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FORAGING EFFICIENCY AND BODY SIZE: A STUDY OF OPTIMAL DIET AND HABITAT USE BY BLUEGILLS¹

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Abstract. A foraging model was developed to predict the optimal diet breadth and maximum energetic intake of a given-sized fish foraging in each of three aquatic habitats: the open water, vegetation, and bare sediments. Model parameters of prey encounter rates and prey handling times were quantified as functions of fish size, prey density, and prey size through a series of laboratory feeding experiments using the bluegill sunfish (*Lepomis macrochirus*). Results of these experiments show both searching ability and prey handling efficiency to increase with increasing fish size.

Predictions of prey size selection and optimal habitat use based upon maximizing energetic gain were then examined in a small Michigan lake for three size classes of bluegills. Bluegills >100 mm standard length were highly size selective in their feeding and their diets closely matched predictions of an optimal diet model. From two estimates of relative prey visibilities I show that these fish selected larger prey items than would be predicted if prey were consumed "as encountered." Habitat use of large bluegills was also shown to maximize foraging return as fish switched from utilizing vegetation-living prey to utilizing open-water zooplankton as relative foraging profitabilities in the two habitats changed across the summer. Bluegills <100 mm standard length were restricted in their habitat use, remaining in or near the vegetation despite demonstrated increases in foraging return available in the open-water habitat. Size-related predation risk apparently accounts for differences in habitat use between bluegill size classes, and its consequences for intra- and interspecific competition between size classes are discussed.

Key words: body size; foraging efficiency; habitat switching; *Lepomis*; Michigan; Osteichthyes; predation risk; size selection.

INTRODUCTION

At the heart of the rapidly expanding theory of optimal foraging is the goal of predicting the diet and habitat use of organisms as a function of resource availability and utility to the consumer. To date, this theory has largely been concerned with the processes of individual consumer choice. However, its potential applicability to the study of community level questions is large (e.g., Werner 1977). Clearly, the ability to predict the diet and habitat use of organisms in nature represents a potential foundation upon which more mechanistic theories of competition and species packing may be built. The eventual usefulness of optimal foraging theory in unraveling the nature of community structure will depend in large part on the degree to which the theory can quantitatively predict forager behavior in the field (Pyke et al. 1977).

There have been relatively few field studies of optimal foraging (Davies 1977, Goss-Custard 1977), and only the work of Belovsky (1978) on moose has actually attempted to predict an animal's diet quantitatively in nature through optimal foraging criteria. This slow progression from theory to empirical test is understandable, as major difficulties stand in the way of extending optimal foraging models to the field. Not the least of these difficulties is the need to measure the

availability of various prey types to the consumer and the quantification of actual resource use by the foraging animal. Crucial in the testing of any foraging model is a means by which prey abundances, measurable in the field, can be translated into actual rates of prey encounters by a forager.

This paper develops an optimal foraging model for the bluegill sunfish (*Lepomis macrochirus*) and examines its predictions in a natural environment. Since bluegills capture prey individually and swallow them intact, the size and type of prey consumed by a foraging fish are easily determined from gut contents. Further, the close association between prey type and habitat which exists for many groups of aquatic animals (e.g., open-water zooplankton, vegetation-dwelling insects, etc.) permits the determination of a fishes' habitat use through dietary analysis. In these respects, the bluegill represents an ideal organism for the study of diet selection and habitat use in nature.

The size-distributed nature of fish populations also allows an examination of the functional relationships between body size and foraging efficiency so that relative differences in resource utilization can be related to potential competitive interactions between size classes. The determination of such relationships represents an important first step in understanding the nature of exploitative competition both within and between size-structured populations.

In this study I utilize a series of laboratory foraging experiments to quantify foraging parameters of prey encounter rates and handling times as functions of fish

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size, prey size and prey density. These experiments were designed to simulate the physical structure and prey types found in each of three aquatic habitats (the open water, bare sediments and vegetation) which previous studies have demonstrated to be key divisions of the bluegill's natural environment (Werner and Hall 1976, 1979, Werner et al. 1981). Seasonal prey abundances were then measured in these three habitats in a small Michigan lake and translated into prey encounter rates and profitabilities using results of the laboratory experiments. A foraging model was then used to make predictions of optimal diet breadth and habitat use for a given sized fish, and these predictions were compared to the actual diets and habitat use of three size classes of bluegills occurring in the lake.

THE MODEL

To predict the range of prey sizes eaten and maximum net energetic intake for a given-sized bluegill foraging in habitat type *j*, an optimal foraging model similar to those developed by Werner and Hall (1974), Charnov (1976), Pearson (1976), and others was formulated. As in these models, the net rate of energy intake from habitat *j*, $E_{nj}/T_{(j)}$ (J/s), can be described as

$$E_{nj}/T_{(j)} = \frac{\sum_{i=1}^n (B_{(ij)}E_{(ij)}) - C_s}{1 + \sum_{i=1}^n B_{(ij)}H_{(ij)}} \quad (1)$$

where $E_{(ij)} = Ae_{(ij)} - C_h H_{(ij)}$,

where *A* = assimilable fraction of energetic content, $e_{(ij)}$ = energetic content of prey size class *i* found in habitat type *j* (J), $H_{(ij)}$ = handling time of prey size class *i* in habitat type *j* (s), and C_h = energetic cost of handling prey (J/s), C_s = energetic cost of searching (J/s) and $B_{(ij)}$ = number of individuals of prey size *i* encountered per second of search. (Other symbols used in the text are defined in Table 1.)

The optimal diet for a predator (i.e., that subset of available prey sizes which maximizes its net rate of energetic intake (E_n/T)) can now be determined by ranking prey sizes from highest to lowest $E_{(ij)}/H_{(ij)}$ and then adding prey sizes to the diet until the ratio E_n/T is maximized. A proof of this theorem can be found in Charnov (1976).

The inclusion of the energetic costs of searching and handling in Eq. 1 is of course necessary when comparing the energetic intakes of foragers of differing body size. In fish and many other organisms, searching ability and efficiency at handling prey will also be functions of body size. Therefore, in order to predict the diet and net energetic intake of different size classes of the bluegill it is necessary to determine the functional relationships between predator size and the parameters in Eq. 1.

For fish, the assimilable fraction of energy ingested

TABLE 1. Definition of symbols used in the text.

E_n	Net energy gained while foraging (J)
T	Time spent foraging (s)
$e_{(i)}$	Energetic content of prey size class <i>i</i> (J)
$H_{(i)}$	Handling time for prey size class <i>i</i> (s)
$B_{(i)}$	Encounter rate for prey size class <i>i</i> (number/s)
l	Prey length (mm)
A	Assimilable fraction of energy content
C_s	Energetic cost of searching (J/s)
C_h	Energetic cost of handling (J/s)
L	Fish standard length (mm)
S	Swimming speed (m/min)
t	Water temperature (°C)
M	Fish live mass (g)
D	Prey density (units appropriate to each habitat)
m	Prey dry mass (mg)

(*A*) appears to be independent of body size (Elliot 1976) and a value of 0.7 is appropriate for most invertebrate prey (see Ware 1975 for a general discussion, also Elliot 1976).

The energetic costs of searching and handling (C_s and C_h) can be estimated for bluegills using the data of Wohlschlag and Juliano (1959). These investigators measured the oxygen consumption of bluegills as a function of body mass (*M*), swimming speed (*S*) and water temperature (*t*) using a rotating respirometer suspended in a lake. Oxygen consumption was converted to joules expended by assuming 1 mg oxygen consumed equals 13.6 J (Elliot and Davison 1975). Since other parameters of the foraging model were determined as functions of fish standard length (length from anterior end of head to posterior end of vertebral column), the measure of fish size contained in Wohlschlag and Juliano's energetic equation was converted from live mass in grams (*M*) to standard length in millimetres (*L*) using a length-mass relationship for bluegills of $M = 0.000026 L^{3.043}$ (E. E. Werner and D. J. Hall, *personal communication*). The resultant equation:

$$\log C = -7.2296 + 2.5847 \log L + 0.0142 S + 0.0198 t \quad (2)$$

was used to calculate C_s and C_h . C_s was calculated using the swimming speed exhibited by a fish while searching. C_h should include the costs of masticating prey and swallowing as well as any movement which occurs. At present, no measures of the costs of processing prey exist for bluegills. Since most of the bluegill's prey are small, soft-bodied invertebrates, which the fish swallows whole, it is probably reasonable to assume its energetic expense of chewing and swallowing is small relative to that of swimming. Therefore, C_h was approximated using Eq. 2 and the swimming speeds exhibited by fish while handling prey.

Swimming speeds of bluegills engaged in searching and handling were determined from a series of laboratory foraging experiments designed also to measure

TABLE 2. Mean swimming speeds in metres per minute (± 1 SE) for bluegills of different standard lengths (SL) searching out and handling two sizes of prey in laboratory representations of the vegetation and sediment habitats.

Prey length (mm)	Swimming speeds							
	110 mm SL		65 mm SL		45 mm SL		21 mm SL	
	Searching	Handling	Searching	Handling	Searching	Handling	Searching	Handling
	Vegetation habitat							
9.5	1.9 \pm .21	0.5 \pm .23	2.2 \pm .14	1.3 \pm .11	2.6 \pm .16	1.3 \pm .16	1.1 \pm .16	0.5 \pm .16
13.1	1.8 \pm .24	0.8 \pm .54	2.0 \pm .09	0.7 \pm .05	2.2 \pm .10	1.4 \pm .14
Prey length (mm)	110 mm SL		80 mm SL		45 mm SL		25 mm SL	
	Searching	Handling	Searching	Handling	Searching	Handling	Searching	Handling
	Sediment habitat							
11.1	1.3 \pm .08	0.6 \pm .05	1.3 \pm .08	0.6 \pm .06	2.3 \pm .10	0.9 \pm .05	1.0 \pm .06	0.4 \pm .07
19.5	1.4 \pm .12	0.5 \pm .06	1.4 \pm .11	0.7 \pm .08	2.3 \pm .19	0.8 \pm .12	1.0 \pm .06	0.5 \pm .30

prey encounter rates and handling times (a complete description of the laboratory system can be found in the following section). Average swimming speeds were calculated for each experiment by dividing the total distance traveled while searching or handling by the total time spent in the activity. Table 2 lists the swimming speeds ($\bar{x} \pm 1$ SE) of fish while searching or handling prey in laboratory representations of vegetation and sediment habitats. As would be expected, fish swam slower while handling prey than while actively searching. Also, fish size and habitat type had a significant effect on swimming speeds: two-way ANOVA (searching): fish size $F = 48.3$, $P < .001$; habitat type $F = 10.5$, $P < .002$; two-way ANOVA (handling): fish size $F = 15.9$, $P < .001$; habitat type $F = 3.2$, $P > .05$; $n = 96$. However, the total range of swimming speeds observed across all fish sizes or habitats was small, and over this range in swimming speeds only minor changes in energetic costs occur. For example, a 50-mm bluegill at 18° expends 3.4 mJ/s swimming at 1.0 m/min and 3.6 mJ/s swimming at 3.0 m/min (by Eq. 2). Therefore, to simplify calculation of optimal diets, average swimming speeds taken across all bluegill sizes and both habitats were used to calculate the energetic costs of searching and handling. Bluegill swimming speeds while searching and handling were 1.7 ± 0.08 m/min and 0.80 ± 0.05 m/min ($\bar{x} \pm 1$ SE, $n = 96$), respectively; these values fall within the range of swimming speeds observed for feeding fish in nature (Ware 1975).

The energetic content of prey size class i ($e_{(i)}$) was determined by converting prey lengths to dry masses and then multiplying by the appropriate energy equivalent. Prey lengths were converted to masses by the following regressions: open-water habitat, $m = 0.012l^{2.63}$; bare-sediment habitat, $m = 0.003l^{2.35}$ ($r = .93$, $n = 64$); vegetation habitat, $m = 0.005l^{2.16}$ ($r = .93$, $n = 179$). The open-water regression is for four species of *Daphnia* (Burns 1969); the bare sediment regression is for *Chironomus* larvae (G. G. Mittelbach, *personal observation*), and the vegetation

regression contains a number of prey groups, including: amphipods, caddisfly larvae, damselfly naiads, midge larvae, *Sida*, *Simocephalus*, copepods, *Bosmina*, and mayfly nymphs (Dumont et al. 1975, E. E. Werner and D. J. Hall, *personal communication*, G. G. Mittelbach, *personal observation*). Prey dry masses were then converted to joules using the following energy equivalents: 21 J/mg dry mass for *Daphnia* (Richman 1958, Cummins and Wuycheck 1971), 23 J/mg dry mass for Chironomidae (Cummins and Wuycheck 1971, Elliot 1976), and 21 J/mg dry mass for vegetation prey (Cummins and Wuycheck 1971).

To quantify prey encounter rates (B) and handling times (H) a large number of laboratory experiments were performed using various combinations of prey size, fish size and prey density. These experiments were designed to simulate the structure and prey type found in each of three distinct aquatic habitats: the open water, bare sediments, and vegetation. Experimental field studies (Werner and Hall 1976, 1979, Werner et al. 1981) have shown that the bluegill treats these habitats as distinct divisions of the environment; each habitat differs markedly in physical structure and associated prey and therefore requires unique modes of foraging by the fish. Within a habitat type, prey were characterized by body size and density since the responsiveness of fish to both parameters is well recognized (Ivlev 1961, Werner and Hall 1974, Eggers 1977).

LABORATORY EXPERIMENTS

Methods

In the laboratory, realistic approximations of each of the three habitat types were constructed as follows:

Habitat	Laboratory
Open water	structure = open aquaria prey = zooplankton (<i>Daphnia pulex</i>)

Bare sediments	structure = aquaria containing 4–5 cm layer of marl sediments
	prey = midge larvae (predominantly <i>Chironomus plumosus</i>)
Vegetation	structure = aquaria containing anchored, live <i>Elodea</i> (100 plants/m ²)
	prey = damselfly naiads (Coenagrionidae)

The particular prey types chosen commonly occur in each habitat in nature and in general represent the degree of crypsis and mobility characteristic of prey in the habitat (i.e., tube-dwelling midges in the sediments, free-swimming zooplankton in the open water, clinging damselfly naiads in the vegetation). The physical structure of each habitat was represented by natural substrates where appropriate.

The general format for each experiment involved dividing a 214-L aquarium into two unequal sized sections, 26 L and 188 L, by a removable glass partition. The larger volume contained a prey distribution of known composition (prey type, size, and density). *Daphnia* were size-sorted by washing them through a series of United States standard sieves, and a known number of a specific size class were then introduced into the larger division of the aquarium immediately prior to the initiation of a feeding experiment. Two sizes of *Daphnia* (2.20 ± 0.04 mm and 1.14 ± 0.02 mm body length) and five prey densities (0.1, 0.5, 2.5, 5, 15 individuals/L) were used. For the sediment habitat *Chironomus* larvae were sized, counted, and then distributed over the surface of the larger section of the aquarium. Midges were introduced during the late afternoon of the day prior to an experiment as this permitted the larvae to burrow into the sediments. Two midge sizes (19.53 ± 0.46 mm and 11.07 ± 0.34 mm body length) were used at densities of 50, 300, and 1000 individuals/m². Experiments simulating the vegetation habitat used Coenagrionidae naiads (9.51 ± 0.27 mm, 13.15 ± 0.33 mm, and 22.30 ± 0.28 mm body length) at densities of 38 and 192 individuals/m³ for large damselflies, 192 individuals/m³ for medium damselflies and 192, 385 and 1538 individuals/m³ for small damselflies. Damselfly naiads were introduced into an aquarium the day prior to an experiment. All prey were either collected from local ponds or cultured in the laboratory.

After the introduction of prey a fish which had been starved for 24 h was placed into the smaller section of the aquarium and allowed to acclimate for 30–60 min. An experiment was then initiated by removing the glass partition and allowing the fish to feed. Data recorded were handling time for each prey captured, time between strikes, success or failure of a strike,

and the distance traveled by a fish while handling prey and while searching (excepting the plankton experiments where no distance measurements were taken). Fish were observed directly and feeding behaviors timed by speaking into a tape recorder, which was then replayed and timed with a stopwatch. Handling times for *Chironomus* and Coenagrionidae were measured as the time from prey capture until the reinitiation of search. Handling times for *Daphnia* were too short to be measured accurately in this manner. For these prey, handling times were determined by examining the time per prey item captured as a function of prey density. The asymptotic value of time per prey item as density increased was used as a measure of baseline or minimum handling time (Ware 1972, Werner 1977).

Experiments were performed over short time periods (30 s for *Daphnia*, 3 min for Coenagrionidae, and 10 min for *Chironomus*) to minimize the effect of prey depletion. Maximum prey depletion was <25% of total, excepting the lowest *Daphnia* and Coenagrionidae densities, where prey depletion was $\approx 45\%$.

Over 500 feeding experiments were conducted. Ten bluegills (33–109 mm SL) were used in the open-water experiments, nine (21–115 mm SL) in the vegetation experiments and six (21–109 mm SL) in the sediment experiments. Each combination of prey size, fish size, and prey density was replicated from three to six times. Water temperatures ranged from 17°–22°C.

Results

Naive bluegills exposed to these laboratory habitats show a marked increase in prey capture rate with successive feeding experiments (see Fig. 1 in Werner et al. 1981). Since I wished to determine the maximum energetic return available to a fish in a given habitat, measurements of prey encounter rates and handling times were taken after fish were experienced in a habitat and prey capture rate had levelled off (generally after 6–8 trials).

Fig. 1 shows handling time per prey item (H) plotted as a function of relative prey size (prey length/fish length) for prey in each of the three habitats. For each prey type, handling time increases exponentially above a critical ratio of prey length/fish length (l/L_{crit}). Below this ratio handling time remains approximately constant. These results are in agreement with the general relationship postulated by Schoener (1969), who argues that below a critical prey length handling time should remain constant and above this prey length handling time should increase sharply. Werner (1974) also found that bluegill handling times when feeding on either *Daphnia* or artificial prey were constant at ≈ 1 s/prey item for small prey and increased exponentially with larger prey sizes. Handling times for bluegills feeding on *Chironomus* did not approach 1 s at small prey sizes; rather, handling times for these prey reached a minimum at about 10 s/prey. When a fish

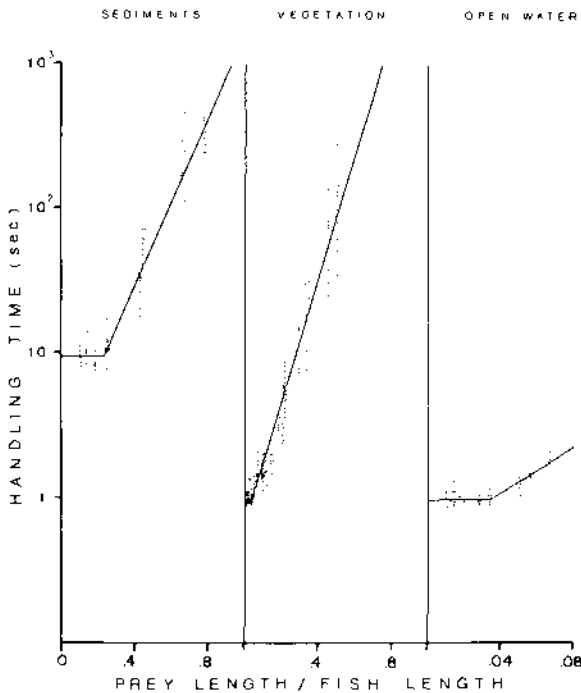


FIG. 1. Prey handling time as a function of relative prey size in each of three habitats. Prey used were *Chironomus* larvae for the sediments, Coenagrionidae naiads and *Daphnia* for the vegetation, and *Daphnia* for the open water. Handling times for *Daphnia* were combined with those for Coenagrionidae to complete the range of prey sizes commonly found in natural vegetation. Fish sizes ranged from 22–110 mm. Curves were fitted by the regression equations in Table 3.

captures a midge larva it engulfs a mouthful of sediments along with the prey. The bluegill must separate a prey item from these sediments before swallowing, and this "sieving" action functions to increase the handling time for fish feeding on sediment-dwelling prey. For each prey type an exponential equation was fitted by least-squares regression to values greater than the minimum handling time per individual prey. The fitted equations, minimum handling times, and critical ratios of prey length/fish length are listed in Table 3.

The rate at which a fish encountered prey (B) was a function of prey density (D), prey length (l), and fish size (L) in each habitat (Fig. 2). Prey encounter rate was defined operationally as the mean number of prey captured per unit search time; this rate was calculated for each experiment by dividing the number of prey captured by the total experimental time minus total handling time. The relationships shown in Fig. 2 can be qualitatively interpreted from known information on the visual abilities of fish. Numerous studies (Ware 1971, Werner and Hall 1974, Vinyard and O'Brien 1976, and Confer et al. 1978) have demonstrated a positive relationship between reactive distance (the distance at which a fish can detect a prey) and prey body length. Schmidt and O'Brien (referenced in O'Brien 1979) have also shown that reactive distance increases with fish body length. However, while reactive distances may be measured as functions of prey length and fish length in simple environments, the translation of these reactive measures into actual rates of prey encounter in habitats containing physical structure and cryptic prey is a complex if not hopeless task. A regression approach was chosen instead as a means of predicting prey encounter rates in each of the habitats studied.

The variables B , D , l , and L , as well as their logarithmic transforms, were examined using stepwise multiple regression to determine which combination of variables provided the best predictor of prey encounter rate (B) in a habitat. A regression model of the form:

$$\log B = a + b_1 \log D + b_2 \log l + b_3 \log L$$

yielded the best overall fit to the data, and the fitted constants for each habitat are listed in Table 4. The complete regression for each habitat is highly significant ($P < .001$) as are each of the variables within the regressions ($P < .05$). Inspection of residuals revealed no strong bias in the equations. A hierarchical F test was used to test for significant interactions between the variables. No three-way interactions were found to be significant ($P > .05$). Of the nine possible two-way interactions only one, $D \times L$ for the vegetation habitat, was significant ($P < .05$). Therefore, a simple model excluding interaction terms was used.

TABLE 3. Handling time relations for bluegill feeding on each of three prey types. The values l/L_{crit} represent ratios of prey length/fish length below which handling time remains constant and above which handling time increases exponentially. Minimum handling times are $\bar{x} \pm 1$ SE.

Prey type	Handling time (H) ($l/L \geq l/L_{crit}$)	Minimum handling time (H) ($l/L < l/L_{crit}$)	l/L_{crit}
<i>Daphnia</i>	$H = 0.536 e^{16.468 l/L}$ $r = .92; n = 18$	$H = 1.02 \pm .02$ $n = 24$	0.034
<i>Chironomus</i>	$H = 2.364 e^{6.492 l/L}$ $r = .96; n = 62$	$H = 9.63 \pm .21$ $n = 20$	0.22
Coenagrionidae and <i>Daphnia</i>	$H = 0.639 e^{9.966 l/L}$ $r = .96; n = 112$	$H = 1.02 \pm .02$ $n = 30$	0.045

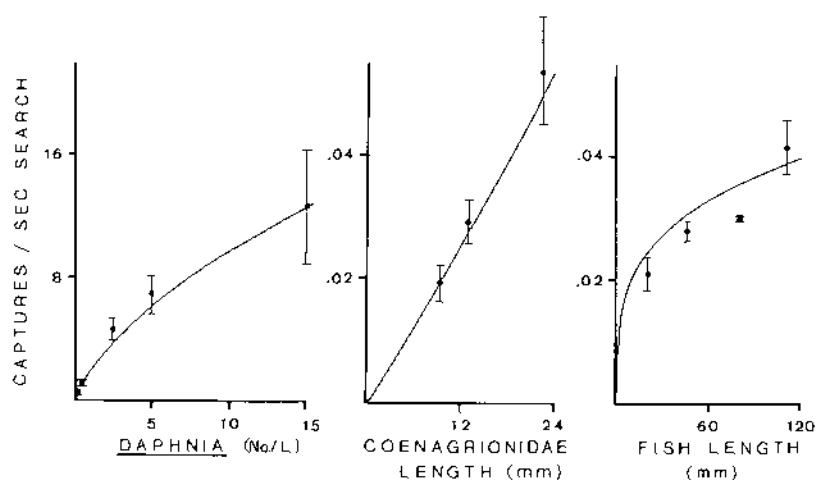


FIG. 2. Representative examples of laboratory prey encounter rates ($\bar{x} \pm 1$ SE) in relation to prey density, prey length and fish length. Results shown in the first panel are from two 65-mm bluegills feeding on *Daphnia* (1.14-mm body length). The second panel shows results from two 110-mm bluegills feeding on *Coenagrionidae* (192 naiads/m²) and the third panel shows data from eight bluegills feeding on 11.1-mm *Chironomus* larvae at 1000 larvae/m². Curves were fitted by the regression equations in Table 4.

To illustrate the relative effects of prey density, prey length, and fish length on the rate of prey encounter by bluegills, response surfaces constructed using the regression equation for the vegetation habitat are shown in Fig. 3. As can be seen, fish size has a dramatic effect on prey encounter rate, larger fish encountering more prey per unit time than smaller fish. This result is consistent with the visual physiology of fish which predicts an "increased acuity or sensitivity or both in larger fish of any species" (Hester 1968). Qualitatively, the effects of prey size, fish size, and prey density were similar in all three habitats. Important quantitative differences, however, exist between habitats (Table 4). Notably, encounter rates for the same size and density of prey are much greater in the open water than in the vegetation or sediments. The open water provides no structural refuges for prey, and consequently zooplankton occurring in the lighted epilimnion are considerably more available to fish than littoral prey. The effect of fish size on prey encounter rate is also greatest in the open-water habitat where no environmental structure limits visibility.

The basic trade-offs involved in determining habitat utility to the bluegill are thus apparent from the rela-

tionships of prey handling times and encounter rates characteristic of each habitat. Prey found in the open-water habitat are highly visible and are encountered at high rates by a foraging fish. However, since these prey are small and must be handled individually, the profitability (E/H) of any single zooplankter is low. Vegetation-dwelling prey are generally larger than zooplankton and will have higher individual profitabilities (E/H); however, the structure of the vegetation reduces the rate at which bluegills can find these prey. Encounter rates with sediment-dwelling prey are similar to those found in the vegetation, but the time required by fish to extract these prey results in higher handling times and lowered prey profitability.

The foraging model (Eq. 1) can now be used to weigh the relative magnitudes of these effects and determine the net energy available from a habitat. Because parameters of the model are calculable functions of prey size, fish size, and prey density, the net energetic return and optimal diet of a given-sized bluegill can be predicted from a knowledge of available prey sizes and abundance alone. Measures of the prey sizes and abundances naturally available in each habitat were determined in a small Michigan lake. These data

TABLE 4. Fitted parameters (± 1 SE) of the multiple regression equations describing prey encounter rates (B) in each habitat. The form of each regression equation is $\log B = a + b_1 \log D + b_2 \log l + b_3 \log L$.

Habitat	a	b_1	b_2	b_3	R^2	Overall significance	n
Open water	$-3.374 \pm .50$	$0.667 \pm .06$	$0.921 \pm .28$	$2.006 \pm .29$.79	$P < .001$	68
Sediments	$-5.114 \pm .30$	$0.719 \pm .05$	$0.971 \pm .20$	$0.262 \pm .10$.84	$P < .001$	58
Vegetation	$-5.905 \pm .41$	$0.779 \pm .07$	$1.045 \pm .22$	$0.694 \pm .13$.58	$P < .001$	110

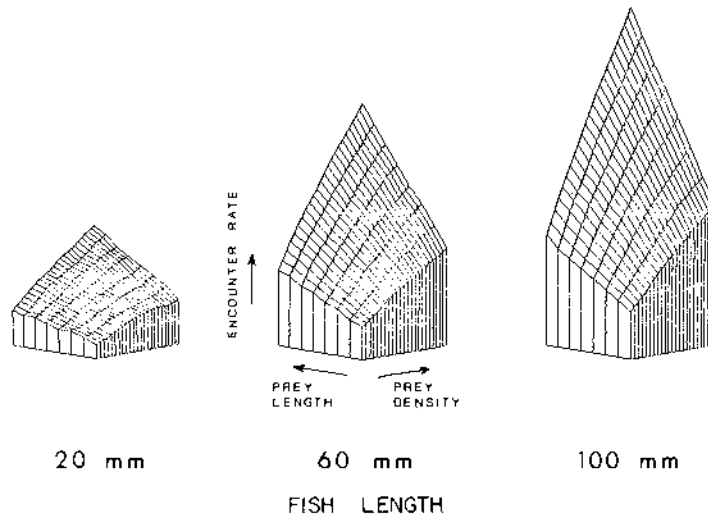


FIG. 3. Rate of prey encounter as a function of prey density and prey length for three sizes of bluegills (20, 60, 110 mm) foraging in the vegetation on Coenagrionidae. Response surfaces were constructed from the equation $\log B_i = 5.905 + 0.779 \log D + 1.045 \log l + 0.694 \log L$ (Table 4). Prey densities of 10–45 prey/m³ and prey lengths of 5–12 mm were used for each fish size.

were used to generate predictions of optimal diets and habitat use for bluegills in this lake, which were then compared to actual diets and habitat use of the fish.

FIELD STUDY

Site

Lawrence Lake, a mesotrophic marl lake, 4.9 ha in surface area, located 2.1 km east of Hickory Corners, Barry County, Michigan, USA, was chosen as the study site because it contains a large and apparently stable population of bluegills (Hall and Werner 1977), a simple vegetational community (79% *Scirpus subterminalis* by mass (Rich et al. 1971)) and distinct habitat types similar to those used in the laboratory experiments. Prey resources and fish were sampled from each of three habitats (barren marl bench, vegetated bench and slope, and open water) on the east shore of Lawrence Lake during the months of May–August 1979.

Prey living in the bare, marl sediments were sampled with a corer (6.5 cm diameter; 8 cm deep) operated by a diver wearing mask and snorkel or SCUBA. Five random samples were taken on each date. Samples were gently washed through a series of three sieves (2.83-, 0.710-, 0.180-mm mesh), from which prey were collected and preserved in 10% formalin. Contents of the smallest mesh sieve were mixed with a 20% solution of MgSO₄, allowing the separation of live prey from inorganic sediments and debris.

The vegetation habitat was sampled by a diver using a modified version of Gerking's sampler (Gerking 1957), described fully in Mittelbach (1981). This sampler has proven to be effective in capturing prey from

the size of small cladocerans to large, motile prey such as damselflies, mayflies, and occasionally small fish. Sampling was stratified with five samples taken randomly along the bench (0.5–1.5 m depth) and five samples taken randomly along the slope (2–4 m depth) on each date. Vegetation samples were carefully washed into a series of three sieves (2.83-, 0.710-, 0.180-mm mesh). Contents of the two largest sieves were sorted by hand and the live prey removed and preserved in 10% formalin, while contents of the smallest sieve were separated using 20% MgSO₄ solution.

Open-water prey were sampled at two locations in the lake using a 30 cm diameter number 10 plankton net. Two vertical tows were taken from a depth of 4 m at a location in the limnetic zone approximately 60 m from shore. A depth of 4 m was chosen as it defines the usual limit of the thermocline in Lawrence Lake during the summer (Wetzel 1975). Previous work has suggested that bluegills remain above the thermocline when feeding (Hall et al. 1979), and echo soundings taken in Lawrence Lake on 29 July 1979 confirmed that all fish were located between the surface and a depth of 4–4.5 m (thermocline at 4 m; R. G. Wetzel, *personal communication*). Plankton abundances near shore were determined by taking two vertical tows from 3 m deep at locations along the slope (water depth 4–5 m). All plankton samples were preserved in 95% alcohol.

The bluegill is largely a diurnal feeder, showing a major feeding peak around sunrise (Sarker 1977, Wilsman 1979). On average, plankton sampling began 15 min before sunrise and was completed by 10 min post-sunrise. Vegetation and sediment sampling began on average 30 min postsunrise and was completed by 70

min postsunrise. Resources sampled thus represent prey availabilities during this morning feeding period.

Prey samples were enumerated under a dissecting microscope and organisms classified, generally to genus or family level. Large vegetation- and sediment-dwelling prey were counted in their entirety. Prey collected on the smallest sieve and the open-water plankton were subsampled due to the large numbers of individuals present. Fifteen to 50 randomly chosen individuals in each prey category were measured for total body length in each sample. Prey size-frequency distributions were then constructed for each sample by grouping prey into 0.5-mm classes for the vegetation and sediment habitats and into 0.1-mm classes for the open-water plankton. The overall size-frequency distribution of prey available in a habitat was determined by averaging across all samples from a given date.

The distribution of prey by size (length) in each habitat was described by a lognormal distribution. Within each habitat the abundance and size of prey changed dramatically across the summer, resulting in marked changes in profitability of these habitats to the fish (see section on habitat switching). A complete description of the dynamics of these prey resources can be found in Mittelbach (1981).

Bluegill diet and habitat use

Fish were sampled from areas of bare sediments and the vegetated bench and shallow slope using a 15.25-m seine, whereas bluegills found along the deeper portions of the slope and in the open water beyond were collected by angling. On average sampling began 45 min postsunrise and was completed by 80 min postsunrise. Thus the location and timing of the fish collections were coincident with that of the prey sampling. After capture fish were anesthetized and killed with MS-222 (tricaine methanesulfonate) and preserved in 10% formalin.

Bluegills were grouped into three size classes; 10–50 mm SL, 51–100 mm SL, and 101–150 mm SL, corresponding to age classes 1–2 yr, 3–4 yr, and >4 yr, respectively (E. E. Werner and D. J. Hall, *personal communication*). Stomach contents of fish in each size class were counted, measured and identified to the lowest taxonomic level possible (42 different prey groups, about 50% to genus or species). Length-mass regressions were obtained for each prey taxon, permitting the conversion of counts to mass. The prey were then categorized according to habitat types, i.e., prey found in (1) the open water (plankton), (2) sediments, (3) vegetation, or (4) other, which included prey not specific to any of the first three habitats. The resource samples were used as guides in assigning prey to specific habitat types.

The optimal diet and average net energetic return (E_n/T) available in each habitat was calculated for each bluegill size class using Eq. 1 and the size-frequency

distribution of prey available in the field. In predicting optimal diets from Eq. 1 and the laboratory-derived parameters, encounter rates for different-sized prey were assumed to act independently; i.e., the rate at which a fish encounters a given-sized prey is unaffected by the size and/or density of other prey in the environment. This assumption is necessary in extending prey encounter rates experimentally determined with single prey size classes to the field situation where multiple prey sizes occur concurrently.

Fig. 4 compares available prey distributions, predicted optimal diets, and the actual diets exhibited by the three size classes of bluegills in the field. Optimal diets were computed for fish sizes corresponding to the midpoint of each size class. The largest bluegills were highly size selective in their feeding and the distribution of prey sizes eaten corresponded quite closely to that predicted by the optimal diet model (Fig. 4a). The correspondence with the predicted optimal diet is especially impressive in light of the extreme size selection predicted in two different habitats and across three sampling dates. Further, bluegills of this size in the laboratory will feed on prey smaller than those eaten in the field (minimum prey size tested; 1.1-mm *D. pulex*), indicating that these fish were capable of consuming smaller prey. A taxonomic list of the major prey groups found in the vegetation and open-water habitats and their observed range in body length is provided in the Appendix.

Bluegills (>100 mm) utilizing the plankton fed almost exclusively on large *Daphnia*, ignoring copepods, small cladocera (e.g., *Ceriodaphnia* and *Bosmina*) and the majority of smaller *Daphnia* present (which ranged down to 0.65 mm body length). Since the distance at which a fish can detect a zooplankter increases with prey size (see Confer et al. 1978 for a review), such observed size selection may simply reflect an increased encounter rate with larger, more visible prey. For the open-water habitat, where visibility is unhindered by environmental structure, two methods are available to compute the average prey size ingested by a bluegill consuming prey "as encountered." The first uses a formula derived by Eggers (1977) who, assuming a cylindrical visual field swept out by a swimming fish, calculated the expected proportion of prey size class i ingested as

$$P_i = D_i l_i^2 / \sum_{j=1}^n D_j l_j^2,$$

where P_i = proportion of ingested prey of size class i , D_i = ambient density of size class i , l_i = length of prey in size class i , and n = number of classes. A second estimate of the average prey size encountered can be obtained using the regression equation for the open-water habitat presented in Table 4. From this equation the number of prey size class i encountered per second of foraging can be calculated knowing the

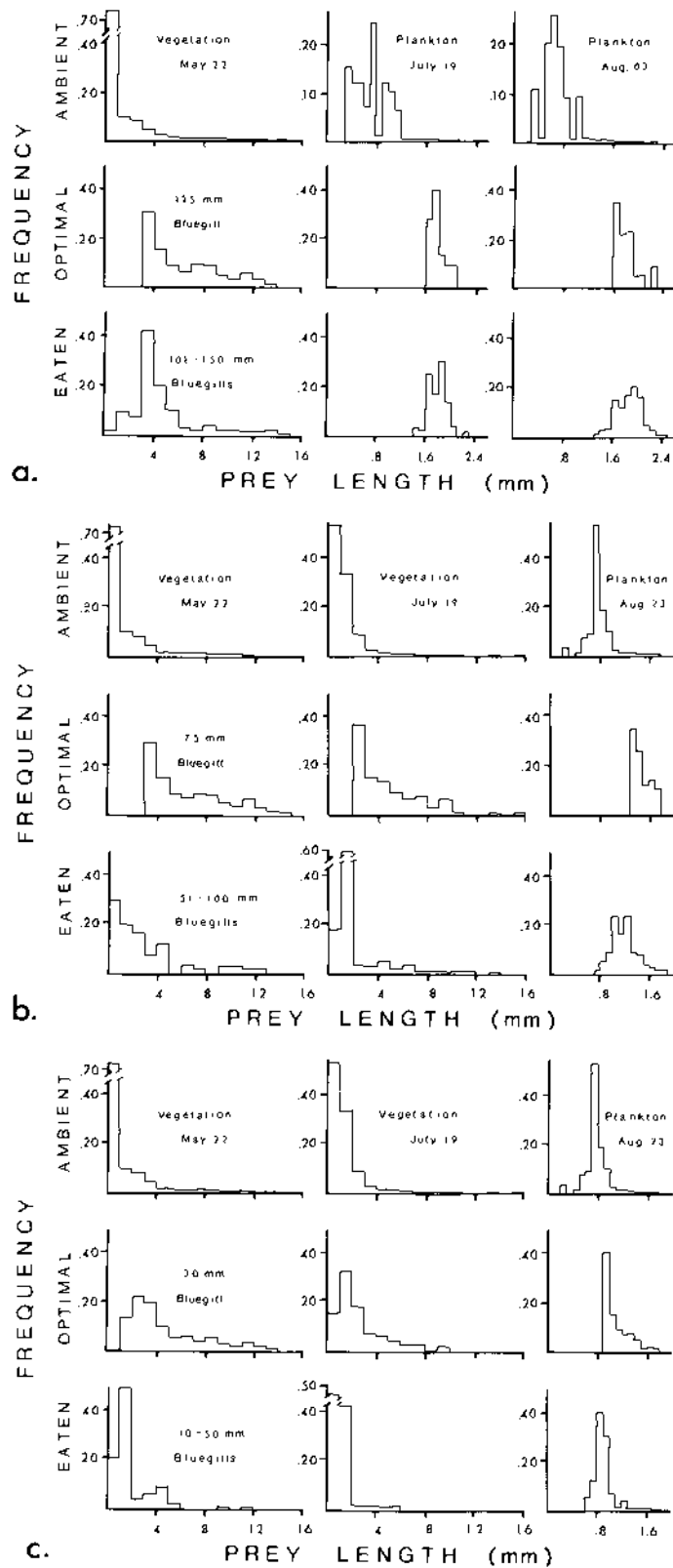


FIG. 4. Size-frequency distributions of prey available in a habitat, predicted optimal diets, and actual diets of three size classes of bluegills. Data represent those dates when prey availability in a habitat could be matched with the diets of four or more fish which had obtained >90% of their diet by mass from that habitat. Sample sizes were 4-9 fish/date.

TABLE 5. Comparison of mean body length of *Daphnia* in the environment, eaten "as encountered," in the optimal diet (125-mm SL bluegill), and actually eaten by bluegills (101–150 mm SL, four fish each date). All means ± 1 SE except where indicated. Ambient and "encountered" means based on $n = 2$ prey samples from each date. Means with a common superscript letter were significantly different with $P < .01$ (t test).

	\bar{x} prey length (mm)	
	19 July	3 August
Ambient	0.88 \pm .06	1.05 \pm .01
"Encountered" (Egger's equation)	1.03 \pm .17 ^a	1.21 \pm .01 ^c
"Encountered" (regression)	1.04 \pm .15 ^b	1.18 \pm .04 ^d
Optimal diet	1.75	1.78
Eaten (± 1 SE)	1.74 \pm .04 ^{ab}	1.86 \pm .04 ^{cd}
Eaten ($\pm 95\%$ CI)	1.74 \pm .13	1.86 \pm .13

body length and density of prey size class i and the size of the fish.

Table 5 compares the mean length of *Daphnia* in the environment with predicted mean length of *Daphnia* if consumed "as encountered," the mean length of *Daphnia* in the optimal diet, and the mean length of *Daphnia* consumed on two sampling dates when at least four large bluegills collected had been eating only *Daphnia*. On both dates the average size of prey consumed was significantly greater ($P < .01$) than predicted if prey were consumed "as encountered." Thus the prey size selection shown by these fish represents actual choice and not simply an increased encounter with large *Daphnia*. Secondly, the optimal foraging model predicted quite accurately the mean prey size eaten, the predicted means falling within the 95% confidence intervals for the average prey size eaten on both dates (Table 5).

The two smaller size classes of bluegills were also size selective in their feeding, although to a much lesser extent than bluegills > 100 mm (Fig. 4b, c). These smaller fish also regularly included in their diet some prey sizes below those predicted by the optimal foraging model. The inclusion of these suboptimal prey sizes may well represent the fact that the net energy intake rate (E_n/T) of these fish shows little change over a broad range of prey sizes. In Fig. 5, E_n/T is plotted as the diets of the three fish sizes expand from including the most profitable to least profitable prey, the optimal diet being defined as including all prey sizes \geq the prey size at which E_n/T is maximized. The E_n/T curve has a distinct peak for the largest size class of bluegills (125 mm) and the optimal diet is clearly defined. For 75-mm bluegills the peak in the E_n/T curve has become a plateau, and for 30-mm bluegills the E_n/T curve has flattened to a gentle rise and fall. Thus, while a unique lower bound on the diet which maximizes E_n/T exists, there is obviously a range of prey sizes of lower profitability, the inclusion of which has only a very slight effect on a small fish's average

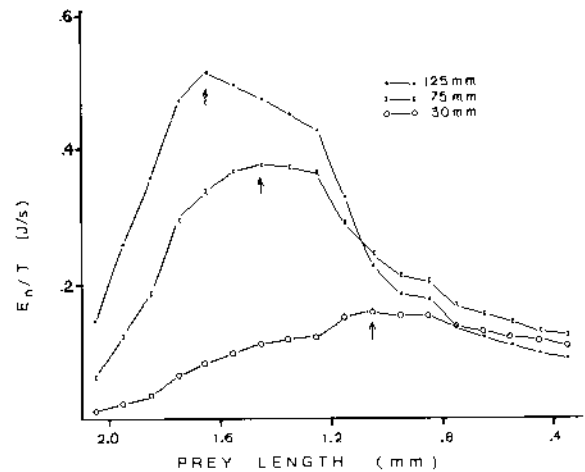


FIG. 5. Average foraging return (E_n/T) of three sizes of bluegills (125, 75, 30 mm) as a function of prey sizes in the diet. Curves were constructed from Eq. 1 and the size-frequency distribution of zooplankton available in Lawrence Lake on 19 July. Over this range of prey sizes, prey profitability (E_i/H_i) is directly related to prey length for all three sizes of fish. The optimal diet of each fish size is defined as including all prey sizes \geq that prey size which maximizes E_n/T (indicated by an arrow).

rate of energetic intake. Therefore, if all fish sizes have equal abilities to estimate average energetic intake, one would expect the same error in estimation of E_n/T to cause an increasing number of suboptimal prey sizes to be included in the diet as fish size decreases. For the data shown in Fig. 4, I determined the percent reduction in E_n/T from maximum which would result from the inclusion of those suboptimal prey sizes eaten by the Lawrence Lake fish. On average, E_n/T was reduced $11 \pm 3.5\%$ for large bluegills, $21 \pm 13\%$ for medium bluegills, and $6 \pm 3.5\%$ for small bluegills. Thus, these limited data suggest that all three bluegill size classes did in fact optimize their diet to approximately the same degree.

Clearly, the optimal foraging model developed in this study, which is based upon simple body size relations determined in the laboratory, quite accurately predicted the diet breadth and prey selection of the largest size class of bluegills in the field. Moreover, the actual and predicted size selection of these fish was greater than that resulting from a simple visibility bias alone. Thus one can confidently use the model to examine the degree to which habitat use by these fish is based upon maximizing foraging intake. The diets of the two smaller bluegill size classes often included some prey sizes smaller than those predicted. However, it was shown that the inclusion of these prey sizes generally has only a small effect on the fishes' average rate of energetic intake. Consequently, the model's predictions of net energetic return should be good estimates of habitat profitability for these fish

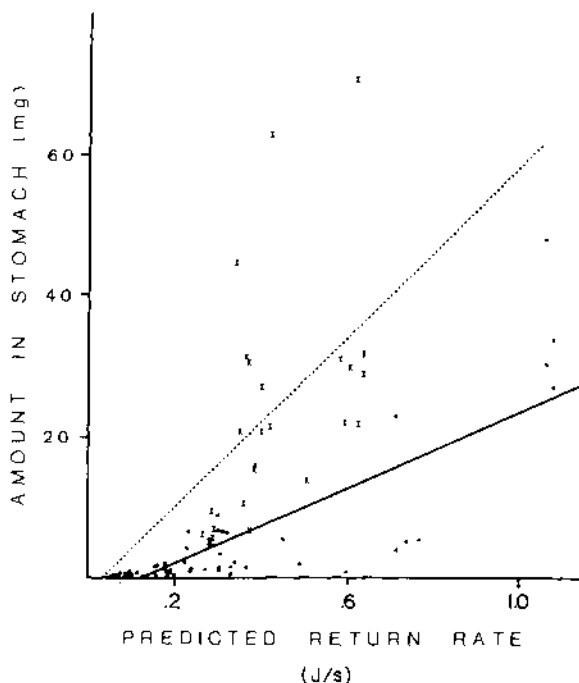


FIG. 6. Linear relationships between predicted foraging return from a habitat, and stomach contents (milligrams dry mass) of bluegills obtaining >80% of their diet from either the open water (x) or vegetation (●) habitats. Fitted regression equations are $Y = -2.35 + 252.1X$ ($r^2 = .22$, $P < .05$, $n = 24$) for the open water (---) and $Y = -4.02 + 117.14X$ ($r^2 = .71$, $P < .01$, $n = 59$) for the vegetation (—).

sizes also. In the next section the seasonal pattern of habitat value is determined for Lawrence Lake and compared to the actual habitat use of the three bluegill size classes.

Habitat profitability and use

If bluegills are feeding so as to maximize their energetic return, one would expect not only to find close correspondence of optimal and actual diet breadths, but also each size class foraging in the habitat yielding the highest net energetic gain. Further, as prey abundances change across the summer one would expect to see fish shift habitats in response to changes in relative habitat profitabilities.

Over the summer bluegills fed extensively from the vegetation and open-water habitats. Therefore, we can plot the predicted energetic return from these habitats against actual foraging intake of fish feeding in the habitats to determine, (1) whether predicted foraging returns are related to actual amounts eaten, and (2) whether any initial bias exists between habitats in the estimation of energetic return. Plotted in Fig. 6 are the model's predicted energetic returns from the vegetation and plankton vs. the actual prey biomass ingested by bluegills feeding in these habitats. For both the

vegetation and plankton there is a significant positive relationship ($P < .05$) between predicted and realized intakes, demonstrating that the model does provide a good index of habitat value to the fish although there was considerable individual variation. Note, however, that points for the vegetation fall below those for the open-water plankton, indicating that energetic intakes for the vegetation habitat have been overestimated relative to those for the plankton (since the times available for foraging each habitat were approximately equal on each sampling date). The basis for this discrepancy may lie in the fact that the vegetation densities used in the laboratory experiments were less than those actually occurring in the field (100 stems/m² vs. ≈ 900 stems/m²), resulting in estimates of prey encounter rates higher than those actually obtainable by the fish in the field. Glass (1971) has shown that increasing environmental structure decreases the rate at which largemouth bass can capture prey in the laboratory. When prey encounter rates in the vegetation are reduced 50% the regression lines shown in Fig. 6 coincide, removing the bias in estimated return rates between the vegetation and open-water habitats. This reduction in encounter rate was applied to the optimal foraging model to generate unbiased predictions for the profitability of the vegetation habitat across the season. The predicted pattern of habitat use is similar, however, using either corrected or uncorrected prey encounter rates in the vegetation.

The first column in Fig. 7 shows the seasonal pattern in predicted net energetic return (joules per second) for a given-sized bluegill foraging in each of the three habitats. These predictions were generated using the optimal foraging model and the habitat-specific prey abundances measured in the field. Clearly, there were marked differences in habitat profitability. The vegetation habitat was by far the most profitable habitat initially, declining steadily in value across the summer. This decline was predominantly caused by a reduction in the abundance of large insect prey (Mittelbach 1981) and had the greatest proportional effect on the largest size class of bluegills.

Plankton profitabilities were initially low, rose in late June, and remained above those of the vegetation habitat throughout July and August. The rise in plankton profitability resulted from an increase in the abundance of large *Daphnia* (*Daphnia* number/L >1.5 mm body length: 0 on 14 June; 0.04 ± 0.01 on 25 June; 0.18 ± 0.14 on 19 July; 0.32 ± 0.05 on 29 July; $\bar{x} \pm 1$ SE, $n = 2$). Throughout the summer the sediment habitat remained very low in profitability, reflecting low prey abundances and a high minimum handling time for bluegills feeding on these prey (recall Fig. 1).

Therefore, the predicted seasonal pattern of habitat use resulting in maximum energy intake for all three size classes is as follows; exclusive use of the vegetation habitat in May, a shift to utilizing the plankton in late June, and a continued exclusive use of plankton

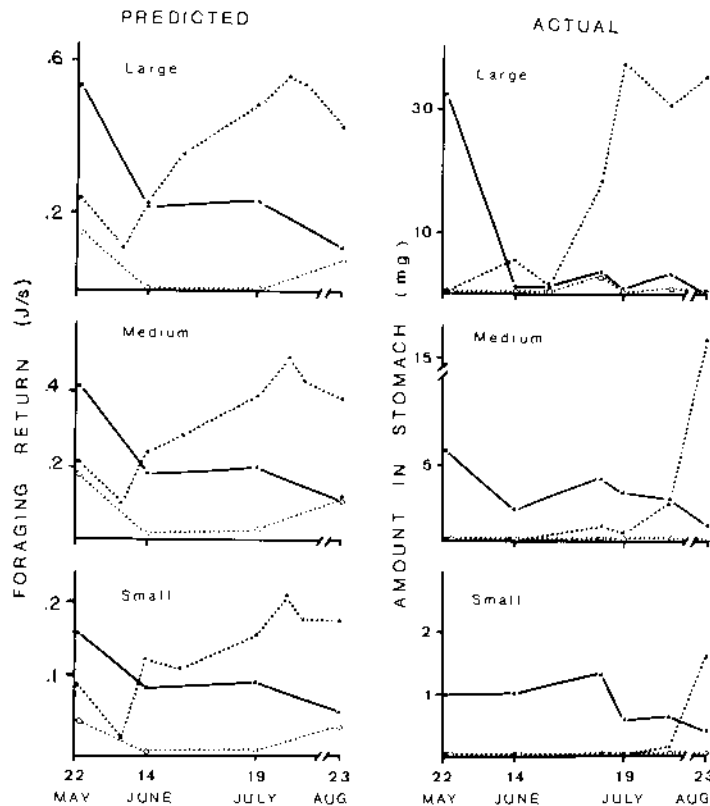


FIG. 7. Seasonal pattern in predicted habitat profitability (left) and actual habitat use (right) for three size classes of bluegills. Actual habitat use determined from the mean amount of prey (milligrams dry mass) foraged from each habitat. Dashed lines and closed circles represent the open water, solid lines and closed circles the vegetation, and dotted lines and open circles the sediments. Sample sizes were 3–6 fish/date for large bluegills (101–150 mm), 5–9 fish/date for medium bluegills (51–100 mm) and 4–9 fish/date for small bluegills (10–50 mm).

throughout July and August. Note that the magnitude of difference in predicted profitabilities between the vegetation and plankton habitats early and late in the summer is considerably greater than the percent error in estimated foraging return (E_n/T) which would result from the inclusion of suboptimal prey sizes in the diets of the Lawrence Lake fish. Therefore any differences between predicted and actual diet breadths exhibited by the fish are not so large as to affect the prediction of a habitat switch from the vegetation to the plankton across the summer.

The actual seasonal diets of the bluegill size classes are shown in the right column of Fig. 7. The habitat use of the largest bluegills was in nearly complete accordance with predictions for maximizing net energetic return, with these fish feeding initially in the vegetation and then shifting to the open-water plankton in July. The shift to the plankton occurred some 2 wk later than predicted.

The two smaller size classes of bluegills also foraged initially from the vegetation as predicted. However, these fish continued to use the vegetation habitat for nearly the entire summer, despite calculations that

they would have increased their foraging return by utilizing the plankton after the middle of June. On the single date when these smaller fish feed extensively on plankton, 23 August, foraging intakes increased dramatically over previous dates, indicating that these fish did profit in utilizing the plankton.

Data from 23 August represent a change in the distribution of the plankton resource from previous dates. Table 6 shows that 23 August was the only date in the summer when *Daphnia* were abundant near the vegetated slope. Consequently, on this date small fish may have been able to feed on *Daphnia* while remaining in close proximity to the structural protection of the vegetation. A comparison of the species of *Daphnia* eaten lends support to this line of reasoning. Three species of *Daphnia* co-occurred in the plankton on 23 August and they differed markedly in their horizontal distribution. Vertical tows taken from the limnetic station contained on average 64% *D. pulex*, 30% *D. retrocurva*, and 6% *D. galeata*, while vertical tows taken at the base of the slope (within 0.05–1.5 m of the vegetation) contained 6% *D. pulex*, 51% *D. retrocurva* and 43% *D. galeata*. The two smallest size classes of

TABLE 6. Mean density (number/L) \pm 1 SE of *Daphnia* sampled at the midlake and nearshore stations for those dates when bluegills were feeding on *Daphnia*; $n = 2$ samples for each case.

	25 June	19 July	29 July	3 August	23 August
Midlake	0.32 \pm .08	2.55 \pm .55	2.25 \pm .75	2.30 \pm .10	3.25 \pm .75
Nearshore	0.03 \pm .01	0.18 \pm .12	0.33 \pm .01	0.07 \pm .01	5.45 \pm .55

bluegills had only *D. galeata* and *D. retrocurva* in their stomachs despite *D. pulex* being the most profitable prey due to its large size. Bluegills >100 mm did feed heavily on *D. pulex*. These data suggest that large bluegills foraged on *Daphnia* in the limnetic zone whereas smaller fish would feed on these prey only when they occurred near the vegetation.

DISCUSSION

Prey size selection by the largest bluegills closely matched predictions of the optimal foraging model, providing field evidence that diet selection in these organisms is based upon maximizing net energetic intake. This corroborates earlier laboratory work by Werner and Hall (1974) who demonstrated that bluegills select prey so as to maximize biomass (energy) ingested. The diets of smaller bluegills generally included more suboptimal prey sizes. Other studies of optimal foraging similarly report a fraction of suboptimal prey eaten (Werner and Hall 1974, Krebs et al. 1977) and the inclusion of these prey has been postulated to represent effects of recognition time, "sampling," and/or detection errors (Krebs et al. 1977, Krebs 1978). It is unlikely that large fish are better at recognizing prey than are smaller fish, as the same visual cues are available to all fish. However, there may well be size-related differences in the abilities of fish to sample their environment and estimate energetic returns. Small fish encounter and capture fewer prey per unit foraging time than large fish due to an increase in searching ability and handling efficiency with fish size (recall Figs. 1 and 3). These differences in capture rate are demonstrated by the diets of bluegills collected on 22 May when all fish sizes had been feeding in the vegetation. On this date the average number of prey items in the stomach was 202 ± 20.3 for large bluegills, 32.8 ± 11.5 for medium bluegills and 12.6 ± 2.6 for small bluegills ($\bar{x} \pm 1$ SE). Therefore, if fish must sample their environment and estimate prey availabilities by encountering and/or capturing prey one would expect the sampling efficiency of a fish to increase with body size. Moreover, small fish will be more likely to have their diets affected by small-scale patchiness in prey distributions, since they encounter fewer total prey per foraging bout. These two factors may in part account for the higher percentage of suboptimal prey sizes included in the diets of small bluegills.

A third factor which may contribute to the reduced correspondence between predicted and actual size se-

lection in these fish is that the average foraging return for smaller fish changes little over a broad range of prey sizes. A comparison of the change in energetic return (E_n/T) as prey sizes are added to the diet (Fig. 5) illustrates that the inclusion of suboptimal prey sizes in the diet has a smaller total effect on energetic intake as fish size decreases. Therefore, if all fish are able to estimate foraging return to the same degree (i.e., $\pm X$ number of joules per unit time) one would expect any errors in the estimation of E_n/T to result in the inclusion of more suboptimal prey in the diets of small fish. If, however, the estimation of foraging return is based on relative values (i.e., $\pm X\%$ of maximum E_n/T), decreasing fish size may or may not result in the inclusion of more suboptimal prey in the diet depending on the exact shapes of the E_n/T curves. The abilities of bluegills or any other organisms to estimate their average energy intake is unknown, and the results of this study clearly demonstrate the importance of understanding the means by which organisms sample their environment and estimate parameters in the continued refinement of optimal foraging theory.

Bluegills of the largest size class (101–150 mm) were found to forage so as to maximize their energetic gain, switching habitats as relative profitabilities changed across the summer. The importance of this habitat shift to the bluegills, in terms of energetic return and potential growth, is evident from examining Fig. 7. In June, prior to feeding on zooplankton, large bluegills averaged <7 mg prey dry mass in their stomachs. Upon switching to zooplankton in July gut contents increased to an average of 20–40 mg dry mass. Thus by utilizing the open-water habitat these larger bluegills were able to maintain a high rate of energy intake after the vegetation habitat had dropped in value.

The timing of the shift to the open-water habitat was delayed approximately 2 wk from that predicted by the optimal foraging model. Werner et al. (1981) postulate that such a delay in habitat switching is to be expected when organisms must estimate foraging returns in complex habitats where the effects of learning or experience are important. These workers have shown that bluegills require six to eight daily exposures to laboratory representations of the open-water habitat before reaching maximum foraging efficiency. Thus if bluegills sample the open water or other new habitats in an inexperienced state, their estimate of energetic return from the habitat will be considerably below that obtainable once they are experienced. This can result in a delay in the timing of habitat switching

relative to predictions based upon experienced foragers (the case in Fig. 7). Further, once a habitat switch is made one would expect to find a rapid increase in foraging intake due to an improvement in efficiency in the habitat. The delay in the switch from the vegetation to the open-water habitat shown by the large bluegills in this study, plus the marked increase in the amount eaten once the switch occurred, matches these predictions. However, the limited number of samples taken during the period in which the bluegills were switching from the vegetation to the plankton precludes a thorough evaluation of the hypothesis of Werner et al. (1981). Also, some of the increase in stomach contents after the switch must be attributed to the increasing profitability of the plankton over this time period as well as to any improvement in foraging efficiency due to experience.

Bluegills <100 mm did not extensively utilize the open-water habitat except when large *Daphnia* were abundant near the vegetation (e.g., the 23 August sampling date). The jump in biomass of prey ingested on this date relative to those previous (see Fig. 7, right side) demonstrates that these fish did in fact profit energetically from foraging on *Daphnia* and would have throughout July and August had these prey always occurred near the vegetation.

The habitat use of these smaller bluegills may be compromised by an increased predation risk in more open environments, as the degree of predation risk to the bluegill is strongly size related. Bluegills >100 mm are beyond the handling capabilities of all but the very largest individuals of its dominant predator in this system, the largemouth bass (*Micropterus salmoides*). With decreasing size bluegills <100 mm become vulnerable to an ever-increasing fraction of the bass population, with 80% of the bass (excluding young of the year) capable of handling bluegills up to 30–46 mm (Hall and Werner 1977). Therefore, one would expect that bluegills >100 mm would be totally unconstrained by predation in their habitat selection, while bluegills of smaller sizes would be forced to balance their potential energetic gain from a habitat against their risk of being eaten. Glass (1971) has demonstrated that the foraging success of the largemouth bass (*Micropterus salmoides*) declines dramatically with an increase in environmental structure (e.g., the vegetation habitat vs. the open water). Further, the majority of the largemouth bass in Lawrence Lake occur in the water column off the slope (Werner et al. 1977). These two factors together suggest that the open-water habitat is a relatively risky environment for small bluegills. That bluegills <100 mm feed on *Daphnia* occurring within a few metres of the vegetation while apparently ignoring opportunities to feed on *Daphnia* located farther offshore suggests that these fish may balance foraging profitability and predation risk when selecting habitats, and that this balance is a dynamic one depending on prey availabilities and relative risks.

A size-specific trade-off between foraging profitability and predation risk is likely to be a common phenomenon among many groups of organisms whose populations are structured by body size. In simple one-habitat systems these trade-offs can result in a single, optimal body size for organisms occupying that habitat (Lynch 1977). In systems containing a number of habitats, each with different size-related foraging efficiencies and predation risks, optimal habitat choice by organisms will involve balancing energetic gain from a habitat against the chance of being eaten in that habitat. In such cases it will be important to consider the time scale over which organisms make decisions, as optimal habitat choice on a day-to-day basis may not be consistent with optimal habitat use over the entire lifetime of the organism. Also, changes in prey availability and predation risk on a diel basis can dramatically affect the relative values of habitats over time scales of a few minutes or hours (see Hall et al. 1979, Bohl 1980 for examples with planktivorous fish). The existence of such restricted feeding periods in which prey may be maximally available and/or predation pressure reduced would be expected to provide strong selective pressure for the evolution of traits maximizing energy intake during the time available for feeding.

Recent laboratory work with notonectids has demonstrated that back-swimmers are apparently able to balance conflicting demands between foraging profitability and predator avoidance in such a way as to maximize their feeding rate (Sih 1980). My results similarly suggest the importance of these two factors in determining the habitat use and resultant size-class segregation of bluegills in natural environments. However, this area of ecology represents the somewhat curious case where the development of relevant theory lags behind empirical demonstration. To date, models of optimal habitat use incorporating both energetic gain and predation risk have been limited to a few, special cases (Rosenzweig 1974, Covich 1976, Pearson 1976). A major difficulty in the development of such theory lies in the fact that foraging profitability and predation risk are basically measured in different units (e.g., energy gained per unit time vs. probability of death per unit time, respectively). Only by translating these measures into common units commensurate with fitness will a more general theory of habitat use emerge.

The pattern of size-class segregation demonstrated by bluegills in this and other studies (Hall and Werner 1977, Keast 1977, Werner et al. 1977) represents a case where predation may function to reduce intraspecific competition by channelling size classes into separate habitats. Bluegill size classes show little tendency to partition the food size dimension of the niche (Hall et al. 1970, Keast 1977) and Werner (1974) has shown from handling time relations alone that bluegills from 50–250 mm in length would be expected to overlap

completely in the range of prey sizes eaten. As a result, diet overlaps between bluegill size classes are often large and the potential for intraspecific competition is strong. By restricting small fish to habitats of low risk (i.e., the vegetation), predation pressure can result in de facto habitat segregation and a reduction in competition between size classes. Unstructured habitats become essentially exclusive resources for individuals large enough to be outside the danger of predation. These exclusive resources can result in large disparities in growth rates between size classes, as evidenced by the foraging return of large and small bluegills in Lawrence Lake late in the summer. This phenomenon of predator-generated habitat segregation is likely to be a general one among species where predation risk is related to body size and its potential importance to the outcome of intraspecific interactions remains to be studied.

The fact that bluegills and many other species stocked in the absence of predators invariably develop "stunted" populations (Swingle and Smith 1940, Wenger 1972) has long demonstrated the importance of predation in mediating intraspecific competition in fish. Historically, the action of predation in these systems has been viewed as reducing population numbers to the point where large individuals can maintain positive growth rates. It is suggested here that this explanation is probably too simple, that in fact the action of predators in generating habitats of exclusive use to the larger size classes (e.g., the open water, bare sediments) may actually be the most important factor in stabilizing intraspecific competition between size classes.

While predation may function to reduce intraspecific competition in some cases, it is also likely to concentrate interspecific interactions at specific points in a species life history. In small lakes such as Lawrence, young-of-the-year of all species are found in the littoral vegetation (Werner et al. 1977, G. G. Mittelbach, *personal observation*), sometimes after spending a brief period in the limnetic zone as fry (Werner 1966). Adults of these species may eventually come to utilize different resources (e.g., fish, zooplankton, mollusks), which often occur in separate habitats. Such habitat segregation is precluded among young fish to the extent that predation risk restricts small individuals of these species to a single habitat, the vegetation (as is apparently the case for bluegills). Moreover, young of different species may exhibit large differences in their abilities to capture vegetation-dwelling prey, as their morphologies and foraging behaviors are fashioned to forage efficiently other habitats and prey types as adults (Werner 1977). Thus, asymmetries in competitive effects between species occupying the vegetation as juveniles are to be expected. Whether strong interspecific competition actually occurs at this stage in a species' life history will depend, of course, on the de-

gree to which vegetation resources are limiting for small fish. This study has demonstrated that small bluegills could often increase their energy intake by feeding outside the vegetation. Also, juveniles of several fish species have been observed to move from the vegetation into more open areas at dawn and dusk (Stuntz 1975, Wilsmann 1979, G. G. Mittelbach, *personal observation*) when lowered light levels presumably reduce predation risk. These observations suggest that resources in the vegetation are in fact reduced relative to other habitats and that species confined by predation to the vegetation are in competition.

Clearly, the ability of ecologists to evaluate the relative impact of predation risk and foraging return in determining an animal's diet and habitat use will be an important step towards the development of a predictive theory of community structure. The success of simple optimal foraging models in predicting the diets and habitat use of organisms in the field (Werner 1977, Belovsky 1978, this study) indicates that an optimal foraging approach will prove extremely useful in examining questions related to resource partitioning, niche overlaps, and the extent of competitive interactions both within and between species.

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APPENDIX

Listed below are the major prey groups found in the vegetation and open-water habitats of Lawrence Lake for dates on which bluegill prey size selection was examined (Fig. 4a, b, c in text). A complete description of prey abundance and biomass by sampling date and habitat can be found in Mittelbach (1981).

Prey in vegetation	Range in body length (mm)		
	22 May	19 July	
<i>Simocephalus</i>	0.6-2.2	0.6-2.0	
<i>Sida</i>	0.8-2.8	0.8-2.0	
Copepoda	0.3-1.7	0.3-1.7	
Ostracoda	0.3-1.0	0.3-1.0	
<i>Hyalella</i>	0.6-5.0	0.6-4.0	
Chironomidae	1.1-12.6	0.5-9.0	
Other Diptera	1.0-17.5	1.2-16.3	
Tricoptera	1.6-12.8	1.3-9.1	
Ephemeroptera	1.8-15.2	0.5-5.9	
Odonata	1.4-15.3	1.6-5.4	
Gastropoda	0.6-6.4	0.6-5.2	
Plankton prey	19 July	3 August	23 August
<i>Daphnia pulex</i>	0.7-2.1	0.7-2.2	0.8-1.4
<i>D. retrocurva</i>	*	0.6-2.0	0.6-1.8
<i>D. galeata mendotae</i>	*	0.6-1.9	0.6-1.3
<i>Bosmina</i>	*	0.3-0.4	*
<i>Ceriodaphnia</i>	*	0.3-0.7	0.5-0.8
<i>Pseudosida</i>	*	0.5-1.2	*
Copepoda	0.3-1.2	0.3-1.3	0.4-1.3

* Rare or absent (density < 0.05 individuals/L).