is not responsible for decreased damselfly encounter rates. There was also a significant upswing in the damselfly encounter rate once the two guppies were captured (the second forty seconds of search during the optimal foraging bouts, Figure 2, B vs. C, $P < .005$), indicating that the bass changed their method of foraging and were then receptive to damselfly prey once two guppies were consumed, as predicted.

Further evidence that the bass in high vegetation had learned to forage for guppies until two were eaten and then accept damselflies into the diet came when the original high structure bass (fishes 4-6) were switched to low structure on day 8 (Table 6). Fishes 5 and 6 foraged in precisely the manner in which they had selected prey in high structure - capturing two guppies, then eating damselflies. Fish 4 began its foraging trial with three guppies; however, the third guppy was captured in close spatial proximity to the second individual without any intervening search. Thus, this bass would have had to reject an accessible, more valuable prey item - the third guppy, if it were to begin consuming damselflies immediately. The three bass seemed to be repeating an inappropriate behavior (for low structure) which had been learned in high vegetation. The fish changed their foraging mode quickly, however - on day 9 all three fish specialized and they continued to do so (with one exception) on days 10-14.

A variety of methods could have been employed by the bass in order to determine the best time to quit specializing on guppies and begin eating damselflies as well, including a time or capture expectancy or a giving up time (Krebs et al. 1974). The appropriate giving up time in high structure would have been approximately 22 seconds, as described earlier. However, if the forty second search time interval following the capture of two guppies is divided in two time periods of twenty seconds each, there is no difference in the damselfly capture rate between these shortened intervals. The immediate increase in damselfly encounters, apparent even in the first twenty seconds following the capture of two guppies, suggests that the bass were not using a giving up time but were hunting by expectation. Indeed, hunting by expectation was an energetically superior strategy. The number of guppies in high structure did not change from day to day - thus, time spent waiting to see if a third guppy could be captured in a short time interval would have resulted in a lowered rate of energy intake.

During the optimal foraging experiments, bass in low and high structure had higher rates of energy acquisition on days when they foraged in the predicted manner. Thus, if the bass were sensitive to differences in rates of energy acquisition, the optimal patterns of prey selection could have been reinforced over the course of the foraging trials. For example, by specializing on day 9, fishes 4-6 increased their energy intake rate (calculated after the first four prey captures) by from 31 to 125% compared to their first day in low structure (day 8), when they had generalized. Overall, fish in low structure acquired energy at a net rate of 34.7 ± 3.1 J/s (n = 32) on days when they specialized vs. 28.4 ± 4.0 J/s (n = 10) for generalized feeding.

Bass in high structure also had higher rates of energy intake on days when they foraged in the predicted manner. By eating two guppy prey at the beginning of foraging bouts, the bass were able to increase E_n/T by 75 to 450% compared to days when the first two prey taken were not fish (Table 7). High structure bass also did better on days when the third prey taken (after the consumption of two guppies) was a damselfly rather than a guppy. The FFD pattern produced an E_n/T of 16.7 ± 1.2 J/s (n = 22) compared with 10.0 ± 1.7 J/s (n = 6) for FFF in high structure.

DISCUSSION

A primary goal of this experimental work was to explore the effects of structural complexity on the foraging behavior of largemouth bass. The conclusion was that variation in structure produced significant changes in almost all aspects of the foraging process, including search times, handling times, rates of predator movement while searching for and handling prey, and overall diet breadths. The effects of structure on foraging behavior were at times unique to the prey type under consideration, however. For example, the decrease in the damselfly encounter rate from low to high structure could be directly related to the proportional decline in the average swimming speed of the bass while searching for damselflies in high structure (Table 1 and Table 3). In contrast, bass swam at the same

TABLE 7. Average rates of energy acquisition (J/s) after consumption of two prey by fishes 1–3 in high structure. An * indicates that the first two prey eaten were guppies, + indicates that a guppy and a damselfly were the first two prey, and ° indicates the first two prey were damselflies.

	E_n/T						
	Day 1	Day 2	Day 3	Day 4	Day 5	Day 6	Day 7
Bass 1	21.6*	10.3^+	14.5^+	15.3^+	24.3*	20.0*	28.8*
Bass 2	10.3*	7.6^+	24.3*	21.4^+	24.0*	24.0*	19.5*
Bass 3	2.0^+	3.9*	16.2*	14.2*	5.3°	45.2*	21.9*

rate while searching for guppies in low and high vegetation, yet there were large differences in the guppy encounter rates between structures, especially once two guppies had been eaten (Table 2). Of course, there were marked behavioral differences between the two prey types. Guppies attempted to swim away from sites of previous capture attempts by the bass, while damselflies did not. Such movement served to conceal guppies in high vegetation; in low structure it seemed to make them more easily detectable.

Handling times per captured prey individual increased significantly for both prey in high structure, but the changes were similar in magnitude (Table 1). Thus, the value (E_i/H_i) of both prey types fell in high structure, but guppies were still about four times as valuable as damselflies. Damselfly value was 17.2 J/s in low structure and 12.7 J/s in high structure; guppies were worth 64.7 J/s in low and 48.3 J/s in high. The major difference in diet selection between habitats seemed to be the result of the lowered encounter rate with guppies in high structure. Bass included damselflies in the diet (in high vegetation) when encounter rates with guppies fell below a certain level. In a field study, similar results were obtained (Anderson 1983b). Bass in an environment with moderate densities of vegetation had higher prey encounter rates and narrower diets than bass in a highly structured field environment.

A second goal of this study involved an evaluation of the efficacy of an optimal foraging model in predicting resource consumption by bass in the differently structured environments. The model's prediction of greater diet generalization in high structure was confirmed and the correspondence between the model's predictions and actual consumption patterns of the fish was generally stronger as the fish became more experienced in their particular environments (Tables 5 and 6). A variety of studies with fish (Werner and Hall 1974, Mittelbach 1981) and other organisms (Belovsky 1978, Erichsen et al. 1980, Pleasants 1981, Ostfeld 1982, Townsend and Hildrew 1980, Jenkins 1980) have yielded results which support predictions based on optimal foraging theory.

While a large amount of evidence has been gathered to support the idea that animals forage optimally, less is known about the specific behavioral mechanisms used by animals to accomplish maximal foraging efficiency (Ollason 1980). It is often hypothesized that animals use simple rules-of-thumb to make appropriate foraging decisions (Townsend and Hildrew 1980), and that such simple foraging rules lead to patterns of prey utilization indistinguishable from those predicted by optimal foraging theory (Breck 1978, Janetos and Cole 1981). A simple rule-of-thumb used by the bass in this study might have been: Attack fish prey - if no fish prey are in view, then search for damselflies. If bass preferred fish prey but would attack a damselfly if a fish were not in view, then one would naturally expect more fish to be taken as prey in low structure compared to high because of the difference in visibilities - a bass can see much farther in low structure. Three lines of evidence lead one to reject the idea that this mechanism was at work. First, in low structure, on several occasions a bass was observed to swim up closely to a damselfly, maintain momentary visual contact, and then swim on in search of the remaining guppies, which at the time were behind the bass and presumably out of view. Second, the behavior of fishes 4-6 on day 8 suggests that the fish were foraging according to a learned expectation of prey availability, even though their new environment, low structure, gave them a broad view of the prey that were present. Third, in high structure, at the beginning of foraging bouts the bass went through lengthy periods of search during which no guppy prey were visible, yet the data show that the bass were actively excluding damselflies from the diet during this period (Figure 2). For example, on days 13 and 14 the three bass in high structure searched for a combined total of 161.9 seconds before detecting the two guppy prey which were captured at the beginnings of each foraging bout. No guppies were in view during this extended search interval, yet no damselflies were taken as prey despite the fact that damselflies should have been encountered every 37 seconds. The evidence seems to support the idea that the bass were sensitive to their rates of energy acquisition.

There were several deviations from the optimal predicted pattern. Fish 1, while in low structure, foraged as predicted only twice (Table 5). Such "mistakes" have been generally attributed to unknown prey recognition times or to sampling and/or detection errors made by the predator (Krebs et al. 1977, Krebs 1978). The problem may actually reside with the application of the model rather than with the predator's ability to estimate energetic reward. For example, E_n/T for fish 1 was 36.0 $\pm$ .8 J/s on days 3 and 6, when it specialized, very close to the rate predicted by the model (35.6 J/s).

Fish 1 averaged 36.0 $\pm$ 4.2 J/s on the five days when it did not specialize, indicating that the model had underestimated its potential energy gain as a generalist and that there were no energetic penalties associated with including damselflies in the diet. The inability of the model to predict this fish's energetic rewards associated with various foraging modes was due to the fact that fish 1 changed its foraging behavior when both prey were present. Fish 1's average handling time with damselflies was 3.9 $\pm$ .4 s when guppies were present vs. 7.0 $\pm$ .5 s when foraging for damselflies alone. Further, during the optimal foraging trials, many damselflies were eaten as parts of multiple captures without intervening search, i.e., the bass often swallowed a damselfly enroute to capturing a fish prey. This inevitably led to an increase in the generalized E_n/T when both prey were present compared with the model's predictions, which were based on the fish's experience with single prey types. Zimmerman (1981) has argued that optimal foraging models are too simplistic because they can not adequately incorporate the behavioral flexibilities of predators; thus, predictions of changes in foraging behavior in response to alterations of environmental conditions may be doomed to failure because the set of behavioral possibilities and capabilities is unknown. In this study, the ability of fish 1 to almost simultaneously capture damselflies and fish prey was unanticipated.

The significant decline in the receptivity of bass to damselflies during the first 35-40 s of the foraging bouts in high structure, the high encounter rates with damselflies thereafter, and the residual effect exhibited by fishes 4-6 on their first day in low structure all suggest that the bass formed expectations regarding the nature of their prey communities and foraged according to those expectations. The gradual development of such expectancies followed by their extinction when new conditions were encountered suggests that they were learned behaviors. The theoretical importance of learning in determining predator-prey interactions has been explored by Murdoch and Oaten (1975), Hughes (1979), and Werner et al. (1981). Tinbergen (1960), Norton-Griffiths (1967), Dawkins (1971), Lawton et al. (1974), and Mittelbach (1981) have shown that the relative use of different prey types (or habitats) can be significantly influenced by experience. Jaeger and Rubin (1982) demonstrated that salamanders learned through foraging experience to assess the profitabilities of prey types. Only those salamanders which had previously encountered two different prey types were able to forage optimally when both prey types were presented together.

Structural complexity apparently influenced the rate at which the foraging behaviors were learned. Transferred bass in low structure achieved day-to-day repeatability in prey selection in one day (Days 8-9) compared with the four to five day interval required by the fish in high structure (Table 6). Obviously, it should be easier for predators in less structured environments to monitor the sizes, distributions, and abundances of their prey. Sampling confidence should also be greater in low structure - note that the variance associated with most of the foraging parameters is smaller there (Tables 1 and 2). Only the variance associated with the velocity required to pursue and capture (handle) prey was greater in low structure (Table 3), and this foraging parameter made the least difference

to the overall rate of energy gain.

In switching from specialized to generalized feeding in high structure, bass did not use a giving up time strategy, but the data did not permit a differentiation between two other strategies - a time or number expectancy. Clearly, the optimal behavior in high structure was more complex than the best foraging mode in low vegetation. To maximize E_n/T, high structure bass had to learn to change their foraging behavior within a feeding bout as the more valuable prey became depleted. The ability of the bass to do so seemed remarkable. An analagous situation may occur under natural conditions if small fish which are potential prey of largemouth bass become more secretive, cautious, and evasive once a nearby prey individual has been captured. Such resource depression might require bass to change their foraging tactics and become less selective in order to continue to acquire energy. Davies (1977) and Holmes et al. (1978) have observed marked changes in prey selection by individual birds on a diel basis which were related to changes in prey type availability.

Based on energetic considerations alone, young bass should prefer to forage in relatively unstructured rather than highly structured environments, as long as resource levels are not strikingly enhanced in high structure. In contrast, predation risk should cause small bass to favor more highly structured habitats. An interesting follow-up to this study would involve the analysis of habitat selection by bass vis-a-vis structural complexity: Do bass choose habitats according to foraging profitability or minimization of predation risk?

The goal of this research has not been to make such predictions but to suggest consequences, in terms of diet selection, for bass once habitat selection has been accomplished. Bass in highly structured habitats can be expected to be more generalized feeders than other bass in less structured areas. This hypothesis has been supported by an initial field study (Anderson 1983b). Structure should then mitigate the effect of predation on preferred prey species of the bass, possibly resulting in changes in the overall composition of the prey community. Such a relationship between structural complexity, predation intensity, and the resultant nature of the prey community has already been documented in a marine epifaunal community (Russ 1980).

LITERATURE CITED

Adams, C. 1975. The nutritive value of foods. United States Department of Agriculture. Washington, D. C.

Anderson, O. 1983a. The effects of structural complexity on foraging behavior and diet breadth. Submitted to Ecology.

Anderson, O. 1983b. Prey selection and growth of largemouth bass at different macrophyte densities. Submitted to Transactions of the American Fisheries Society.

Belovsky, G. E. 1978. Diet optimization in a generalist herbivore: the moose. Theoretical Population Biology 14:105-134.

Breck, J. E. 1978. Suboptimal foraging strategies for a patchy environment. Ph.D. thesis, Michigan State University.

Charnov, E. L. 1976. Optimal foraging; attack strategy of a mantid. American Naturalist 110:141-151.

Cook, R. M., and B. J. Cockrell. 1978. Predator ingestion rate and its bearing on feeding time and the theory of optimal diets. Journal of Animal Ecology 47:529-547.

Cowie, R. J. 1977. Optimal foraging in great tits (*Parus major*). Nature 268:137-139.

Cummins, K. W., and J. C. Wuycheck. 1971. Caloric equivalent for investigations in ecological energetics. Internationale Vereinigung fur Theoretische und Angewandte Limnologie, Mitteilungen 18:1-158.

Curio, E. 1976. The ethology of predation. Springer-Verlag, New York, New York, USA.

Davies, N. B. 1977. Prey selection and social behaviour in wagtails (Aves: Motacillidae). Journal of Animal Ecology 46:37-58.

Dawkins, M. 1971. Shifts of "attention" in chicks during feeding. Animal Behaviour 19:575-582.

Elliot, J. M. 1976. The energetics of feeding, metabolism and growth of brown trout (Salmo trutta) in relation to body weight, water temperature and ration size. Journal of Animal Ecology 45:923-948.

Elliot, J. M., and W. Davidson. 1975. Energy equivalents of oxygen consumption in animal energetics. Oecologia 19:195-201.

Erichsen, J. T., J. R. Krebs and A. I. Houston. 1980. Optimal foraging and cryptic prey. Journal of Animal Ecology 49:271-276.

Gerking, S. D. 1957. A method of sampling the littoral macrofauna and its application. Ecology 38:219-225.

Gill, J. L. 1978. Design and analysis of experiments in the animal and medical sciences. Iowa State University Press, Ames, Iowa, USA.

Glass, N. R. 1971. Computer analysis of predation energetics in the largemouth bass. Pages 325-363 in B. C. Patten, editor. Systems analysis and simulation in ecology. Volume 1. Academic Press, New York, New York, USA.

Heidinger, R. C. 1975. Life history and biology of the largemouth bass. Pages 11-20 in Henry Clepper, editor. Black bass biology and management. Sport Fishing Institute, Washington, D. C.

Holmes, R. T., T. W. Sherry, and S. E. Bennett. 1978. Diurnal and individual variability in the foraging behavior of American redstarts (Setophaga ruticilla). Oecologia 36:141-149.

Hughes, R. N. 1979. Optimal diets under the energy maximization premise: the effects of recognition time and learning. American Naturalist 113:209-221.

Ivlev, V. W. 1961. Experimental ecology of the feeding of fishes. Yale University Press, New Haven, Connecticut, USA.

Jaeger, R. G., and A. M. Rubin. 1982. Foraging tactics of a terrestrial salamander: Judging prey profitability. Journal of Animal Ecology 51:167-176.

Janetos, A. C., and B. J. Cole. 1981. Imperfectly optimal animals. Behavioral Ecology and Sociobiology 9:203-209.

Jenkins, S. H. 1980. A size-distance relation in food selection by beavers (Castor canadensis). Ecology 61:740-746.

Krebs, J. R. 1978. Optimal foraging: decision rules for predators. Pages 23-63 in J. R. Krebs and N. B. Davies, editors. Behavioural ecology. Sinauer Associates, Sunderland, Massachusetts, USA.

Krebs, J. R., Ryan, J. C., and E. L. Charnov. 1974. Hunting by expectation or optimal foraging? A study of patch use by chickadees. Animal Behaviour 25:10-29.

Krebs, J. R., Erichsen, J. T., Webber, M. I., and E. L. Charnov. 1977. Optimal prey selection in the Great Tit (Parus major). Animal Behaviour 25:30-38.

Lawton, J. H., J. R. Beddington, and R. Bonser. 1974. Switching in invertebrate predators. Pages 141-158 in M. B. Usher and M. H. Williamson, eds. Ecological Stability. Chapman and Hall, London.

MacCrimmon, H. R., and W. H. Robbins. 1975. Distribution of the black basses in North America. Pages 56-66 in Henry Clepper, editor. Black bass biology and management. Sport Fishing Institute, Washington, D. C.

Mittelbach, G. G. 1981. Foraging efficiency and body size: a study of optimal diet and habitat use by bluegills. Ecology 62:1370-1386.

Murdoch, W. W. and A. Oaten. 1975. Predation and population stability. Advances in Ecological Research 9:1-130.

Norton-Griffiths, M. 1967. A study of the feeding behaviour of the oyster-catcher Haematopus ostralegus. D. Phil. Thesis, Oxford University.

Nyberg, D. W. 1971. Prey capture in the largemouth bass. American Midland Naturalist 86:128-144.

Ollason, J. G. 1980. Learning to forage - optimally? Theoretical Population Biology 18:44-56.

Ostfeld, R. S. 1982. Foraging strategies and prey switching in the California sea otter (Enhydra lutris). Oecologia 53:170-178.

Pleasants, J. M. 1981. Bumblebee response to variation in nectar availability. Ecology 62:1648-1661.

Pyke, G. H. 1978. Optimal foraging in hummingbirds: testing the marginal value theorem. American Zoologist 18:739-752.

Russ, G. R. 1980. Effects of predation by fishes, competition, and structural complexity of the substratum on the establishment of a marine epifaunal community. Journal of Experimental Marine Biology and Ecology 42:55-69.

Stein, R. A. 1977. Selective predation, optimal foraging, and the predator-prey interaction between fish and crayfish. Ecology 58:1237-1253.

Stoner, A. W. 1982. The influence of benthic macrophytes on the foraging behavior of pinfish, Lagodon rhomboides. Journal of Experimental Marine Biology and Ecology 23:255-266.

Tinbergen, L. 1960. The dynamics of insect and bird populations in pine wood. Arch. Néerl. Zool. 13:259-473.

Townsend, C. R., and A. G. Hildrew. 1980. Foraging in a patchy environment by a predatory net-spinning caddis (Plectrocnemia conspersa) larva: A test of optimal foraging theory. Oecologia 47:219-221.

Vince, S., Valiela, I., Backus, N., and J. M. Teal. 1976. Predation by the salt marsh killifish Fundulus heteroclitus in relation to prey size and habitat structure: consequences for prey distribution and abundance. Journal of Experimental Marine Biology and Ecology 23:255-266.

Ware, D. M. 1973. Risk of epibenthic prey to predation by rainbow trout (Salmo gairdneri). Journal of the Fisheries Research Board of Canada 30:787-797.

Werner, E. E., and D. J. Hall. 1974. Optimal foraging and the size selection of prey by the bluegill sunfish (Lepomis macrochirus). Ecology 55:1042-1052.

Werner, E. E., and G. G. Mittelbach. 1981. Optimal foraging: field tests of diet choice and habitat switching. American Zoologist 21:813-829.

Werner, E. E., Mittelbach, G. G., and D. J. Hall. 1981. Foraging profitability and the role of experience in habitat use by the bluegill sunfish. Ecology 62:116-125.

Zimmerman, M. 1981. Optimal foraging, plant density, and the marginal value theorem. Oecologia 49:148-153.

THE EFFECTS OF STRUCTURAL COMPLEXITY

ON FORAGING BEHAVIOR

AND DIET BREADTH

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INTRODUCTION

Ecologists have long been interested in how changes in patterns of habitat or prey utilization are related to modifications in resource levels (Emlen 1966, MacArthur and Pianka 1966). Questions linking habitat use and prey choice to the availability of resources are of fundamental importance in understanding the effects of competition at the community level (Mittelbach 1981a).

MacArthur and Pianka (1966) theorized that as resource levels declined, populations would tend to limit their foraging activities to those patches in which they were most efficient, thus decreasing their breadth of habitat utilization. Ivlev (1961) and Curio (1976) documented increases in diet breadth with decreasing levels of prey abundance, a relationship predicted by the theoretical work of Emlen (1966) and Schoener (1971). Krebs et al. (1977) and Goss-Custard (1977) demonstrated that changes in diet breadth were primarily dependent on alterations in the abundance of preferred, but not non-preferred, prey. Non-preferred prey were not included in the diet unless the availability of preferred prey declined; increasing the density of non-preferred prey did not lead to their inclusion in the diet (but see Elner and Hughes 1978).

One factor which reduces the availability of prey is the amount of structure in the environment in which a predator forages (Ware 1973). Here structure can be defined as the discrete, physical components of an environment (vegetation, rocks, debris, etc.) which interfere with a predator by restricting its field of vision or rate of movement.

Generally, increases in structural complexity have been shown to reduce rates of prey capture (Glass 1971, Ware 1973, Vince et al. 1976).

Considering only structure's influence on prey availability, it would appear that increased amounts of structure should lead to more generalized diets for predators which are sensitive to their rates of energy acquisition. By lowering prey capture rates (and thus energy intake), increased structural complexity should make predators more receptive to lower quality food items (Figure 1). Vince et al. (1976) examined patterns of prey choice by killifish (*Fundulus heteroclitus*) and found that the killifish were generalists in high structure and were highly selective at low macrophyte densities.

This simple view of the functional relationship between structure and diet breadth was contradicted by the experimental manipulations of Stoner (1982), who observed narrower diets in pinfish (*Lagodon rhomboides*) at increased structural levels. Apparently, one of the prey types utilized by Stoner gained almost complete refuge from predation in high structure and was rarely part of the diet. Thus, if a portion of the prey community becomes unavailable at high levels of structure, predators might appear to be more selective only because there are fewer prey types from which to choose.

In high structure, large, mobile prey should be less likely to become unavailable than small, sedentary prey. Indeed, Crowder and Cooper (1982) reported that at high macrophyte levels, the proportional representation of large invertebrate prey in the diets of bluegill sunfish increased. At low macrophyte levels, bluegills ate more small prey. It should be pointed out, however, that structural complexity

FIGURE 1. Proposed mechanism by which diet breadth increases as prey encounter rates decline. The solid line plots net energy gained (E_n) vs. time spent foraging (T) for a predator when prey availability is high. The dashed line is for the same relationship but with low prey availability. Symbols (stars, closed circles, and open circles) show net energy gained (E_i) from eating an individual of a particular prey type vs. the handling time (H_i) for that prey type. Stars represent prey types eaten under both conditions of prey availability; prey represented by closed circles are not consumed when the availability of preferred prey is high (the solid line) because such consumption would lower E_n/T. Prey represented by open circles are excluded from the diet in both cases.

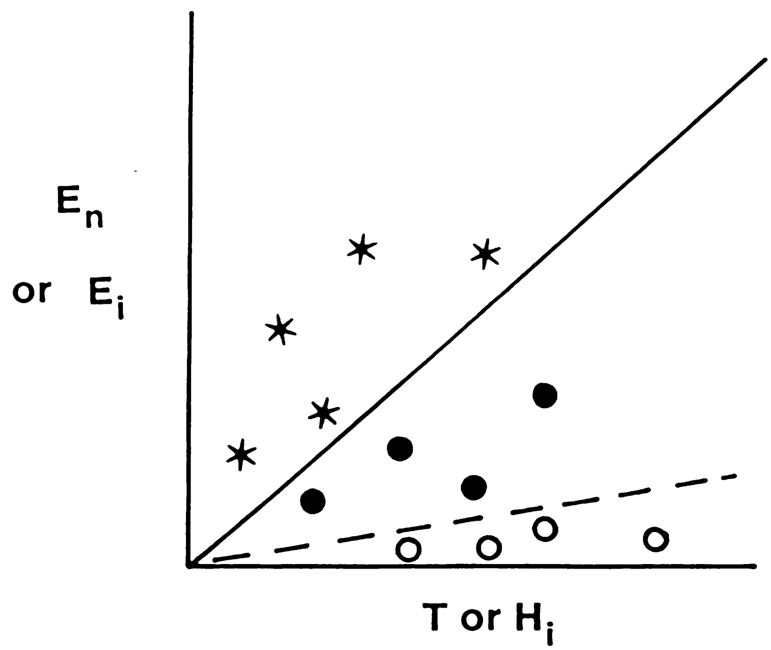


FIGURE 1.

and prey densities are usually positively correlated. Crowder and Cooper (1982) argued that broad diets should prevail in low structure because of resource impoverishment with consequent low energetic yields for predators.

Further complexity is added to the structural complexity - diet breadth relationship with the realization that even perfect knowledge of prey availability is alone insufficient to completely predict diet composition. Foraging models which incorporate not only prey encounter rates but also prey handling times and net energetic contents have been successful in predicting diet selection (Werner and Hall 1974, Mittelbach 1981a, Werner and Mittelbach 1981). It is reasonable to think that structural complexity will influence these additional components of the foraging process. For example, Glass (1971) reported that fish prey were adept at using structure to evade largemouth bass predators, thus lengthening the total time required by bass to handle such prey in highly structured environments. In the same study Glass suggested that the energetic costs of capturing prey increased markedly at higher structural levels, implying that the net energy gained per prey item declined with increased structure. If increased levels of structure acted to dramatically increase the energetic costs associated with pursuing certain prey or the time required to handle certain prey, increased structure might then lead to active rejection of such prey by predators and thus greater selectivity. Alternately, if structure reduced the probability of capturing some prey after predator detection and attack, increased structure could produce greater apparent selectivity (narrower diets). Thus the effects of structural complexity on prey selectivity can potentially be mediated by many factors, including prey densities and encounter rates, handling times, and the energetic costs of foraging.

A logical first step toward: (1) assessing the relative importance of these factors, and (2) understanding how structure influences patterns of prey selection by predators, would be to break the foraging process into discrete parts and then examine how each part varies with structural complexity for a variety of prey types. In this study I quantify prey encounter rates, handling times, prey values, capture success, and the energetic costs of searching for and handling prey as functions of structural complexity using a predator, the largemouth bass (*Micropterous salmoides*), which commonly forages in structured environments, and three representative prey types. I then integrate the components of the foraging process and use an optimal foraging model to predict general patterns of resource utilization by bass in differently structured environments. These predictions are then compared with what is known about the foraging behavior of bass in differently structured, multi-prey communities.

METHODS

In the laboratory three structurally different foraging environments were created by placing either 5, 10, or 15 plastic *Elodea* plants (12 stems/plant) in three separate 208-L aquaria. The plants were uniformly spaced and anchored in a sand substrate. Stem densities ranged from 200-600/m^2.

Each aquarium possessed a small volume (24L) at one of its ends with no plants. This portion of the aquarium, separated from the rest of the foraging area by an opaque Plexiglas sliding door, served as an acclimation chamber for the largemouth bass.

Prior to each foraging trial, a single bass was placed in the small chamber and allowed to acclimate for thirty minutes. The Plexiglas door was then raised, allowing the bass to swim into the larger volume, which contained the plants and prey.

Nine largemouth bass were used in the experiments, three in each environment. The bass were randomly selected from a group of largemouth bass provided by the New London National Fish Hatchery, New London, Minnesota, USA, for a field study at an EPA outdoor laboratory in Monticello, Minnesota. The fish, which had an initial total length of approximately 35 mm, were allowed to grow in semi-natural stream environments which contained a full complement of natural aquatic prey until they reached 60 mm in length. The nine fish were then selected, brought into the laboratory, and housed separately in 110-L aquaria. On days when the bass were not being tested, they were fed small aquatic invertebrates, mainly amphipods. The bass averaged 70 mm in total length during the experiments. A complete foraging record was maintained for each fish.

Three different prey types were used in the experiments - fathead minnows (Pimephales promelas), Callibaetis mayflies, and Coenagrionid damselflies. Mayflies and damselflies are common prey of small largemouth bass, and it was hoped that the fathead minnows would be representative of the small fish prey for which 70 mm bass often forage.

The bass foraged for only a single prey type during any specific trial; no combinations of prey types were utilized. Various densities of minnows and mayflies were used, ranging from 42-333/m^3. Each density was replicated at least twice. A single density of damselflies was used, 416/m^3, with triplicate replication.

Uniform sizes of each prey type were utilized during the experiments. Dry weights were obtained by drying thirty representative individuals of each type for 48 hours at 45 C and then weighing to the nearest .1 mg. Dry weights in mg. ($\pm$ 1 SE) were: fathead minnows, 9.9 $\pm$ .6; mayflies, 2.0 $\pm$ .1; and damselflies, 2.3 $\pm$ .1. These dry weights were used to compute the energetic contents of the prey in order to predict patterns of diet breadth for largemouth bass in relation to structural complexity (see below).

The bass had not eaten for 24 hours prior to each test and foraged actively for the prey. From behind a blind an observer recorded the foraging behavior on a voice tape recorder. Foraging time spent by the bass was categorized as either search time or handling time, where handling time included the time required to pursue, capture, and swallow a prey item, plus the pause after swallowing. The bass searched for prey by swimming steadily through the water, frequently changing their direction of movement and adjusting the position of the eyes. The beginning of handling time was easily distinguishable from searching behavior because it involved an accelerated, unidirectional movement toward a prey item which could usually be seen by the observer as well. At the end of the handling period for a particular prey individual a bass was usually stationary, with its gill covers flaring in and out in a pumplike manner. Search was reinitiated when the bass stopped the pronounced gill cover movement and resumed swimming with a strong thrust of the caudal fin.

At the end of each day's nine trials, the tape recording of the foraging behavior was replayed, and a Heuer 410 microsplit digital stopwatch was utilized to obtain the time required to search for and handle each prey individual. The success or failure of each capture attempt was also noted.

Additionally, the aquaria had been marked in a grid-like pattern with 5 cm markings so that the spatial positions of the bass could be recorded throughout the trials. Coupling the spatial positions with the times when searching or handling behaviors commenced and ended made it possible to calculate the velocities of the bass while searching for and handling prey. The velocities were employed to estimate the energetic costs incurred by the bass while handling or searching.

The foraging trials were usually short, both to eliminate any problems associated with significant changes in prey density within the aquaria during a foraging bout and to guard against alterations in search or handling times due to changes in motivational state. Generally, the bass ate four or fewer minnows and six or less damselflies or mayflies, and only at the lowest density of fathead minnows and mayflies were prey densities reduced by greater than 25% during a foraging trial.

Data recorded during the time that the bass were learning to use the foraging environments and/or search for or handle a particular type of prey were not used in the analyses. When a bass foraging in a particular level of structure had similar average search and handling times over the course of three consecutive foraging bouts for a specific prey type at a given density, it was judged that the learning process was complete.

Using these methods it was possible to relate the encounter rate, defined as the number of prey captured per second of search, to the amount of structure for each prey type and to examine the influence of structural complexity on prey handling times, capture success, and the rates of movement by bass while searching for and handling prey.

To predict general patterns of resource utilization by bass in differently structured environments, an optimal foraging model similar to that developed by Charnov (1976) and utilized successfully by Mittelbach (1981a) was employed. This foraging model takes the form:

$$(1) \quad E_n/T = \frac{\sum_{i=1}^{n} B_i E_i - C_s}{1 + \sum_{i=1}^{n} B_i H_i}$$

where E_n = the net energy gained while foraging (cal), T = the time spent foraging (s), B_i = the encounter rate with prey type i (# captures/s), E_i = the net energetic gain associated with prey type i (cal), C_s = the cost of searching (cal/s), and H_i = the time required to handle prey type i (s).

E_i, the net energetic gain associated with prey type i, can be defined as:

$$(2) \quad E_i = Ae_i - C_h H_i,$$

where e_i = the actual energetic content of prey type i, A = the fraction of the prey's energy content which can be assimilated by the bass, and C_h = the cost of handling prey type i (cal/s).

A, the assimilable fraction of energy ingested, was assumed to be .7 (Elliot 1976). The e_i's were estimated by using the dry weights of the prey types and assuming that 1 mg dry mass = 5.1 cal for the mayflies and damselflies (Cummins and Wuycheck 1971) and 1 mg = 5 cal for the fathead minnows (Adams 1975).

The costs of searching for and handling different prey types were calculated using the mean velocities of the bass while foraging for different prey types. Translation of velocity into cost was accomplished using the relationship described by Glass (1971),

$$(3) \quad Y = RM + bV^{c},$$

where Y is the oxygen consumption in mg/hour, RM is the rate of oxygen consumption at zero velocity (routine metabolic level), V is the velocity of the bass in cm/s, and b and c are constants. For 70 mm bass, the appropriate equation (Glass 1971) is:

$$(4) \quad Y = 2.08 + (.26)\,V^{(1.7)}$$

for the ambient temperatures (18-21^{o}C.) utilized in these experiments. Oxygen consumption was converted to calories expended/second by assuming that 1 mg oxygen consumed equals 3.25 cal (Elliot and Davison 1975).

Average handling velocities were used to compute the costs of handling even though the handling process itself actually combines periods of burst swimming activity and small amounts of time when the bass is relatively motionless. Rice and Breck (1982) have shown that such averaging results in only minor changes in the estimates of metabolic costs of the largemouth bass.

Since all the parameters of the optimal foraging model could be quantified for each prey type as functions of structural complexity, it was possible to predict diet breadth for the bass over a wide range of prey densities in differently structured environments.

To make such predictions, the concept of prey value is a useful tool. Value can be defined as E_i/H_i, the net energy gained from an individual of a particular prey type divided by its handling time. Value is thus the average rate of energy acquisition while handling individuals of a particular prey type. In the optimal foraging model, a prey type, i, should be included in the diet if its value exceeds the rate of energy intake garnered by a predator while foraging for those prey types already in the diet (Charnov 1976). Since E_i's and H_i's were determined during the foraging trials, it was possible to examine how each prey type's value changed with structure and to predict dietary inclusion or exclusion of a prey type at various prey densities and structural levels.

RESULTS

Encounter Rates

Structure had a predictable effect on the encounter rates (# captures/second of search) by bass with *Callibaetis* mayflies. At each structural level there was a highly significant elevation of the encounter rate with increases in prey density (Figure 2, Table 1), but the slopes of the three regression lines are significantly different ($L > M$, $M > H$, $P < .05$). Thus, for a given *Callibaetis* density, the encounter rates can be ranked: L M H.

A quite different relationship was observed with the fathead minnow, *Pimephales promelas*, as prey. Here the slope of the regression

FIGURE 2. Mean encounter rates (# captures/second of search, $\pm$ 1 SE) for largemouth bass in relation to the density of *Callibaetis* mayflies in laboratory environments with low (L), medium (M), and high (H) amounts of structure. Multiply mayfly densities by 8.33 to obtain $\#/m^3$. Lines were drawn from the regression equations in Table 1.

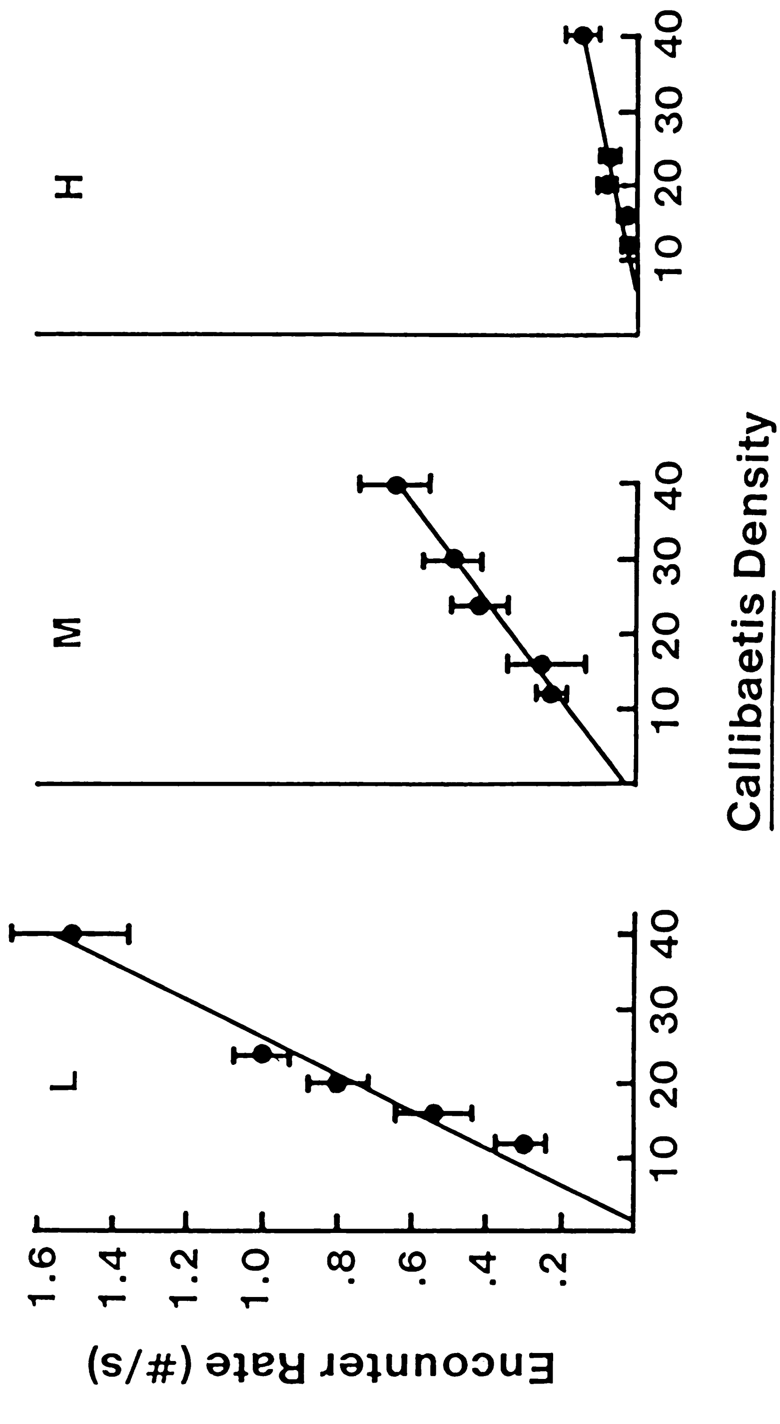

Encounter Rate (#/s)
1.6
1.4
1.2
1.0
.8
.6
.4
.2
L
M
H
10 20 30 40
10 20 30 40
10 20 30 40
Callibaetis Density

FIGURE 2.

TABLE 1. Fitted parameters ($\pm$ 1 SE) of the linear regression equation describing encounter rates (B) by largemouth bass with mayflies in three structurally different environments. The form of each equation is $B = a + b_1x$, with x = mayfly density (number per aquarium).

Environment	a	b_1	Significance level	n
Low structure	$-.06 \pm .21$	$.040 \pm .008$	.001	83
Medium structure	$.04 \pm .12$	$.015 \pm .004$	.005	84
High structure	$-.02 \pm .03$	$.004 \pm .001$	.005	85

line relating encounter rate to prey density was actually increased in medium structure compared to low or high structure ($P<.05$) and there was no significant difference between low and high structures (Figure 3, Table 2). Higher encounter rates with fathead minnows in medium structure were the result of the combined effects of structural complexity and the behavior of the prey. The fathead minnows tended to aggregate in schools, doing so most dramatically in the low structure environment and to a much lesser extent in the more structured aquaria. The bass avoided dense aggregations of fatheads, lowering the encounter rate in low structure. Although the fatheads schooled little in high structure, the bass had difficulty finding them because of the increased amount of structure. As a result, the encounter rates were highest in medium vegetation.

The bass in low structure seemed to search for solitary fathead minnows, bypassing aggregated groups of the prey. Many studies have demonstrated that schooling reduces the susceptibility of fish prey to predators (Radakov 1958, Neill 1970 and 1974, Shaw 1978). In this study no quantitative record was kept relating capture success to the spatial position of a prey item relative to other prey, but qualitatively it did seem that fewer captures resulted on occasions when bass attacked a group of fatheads. Also, the regression of handling time on fathead density in low structure had a positive slope and was moderately significant ($P<.10$). Prey density should be positively related to the probability of schooling and the average number of prey individuals in a group. Since handling time increased with density, there was an indication that schooled prey had reduced value (E_i/H_i).

FIGURE 3. Mean encounter rates (# captures/second of search, $\pm$ 1 SE) for largemouth bass in relation to the density of fathead minnows (*Pimephales promelas*) in laboratory environments with low (L), medium (M), and high (H) amounts of structural complexity. Multiply prey densities by 8.33 to obtain $\#/m^3$. Lines were drawn using the regression equations in Table 2.

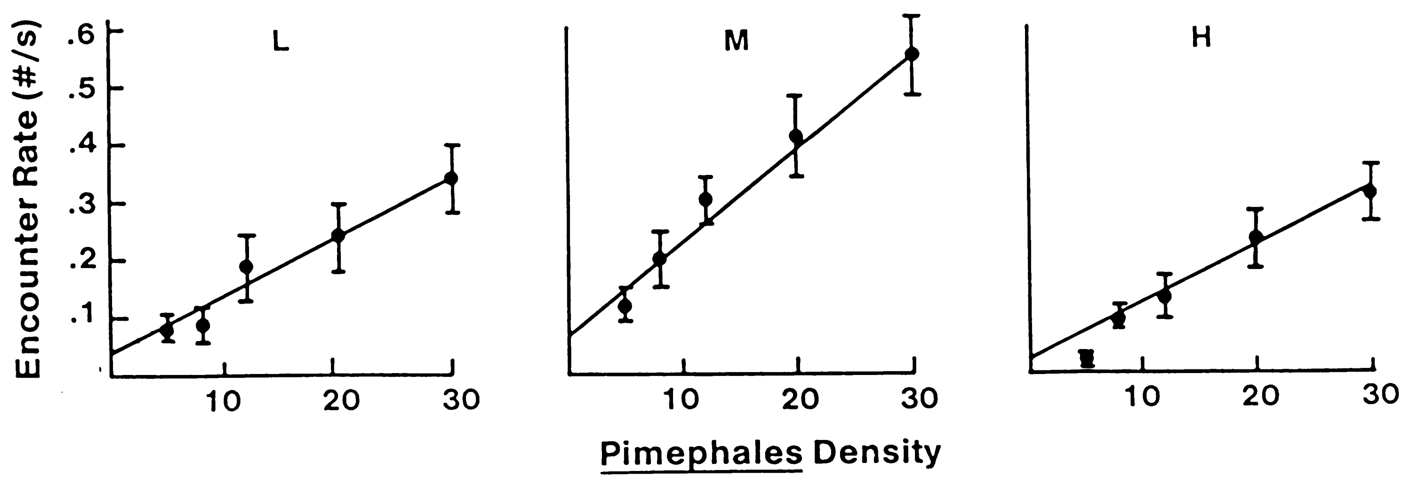


FIGURE 3.

TABLE 2. Fitted parameters ($\pm$ 1 SE) of the linear regression equations describing encounter rates (B) by largemouth bass with fathead minnows in three structurally different environments. The form of each regression equation is: $B = a + b_1x$, with x = fathead minnow density (number per aquarium).

Environment	a	b_1	Significance level	n
Low structure	$-.04 \pm .07$	$.010 \pm .003$	.005	83
Medium structure	$.07 \pm .06$	$.018 \pm .003$	.001	99
High structure	$-.02 \pm .05$	$.010 \pm .003$	.001	93

The positive relationship between handling time and fathead minnow density did not occur in medium or high structure, where schooling behavior was reduced.

The magnitude of the effect that structure has on encounter rates should be quite prey-specific. Larger, more mobile prey should have encounter rates which, relative to smaller, more sedentary prey, are less influenced by changes in the quantity of environmental structure. Thus it was expected that bass would have higher encounter rates with actively swimming, larger *Pimephales* than with sedentary *Callibaetis*, and that the changes in encounter rates associated with differences in structure would be smaller for *Pimephales*.

Indeed, for a given prey density, the highest encounter rate (in medium structure) was only 1.8 - 2 times greater than the lowest encounter rates (in low and high structure) for *Pimephales*, whereas for *Callibaetis* there was a tenfold increase in the encounter rate from high to low structure (Table 3).

At medium and high structures, the encounter rate was higher with *Pimephales* than with *Callibaetis* at any given density, as expected (Table 3). But in low structure, mayfly encounter rates were higher, due to the fathead schooling effect and an additional factor. In low structure, where bass obtained unobstructed views of their surroundings, it was possible for there to be several mayflies within the reactive field (that region of space within which the bass can detect prey). Thus, several prey could be captured without the necessity of intervening search, increasing the mayfly encounter rate, which was expressed in captures per second of search. This phenomenom could not

TABLE 3. Predicted mean encounter rates (captures per second of search with 95% C. I.) by largemouth bass with *Callibaetis* and fathead minnow (*Pimephales*) prey at different prey densities (#/m^3) in environments with different amounts of structural complexity. L - low structure, M - medium structure, and H - high structure. Encounter rates and intervals were calculated using the linear regression relationships described in Tables 1 and 2.

	ENCOUNTER RATES					
	Callibaetis			*Pimephales*		
Density	L	M	H	L	M	H
50	.18 ± .35	.13 ± .20	.004 ± .06	.10 ± .10	.18 ± .08	.08 ± .09
100	.42 ± .27	.22 ± .16	.03 ± .04	.16 ± .08	.29 ± .06	.14 ± .06
150	.66 ± .20	.31 ± .12	.05 ± .03	.22 ± .07	.39 ± .05	.20 ± .05
200	.90 ± .17	.40 ± .09	.08 ± .02	.28 ± .08	.50 ± .07	.26 ± .06
250	1.14 ± .17	.49 ± .09	.10 ± .03	.34 ± .10	.61 ± .10	.32 ± .08
300	1.23 ± .22	.58 ± .13	.12 ± .04	.40 ± .14	.72 ± .13	.38 ± .10

occur with fatheads, which fled from sites of prey capture and had to be searched for anew, nor could it occur at higher structural levels where the shielding effect of the vegetation reduced the probability of there being multiple prey simultaneously in view. Thus prey behavior and spatial distribution, in addition to size, are important factors in determining prey encounter rates at different levels of structure.

Bass predators had much higher encounter rates with *Callibaetis* than with Coenagrionid damselflies at all structural levels (Table 4). Despite the fact that individuals of the two prey types were very similar in size, the two prey were quite different behaviorally. The Coenagrionids were climbers, always positioning themselves on the vegetation, whereas many *Callibaetis* individuals were found on the sand substrate. As a result, in low structure the Coenagrionids were hidden by the stems and leaves of the small amount of vegetation that was present while *Callibaetis* individuals were relatively unprotected. Average Coenagrionid search times were eleven times greater than *Callibaetis* search times in low structure (Table 4). As the amount of structure increased and *Callibaetis* gained protection from the interposed vegetation, the differences in average search times between the two prey became proportionately smaller but were still highly significant. Welch's t' statistic (Gill 1978) was employed to make comparisons between prey types because of heterogeneous variance. The large observed differences in the search times for these similar sized prey indicate that the specific effects of structure will depend on whether structure intervenes between a predator and its prey (as it did

TABLE 4. Comparisons of search times ($\pm$ 1 SE, in seconds) required by largemouth bass to detect *Callibaetis* mayflies and Coenagrionid damselflies in differently structured environments. Mayfly density was $333/m^3$, damselfly density equaled $416/m^3$. Values of Welch's t' statistic, degrees of freedom, and probability of Type I error are given for each comparison.

Structure	Mayfly Search Time	Damselfly Search Time	t'	v	P
Low	$1.1 \pm .2$	11.8 ± 2.9	3.6	30	.0005
Medium	$2.8 \pm .3$	22.9 ± 3.9	5.1	35	.0005
High	14.7 ± 4.0	83.0 ± 16.4	4.3	19	.0005

with *Callibaetis*) or is actually the source of the prey (as with Coenagrionids). In the latter case, the masking effect of structure should be greater, especially at low levels of structure.

Both invertebrate prey types were easier to capture than the fish prey (Table 5). Structure had little influence on capture success within a prey type (# successful captures X 100 / # captures attempted) except when fathead minnows were the prey. 24% of the minnow capture attempts ended in failure in high structure.

HANDLING TIMES

The time required to handle prey increased as a function of structural complexity for all prey types (Tables 6 and 7). The average handling time for fathead minnows increased from 10.4 to 14.5 s in high structure, as the minnows in high structure lengthened pursuit times by darting in and out of the abundant vegetation and increased the average handling time per captured prey item by escaping more often.

Mayfly handling time was markedly affected, almost doubling from low to high structure. Two proximate factors should act to reduce mayfly handling times at lower levels of structure. First, since vision is relatively unrestricted in low structure, there is an increased probability that another prey will be in sight while a mayfly is being eaten. The stimulus of the second prey in view may cause the bass to quicken or shorten the handling behavior with the original prey. Also, the attack on the first prey may bring the bass somewhat close to the

TABLE 5. Percentage of capture attempts which are successful for largemouth bass with three prey types at three structural levels. L - low, M - medium, and H - high levels of structure. N is greater than 90 for each combination of structure and prey type.

Prey	L	M	H
Mayflies	100%	100%	97%
Damselflies	98%	99%	99%
Fathead minnows	82%	86%	76%

TABLE 6. Mean handling times (± 1 SE) in seconds for largemouth bass with three different prey types in structurally complex environments - low (L), medium (M), or high (H).

Prey	L	M	H
Mayflies	3.9 ± .2	4.4 ± .2	7.1 ± .4
Damselflies	7.4 ± .6	8.4 ± .7	9.4 ± .7
Fathead minnows	10.4 ± .9	12.2 ± .8	14.5 ± 1.1

TABLE 7. Tests of significance for structure-related differences in handling times by bass with three different prey types. For each prey type, two mutually orthogonal contrasts are shown. For each contrast, $delta_k$ (the difference between the averages of the observations on either side of the contrast), the t statistic, and probability of Type I error are given. H = high structure, M = medium structure, and L = low structure.

Prey Type	Contrast	$delta_k$	t	P
Mayflies	M vs. L	.5	1.3	.10
	H vs. M & L	3.0	8.8	.0005
Damselflies	M vs. L	1.0	1.1	.15
	H vs. M & L	1.5	1.9	.05
Fatheads	M vs. L	1.8	1.3	.10
	H vs. M & L	3.0	2.6	.01

second prey - closer than would be expected if the first prey were not present and the second prey were simply detected at the periphery of the reactive field. In this case the time required to pursue the second prey item, and thus the overall handling time, would be reduced. Both of these mechanisms should be enhanced by increases in prey density. Indeed the regression of handling time on mayfly density in low structure is significant ($P < .05$, Figure 4).

To check the importance of these factors, the handling times by bass with mayflies in low structure were divided into categories and reevaluated (Table 8). "Isolated" handles were defined as those prey handling periods which were immediately preceded and followed by searching behavior. Isolated handles should involve the longest pursuit times, since prey are presumably sighted at the limits of the reactive field. Since isolated handles are terminated by searching behavior, there is no direct prey stimulus to cut short the handle, either. "Cut short" handles follow searching behavior but are terminated, not by search, but by the attempted capture of another prey item. Thus the pursuit time portion of cut short handles should be similar to isolated handles, since they both follow searching behavior, but the stimulus to end cut short handles is stronger. "Following" handles follow cut short handles; they are terminated by search. Thus pursuit times of following handles should be the shortest of all handling types, but the strong stimulus to end the following handles is lacking.

There are marked differences between the handling types

FIGURE 4. Handling times ($\bar{x} \pm 1$ SE) in seconds for largemouth bass feeding on Callibaetis mayflies at different mayfly densities in low structure. Multiply mayfly densities by 8.33 to obtain $\#/m^3$. The form of the regression equation is: $Y = 5.8 - .08(x)$.

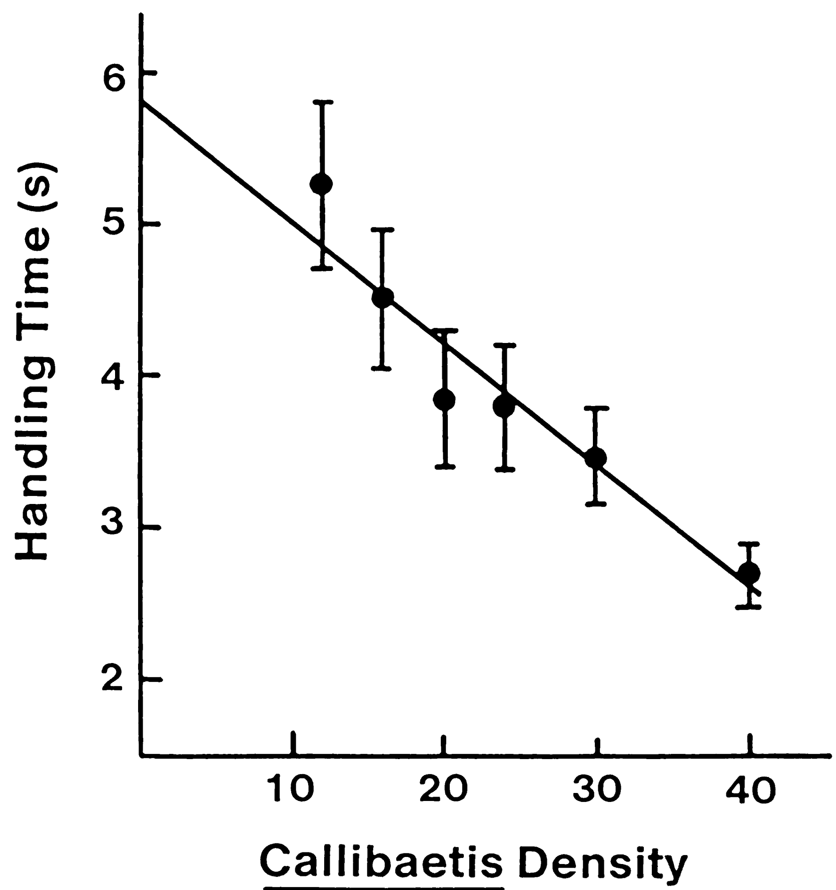


FIGURE 4.

TABLE 8. Categorization of handling times (in seconds) for largemouth bass with *Callibaetis*. Two contrasts are presented as well as the 95% confidence interval for the differences between the means on opposite sides of the contrast (Scheffe's Interval).

Handling Time Characteristic	Mean Handling Time ± 1 SE
Isolated	5.8 ± .3
Following	3.6 ± .3
Cut short	2.6 ± .2
Contrast	95% Confidence Interval
Isolated vs. Following	2.2 ± 1.0
Following vs. Cut short	1.0 ± .9

(Table 8). Isolated handles are the longest, as one would expect. Following handles take less time, presumably because of shortened pursuits, and cut short handles are the shortest of all, a full three seconds less than isolated handles. Apparently, the stimulus provided by a nearby prey item is the strongest factor in shortening handling times, with decreases in pursuit distance (time) also important. For each contrast between the means of the handling types, a 95% confidence interval is given. Scheffé's interval was utilized since the contrasts were selected postdata (Scheffé 1953).

RATES OF MOVEMENT AND ENERGETIC COSTS

Structure also affected the rates of movement of bass while searching for or handling prey (Table 9). A threshold effect was apparent. Rates of searching for *Callibaetis* and *Pimephales* were similar, with a marked decline in the rate of search for each prey type in high structure. Handling velocities were higher for *Pimephales* than *Callibaetis*, especially in high structure; greater pursuit velocities were required to capture the fish prey.

The average *Pimephales* handling velocity increased in high structure compared to medium and low (Table 9). Apparently a high velocity of pursuit was needed in high structure to overcome the fatheads' propensity to escape by abruptly and erratically turning while moving through the dense vegetation. In contrast, the average *Callibaetis* handling velocity dropped in high structure. Since metabolic

TABLE 9. Average velocities (cm/s ± 1 SE) of largemouth bass while searching for or handling two types of prey in three differently structured environments. L - low structure, M - medium structure, and H - high structure.

	Search Velocities		
Prey Type	L	M	H
Callibaetis	6.2 ± .5	6.1 ± .5	3.6 ± .3
Pimephales	6.8 ± .6	6.7 ± .4	3.8 ± .4
	Handling Velocities		
Callibaetis	3.2 ± .3	3.1 ± .3	1.7 ± .2
Pimephales	4.7 ± .4	4.7 ± .3	5.5 ± .5

cost is related to activity level, the cost of handling *Callibaetis* decreased while the cost of handling *Pimephales* increased in high structure, implying that E_i, the net energetic gain associated with a particular prey item, declines for *Pimephales* in high structure and is enhanced for *Callibaetis*, relative to less structured environments.

The differences in costs associated with the changes in velocity in high structure are small, however. By increasing its *Pimephales* handling velocity from 4.7 cm/s in medium structure to 5.45 cm/s in high structure, a 70 mm largemouth bass increases its cost from .0022 cal/s to .0023 cal/s (from Equation 4). Thus bass in medium and high structure would have to handle fatheads for almost three hours a day for there to be even a 1 calorie savings in cost in medium structure.

Similarly, bass handling *Callibaetis* in high structure reduce their cost of handling by .0001 cal/s compared to medium structure. If handling times and encounter rates were similar between structures, with handling time set at six seconds, the bass would have to handle almost 1700 mayflies/day in order for bass in high structure to have a 1 calorie/day advantage based on reduced cost.

Thus the small differences in costs of handling prey associated with different structural levels have little effect on the expression describing net energetic gain per prey item:

$$E_i = Ae_i - C_h H_i$$

Since the bass are able to capture fairly large prey, the equation is swamped by the e_i term, the total energy content of the prey. e_i is expressed in calories, while C_h, the cost of handling, is expressed in calories X 10^{-3}/s. Accordingly, the increased Pimephales handling cost in high structure results in an E_i of 34.6167 in high structure compared to 34.6231 cal in medium, a reduction of only 6.4 X 10^{-3} cal per fathead. Since handling time (H_i) is multiplied by the cost of handling term, changes in handling time also have minimal effects on E_i. For example, increasing the Pimephales handling time to 20 seconds in high structure reduces E_i to 34.6039 cal, a .019 calorie reduction in energy per fathead compared to medium structure.

The significant differences in growth observed between bass in differently structured field environments (Anderson 1983b) are thus not caused by structure related changes in energetic cost per prey item. It is doubtful whether differences in search costs are important, either. Bass in high structure might have to search longer to obtain a given amount of energy than bass at intermediate structures because of lowered prey encounter rates in high structure. But this extended searching would only tend to balance out the energy costs between structural types, since it is actually slightly cheaper to forage at higher structures, with lower search velocities.

DIET BREADTHS

Even though structure has a miniscule effect on the net energy gained per prey item, structure should have important effects on prey selection. Structure alters prey encounter rates (Figures 1 and 2, Table 4) and can have strong effects on prey values (Table 10), two

TABLE 10. Calculated values (cal/s) of three different prey of largemouth bass at three levels of structural complexity. L, M, and H stand for low, medium, and high levels of structure.

Prey	L	M	H
Fathead minnows	3.4	2.9	2.4
Mayflies	1.8	1.6	1.0
Damselflies	1.1	1.0	.9

factors which are important in determining patterns of prey selection (Mittelbach 1981a).

The value of a prey item (E_i/H_i) should be an indicator of its desirability for a predator. For the three prey types utilized in this study, the major shift in value across structures occurs for *Callibaetis* (Table 10), with its value dropping almost in half from low to high structure. This is because *Callibaetis* handling times are so sensitive to structure, almost doubling over the range of structures used in these experiments. There are moderate changes for *Pimephales*. Note that it has a value 1.8 times greater than *Callibaetis* in low structure and is worth 2.5 times as much in high structure, a trend which is opposite to what one would expect based on the reduced *Pimephales* capture success in high structure. Coenagrionids are relatively resistant to changes in value because their handling times change little with structure. The result is that Coenagrionids and *Callibaetis* become very similar in value in high structure. Thus, if mayflies are included in the diet in high structure, slightly larger damselflies should also be included whereas in low structure the probability of damselflies and mayflies occurring together in the diet is lower. In fact, in a field study done with bass (Anderson 1983b), damselflies were absent from the diet in low and medium structures (even though present in the environment at high densities) and strongly represented in the diet in high structure (mayflies were frequent prey in all habitats.

In a separate laboratory study, an optimal foraging model proved to be an adequate predictor of the foraging behavior developed by bass in differently structured environments (Anderson 1983a). Therefore, the energy-maximizing model described earlier (Equation 1) was employed, using the foraging parameters determined in these experiments, to predict general patterns of diet breadth for bass in structured environments. Figure 5 represents predicted diet breadths of bass at three structural levels with a simple prey community of fathead minnows and *Callibaetis* mayflies. Under natural conditions bass would never encounter such a simple prey community, but the relationships shown in Figure 5 are meant to portray structure-related diet breadths of bass when fish and invertebrate prey types are present. The hatched areas represent combined densities of fatheads and mayflies wherein a 70 mm bass can maximize its rate of energy intake by specializing on the more valuable prey - fathead minnows. Note that the highest probability of specialization occurs in medium structure, where bass have the highest encounter rates with minnows. Despite the fact that encounter rates with fathead minnows are similar in low and high structures, bass in low structure should be generalists at minnow densities up to $58/m^3$, whereas in high structure bass should begin specializing at a fathead density of $25/m^3$ (Figure 5). This difference is due to the increased value of *Callibaetis* in low structure. Thus, when the prey community consists of large individuals which change little in value with structure (the fatheads in this case) and smaller prey types which change more dramatically, it is quite possible that greater foraging specialization will occur at higher levels of structure instead of in low structure. This may be the mechanism underlying the greater consumption of large prey by bluegills at higher structural levels in Crowder and

FIGURE 5. Graphical representation of the predicted foraging modes of 70 mm largemouth bass at different densities of two prey types, fathead minnows (Pimephales promelas) and Callibaetis mayflies, in environments with low (L), medium (M), or high (H) levels of structure. Specialization on the preferred prey, Pimephales, is predicted in the hatched areas. Open areas of the graphs represent combined prey densities at which bass should be generalists, taking both prey as encountered. Fathead dry weight = 9.9 mg, mayfly dry weight = 2.0 mg.

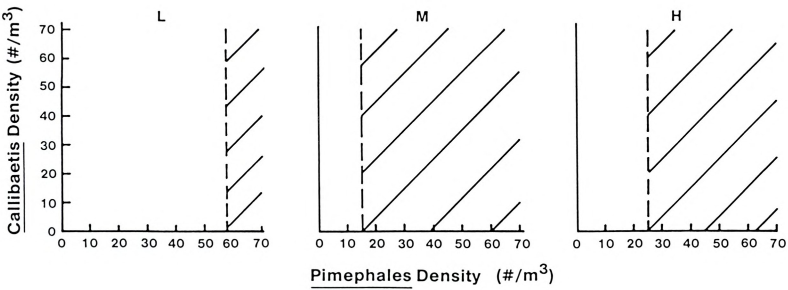

L
M
H
Callibaetis Density (#/m3)
0
10
20
30
40
50
60
70
Pimephales Density (#/m3)

Figure 5.

Cooper's experimental work (1982). Note that the graphical representation neglects the positive relationship between *Callibaetis* density and value in low structure. Such an effect increases the probability of specialization on *Pimephales* at low *Callibaetis* densities and makes inclusion of *Callibaetis* more likely at high densities. Thus a vertical line separating regions of specialization and generalization would be inappropriate.

Using a simple prey community of *Pimephales* and another invertebrate prey, Coenagrionid damselflies (Figure 6), predicted regions of specialization are greater than in the *Callibaetis* case because the Coenagrionids were less valuable. Generalization is predicted in medium structure only when fathead densities drop almost to zero. There is a slight difference in the predicted pattern of resource utilization between low and high structures. The *Pimephales* encounter rates are similar in the two environments but specialization is predicted at a slightly lower minnow density in high structure (15 vs. $23/m^3$) because of the small decrease in Coenagrionid value with structure.

If one looks at an invertebrate community (Figure 7) of mayflies and damselflies, the simple trend of greater generalization with increased structure finally holds. This is because for any given density of the preferred prey, *Callibaetis*, the encounter rate is decreased as structure is increased, making it more likely that Coenagrionids would be an energetically acceptable part of the diet. In high structure generalization is predicted over the entire range of *Callibaetis* densities examined (0–$700/m^3$). Note, however, that the patterns of predicted diet breadth would change markedly if the damselflies were

FIGURE 6. Graphical representation of predicted foraging modes utilized by 70 mm largemouth bass at different densities of fathead minnows (*Pimephales*) and Coenagrionid damselflies in three differently structured environments. Specialization on *Pimephales* is predicted in the hatched areas. Both prey should be eaten if their combined densities lie in open areas of the graphs. Fathead dry mass = 9.9 mg, damselfly dry mass = 2.3 mg.

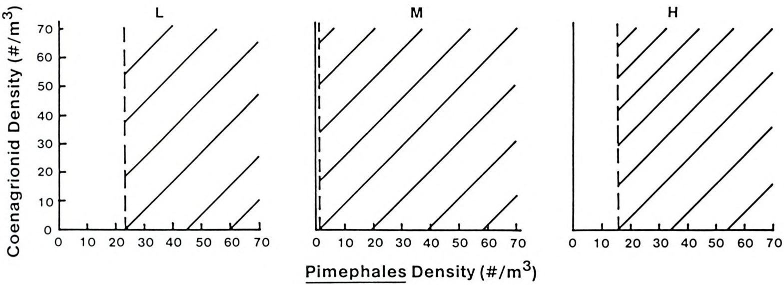
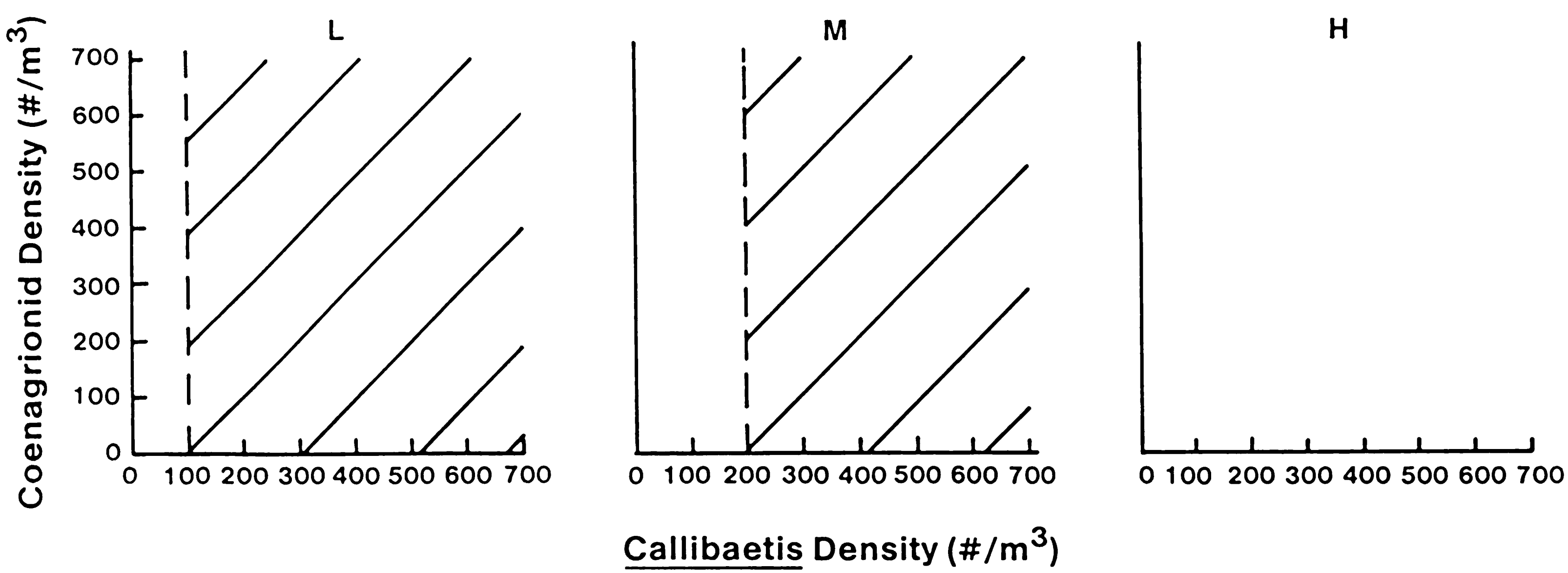

Coenagrionid Density (#/m3)
70
60
50
40
30
20
10
0
L
M
H
0 10 20 30 40 50 60 70
0 10 20 30 40 50 60 70
0 10 20 30 40 50 60 70
Pimephales Density (#/m3)

FIGURE 6.

FIGURE 7. Graphical representation of predicted diets of 70 mm largemouth bass at different densities of *Callibaetis* mayflies and Coenagrionid damselflies in low, medium, and highly structured environments. Specialization on *Callibaetis* is predicted in hatched areas; generalization (taking both prey) is energetically advantageous in open portions of the graphs. Mayfly dry weight = 2.0 mg, damselfly dry weight = 2.3 mg.



L
M
H
Coenagrionid Density (#/m3)
700
600
500
400
300
200
100
0
0 100 200 300 400 500 600 700
0 100 200 300 400 500 600 700
0 100 200 300 400 500 600 700
Callibaetis Density (#/m3)

FIGURE 7.

somewhat larger (more valuable) than the mayflies. In that case, the sensitivity of mayfly value to structure would produce larger regions of predicted generalization in low structure. In fact, increased generalization should occur in low structure whenever there are high numbers of prey which are not associated with (hidden by) structure and which have values dependent on their densities.

The validity of the predicted patterns of Figure 7 have been examined under field conditions using largemouth bass as predators and a prey community which consisted entirely of invertebrates and had Callibaetis mayflies as the most valuable common prey (Anderson 1983b). Despite the presence of more than 20 prey taxa, diet breadths of bass in the field corresponded with the generalizations permitted from examination of Figure 7. Bass in the highly structured field environment had broader diets than their medium vegetation counterparts, even though prey densities were significantly greater in high vegetation. Bass in low structure also foraged in a more generalized manner than bass in medium vegetation. Corresponding with Figure 7, Baetid mayfly densities in the low vegetation field habitat were close to $100/m^3$, and most mayflies were smaller (less valuable) than those used in this study.

DISCUSSION

At a given density of either of the two invertebrate prey types, encounter rates decreased as the amount of structure increased. However, under natural conditions prey densities are generally enhanced with increased amounts of structure (Gerking 1957). Potentially, such increases in prey densities might be sufficient to make prey encounter rates in highly structured environments comparable to those found in less structured environments.

The relationship between structural complexity and the actual adjustments which must be made in prey densities to equalize encounter rates across structural levels are illustrated in Figure 8. The prey weighting factors are simply numbers which must be multiplied by the density of a prey type at a given level of structure so that the encounter rate by bass with that prey type is equal to the encounter rate at the lowest level of structure used in this study (200 stems/m^2). The weighting factors are estimated from the slopes of the regression lines relating encounter rates to prey densities for Callibaetis (Table 1) and from the relationship between structure and mean search times for Coenagrionid prey (Table 4). For example, from Table 1 the slope of the line relating encounter rate to prey density is ten times greater in low structure than in high (.04 vs. .004). Thus, for a given density in low structure, prey density in high structure must be ten times greater for encounter rates to be equal. Only one density of Coenagrionid damselflies was utilized, so there is no regression of encounter rate on density for this prey type; however, prey weighting factors can still be computed by using the inverse of search times (Table 4) for encounter rates and by assuming a direct linear relationship between prey density and encounter rate. Note (Figure 8) that prey density must increase exponentially as a function of structure to equalize encounter rates across structural levels.

FIGURE 8. Relationship between structural complexity (macrophyte stems/m^2) and prey weighting factors for two prey types. Prey weighting factor = the number which must be multiplied by the prey density at any level of structure so that the encounter rate by largemouth bass with that prey type at that level of structure is equal to the encounter rate at the lowest level of structure (200 stems/m^2). Dashed line represents plot of weighting factor vs. structure for Coenagrionid prey, dash-dot line is for *Callibaetis*. Solid line represents plot of factors by which prey densities are actually increased across changes in structure (from Gerking 1957).

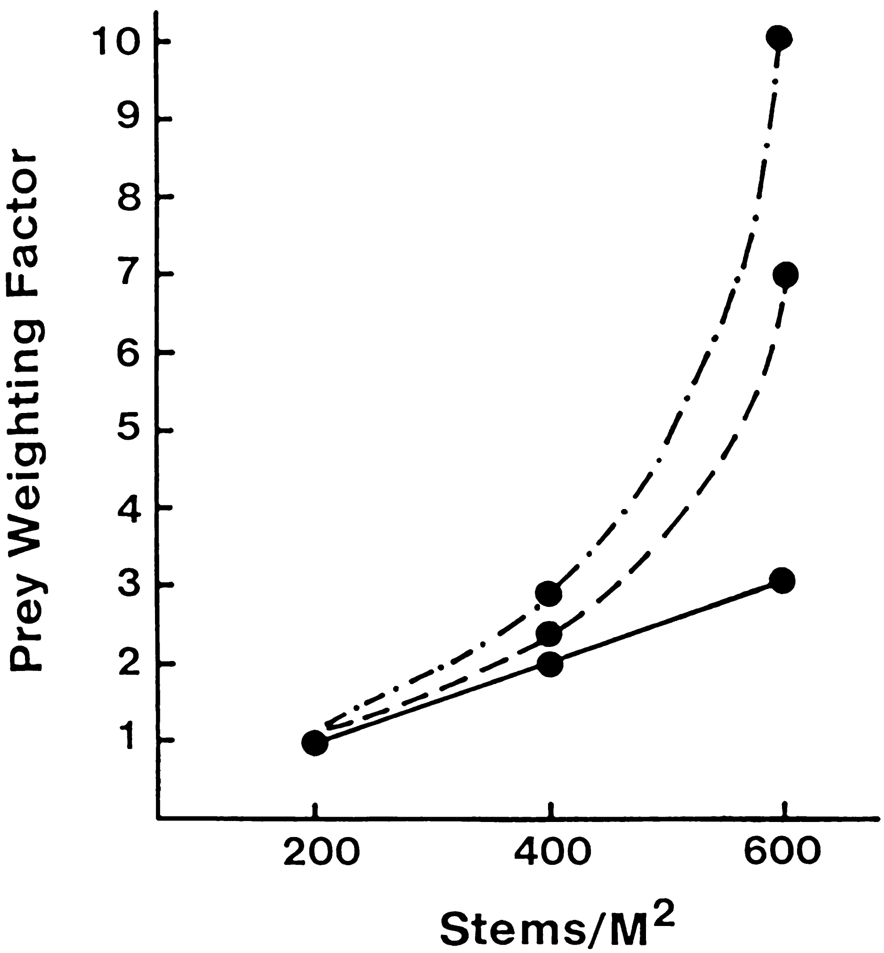


FIGURE 8.

Gerking (1957) examined the relationship between prey and vegetation biomass in Bryant's Creek Lake, Indiana. His vegetation and prey dry weights can be converted to number of stems and number of prey individuals, respectively, by assuming that the average dry mass of a stem of aquatic vegetation is 400 mg (Anderson, pers. obs.) and that average prey dry weight is .03 mg (Mittelbach 1981b). One can then plot prey density vs. stem density (Figure 9). A simple linear regression model fits the available data better (linear model $r^2 = .44$) than either exponential ($r^2 = .41$), logarithmic ($r^2 = .41$), or power functions ($r^2 = .38$), indicating that there is a relatively constant number of prey individuals per stem regardless of stem density. While prey densities do increase with structure (the straight line in Figure 8), the higher densities are inadequate to compensate for the loss of foraging efficiency in highly structured environments. Predators in such environments can be expected to acquire energy at reduced rates.

Although the analysis of handling times provided a mechanism underlying the reduction of handling time in low structure, it left one with an unsettling question. That is, if bass have the ability to shorten handling times (the "cut short" handles), why do they not always do so? Such reductions can only increase the rate of energy acquisition. Furthermore, the two hypotheses put forth to explain the minimization of handling time did not completely account for the difference in handling times between low and high structures, since isolated handles in low structure were 5.8 s, still less than the 7.1 s average in high. In addition, damselfly handling times increased steadily with structure (Tables 6 and 7) yet damselflies, concealed on the

FIGURE 9. Relationship between prey density and density of aquatic macrophytes in Bryant's Creek Lake, Indiana (from Gerking 1957). The straight line is drawn from the linear regression equation: $Y = 281.9 + 19.96(x)$. $r^2 = .44$, $P < .05$.

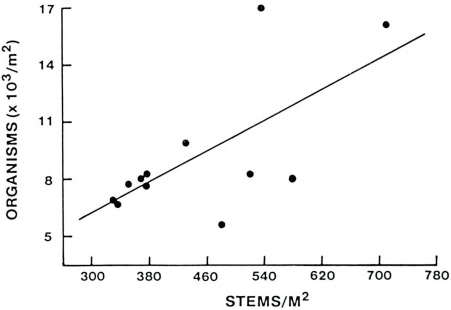

17
14
11
8
5
ORGANISMS (x 10³/m²)
300
380
460
540
620
700
780
STEMS/M²

FIGURE 9.

vegetation, were captured one at a time - thus no multiple capture effects could have been working.

The only other explanation that can be given is that the energetic penalties associated with increasing the handling time for a particular prey type are much greater in low structure than in high (Table 11). In high structure, if an extra second or two is spent handling a prey item instead of searching for new prey, little energy is lost because prey encounter rates are low in high structure and the probability of detecting another prey item in that short time interval is small. On the other hand, extra seconds spent handling prey in low structure can have a more profound effect on the rate of energy acquisition, since encounter rates in low structure are high - thus the benefits of using even small amounts of time for searching are greater. From Table 11, one can see that increasing the handling time from five to seven seconds for mayfly prey in low structure results in a greater than 25% drop in the rate of energy return. The same handling time change in high structure produces only an 11.5% reduction in energy intake.

The observed fluctuations in handling times between densities and structures are of concern when considering the value of a prey item to a predator, when prey value = E_i/H_i. Ecologists are used to thinking of a particular prey type as having a relatively fixed value; yet with handling times changing so markedly with density and structure such a view seems untenable. Furthermore, the optimal foraging model developed by Charnov (1976) and utilized by Mittelbach (1981a) postulates that whether a prey item should be included in a predator's diet depends

TABLE 11. Hypothetical rates of energy acquisition (E_n/T) in cal/s for largemouth bass foraging for mayflies in three structured environments, low, medium, or high, with three different handling times. E_n/T is calculated for each combination of handling time and structure using the optimal foraging model described in the text and the encounter rates given in Table 3 (with density = $300/m^3$). The mayflies are assumed to be worth 7 calories net.

	E_n/T		
Handling Time	L	M	H
5s	1.22	1.04	.52
6s	1.04	.91	.49
7s	.90	.80	.46

only on its value to the predator, not its density (availability). This view was defended by Sih (1979). However, if prey value is dependent on density, this hypothesis is fallacious.

The handling time - density dependency suggests that the value of a prey type can be affected by the density or distribution of other prey types as well. In Figure 10, a largemouth bass is depicted foraging in environments with two prey types, M and N. Arc X represents the limit of the reactive field of the bass when it is in the position shown. Arc Y defines the field's limit when the bass has reached prey M. Note that in Figure 10b, the increased density (or increased clumping) of prey N will lead to a shorter pursuit time for prey M because there is a type N individual between the bass and M; it will also cut short the handling time on M, since the individual of prey type N between arcs X and Y will be visible from the capture site of M. Thus the value of prey type M is increased in environment 10b, even though its density is unchanged from 10a.

Obviously, the kind of relationship described here will work best in relatively unstructured environments, or with prey which are not strongly associated with structure. In this study the Coenagrionids, always found on the vegetation, had handling times that were not affected by density even in low structure; mayfly handling times were sensitive to density in low but not in high structure. Overall, the multiple prey in view phenomenom, by increasing the value of certain prey, should tend to make predators' diets in unstructured environments more generalized than might otherwise be expected.

Structure should also affect the ability of predators to

FIGURE 10. Schematic representation of the alteration in value of one prey type due to the change in distribution of another prey species. Individuals of the two prey species are represented by dots labelled M and N. Curved line X designates the limit of the fish's reactive field when it is in the position shown. Y designates the reactive field limit once the fish has reached prey type M. In 10a, species N is at low density or is not clumped; in 10b the density or clumping of N has increased.

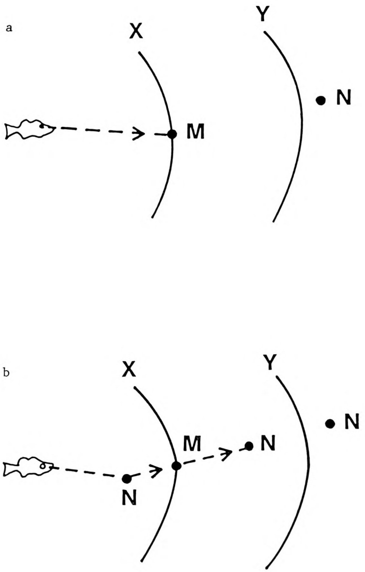


FIGURE 10.

change their patterns of prey selection as familiar prey decline in abundance or new prey become available. At first glance it would seem that predators in low structure would be at an advantage in tracking changes in resource levels; they have higher encounter rates with prey and a better view of what prey may be present. In a set of experiments designed to investigate the interaction between structure and learning, bass in low structure which had been trained in the laboratory to forage only for damselflies were much quicker at detecting and capturing novel fish prey than were their high structure counterparts (Anderson 1983c). On the other hand structure can have surprising effects on the ability of fish to adjust their diets. In another experiment, bass in low and high structure were given the opportunity to forage for a simple prey community of fish and damselflies. The low structure bass specialized on fish; the high structure bass generalized. Then a third prey was added - *Anax* dragonflies of sufficient size to be an energetically favorable prey in both structure types. In this case the bass in high structure added the new prey to the diet more quickly. The potential mechanism underlying the unpredictability of the effect of structure on learning could be that at high levels of structure all prey types become spatially associated with structure and searching for prey becomes a simple process of scanning vegetation. In high vegetation new prey will eventually be detected even if they are encountered at a low rate. At lower levels of structure, the environment may be split into discrete parts - vegetation, open water, and sediments in the aquatic case - and specialization on a prey type found in one of the environmental subdivisions may make predators less able to track

changes in resources elsewhere. In the example given, low structure bass temporarily continued to forage for fish in open water even though more profitable prey were located in the vegetation.

Apparently, it will be difficult to make sweeping generalizations regarding the effects of structural complexity on predators' foraging behavior and patterns of prey selection. Since structural complexity can influence almost all aspects of the foraging process, including the ability of predators to encounter, handle, and learn about prey as well as prey value and behavior, and since the magnitudes of these effects are prey-specific, it may be more prudent to analyze particular ecological settings and make concrete appraisals of the effects of structure on predators and their prey. Indeed, experimental investigations of the relationship between structure and diet breadth have thus far yielded somewhat contradictory results. Vince et al. (1976) and Anderson (1983a) observed broader diet breadths at high structural levels; in contrast Stoner (1982) obtained narrower predator diets in high structure, where one prey type gained almost complete refuge from predation.

The relationship between the foraging behavior of predators and structural complexity may be of critical importance in understanding the mechanisms which regulate the community ecology of littoral zone areas. Nelson (1979) has argued that predation by fishes and decapods is the most important factor in determining the distribution, diversity, species composition, and abundance of amphipods associated with macrophytes in an eelgrass community. Of course the intensity of such predation will be governed by the structural complexity of the environment.

In turn, specific foraging behaviors and patterns of resource utilization should determine the amount of competition between predator species. The recent successes of optimization theory in predicting such patterns (Belovsky 1978, Mittelbach 1981a) have created hope that the extent of interspecific interactions can be quantitatively predicted and mechanistically described. The present study suggests that optimal foraging models should be used with great care. A key element in such models is the time required by predators to handle prey items. Handling time, traditionally viewed as dependent on physical attributes of the predator and its prey (Werner 1977), can also be influenced by prey density and the spatial distribution of prey and may to a certain extent be under the predator's control - witness the difference in handling time between low and high structure even when multiple prey in view phenomena have been accounted for. Such control of prey value should not be surprising. Staddon (1977) has described cases wherein the rapidity with which animals become responsive (search for food) following reinforcement is proportional to their expectancy of future reward. Nonetheless the dependency of prey value on so many variables is troublesome since prey value constitutes such an important part of the optimal foraging model. Either the notion of prey value may have to be redefined or else the ranking of prey items and the precise predictions of predators' diets under complex field conditions will be exceedingly difficult.

LITERATURE CITED

Adams, C. 1975. The nutritive value of foods. United States Department of Agriculture. Washington, D. C.

Anderson, O. 1983a. Optimal foraging by largemouth bass in structured environments. Ecology 64:000-000.

Anderson, O. 1983b. Prey selection and growth of largemouth bass in differently structured stream environments. Submitted to Animal Behaviour.

Anderson, O. 1983c. The interaction between structural complexity and the composition of the prey community in determining changes in the foraging behavior largemouth bass. In preparation.

Belovsky, G. E. 1978. Diet optimization in a generalist herbivore: the moose. Theoretical Population Biology 14:105-134.

Charnov, E. L. 1976. Optimal foraging: attack strategy of a mantid. American Naturalist 110:141-151.

Crowder, L. B., and W. E. Cooper. 1982. Habitat structural complexity and the interaction between bluegills and their prey. Ecology 63:1802-1813.

Cummins, K. W., and J. C. Wuycheck. 1971. Caloric equivalent for investigations in ecological energetics. Internationale Vereinigung für Theoretische und Angewandte Limnologie, Mitteilungen 18:1-158.

Curio, E. 1976. The ethology of predation. Springer-Verlag, New York, New York, USA.

Elliot, J. M. 1976. The energetics of feeding, metabolism and growth of brown trout (Salmo trutta L.) in relation to body weight, water temperature, and ration size. Journal of Animal Ecology 45:923-948.

Elliot, J. M., and W. Davison. 1975. Energy equivalents of oxygen consumption in animal energetics. Oecologia 19:195-201.

Elner, R. W., and R. N. Hughes. 1978. Energy maximization in the diet of the shore crab, Carcinus maenas. Journal of Animal Ecology 47:103-116.

Emlen, J. M. 1966. The role of time and energy in food preference. American Naturalist 100:611-617.

Gerking, S. D. 1957. A method of sampling the littoral macrofauna and its application. Ecology 38:219-225.

Gill, J. L. 1978. Design and analysis of experiments in the animal and medical sciences. Iowa State University Press, Ames, Iowa, USA.

Glass, N. R. 1971. Computer analysis of predation energetics in the largemouth bass. Pages 325-363 in B. C. Patten, editor. Systems analysis and simulation in ecology. Volume 1. Academic Press, New York, New York, USA.

Goss-Custard, J. D. 1977. Optimal foraging and the size selection of worms by redshank, Tringa totanus. Animal Behavior 25:10-29.

Ivlev, V. W. 1961. Experimental ecology of the feeding of fishes. Yale University Press, New Haven, Connecticut, USA.

Krebs, J. R., J. T. Erichsen, M. I. Webber, and E. L. Charnov. 1977. Optimal prey selection in the great tit (Parus major). Animal Behavior 25:30-38.

MacArthur, R. H., and E. R. Pianka. 1966. On optimal use of a patchy environment. American Naturalist 100:603-609.

Mittelbach, G. G. 1981a. Foraging efficiency and body size: a study of optimal diet and habitat use by bluegills. Ecology 62: 1370-1386.

Mittelbach, G. G. 1981b. Patterns of invertebrate size and abundance in aquatic habitats. Canadian Journal of Fisheries and Aquatic Science 38:896-904.

Neill, S. R. St.J. 1970. A study of antipredator adaptations in fish with special reference to silvery camouflage and shoaling. Ph.D. Thesis, Oxford University. 159 pp.

________________. 1974. Experiments on whether schooling by their prey affects the hunting behavior of cephalopods and fish. Journal of Zoology, London, 549-569.

Nelson, W. G. 1979. An analysis of structural pattern in an eelgrass (Zostera marina L.) amphipod community. Journal of Experimental Marine Biology and Ecology 39:231-264.

Radakov, D. V. 1958. On the adaptive significance of shoaling of young coalfish (Pollachius virens). Vop. Ikhtiol 11:69-74.

Rice, J. A., and J. E. Breck. 1982. Synthesizing fish respiration data for bioenergetics modeling; examples using largemouth bass and striped bass. Submitted to Ecology.

Scheffe, H. 1953. A method of judging all contrasts in the analysis of variance. Biometrika 40:87-104.

Schoener, T. W. 1971. Theory of feeding strategies. Annual Review of Ecology and Systematics 2:369-404.

Shaw, E. 1978. Schooling fishes. American Scientist 66:166-175.

Sih, A. 1979. Optimal diet: The relative importance of the parameters. American Naturalist 113:460-463.

Staddon, J. E. R. 1977. The handbook of operant behavior. J. E. R. Staddon and Werner K. Honig, eds. Prentice-Hall, Englewood Cliffs, New Jersey, USA.

Stoner, A. W. 1982. The influence of benthic macrophytes on the foraging behavior of pinfish, *Lagodon rhomboides*. Journal of Experimental Marine Biology and Ecology 58:271-284.

Vince, S., Valiela, I., Backus, N., and J. M. Teal. 1976. Predation by the salt marsh killifish *Fundulus heteroclitus* in relation to prey distribution and abundance. Journal of Experimental Marine Biology and Ecology 23:255-266.

Ware, D. M. 1973. Risk of epibenthic prey to predation by rainbow trout (*Salmo gairdneri*). Journal of the Fisheries Research Board of Canada 30:787-797.

Werner, E. E. 1977. Species packing and niche complementarity in three sunfishes. American Naturalist 111:553-578.

Werner, E. E., and D. J. Hall. 1974. Optimal foraging and the size selection of prey by the bluegill sunfish (*Lepomis macrochirus*). Ecology 55:1042-1052.

Werner, E. E., and G. G. Mittelbach. 1981. Optimal foraging: field tests of diet choice and habitat switching. American Zoologist 21:813-829.

PREY SELECTION AND GROWTH OF LARGEMOUTH BASS

AT DIFFERENT MACROPHYTE DENSITIES

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Littoral zone aquatic macrophytes can have important effects on the interactions between fish predators and invertebrate prey. Macrophytes provide attachment surfaces for periphyton and harbor a variety of invertebrate organisms which serve as food for fish populations. Increased amounts of aquatic vegetation have been shown to be associated with greater biomasses and numbers of invertebrates (Gerking 1957, Hruska 1961).

Although macrophyte and prey densities are positively related, macrophytes reduce the efficiency of fish predators by decreasing the velocity with which they search for prey, by making prey more difficult to detect, and by making some prey more difficult to capture (Anderson 1983). When resource levels are held constant, increased macrophyte levels have been shown to lower the rate of energy acquisition of fish predators (Vince et al. 1976, Stoner 1982, Anderson 1983). In fact, most prey populations would have to increase exponentially as a function of macrophyte density in order for fish predators to have equal prey encounter rates at all macrophyte levels (Anderson 1983). However, prey density appears to be linearly related to macrophyte density (Gerking 1957, Anderson 1983). Thus, fish predators should have steadily declining prey encounter rates as macrophyte levels are increased except that, in areas with small numbers of macrophytes, prey communities tend to be impoverished. Thus, Crowder and Cooper (1982) predicted that fish would have highest growth rates at intermediate macrophyte densities, a prediction which was corroborated in their experimental work with bluegill sunfish.

Crowder and Cooper (1982) hypothesized that fish which foraged in intermediately vegetated environments would have narrower diet breadths than fish in low or high vegetation. The rationale for this argument can be understood by studying Figure 1. Basically, as the rate of energy acquisition declines from intermediate to high or low levels of vegetation due to decreased encounters with prey, more prey types become acceptable parts of the diet (consumption of such prey can increase the overall rate of energy intake). Ivlev (1961) and Werner and Hall (1974) have documented increases in diet breadth with lowering of resource levels for fish.

However, Crowder and Cooper (1982) generally observed narrowest diet breadths in low vegetation despite the fact that greatest growth occurred in medium vegetation, suggesting that a simple energetic explanation of diet breadth may be inappropriate. The factors which influence diet breadth as a function of macrophyte density may be quite complex and interrelated. In addition to the energetic feedback mechanism proposed by Crowder and Cooper, at least three other models can be proposed: (1) First, the manner in which fish search for prey might differ as a function of vegetational density. In littoral zones with modest amounts of vegetation, the overall environment can be more readily partitioned into discrete subdivisions of vegetation, substrate, and open water. Fish which search for prey in one of these microhabitats may have reduced efficiencies in exploiting prey found in the other microhabitats (Werner et al. 1981). Increased specialization would then be expected at reduced macrophyte levels. At high macrophyte densities,

FIGURE 1. Representation of mechanism by which diet breadth increases at high or low macrophyte densities. The solid line plots net energy gained (E_n) vs. time spent foraging (T) for a fish predator in an environment with intermediate amounts of vegetation. The dashed line is for the same relationship at high or low macrophyte densities. Symbols show net energy gained from eating an individual of a particular prey type (E_i) vs. the handling time for that prey type. Stars represent prey types selectively preyed upon at all macrophyte densities; prey represented by closed circles are not consumed in intermediate vegetation because consumption of such prey would lower E_n/T. Open circles represent prey types which are not eaten at any macrophyte level.

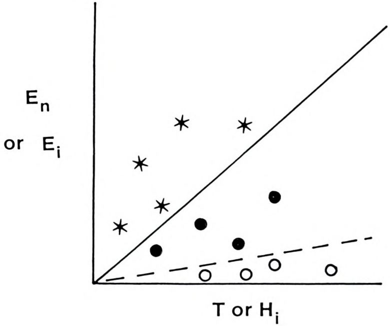

FIGURE 1.

all prey types would be associated with vegetation, and fish predators which simply scanned the vegetation for prey might have broad diets. This mechanism could account for the patterns observed by Crowder and Cooper (1982). In their study, bluegills in low vegetation specialized to the greatest extent on zooplankton found in open water. (2) Alternately, high macrophyte levels might lessen competition between invertebrate species and promote prey community diversity because of either greater productivity or increased opportunities for spatial partitioning of the environment by invertebrates. Fish diets might then tend to expand at higher macrophyte levels because there would be more prey species available and/or fewer rare, seldom encountered prey types. (3) Finally, prey species might be differentially shielded from predation at high macrophyte densities. Small prey species could gain complete refuge and be unavailable in densely vegetated environments. Substrate prey would have a protective blanket of vegetation covering them. Diet breadth might then be negatively related to the abundance of macrophytes, due to the reduced number of prey species actually available to fish at high macrophyte densities.

Hypothetical patterns of diet breadth in relation to macrophyte density are summarized in Table 1. The energetic feedback model proposed by Crowder and Cooper for structured environments is number 4 in the table. Note that models 1 and 2 predict the same pattern of diet breadth. It is possible to differentiate between the two, however, because model 1 predicts that fish in sparse vegetation will tend to consume prey types from only one microhabitat whereas model 2 says

TABLE 1. Expected patterns of diet breadth in relation to macrophyte density based on four possible underlying mechanisms. Mechanisms are numbered as in the text. L = low, M = medium, and H = high macrophyte density in this and all other tables. M>H means that diet breadth is greater at medium than at high macrophyte levels.

Mechanism	Predicted Diet Breadth
(1) Reduced macrophyte levels produce greater microhabitat (open water, substrate, or vegetation) specialization by fish. Fewer prey types are available to fish foraging in only one microhabitat.	H>M>L
(2) Macrophytes promote prey diversity; fish predators are relatively non-selective.	H>M>L
(3) Macrophytes offer almost complete refuge from predation for some prey types; fish predators are relatively non-selective.	L>M>H
(4) Macrophytes alter rate of energy intake while foraging; fish exclude prey which lower energy return.	H,L> M

only that fish in low vegetation will eat fewer prey types but does not specify that they be from one subhabitat. Note also that model one applies to the diet breadths of individual fish rather than an entire population of fish. Obviously, a fish population as a whole might be quite generalized in terms of prey consumption while individuals within the population were specialized if there were significant differences between fish in the ability to exploit different microhabitats.

Unlike models one and four, models two and three imply no feedback between rate of energy intake and prey selection. In models two and three, prey are eaten as encountered, with little active selection or rejection of prey occurring. If selection of prey does occur, the same criterion of prey acceptability is used at each vegetation level. If only prey above a certain size are eaten, that same size requirement is utilized at each macrophyte density. Mechanisms one and four imply a causal relationship between the rate of energy acquisition and prey selection. Fish avoid certain microhabitats (model one) or certain prey types (model four) because their foraging efficiency would be compromised by utilizing such resources.

Models two and three are not mutually exclusive. In fact, if the two mechanisms acted in concert, one would expect little change in diet breadth in relation to macrophyte density. Furthermore, the macrophyte effects of models two and three could be coupled with the energy sensitive fish of model four to produce additional patterns of diet breadth. An examination of how the models' predictions compare with actual prey consumption patterns requires the collection of accurate quantitative information regarding how changes in fish energy intake rates, relative prey encounter rates and energetic values, and prey community diversities are associated with alterations in macrophyte densities.

The relationship between diet breadth and macrophyte density is important for several reasons: (1) If diet breadth changes with vegetational density, interspecific competition among fish and fish predator-prey relationships may be affected by the level of macrophytes found in a given lake. (2) Effective management of a given fish species may require knowledge of that species' ability to use resources in relation to macrophyte density. (3) Analysis of the relationship between macrophyte levels and diet breadth can provide insights into the mechanisms underlying prey selection. The manner in which predators select prey has been a subject of much recent interest to ecologists (Krebs 1978, Werner and Mittelbach 1981).

In this study I quantify growth rates and patterns of prey selection for young largemouth bass (*Micropterous salmoides*) in field environments in which macrophyte densities have been manipulated. Largemouth bass were studied because of their ubiquity and ecological importance in North American lakes (see Heidinger 1975). Furthermore, after an initial short period in the open water, largemouth bass spend the early parts of their lives foraging in aquatic vegetation, first for invertebrates and then for other fish prey (McCammon et al. 1964).

METHODS

The study was carried out from June - September, 1979, in an experimental stream channel at an EPA outdoor laboratory in Monticello, Minnesota. The stream, which contained a full complement of natural prey types (see Appendix), was 2.5 m wide and 523 m in length and featured an alternating pattern of 30.7 m long riffles and pools. The riffles had a stony substrate and no vegetation; the pools had muddy bottoms and varying levels of aquatic macrophytes, primarily *Elodea canadensis* and *Ceratophyllum demersum*. Current velocities, measured at the surface, averaged 6 cm/s in the pools and 11 cm/s in the riffle areas. Stream temperatures varied from 11 to 26°C. over the course of the summer.

In the stream, three different habitat types were created with either low, medium, or high amounts of vegetation in the pools. Each habitat was 122.8 m long and contained two pools, each preceded by a riffle area. Pool macrophytes were manipulated from the stream banks using long handled rakes. Seven observers independently rated the vegetation with regard to both horizontal density and vertical height, and the macrophyte densities were altered until there was uniform observer agreement on differences between habitat types. The high vegetation habitat had no areas of bare substrate, and the dense vegetation extended vertically almost to the water surface (1 m). The medium vegetation habitats were thinned lightly; vegetation extended about 2/3 of the way to the water surface, stems were slightly further apart, and there were small areas of exposed substrate. In low vegetation, approximately 1/3 of the substrate had no vegetation, and the vertical extent was limited to 1/2 m. Vegetation was maintained at the appropriate level in each treatment throughout the remainder of the summer. Quantitative samples taken at the end of the summer revealed that stem densities in low, medium, and high vegetation were approximately 200, 450, and 700 stems/m^2, respectively.

Barriers were created at the ends of each 123 m long habitat by attaching rigid hardware screen to extended railroad ties, placing one end of each tie on opposite stream banks, and anchoring the screen to the stream substrate using large boulders, sand, and gravel. The screen permitted free movement of water, but not fish, between habitat types. 200 largemouth bass and 200 smallmouth bass (<u>Micropterous dolomieu</u>) were placed in each of the three habitats - low, medium, and high vegetation - on June 26, 1979. The foraging behavior and growth of the smallmouth bass will be described in a forthcoming paper. Initial largemouth total length was 41.8 $\pm$ .4 mm (n = 63); the smallmouth were 38.0 $\pm$ .4 mm (n = 133). Both species were generously provided by the New London National Fish Hatchery, New London, Minnesota. The bass density (26.4 kg/ha) utilized was well within the limits found in natural bass populations (Hackney 1975).

At approximately weekly intervals from 7/3/79 to 9/10/79, prey samples were taken in each of the treatments by tying together ten <u>Elodea</u> stems, weighting each vegetation clump with lead sinkers, and placing the vegetation in the center of a collapsed 23 cm diameter blind end plankton net (# 10 mesh, 153 um) which was then lowered into

place on the pool substrate. On each date, two samples were placed at random locations in each pool (4 samples/treatment/date). Each clump was left in the stream for one week and then removed by pulling up monofilament lines which connected bobbers at the stream's surface with the collapsed plankton nets on the stream bottom. Invertebrates were washed from the vegetation, preserved in 10% formalin, and were later placed into one of twenty-six taxonomic categories. The invertebrates were counted and measured, and their weights were calculated using established length-weight regressions (E. Werner, D. Hall, D. Laughlin, unpublished).

Beginning on 7/18/79, approximately six fish were taken at ten day intervals from each treatment to determine weights and examine gut contents. The fish were trapped using Plexiglas boxes 50 x 75 x 90 cm fitted on three sides with fibreglass screening and possessing on the fourth side two sliding Plexiglas doors arranged in a V - pattern. These doors extended 40 cm in front of each trap, with the open part of the V facing outward. The narrow part of the V was left open 3 cm so that bass could swim into the box. On each date a trap was placed in each pool shortly after dawn and then removed two hours later. Three largemouth were randomly selected from each pool (six/treatment) and were weighed, measured, and sacrificed. The stomach contents were preserved in formalin for later analysis, and 85 total stomachs were analyzed.

Prey organisms found in the stomachs were measured and placed into one of the twenty-six taxonomic categories. To examine the breadths

of diet of the bass in the different treatments, the taxa were not further subdivided into prey categories by weight because most of the prey consumed by the bass were small (<1 mg dry weight). Such small prey should differ by less than 5 cal in energetic value (Cummins and Wuycheck 1971), and over this size range the time required for bass to pursue, capture, and swallow individuals of a particular prey type should change very little (Anderson, pers. obs.).

Repeated seinings of the riffle areas of the streams at various times of day throughout the summer yielded many smallmouth but no largemouth bass. Thus it was assumed that the largemouth actually foraged for prey in the vegetated pools, not the riffle areas, and that differences in their growth and foraging behavior across treatments were related to the vegetational differences between pools.

On 9/10/79 the stream was treated with rotenone and the bass were removed. The bass were measured to the nearest mm (total length) and preserved in formalin.

RESULTS

The bass had little impact on the prey communities in the extremely productive stream; prey communities in the different treatments did not decline in numbers or total biomass over the course of the summer. Therefore, prey samples taken on different dates were combined to provide an estimate of the nature of the prey community in each habitat type (Table 2). As expected, both the total number

TABLE 2. Prey community characteristics in stream areas with different amounts of vegetation. Mean values ± 1 SE are given.

	LV	MV	HV
Prey Density ($\#/m^3$)	31,833.3 ±3,058.4	56,360.0 ±3,304.0	83,779.4 ±10,122.2
Prey Biomass (mg dry weight/m^3)	6781.5 ±691.9	13,776.6 ±1,058.2	16,729.9 ±1,805.6
Average Individual Prey Biomass (mg dry weight)	.21	.24	.20
Number of Taxa per Sample	15.8±.6	17.5 ± 1.0	16.5 ± .7
Mean Diversity (H')	1.32	1.89	1.07

and biomass of prey were positively related to the amount of vegetation in a treatment. However, within the stream, there was little difference between vegetation types in the average biomass/prey individual or in the total number of taxa present.

Largemouth bass grew better in medium vegetation than they did in low and high vegetation (ANOVA, $p < .05$, see Table 3). Additionally, these length differences translated into greater average biomasses (wet weights) for bass in medium vegetation. The regression of log weight vs. total length had a greater slope for bass in medium vegetation than in low and high ($p < .10$, $r^2 \geq .95$ for each regression). Thus, a 115 mm bass had a greater biomass in medium than in low or high vegetation.

Initial mortality of the fish after stocking was much higher in low and high vegetation habitats. For example, in the first week after stocking the stream, 26 largemouth were discovered dead in the low vegetation habitat, 14 were dead in high vegetation, and only 4 were found dead in the medium vegetation habitat. All dead fish were replaced with similar sized bass, but the number of bass ultimately recovered from the medium vegetation habitat exceeded the numbers in the other two habitats (Table 3 - recall that 200 largemouth were originally placed in each habitat). Thus, bass grew better in medium vegetation even though their density was probably higher there.

The size difference between bass in medium and low vegetation is even greater if one looks at median instead of mean size differences. The median length in medium vegetation was 118 mm; the median in low

TABLE 3. Mean final total lengths (± 1 SE, in mm) of largemouth bass at different levels of vegetation.

	LV	MV	HV
Number of Bass Recovered	82	112	85
Total Length (mm)	115.1 ± 1.0	119.0 ± .8	116.0 ± 1.1

vegetation was only 112 mm. Mean size of largemouth in low vegetation was increased by the presence of a few very large individuals. Eight individuals larger than 134 mm were recovered from low vegetation; only two bass of that size were found in medium. Presumably, those individuals were cannibalistic, a phenomenon which is not uncommon with largemouth bass. There was a tendency for the distribution of bass lengths in low vegetation to depart from normality, although the departure was not significant. 41% of the length values fell between one standard deviation below the mean and the mean, and the distribution was slightly skewed in the direction of large sizes.

Four prey types - Simocephalus, a cladoceran; Hyallela azteca, an amphipod; Coenagrionid damselflies; and Baetid mayflies - were the most common prey found in the bass stomachs. In all treatments, these four prey categories accounted for greater than 90% of the total prey consumed by the bass.

As the summer progressed, two trends became apparent, both of which were expected. First, as the bass grew, they consumed fewer Simocephalus individuals, which were quite small (~.04 mg dry weight). Second, as the bass became larger, there tended to be more food present in the stomach. However, both trends were apparent in all treatments, and so stomach content data within each treatment were pooled for all dates to make comparisons between the habitat types. A number of patterns emerged (Table 4): (1) Largemouth bass in medium vegetation had the fewest prey items/gut; bass in low vegetation had the most. (2) Bass in medium vegetation consumed larger prey items than bass in high and low vegetation. (3) Bass in low vegetation had the greatest total

TABLE 4. Prey consumption patterns of largemouth bass in stream habitats with different amounts of vegetation. Mean values are given ± 1 SE.

	LV	MV	HV
Number of Stomachs Examined	33	25	27
Number of Prey Items/Stomach	38.7 ±7.8	12.7 ±2.8	26.9 ±4.4
Prey Biomass/Stomach (mg dry weight)	12.3 ±3.6	6.5 ±1.8	6.5 ±1.5
Biomass/Individual Prey Item in Gut (mg dry weight)	.32 ±.09	.51 ±.05	.24 ±.07
Number of Taxa/Stomach	4.2 ±.3	2.9 ±.4	3.8 ± .3

biomass of prey per gut; bass in medium and high vegetation had about the same total weight of prey. (4) Bass in medium vegetation were most specialized, consuming fewer prey types/fish than their counterparts in high or low vegetation.

The average total prey biomass/stomach was highest for bass in the low vegetation habitat because of the presence of very large prey in several of the guts. Bass in low vegetation had a greater tendency than bass in medium or high vegetation to include terrestrial prey, which were usually fairly large ($>$5 mg dry weight). For example, 9 of the bass in low vegetation had a total of 32 ants (mean ant dry mass = 6.6 mg) in their stomachs whereas only 4 bass from medium vegetation had terrestrial prey (4 total ants) in their stomachs and 3 bass from high vegetation consumed terrestrial prey (2 ants, 1 spider). Apparently, it was easier for bass in low vegetation to detect terrestrial prey on the surface of the water.

Despite the presence of many large terrestrial prey in the stomachs, low vegetation bass still on average consumed smaller prey items than fish in medium vegetation (Table 4) because they ate about 5 times as many Simocephalus individuals (Table 5), which averaged less than .05 mg dry weight, and because Coenagrionids and Baetids, which averaged about .5 mg dry weight, comprised a smaller proportion of their diets (Table 5). If one excludes the 9 bass from low vegetation which had ants in their stomachs, the total prey biomass/stomach for bass in low vegetation drops to 5.8 $\pm$ 1.2 mg, less than the biomass of prey found in the stomachs of bass from medium and high

TABLE 5. Relative utilization of four different prey types by largemouth bass at different levels of vegetation.

Habitat	Prey Type	Number Eaten	% of Total Prey Eaten	Number Eaten Per Fish ($\pm$1 SE)
Low Vegetation	_Simocephalus_	761	59.5	23.1 $\pm$ 7.8
(1278 Total Prey)	_Hyallela_	342	26.8	10.4 $\pm$ 2.4
	Baetids	36	2.8	1.1 $\pm$ .3
	Coenagrionids	21	1.6	.6 $\pm$ .3
	Other	118	9.2	3.6 $\pm$ .6
Medium Vegetation	_Simocephalus_	112	35.3	4.5 $\pm$ 2.1
(317 Total Prey)	_Hyallela_	63	19.9	2.6 $\pm$ 1.0
	Baetids	98	30.9	4.0 $\pm$ 1.1
	Coenagrionids	18	5.7	.7 $\pm$ .3
	Other	26	8.2	1.0 $\pm$ .3
High Vegetation	_Simocephalus_	218	30.0	8.1 $\pm$ 3.1
(727 Total Prey)	_Hyallela_	283	38.9	10.5 $\pm$ 1.7
	Baetids	68	9.4	2.5 $\pm$ .8
	Coenagrionids	112	15.4	4.2 $\pm$ 1.3
	Other	46	6.3	1.7 $\pm$ .4

vegetation (Table 4). Presence of ants in the diets was sporadic; 25 of the 32 ants consumed by low vegetation bass were eaten on one of the five sampling dates when many winged ants were observed flying near the stream channel. Thus, consumption of terrestrial prey may have contributed little to the overall growth of the bass in low vegetation, which had the smallest average size at the end of the summer.

Of the four principal prey types (Simocephalus, Hyallela, Coenagrionids, and Baetids), Baetid mayflies should be considered the most valuable prey type where value = E_i/H_i, the net energetic content of a particular prey type divided by its handling time. Approximate dry weights of individuals found in bass stomachs were: Simocephalus, .04 mg; Hyallela, .14 mg; Coenagrionids, .5 mg; and Baetids, .5 mg. Laboratory studies have shown that bass have shorter handling times with Baetids than with Coenagrionids (Anderson 1983); thus, assuming that handling times for Baetids are not significantly longer than with the two smallest prey types, Baetid prey should have the largest value (E_i/H_i).

Assuming that bass actively searched for Baetid prey, optimal foraging theory allows one to make predictions regarding the extent to which other less valuable prey (besides Baetids) are included in the diet (see Charnov 1976). Basically, optimal foraging theory predicts that the proportional representation of Baetids in the diet will be influenced by the average rate of energy acquisition of the bass. If a high rate of energy intake can be maintained by foraging for Baetids, it will be less likely that other prey types will be included in the diet. Other prey types will be included to the extent that the average rate of energy gain while foraging declines.

If Baetid densities were equal in the three habitats, Baetids would be encountered at the greatest rate in low vegetation and at the lowest rate in high vegetation (Anderson 1983), where encounter rate can be defined as the number of prey captured per second of search. However, Baetid densities were far from equal across habitat types (Figure 2). As expected, the low vegetation environment had an impoverished Baetid community (162.5 $\pm$ 38.5/m^3, mean Baetid biomass = .15 $\pm$ .06 mg dry weight); Baetid density in medium vegetation was 5.5 times greater (895 $\pm$ 93.5/m^3, biomass = .13 $\pm$ .04 mg). Based on a laboratory study which used similar macrophyte densities (Anderson 1983b), these density differences should translate into Baetid encounter rates which are 2.75 - 3 times greater in medium vegetation than in low, since for equal Baetid densities, average Baetid encounter rates in medium vegetation are about half as large as encounter rates in low vegetation. Table 5 shows that there were about 3 times as many Baetids/stomach in medium vegetation compared to low.

Baetid densities were highest in high vegetation (1198.2 $\pm$ 117.6/m^3, mean biomass = .14 $\pm$ .03 mg), but encounter rates with Baetids should have been reduced due to macrophyte shielding (Anderson 1983b). Bass in high vegetation consumed an average of 2.5 $\pm$ .8 Baetids per fish, less than in medium vegetation.

Proportional representation of Baetids in the diet is shown in Table 6. Simocephalus individuals were not enumerated from the vegetation samples, so they are not included in the calculation of the

FIGURE 2. Plots of the number of Baetids or Coenagrionids eaten per fish at three levels of vegetation and actual Baetid or Coenagrionid densities vs. level of vegetation. L = low, M = medium, and H = high vegetation. Dashed lines and open dots characterize Coenagrionid consumption or density. Closed dots, solid lines are for Baetids.

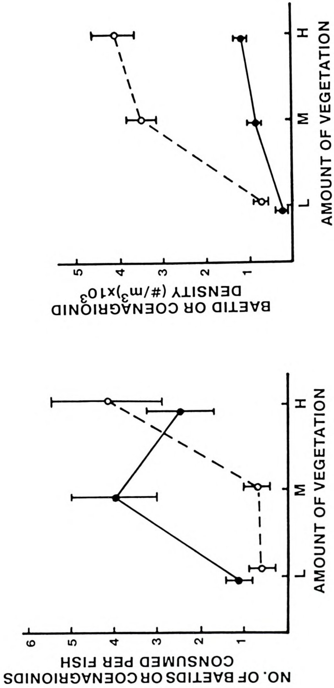
NO. OF BAETIDS OR COENAGRIONIDS CONSUMED PER FISH
1
2
3
4
5
6
L
M
H
AMOUNT OF VEGETATION
BAETID OR COENAGRIONID DENSITY (#/m^3)x10^3
1
2
3
4
5
L
M
H
AMOUNT OF VEGETATION

FIGURE 2.

TABLE 6. Representation of Baetid mayflies in the prey communities and the diets of largemouth bass in three habitat types.

	LV	MV	HV
% of Total Prey Available (not including Simocephalus)	.5	1.6	1.4
% of All Prey Eaten (not including Simocephalus)	7.0	47.8	13.3
Mean Biomass of Individual Baetids in Prey Community ($\pm$ 1 SE)	.15 $\pm$.06	.13 $\pm$.04	.14 $\pm$ .03
Mean Biomass of Baetids Eaten ($\pm$ 1 SE)	.51 $\pm$.10	.53 $\pm$.08	.45 $\pm$.06

proportional representation of Baetids either in the prey communities or the diets. Note that Baetids are always overrepresented in the diet relative to their numerical contribution to the total prey community, but the magnitude of this difference is greatest in medium vegetation - the proportion of Baetids in the diet is 30 times greater than the proportion found in the environment. Corresponding with this increased specialization on mayflies in medium vegetation, fewer total prey types were eaten per bass in medium vegetation compared with bass in high and low vegetation (ANOVA, $p < .05$, Table 4). Bass gained the most weight in medium vegetation, implying that bass in low and high vegetation added other prey types to the diet in relation to their lowered net rates of energy intake.

In a separate study (Anderson 1983b), it was predicted that because similar sized Baetids and Coenagrionids converge in value in high structure (with Baetids worth more in less vegetated environments because of shorter handling times in such habitats), the proportion of Coenagrionids in the diet relative to Baetids should increase in high vegetation. Increased relative consumption of Coenagrionids did occur in high vegetation (Table 5). In low and medium vegetation, bass ate two to six times as many Baetids as Coenagrionids per fish whereas in high vegetation largemouth bass ate 1.7 times as many Coenagrionids, despite the fact that relative densities of the two prey types did not change with differences in vegetation (Figure 2, note that Coenagrionid densities were higher than Baetid densities in each habitat).

Coenagrionid representation in the prey communities and diets is summarized in Table 7. Again, the proportions of Coenagrionids in

TABLE 7. Representation of Coenagrionid damselflies in the prey communities and diets of largemouth bass in three habitat types.

	LV	MV	HV
% of All Prey Available (not including *Simocephalus*)	2.1	6.3	5.1
% of All Prey Eaten (not including *Simocephalus*)	4.1	8.8	22.0
Mean Biomass of Coenagrionids in Prey Community ($\pm$ 1 SE)	.13 $\pm$ .02	.15 $\pm$ .01	.15 $\pm$ .02
Mean Biomass of Coenagrionids Eaten ($\pm$ 1 SE)	.48 $\pm$ .10	.70 $\pm$ .11	.34 $\pm$ .03
% of Eaten Coenagrionids Less than .3 mg dry weight	47.0	20.0	60.6

the diets are increased relative to their numerical contribution to the prey communities. However, the greatest specialization on Coenagrionids occurs in high vegetation, as predicted. Note also that those Coenagrionids eaten in medium vegetation, where energy intake was greater, are significantly larger than the Coenagrionids eaten in low or high vegetation (ANOVA, $p < .05$), again suggesting greater selectivity by the bass in medium vegetation. Bass in medium vegetation were also less likely to eat small Coenagrionids less than .3 mg dry weight (Table 7).

Amphipods were underrepresented in the diets relative to their numerical contributions to the prey communities (Table 8). Again, the largest difference occurred in medium vegetation. The proportion of amphipods in the diet was only 30.2/52.7 = 58% of what it should have been based on the numerical abundance of amphipods in the medium vegetation habitat. (Proportion of amphipods in the diet)/(proportion of amphipods in the prey community) was greater than 80% in low and high vegetation.

DISCUSSION

Reevaluating the models proposed earlier to account for diet breadths at different macrophyte densities, only mechanism 4, the energetic feedback model, fits the available data (see Table 1). Model 2 was found to be based on an incorrect hypothesis, that prey diversity increases at higher macrophyte levels. There is no evidence for this supposed trend (Table 2, plus an additional analysis showed there to

TABLE 8. Representation of amphipods in the prey communities and diets of largemouth bass in three habitat types.

	LV	MV	HV
% of All Prey Available	81.2	52.7	66.5
% of All Prey Eaten	66.2	30.7	55.6

be no tendency for species' abundances to be more evenly distributed at higher levels of vegetation). The premise of model 3, that macrophytes lower encounter rates with prey, is correct; however, the postulated diet breadths (L>M≫H) did not occur due to changing patterns of prey selectivity by bass in the different habitat types (bass in medium vegetation were more selective). Model 1 did not come close to matching actual foraging behavior of the bass - bass in low vegetation, which should have been most specialized according to this model, included the most prey types in their diets. Bass in low vegetation did occasionally include large numbers of a prey type - substrate dwelling Chironomids - which were seldom eaten by bass in medium and high vegetation. However, bass in low vegetation which ate 10 or more Chironomids averaged 5.3 $\pm$ 1.0 prey types per stomach, greater than other bass in low vegetation which had not eaten Chironomids (Table 4). There was no tendency toward microhabitat specialization. Only model 4 fit the data. Diet breadths were narrowest in medium vegetation, and close parallels were observed between degree of selectivity and inferred energy intake.

The results of this study are in agreement with the findings of Crowder and Cooper (1982) regarding fish growth rates at different macrophyte densities but differ with regard to diet breadths. Crowder and Cooper observed little change in diet breadths across macrophyte levels, but there was a tendency for their low vegetation fish to be most specialized. Their low vegetation community, however, was not impoverished - it had high prey densities early in the summer. Furthermore, they utilized bluegill sunfish, which are better equipped than bass for specializing on small zooplankton, which they apparently did in the open water, low vegetation habitat.

In this study, largemouth bass in medium vegetation were at an advantage compared to bass in low or high vegetation. Their growth rates were greater and they were more selective while foraging, taking fewer but larger prey than fish in low or high vegetation and consuming fewer prey taxa per fish. With regard to the management fish populations, questions related to the appropriate amount of vegetation needed to maximize production of a certain species can be put in simple logical terms. Basically, too little vegetation will not provide adequate prey numbers for maximal fish growth; too much vegetation will provide ample prey but hinder foraging. Moderate amounts of vegetation appear to be best, but the quantitative definition of what constitutes "moderate" vegetation will depend on the unique foraging abilities of the fish species of interest. Further, any benefits associated with efficient foraging at a given macrophyte density may be negated if that level of vegetation is also associated with increased predation risk. In such cases, fish may avoid risky areas and forage "suboptimally" in locations where predation risk is reduced (Mittelbach 1981).

LITERATURE CITED

Anderson, O. 1983. Optimal foraging by largemouth bass in structured environments. Ecology 64:000-000.

Anderson, O. 1983. The effects of structural complexity on foraging behavior and diet breadth. Submitted to Oecologia.

Charnov, E. L. 1976. Optimal foraging; attack strategy of a mantid. American Naturalist 110:141-151.

Crowder, L. B., and W. E. Cooper. 1982. Habitat structural complexity and the interaction between bluegills and their prey. Ecology 63:1802-1813.

Cummins, K. W., and J. C. Wuycheck. 1971. Caloric equivalent for investigations in ecological energetics. Internationale Vereinigung fur Theoretische und Angewandte Limnologie, Mitteilungen 18:1-158.

Gerking, S. D. 1957. A method of sampling the littoral macrofauna and its application. Ecology 38:219-225.

Hackney, P. A. 1975. Bass populations in ponds and community lakes. Pages 131-139 in Henry Clepper, editor. Black bass biology and management. Sport Fishing Institute, Washington, D. C.

Heidinger, R. C. 1975. Life history and biology of the largemouth bass. Pages 11-20 in Henry Clepper, editor. Black bass biology and management. Sport Fishing Institute, Washington, D. C.

Hruska, V. 1961. An attempt at a direct investigation of the influence of the carp stock on the bottom fauna of two ponds. Internationale Vereiningung fur Theoretische und Angewandte Limnologie, Verhandlungen 14:732-736.

Ivlev, V. W. 1961. Experimental ecology of the feeding of fishes. Yale University Press, New Haven, Connecticut, USA.

Krebs, J. R. 1978. Optimal foraging: decision rules for predators. Pages 23-63 in J. R. Krebs and N. B. Davies, editors. Behavioural ecology. Sinauer Associates, Sunderland, Massachusetts, USA.

McCammon, G. W., LaFaunce, D., and C. M. Seeley. 1964. Observations on the food of fingerling largemouth bass in Clear Lake, Lake County, California. California Fish and Game 50:158-169.

Mittelbach, G. G. 1981. Foraging efficiency and body size: a study of optimal diet and habitat use by bluegills. Ecology 62: 1370-1386.

Stoner, A. W. 1982. The influence of benthic macrophytes on the foraging behavior of pinfish, Lagodon rhomboides. Journal of Experimental Marine Biology and Ecology 58:271-284.

Vince, S., Valiela, I., Backus, N., and J. M. Teal. 1976. Predation by the salt marsh killifish Fundulus heteroclitus in relation to prey size and habitat structure: consequences for prey distribution and abundance. Journal of Experimental Marine Biology and Ecology 23:255-266.

Werner, E. E., and D. J. Hall. 1974. Optimal foraging and the size selection of prey by the bluegill sunfish (*Lepomis macrochirus*). Ecology 55:1042-1052.

Werner, E. E., and G. G. Mittelbach. 1981. Optimal foraging: field tests of diet choice and habitat switching. American Zoologist 21:813-829.

Werner, E. E., Mittelbach, G. G., and D. J. Hall. 1981. Foraging profitability and the role of experience in habitat use by the bluegill sunfish. Ecology 62:116-125.

APPENDIX

Appendix. Invertebrates identified from vegetation samples and largemouth bass stomachs.

CRUSTACEA: Copepoda; Ostracoda; Isopoda; Cladocera - *Chydorus*, *Simocephalus*, *Daphnia*; Amphipoda - *Hyallela*. INSECTA: Ephemeroptera - Baetidae, Caenidae, Heptageniidae; Odonata - Aeschnidae - *Anax*, Libellulidae, Lestidae, Coenagrionidae; Hemiptera - Corixidae, Notonectidae, Belastomatidae; Trichoptera; Coleoptera - Dytiscidae, Haliplidae; Diptera - Chironomidae - Tanypodinae, Tanytarsus; Ants - *Formica*; Megaloptera; Homoptera; ANNELIDA: Hirudinea.