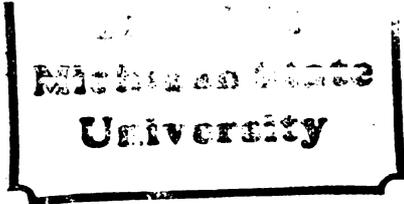




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FORAGING EFFICIENCY AND SIZE-CLASS COMPETITION
IN THE BLUEGILL SUNFISH (Lepomis macrochirus)

By

Gary George Mittelbach

A DISSERTATION

Submitted to
Michigan State University
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ABSTRACT

FORAGING EFFICIENCY AND SIZE-CLASS COMPETITION IN THE BLUEGILL SUNFISH (Lepomis macrochirus)

By

Gary George Mittelbach

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. Prey abundances were measured in the open water, vegetation and bare sediment habitats during the months of May through August 1979 and size-frequency distributions of prey available in each habitat determined. Bluegills >100 mm SL 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 prey to utilizing open water zooplankton as relative foraging profitabilities in the two habitats changed across the summer. Bluegills < 100 mm SL 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. The consequences of size-specific foraging abilities and predation risks to the outcome of competition in size-structured populations are discussed, with particular attention paid to the problem of "stunting" in fish.

To George, Dorothy, Kay, and Lydia

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DEFINITION OF SYMBOLS USED IN THE TEXT

$e(i)$	Energetic content of prey size i (cal)
$H(i)$	Handling time for prey size i (sec)
$B(i)$	Encounter rate for prey size i (number/sec)
i	Prey length (mm)
A	Assimilatable fraction of energetic content
C_s	Energetic cost of searching (cal/sec)
C_h	Energetic cost of handling (cal/sec)
L	Fish standard length (mm)
S	Swimming speed (m/min)
t	Water temperature ($^{\circ}\text{C}$)
W	Fish live weight (g)
D	Prey density (units appropriate to each habitat)
w	Prey dry weight (mg)
E_n	Net energy gained while foraging (cal)
T	Time spent foraging (sec)
P	Search time (sec)

CHAPTER 1

FORAGING EFFICIENCY AND BODY SIZE IN BLUEGILLS

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 (Goss-Custard 1977, Davies 1977) and only the work of Belovsky (1978) on moose has actually attempted to predict an animal's diet 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 chapter 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. It has become increasingly clear that the development of a predictive theory of community structure in fish and other size-distributed species will depend on a thorough understanding of size-specific interactions (Neill 1975, Werner 1977), and Chapter 2 represents an initial attempt at utilizing foraging theory to explore questions relating to size-class competition in fish.

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 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. 1980). Seasonal prey abundances were then measured in these three habitats in a small Michigan lake and a discussion of the distribution and dynamics of this prey resource is presented in Appendix A. Prey abundances were 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.

A FORAGING 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 Charnov (1976), Werner and Hall (1974), Pearson (1976) and others was formulated. Briefly, let

$$E(ij) = A e(ij) - C_h H(ij)$$

where A = assimilable fraction of energetic content, $e(ij)$ = energetic content of prey size i in habitat type j (sec), and C_h = energetic cost of handling prey (cal/sec). Thus $E(ij)$ represents the net energetic gain from eating prey size i . If prey are consumed over time T (sec) which is divided into time spent searching for prey (P) and time spent

handling all prey $\sum_{i=1}^n B(ij)H(ij)$, where $B(ij)$ equals the number of prey size i encountered per second of search, then the net rate of energy intake (E_n/T) from habitat j is

$$E_n/T = \frac{P \sum_{i=1}^n (B(ij) E(ij)) - C_s P}{P + P \sum_{i=1}^n B(ij) H(ij)} \quad \text{or}$$

$$E_n/T = \frac{\sum_{i=1}^n (B(ij) E(ij)) - C_s}{1 + \sum_{i=1}^n B(ij) H(ij)} \quad (1)$$

where C_s = energetic cost of searching (cal).

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 equation 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 expression (1).

For fish, the assimilatable fraction of energy ingested (A) appears to be independent of body size (Elliot 1976) and a value of 0.7 is

appropriate for most prey (Ware 1975, 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 weight (W), swimming speed (S) and water temperature (t) using a rotating respirometer suspended in a lake. Oxygen consumption was converted to calories expended by assuming 1 mg oxygen consumed equals 3.25 calories (Elliot and Davison 1975). Since other parameters of the foraging model were determined as functions of fish standard length, the measure of fish size contained in Wohlschlag and Juliano's energetic equation was converted from live weight in g (W) to standard length in mm (L) using a length-weight relationship for bluegills of $W = .000026 L^{3.043}$ (unpublished data). The resultant equation:

$$\text{Log } C = -7.8512 + 2.5847 \text{ Log } L + 0.0142 S + 0.0198 t \quad (2)$$

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 equation 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 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 1 lists the swimming speeds ($\bar{x} \pm 1 \text{ SE}$) 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°C expends .00081 cal/sec swimming at 1.0 m/min and .00087 cal/sec 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 $1.7 \pm .08$ and $.08 \pm .05$ m/min ($\bar{x} \pm 1 \text{ SE}$, $n = 96$) respectively; values which fall within the range of swimming speeds observed for feeding fish in nature (Ware 1975).

The energetic content of prey size i ($e_{(i)}$) was determined by converting prey lengths to dry weights and then multiplying by the appropriate caloric equivalent (Cummins and Wuycheck 1971). Specific

Table 1. Bluegill Swimming Speeds. Mean swimming speeds in m/min (± 1 SE) for bluegills searching out and handling two sizes of prey in laboratory representations of the vegetation and sediment habitats.

		Vegetation Habitat					
Fish length		110 mm SL	65 mm SL	45 mm SL	21 mm SL		
Prey length (mm)		<u>searching</u>	<u>handling</u>	<u>searching</u>	<u>handling</u>	<u>searching</u>	<u>handling</u>
9.5		1.9 \pm .21	0.5 \pm .23	2.2 \pm .14	1.3 \pm .11	2.6 \pm .16	1.1 \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
						--	--
		Sediment Habitat					
Fish length		110 mm SL	80 mm SL	45 mm SL	25 mm SL		
Prey length (mm)		<u>searching</u>	<u>handling</u>	<u>searching</u>	<u>handling</u>	<u>searching</u>	<u>handling</u>
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
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	0.4 \pm .07
						1.0 \pm .06	0.5 \pm .30

length-weight regressions and caloric equivalents used are detailed in Appendix B.

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. 1980) 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:

<u>Habitat</u>	<u>Laboratory</u>
Open water	structure = open aquaria prey = zooplankton (<u>Daphnia pulex</u>)
Bare sediments	structure = aquaria containing 4-5 cm layer of marl sediments prey = midge larvae (predominantly <u>Chironomus plumosus</u>)
Vegetation	structure = anchored, live <u>Elodea</u> (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 liter aquarium into two unequal sized sections, 26 liters and 188 liters, 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 U.S. standard sieves and a known number of a specific size class were then introduced into the larger division of the aquaria immediately prior to the initiation of a feeding experiment. Two sizes of Daphnia ($2.20 \pm .04$ and $1.14 \pm .02$ 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 aquaria. 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 ($19.53 \pm .46$ mm and $11.07 \pm .34$ mm body length) were used at densities of densities of 50, 300, and 1000 individuals/m². Experiments simulating the vegetation habitat used Coenagrionidae naiads ($9.51 \pm .27$, $13.15 \pm .33$, and $22.30 \pm .28$ mm body length) at densities of 38 and 192 individuals/m³ for large damselflies, 192 individuals/m³ for medium

damselflies and 192, 385 and 1,538 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 minutes. 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). 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 sec. 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 about 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 3 to 6 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 (Figure 1). 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).

Figure 2 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 (i/L_{crit}). Below this ratio handling time remains approximately constant. These results conform to the general relationship postulated by Schoener (1969) and are in close agreement with the data obtained by Werner (1974) for bluegills and green sunfish (Lepomis cyanellus). For each prey type an exponential equation was fit by least-squares regression to all 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 2.

It is interesting to note the high minimum handling time for fish feeding on Chironomus (9.6 sec compared to 1.0 sec for Daphnia). When a fish captures a midge larvae it engulfs a mouthful of sediment along with the prey. The cost of separating the prey from these sediments is

Figure 1. Increase in Capture Rate with Experience for Bluegill Sunfish Feeding on Chironomus and Daphnia. One experiment was performed per day. Excepting one point, points represent the mean \pm 1 SE for 2-6 fish/experiment.

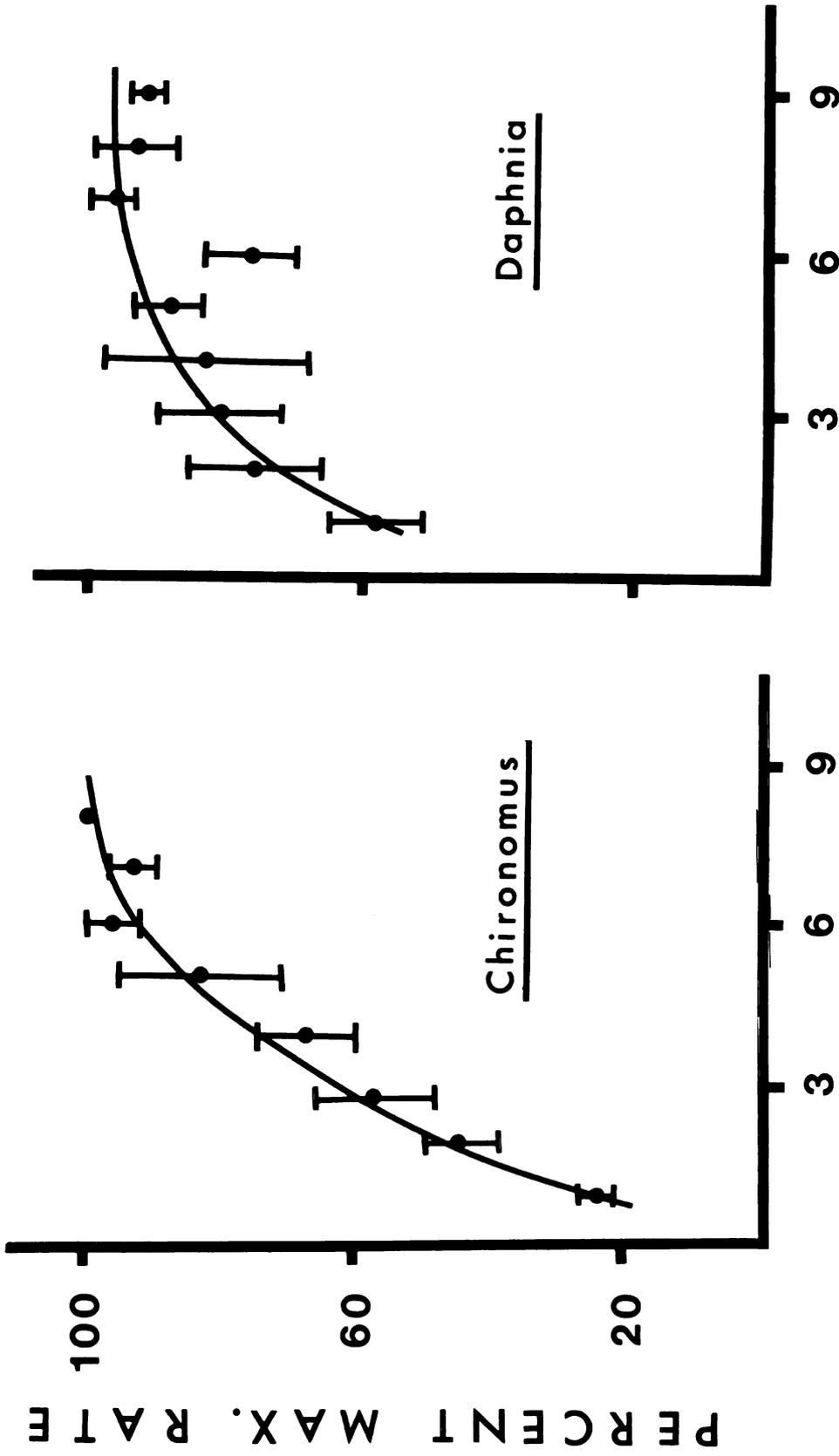


Figure 1

EXPERIMENT NO.

Figure 2. 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. Daphnia were included with Coenagrionidae to represent the size and shape of cladoceran prey common to the vegetation. Fish sizes ranged from 22-110 mm. Curves were fit by the regression equations in Table 3.

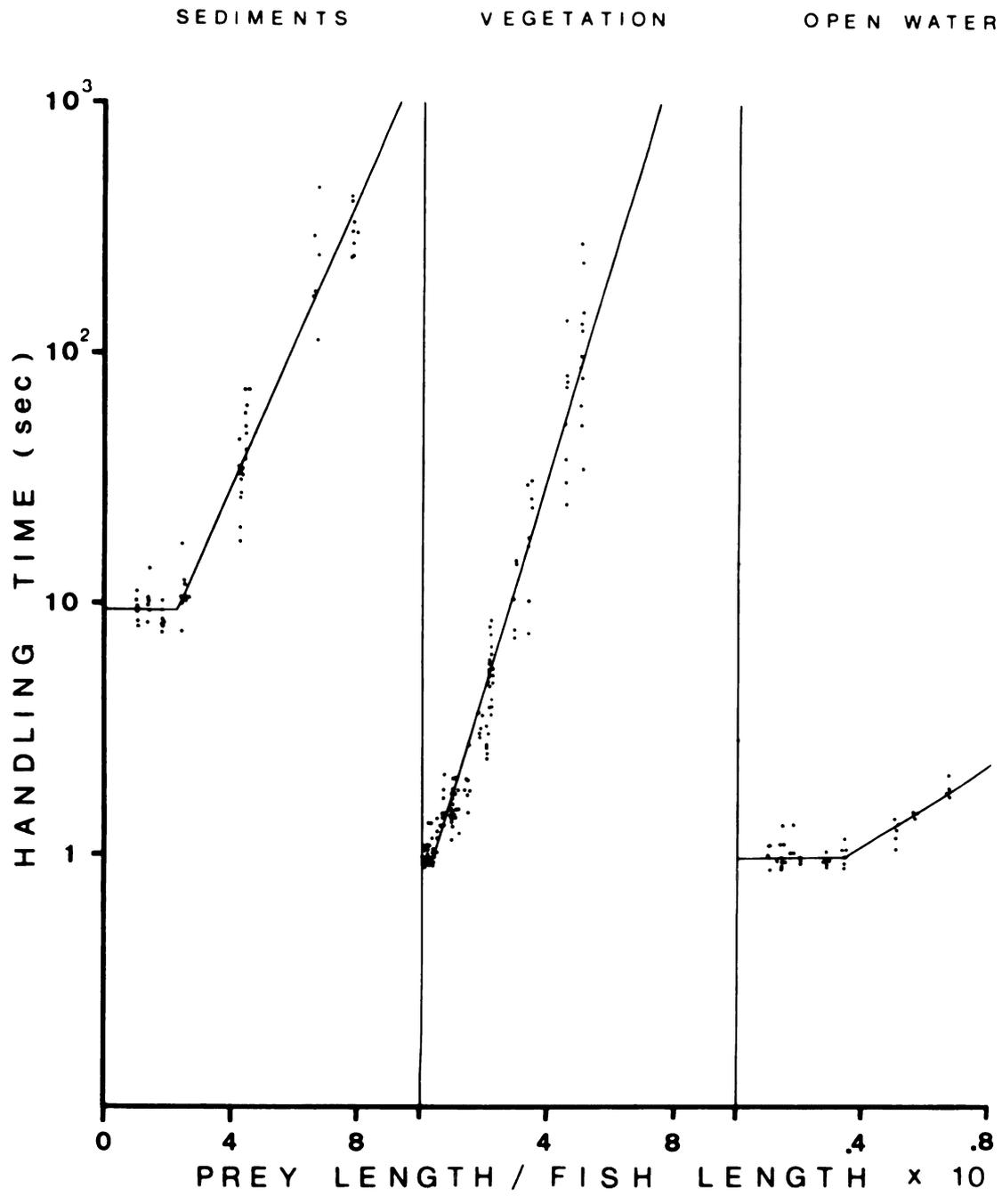


Figure 2

Table 2. Handling Time Relations for Bluegills Feeding on Each of Three Prey Types. The values i/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 $\bar{x} \pm 1$ SF.

Prey type	Handling time (H) $i/L \geq i/L_{crit}$.	Handling time (H) $i/L < i/L_{crit}$.	i/L_{crit} .
Daphnia	H = 0.536 e ^{18.488 i/L} r = .92 n = 18	H = 1.02 + .02 n = 24	0.034
Chironomus	H = 2.364 e ^{6.492 i/L} r = .96 n = 62	H = 9.63 + .21 n = 20	0.22
Coenagrionidae and Daphnia	H = 0.639 e ^{9.966 i/L} r = .96 n = 112	H = 1.02 + .02 n = 30	0.045

significant and functions to increase the handling time for sediment prey.

The rate at which a fish encountered prey (B) was a function of prey density (D), length (i), and fish size (L) in each habitat (Figure 3). 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 Figure 3 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, i, 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:

$$\text{Log } B = a + b_1 \text{ Log } D + b_2 \text{ Log } i + b_3 \text{ Log } L$$

Figure 3. Laboratory Prey Encounter Rate ($\bar{x} + 1$ 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/m³) and the third panel shows data from 8 bluegills feeding on 11.1 mm Chironomus larvae at 1000 larvae/m². Curves were fit by the regression equations in Table 3.

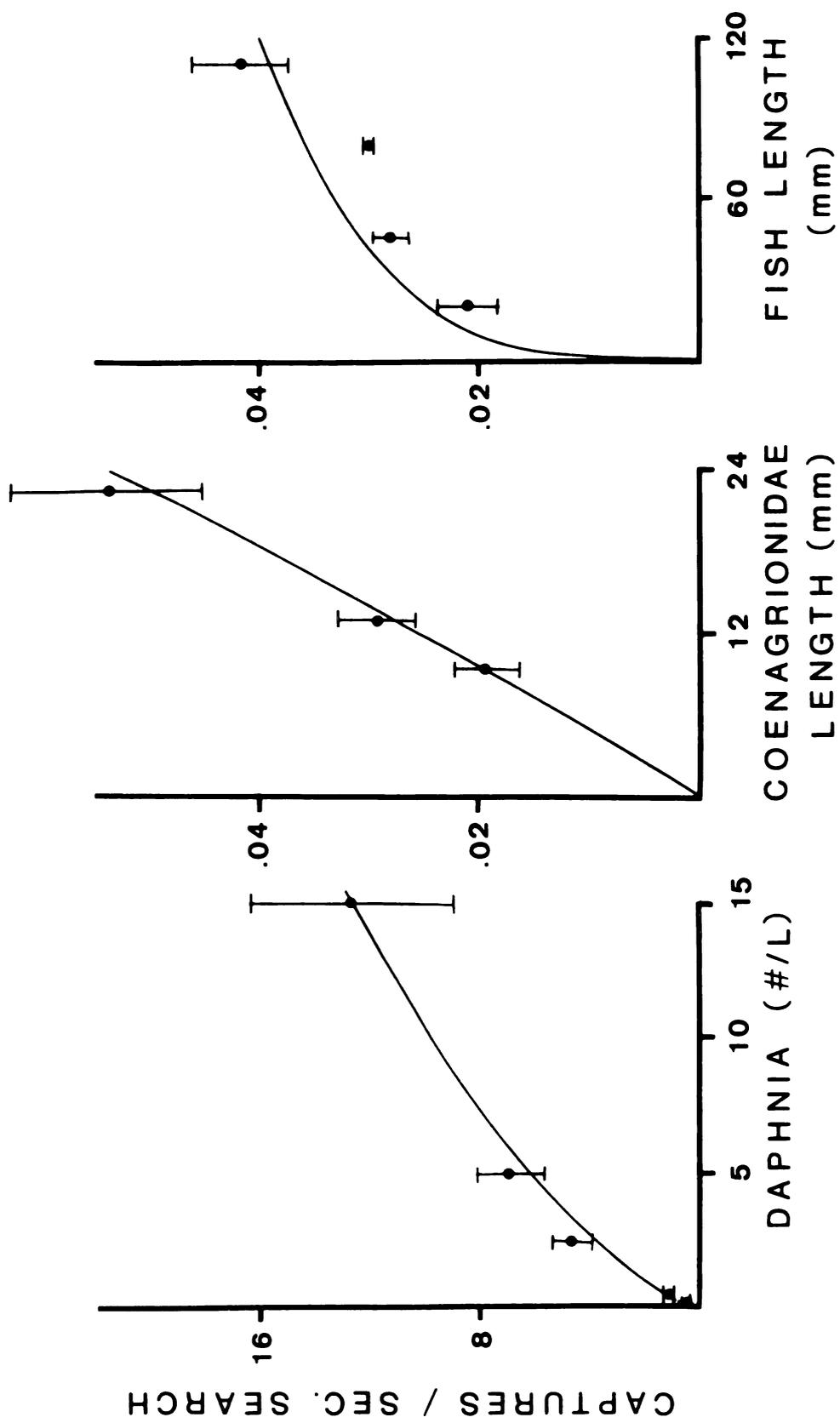


Figure 3

Figure 3. Laboratory Prey Encounter Rate ($\bar{x} + 1 \text{ SE}$) 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 8 bluegills feeding on 11.1 mm Chironomus larvae at 1000 larvae/m². Curves were fit by the regression equations in Table 3.

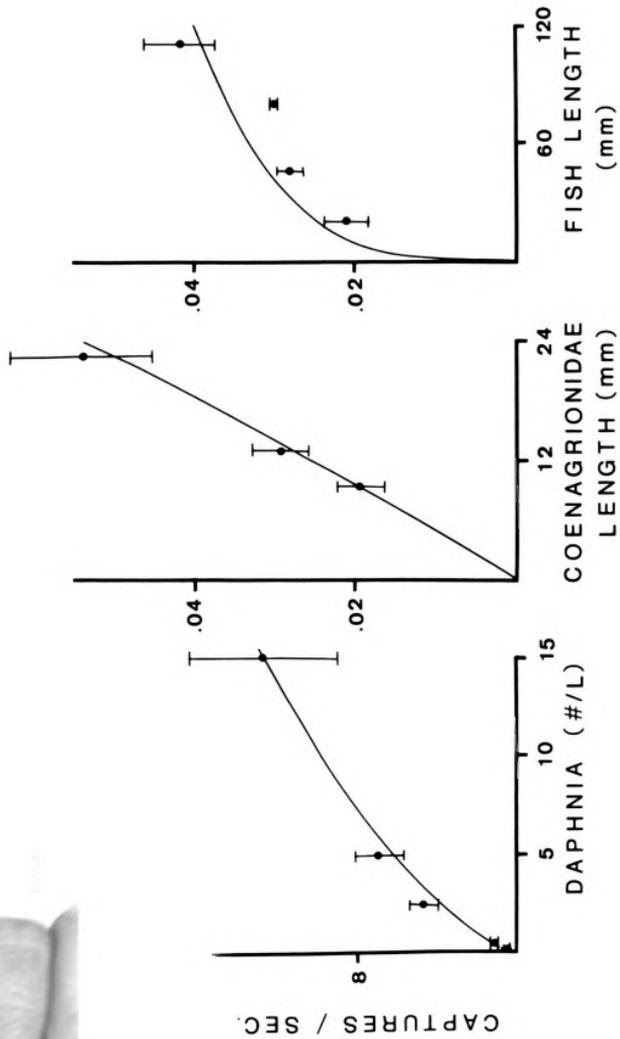


Figure 3

Table 3. Prey Encounter Rate Equations. Fitted parameters (± 1 SE) of the multiple regression equations describing prey encounter rates in each habitat. The form of each regression equation is $\text{Log } B = a + b_1 \text{ Log } D + b_2 \text{ Log } i + b_3 \text{ Log } L$.

<u>Habitat</u>	<u>a</u>	<u>b₁</u>	<u>b₂</u>	<u>b₃</u>	<u>R²</u>	<u>overall significance</u>	<u>n</u>
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

yielded the best overall fit to the data and the fitted constants for each habitat are listed in Table 3. The complete regression for each habitat is highly ($p < .001$) 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 3-way interactions were found to be significant ($p > .05$). Of the nine possible 2-way interactions only one, D x L for the vegetation habitat, was significant ($p < .05$). Therefore, a simple model excluding interaction terms was used.

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 Figure 4. 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 3). 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 tradeoffs involved in determining habitat utility to the

Figure 4. 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. Response surfaces were constructed from the equation $\text{Log } B_i = 5.905 + 0.779 \text{ Log } D + 1.045 \text{ Log } l + 0.694 \text{ Log } L$ (Table 3). Prey densities of 10-45 prey/m³ and prey lengths of 5-12 mm were used for each fish size.

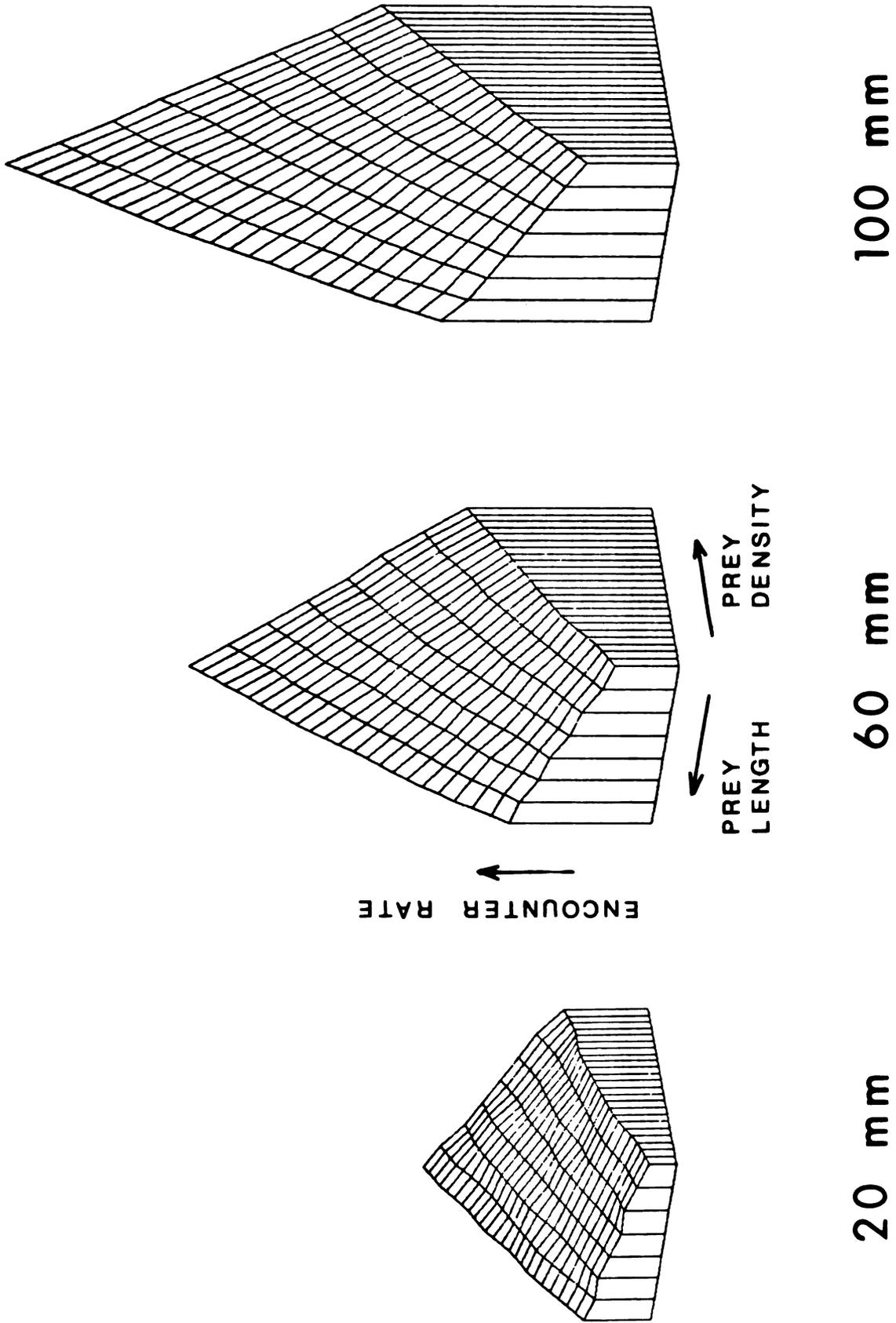


Figure 4

bluegill are thus apparent from the relationships 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 zooplankton 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 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.

A 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 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 weight (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 (Figure 5) during the months of May-August, 1979.

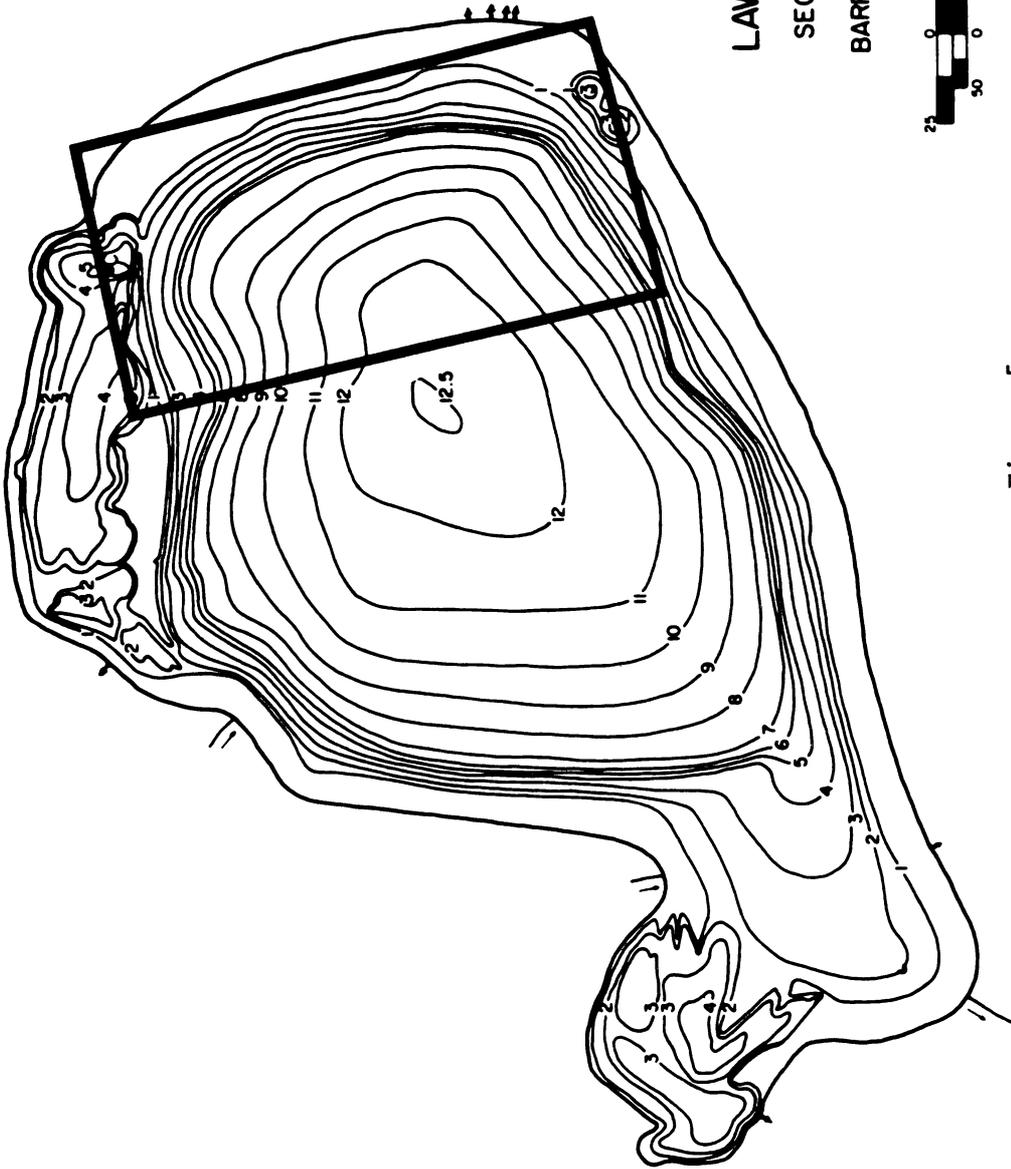
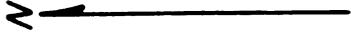
Prey living in the bare, marl sediments were sampled with a corer (6.5 cm dia.; 8 cm deep) operated by a diver wearing mask and snorkel or SCUBA. Five random samples were taken on each date. Samples were gently washed through a series of 3 sieves (2.83, 0.710, 0.180 mm), from which prey were collected and preserved in 10% formalin. Contents of the smallest mesh sieve were mixed with a 20% solution of $MgSO_4$, 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 Appendix A. 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 (.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 3 sieves (2.83, 0.710, 0.180 mm). Contents of the 2 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% $MgSO_4$ solution.

Open water prey were sampled at two locations in the lake using a

Figure 5. Bathymetric Map of Lawrence Lake, Michigan. Sampling location is indicated.

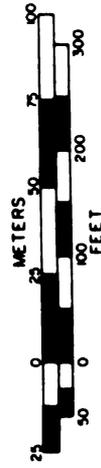
D.M. 6
2016 m



LAWRENCE LAKE

SEC 27 T. 1N. R. 9W.

BARRY COUNTY, MICHIGAN



CONTOUR INTERVALS IN METERS

Figure 5

30 cm diameter #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 July 29, 1979 confirmed that all fish were located between the surface and a depth of 4-4.5 m (thermocline at 4 m (Wetzel, personal communication)). Plankton abundances near shore were determined by taking 2 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 post-sunrise and was completed by 70 min post-sunrise. 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 fifty 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 Appendix A.

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 post-sunrise and was completed by 80 min post-sunrise. 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 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 years, 3-4 years, and > 4 years respectively (Werner and Hall unpublished data). 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-weight regressions were obtained for each prey taxon permitting the conversion of counts to weight. 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 equation 1 and the size-frequency distribution of prey available in the field. In predicting optimal diets from equation 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.

Figure 6 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 (Figure 6). 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.

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 zooplankton increases with prey size (see Confer et al. 1978

Figure 6 a,b,c Size-frequency Distribution of Prey Available in a Habitat, Predicted Optimal Diets, and Actual Diets of Three Size Classes of Bluegills. Data presented represent those dates where prey availability in a habitat could be matched with the diets of 4 or more fish which had obtained $>90\%$ of their diet by weight from that habitat. Sample sizes ranged from 4-9 fish/date.

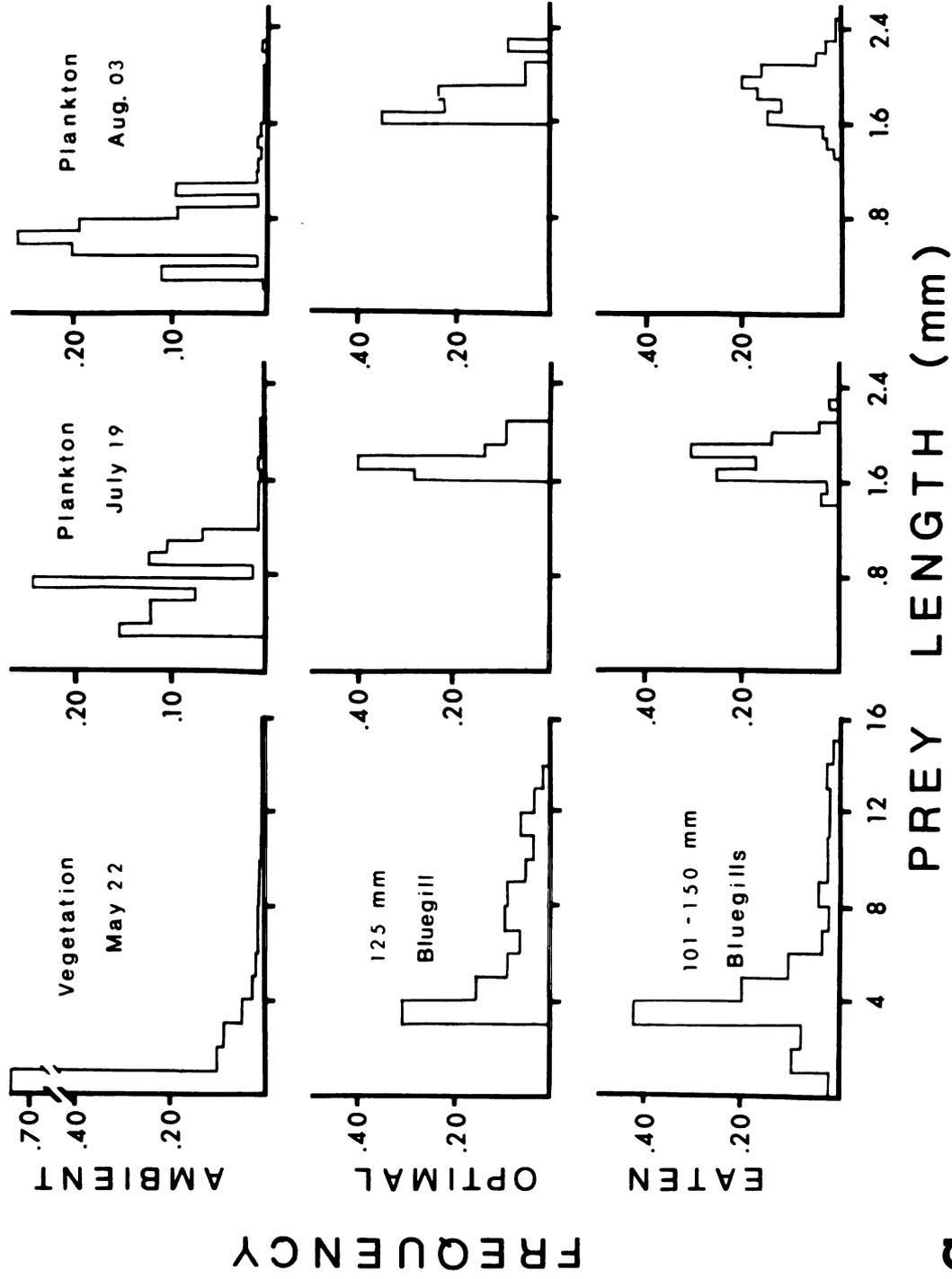


Figure 6

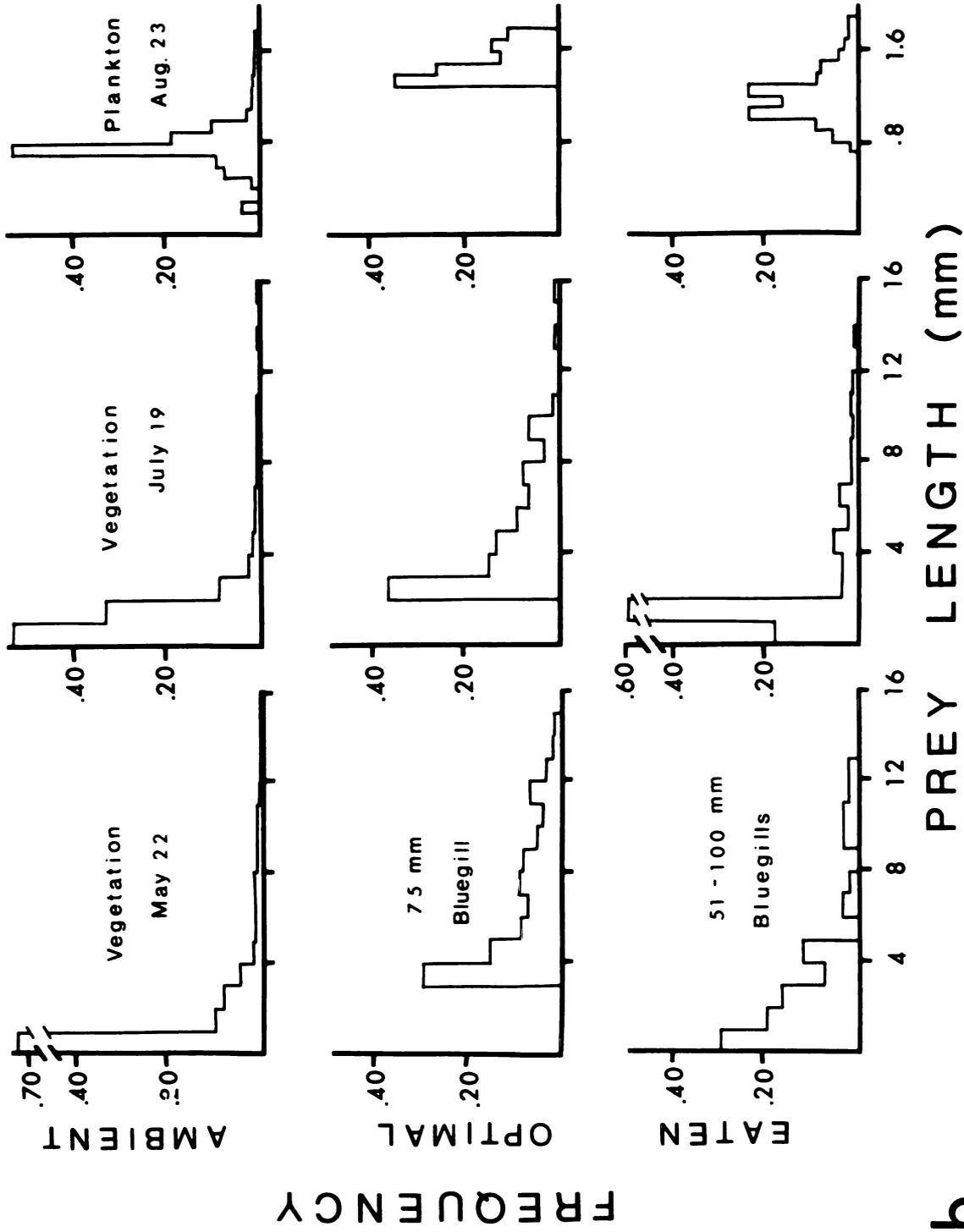


Figure 6 cont.

b.

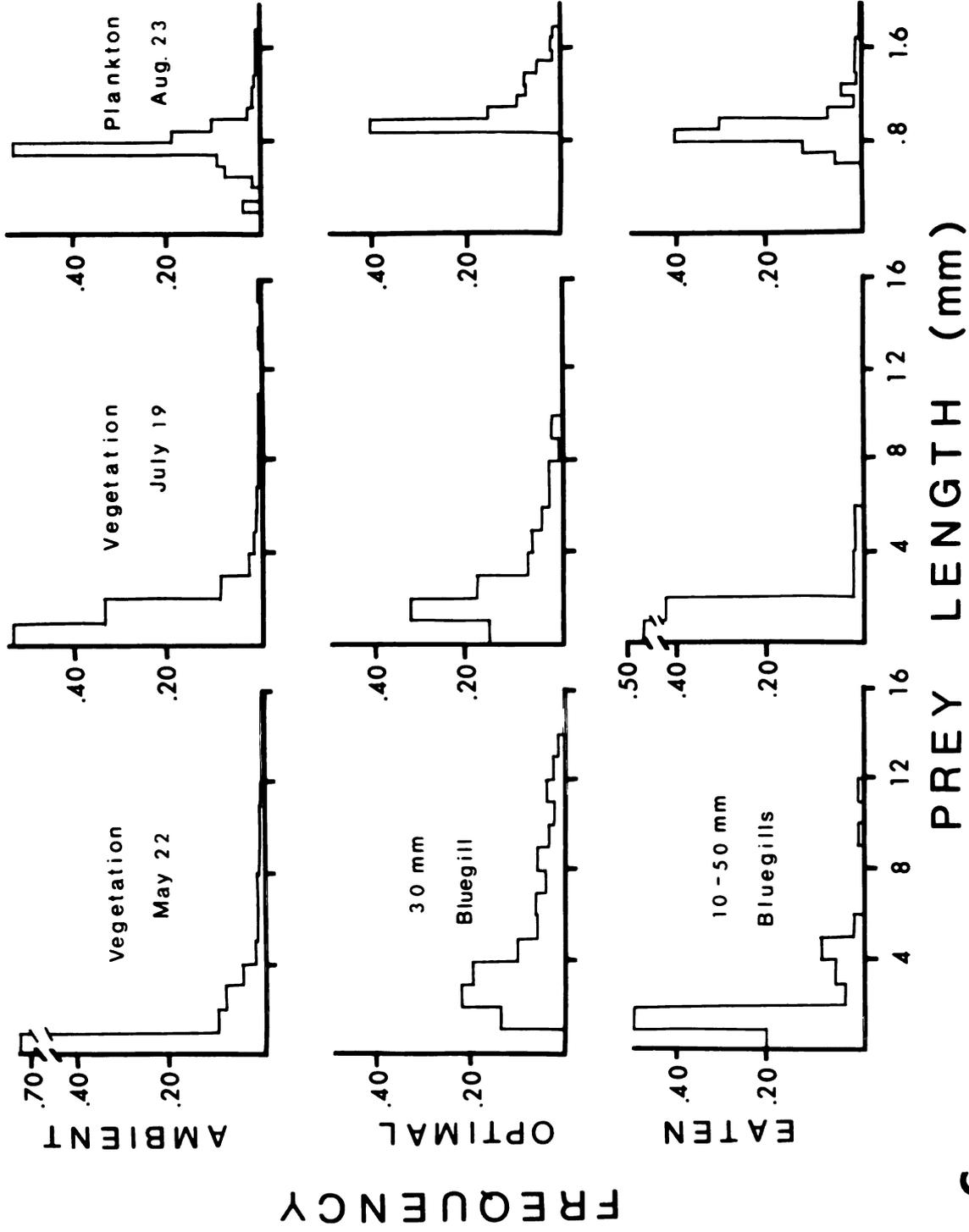


Figure 6 cont.

C.

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 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 3. From this equation the number of prey size-class i encountered/sec foraging can be calculated knowing the body length and density of prey size-class i and the size of the fish.

Table 4 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 4 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

Table 4. Prey Size-selection by Large Bluegills. 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.) (4 fish each date). All means \pm 1 SE except where indicated. Ambient and "encountered" means based on n = 2 prey samples from each date.

<u>\bar{X} Prey Length (mm)</u>	<u>July 19</u>	<u>August 3</u>
Ambient	0.88 \pm .06	1.05 \pm .01
"Encountered" (Egger's eq.)	1.03 \pm .17	1.21 \pm .01
"Encountered" (regression)	1.04 \pm .15	1.18 \pm .04
Optimal Diet	1.75	1.78
Eaten	1.74 \pm .04 \pm .13	1.86 \pm .04 \pm .13

* p < .01

the 95% confidence intervals for the average prey size eaten on both dates (Table 4).

The two smaller size classes of bluegills were also size-selective in their feeding, although to a much lesser extent than bluegills > 100 mm (Figure 6b,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 sub-optimal prey sizes may well represent the fact that the net energy intake (E_n/T) of these fish shows little change over a broad range of prey sizes. In Figure 7, 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 fishes' average 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 sub-optimal prey sizes to be included in the diet as fish size decreases. For the data shown in Figure 6, the percent error in estimating E_n/T which would account for the consumption of sub-optimal prey sizes by the Lawrence Lake fish is on average $11 \pm 3.5\%$ for large bluegills, $21 \pm 13\%$ for medium bluegills and $6 \pm 3.5\%$ for small

Figure 7. 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 equation 1 and the size-frequency distribution of zooplankton available in Lawrence Lake on July 19. 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).

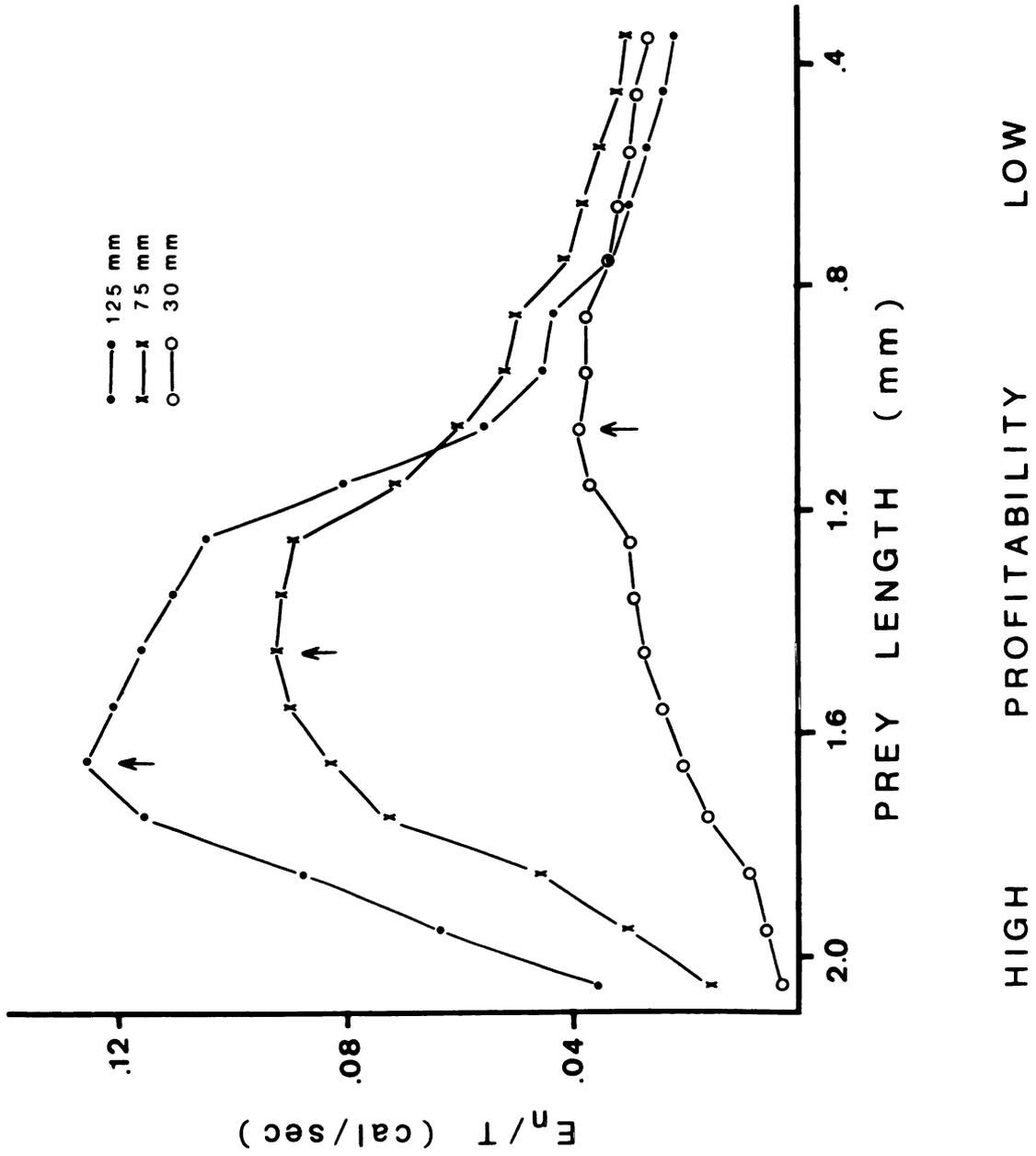


Figure 7

bluegills. Thus, these limited data suggests that all three bluegill size class 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 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 in the estimation of energetic return between habitats. Plotted in Figure 8 are the model's predicted energetic returns from the vegetation and plankton versus 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. 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 Figure 8 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

Figure 8. Linear Relationships Between Predicted Foraging Return from a Habitat and Stomach Contents (mg dry wt.) of Bluegills Foraging > 80% of Their Diet from that Habitat for the Open Water (x) and Vegetation (●) Habitats. Fitted regression equations are $Y = -2.35 + 252.1 X$ ($r = .47$, $p < .05$, $n = 24$) for the open water and $Y = -4.02 + 117.14 X$ ($r = .84$, $p < .01$, $n = 59$) for the vegetation.

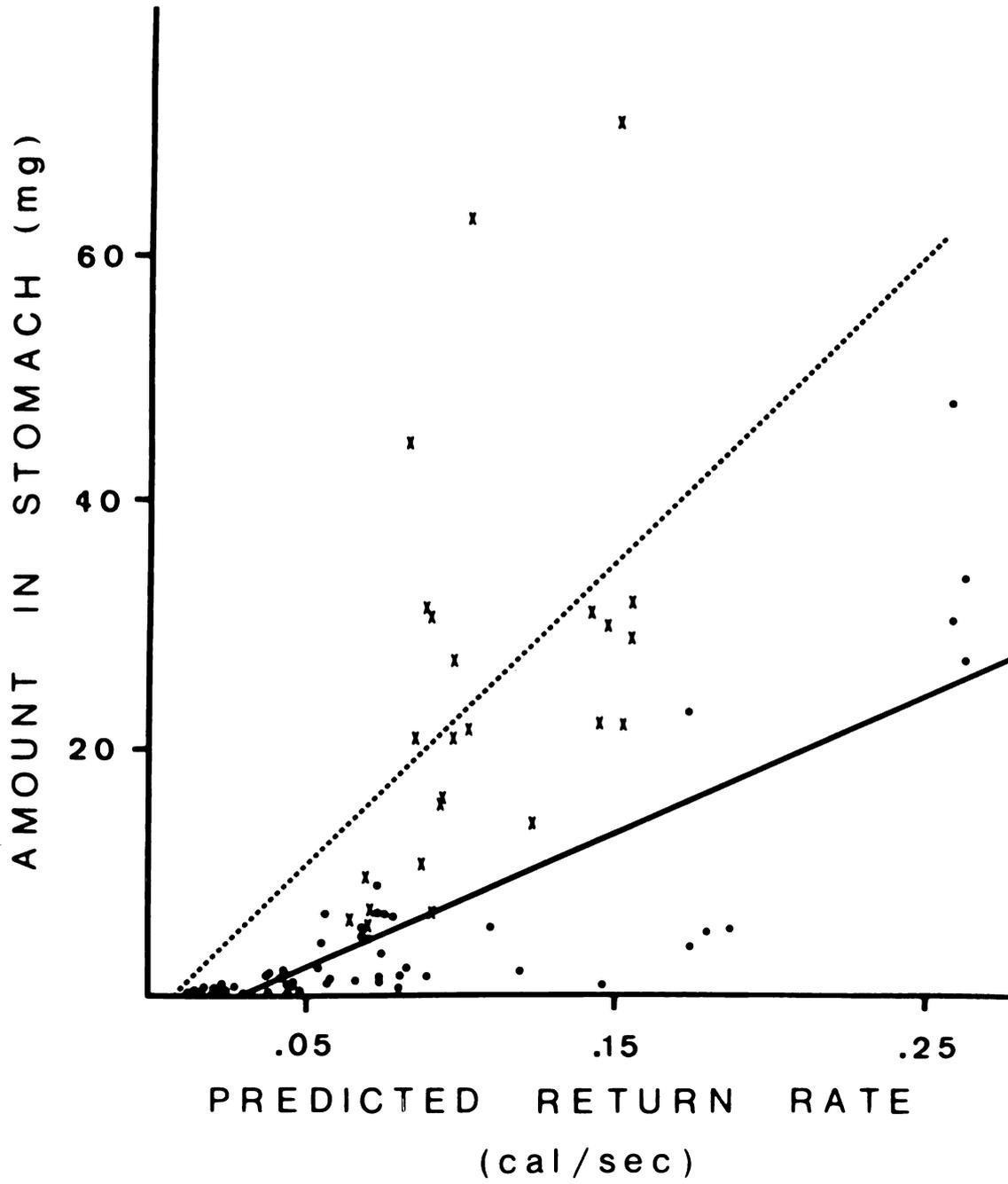


Figure 8

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 Figure 9 shows the seasonal pattern in predicted net energetic return (cal/sec) 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 (Appendix A) 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 #/l > 1.5 mm body length: 0 on June 14; .04 \pm .01 on June 25; .18 \pm .14 on July 19; .32 \pm .05 on July 29 (\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 Figure 2).

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 throughout July and August. Note that the magnitude of difference in

Figure 9. Seasonal Pattern in Predicted Habitat Profitability (left) and Actual Habitat Use (right) for Three Size Classes of Bluegills. Actual habitat use determined from the \bar{x} amount of prey (mg dry wt.) 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 (10-50mm).

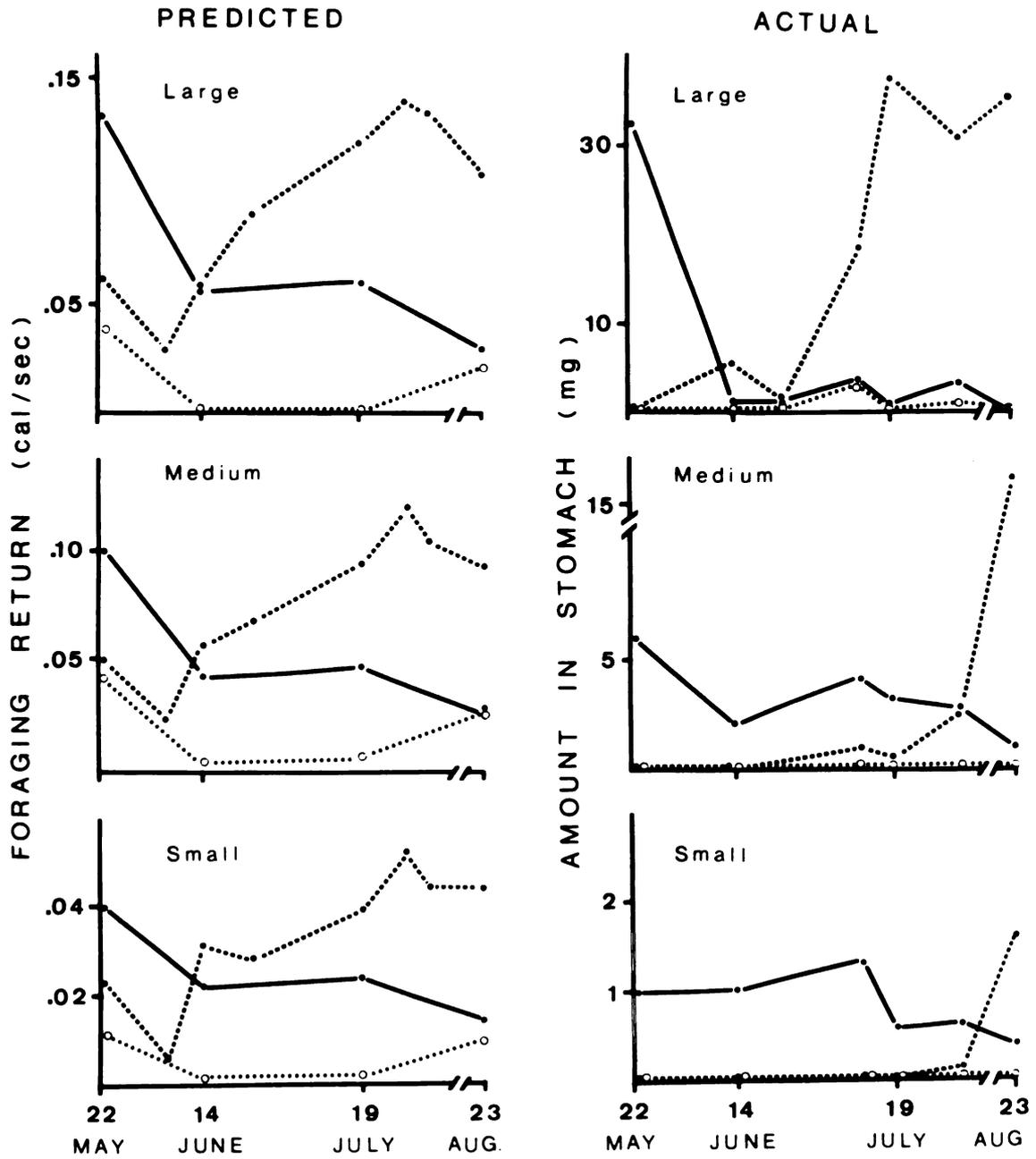


Figure 9

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 column 2 of Figure 9. The habitat use of the largest bluegills was nearly in 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 occurring some 2 weeks 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, August 23, foraging intakes increased dramatically over previous dates indicating that these fish did profit in utilizing the plankton.

August 23 represents a change in the distribution of the plankton resource from previous dates. Table 5 shows that August 23 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

Table 5. Distribution of Daphnia in Lawrence Lake. Mean density (#/l) + 1 SE of Daphnia sampled at the midlake and nearshore stations for those dates when bluegills were feeding on Daphnia; n = 2 for each case.

	<u>June 25</u>	<u>July 19</u>	<u>July 29</u>	<u>August 3</u>	<u>August 23</u>
Midlake	0.32 <u>+ .08</u>	2.55 <u>+ .55</u>	2.25 <u>+ .25</u>	2.30 <u>+ .10</u>	3.25 <u>+ .25</u>
Nearshore	0.03 <u>+ .01</u>	0.18 <u>+ .12</u>	0.33 <u>+ .01</u>	0.07 <u>+ .01</u>	5.45 <u>+ .55</u>

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 August 23 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 .5-1.5 m of the vegetation) contained 6% D. pulex, 51% D. retrocurva and 43% D. galeata. The two smallest size classes of 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 suggests 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 in the field closely matched predictions of the optimal foraging model, providing strong 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 Figures 2 and 4). These differences in capture rate are demonstrated by the diets of bluegills collected on May 22 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 ($\bar{x} \pm 1 \text{ SE}$). 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 selection 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 (Figure 7) 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 cal/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 Figure 9. In June, prior to feeding on zooplankton, large bluegills averaged < 7 mg prey dry weight in their stomachs. Upon switching to zooplankton in July gut contents increased to an average of 20-40 mg dry weight. 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 weeks from that predicted by the optimal foraging model. Werner et al. (1980) 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 6-8 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 Figure 9). 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 Werner et al.'s hypothesis. 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 smaller than 100 mm did not extensively utilize the open water habitat except when large Daphnia were abundant near the vegetation (e.g. the August 23 sampling date). The jump in biomass of prey ingested on this date relative to those previous (see column 2, Figure 9) 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 versus the open water). Further, largemouth bass in Lawrence Lake are distributed with the majority of the population occurring 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 meters 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 tradeoff 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 tradeoffs 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 effect 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 backswimmers are apparently able to balance conflicting demands between foraging profitability and predator avoidance in such a way as to maximize their feeding rate (a measure of relative fitness) (Sih, in prep.). 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/unit time versus probability of death/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 (Werner et al. 1977, Hall and Werner 1977, Keast 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 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, 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 efficiently forage 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 degree 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, 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 1979, 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.

CHAPTER 2
SIZE-CLASS COMPETITION

INTRODUCTION

A major goal in the development of an optimal foraging model which incorporates the effects of predator body size was to utilize foraging theory to provide a mechanistic understanding of the action of competition in size-structured populations. This goal has proven to be both distant and elusive. However, I would like to devote a few pages to some thoughts on the subject of size-class competition and hope that an interested reader might profit from my mental wanderings. Attention is restricted primarily to the Centrarchid fish communities of small lakes, but many of the ideas are generalizable to other systems of size-structured species..

INTRASPECIFIC COMPETITION

For simplicities sake, let us first consider a homogeneous environment in which all prey types are substitutable resources (sensu Tilman 1980) which can be arrayed by body size. For any given pattern of resource availability one can calculate the optimal resource utilization for a given-sized fish from the foraging model developed in Chapter 1. Utilization curves for two sizes of bluegill sunfish feeding on a lognormally distributed resource will in general resemble those shown in Figure 10. Having generated utilization curves for different

Figure 10. Hypothetical Distribution of Net Caloric Gain from the Diets of Two Bluegill Size Classes Utilizing the Same Prey Resource.

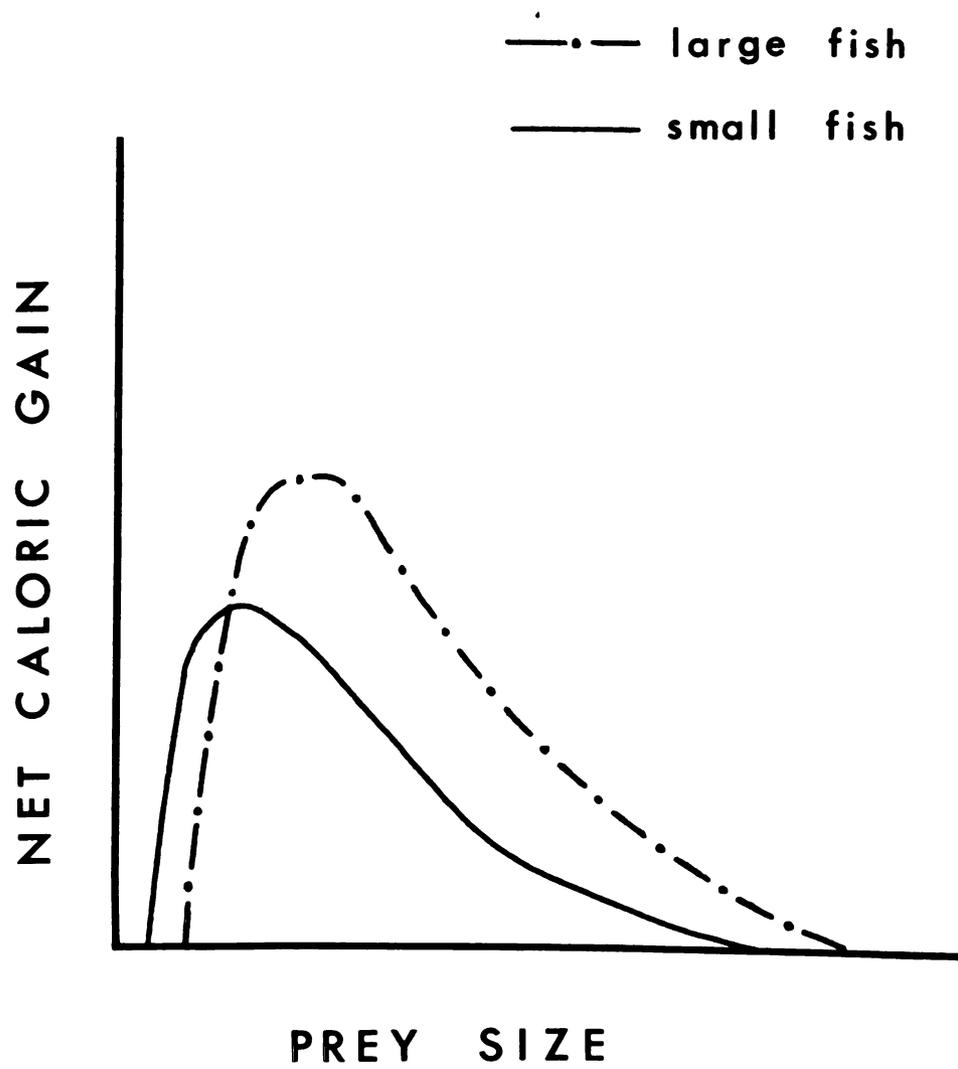


Figure 10

size classes one can then measure overlaps in resource use between size classes. These overlaps will in general be asymmetrical (due to size-specific differences in foraging ability) and the direction and magnitude of these asymmetries estimate the strength of competitive interactions (α 's) between size classes. Note that utilizing foraging theory to calculate the competition coefficients is in itself some accomplishment for these α 's are based upon the net energy gained by each competitor and can be calculated for any specified level of resource abundance. One would now like to use these measures of α to determine the relative success of different size classes and ultimately equilibrium population size structure. However, at this point a number of problems arise. First of all, one must either know the dynamics of resource renewal or assume that resource levels used in calculating the competition functions are at equilibrium values. While assuming equilibrium resource levels is a common simplifying assumption (both explicit or implicit) in many theoretical approaches to competition (Schoener 1974, 1976, 1978, Wilson 1975, Werner 1977 and others), the specification of equilibrium resource levels is especially important in examining size-class competition; for the direction and magnitude of the competitive asymmetry between different size classes can shift depending on the absolute abundance and shape of the resource distribution. This shift in asymmetry is illustrated in Figure 11 which shows how the competitive advantage can change from larger to smaller individuals as resources decline in abundance and size. The results shown in Figure 11 are not surprising as they simply demonstrate that the increased searching and handling efficiency of larger predators can be outweighed by higher metabolic costs as resources become rare or are shifted to small prey sizes.

Figure 11. Hypothetical Distribution of Net Caloric Gain from the Diets of Two Bluegill Size Classes Feeding at High Resource Levels (upper panel) and Low Resource Levels (lower panel).

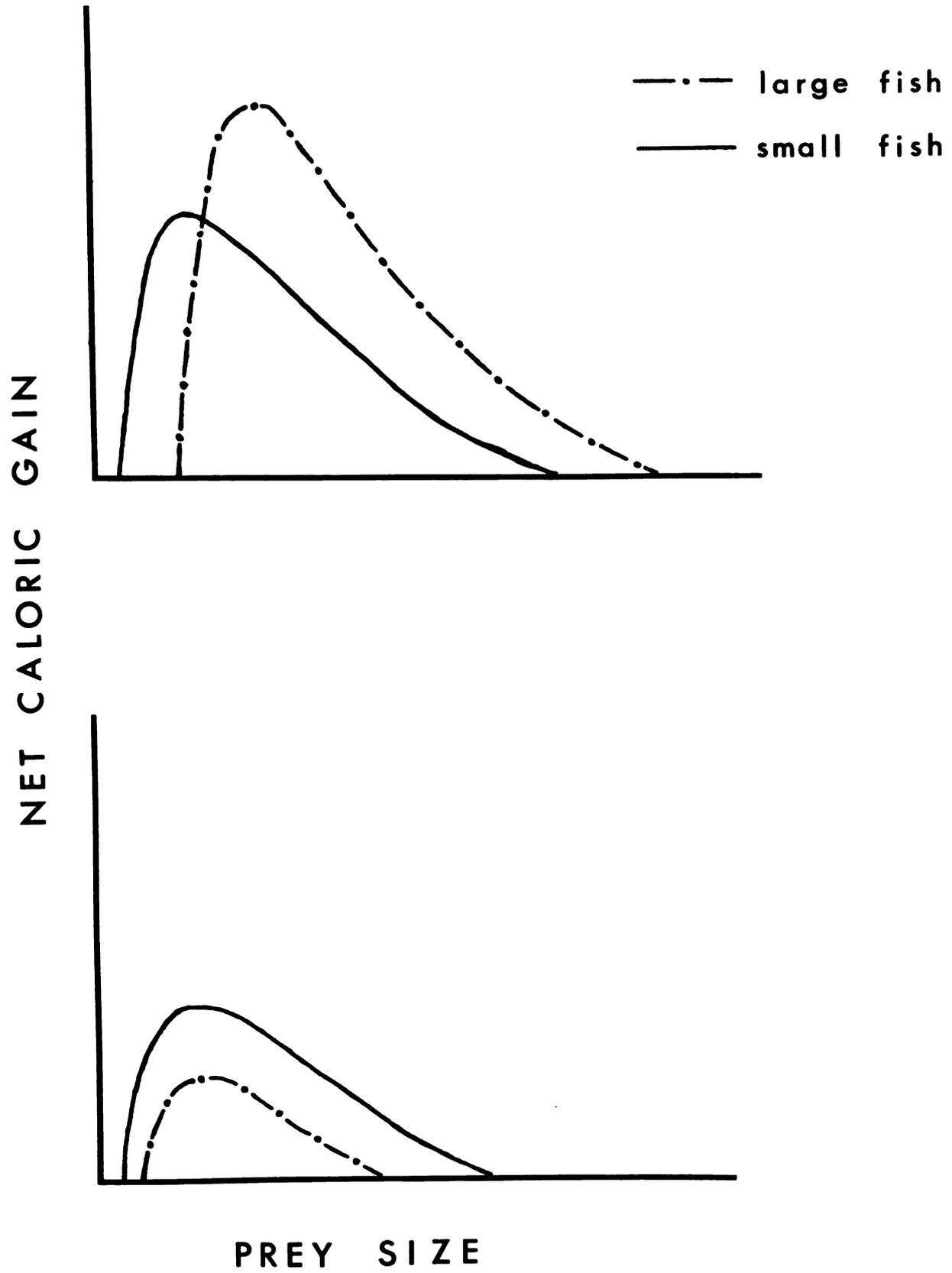


Figure 11

Such shifts in competitive asymmetries as resources decline provide a mechanistic explanation for the phenomenon of "stunting" in many fish populations stocked in monoculture. Consider for example a bluegill population stocked in the absence of predators or competitors. As bluegill population numbers increase one would expect resources to decline in abundance and to be shifted towards smaller sizes (due to the size-selective nature of fish predation). The effects of these shifts in resource availability on the net energetic intake (potential growth) of various fish sizes are illustrated in Figure 12. In this case I have plotted net energetic intake against fish length for 3 levels of resource availability in a vegetation habitat. As the abundance of large prey in the environment is decreased (by reducing the variance of the prey distribution) the fish size which achieves maximal growth rate declines. Further, the net energetic intakes of larger fish are disproportionately reduced relative to small fish, so that at low resource levels only small size classes show significant, positive growth rates. Ultimately, as resource levels drop, one would expect the population to be dominated by small fish, i.e. a stunted population.

The degree to which a fish population can depress resources and cause a shift in size-specific growth rates will of course depend on the vulnerability and renewal rates of the prey species and on the degree to which other factors (e.g. predation) may regulate fish numbers. All of these factors are likely to vary with the structure of the environment and with the overall productivity of the lake. Seasonal dynamics of the prey resource are also likely to affect size-class competition for aquatic systems are in general characterized by flushes in prey resources at certain times of the year (see Appendix A)

Figure 12. Calculated Net Caloric Intake (E_n/T) for Bluegills Feeding on Three Different Distributions of Vegetation Prey. Prey distributions are normal curves of \ln prey length with mode = 0.60 (density at the mode = 20,000 ind./m³) and variances of 0.35, 0.45, and 0.55. E_n/T calculated using a continuous form of the foragingⁿ model developed in Chapter 1 (see page 5).

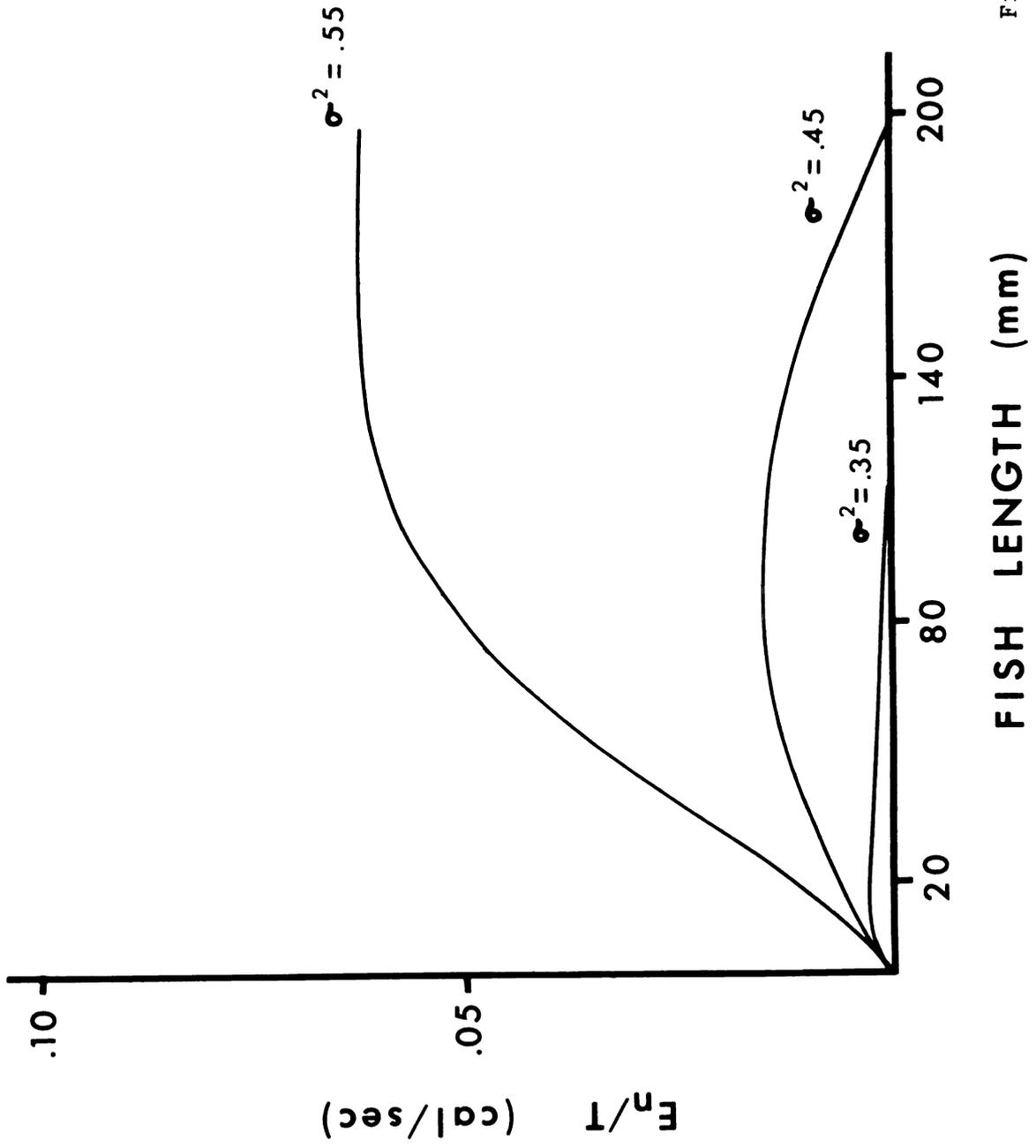


Figure 12

and it may well be that large fish are able to achieve most of their yearly growth during periods of super-abundant prey. If Figure 12 can be taken to represent the common seasonal decline in prey availability from spring to fall in temperate lakes (Appendix A) one would predict that large fish would show much higher seasonal changes in growth rate than would small fish.

The fact that most natural systems are not composed of a single habitat type, but rather contain a number of discrete habitats differing in structure, prey type and associated predation risk, radically alters the simplified view of size-class competition presented above. The field study in Chapter 1 demonstrated that as resource levels declined in a habitat (the vegetation) large bluegills shifted their habitat use to the open water and were thereby able to maintain high levels of energetic intake over most of the summer. Predation risk apparently restricted smaller fish from using the open water habitat, which provided large bluegills with an abundant resource of almost exclusive use. Had the entire bluegill population switched to utilizing the plankton, one would expect the higher rate of predation to rapidly deplete the abundance of large zooplanktors and cause a marked decline in the profitability of the open water habitat. Whether habitat-specific predation risk will have a significant effect on competition between size classes will depend of course on the dynamics of prey resources in open versus structured habitats. For if resource levels change in synchrony between both habitat types, predation risk will have a minimal effect in mediating size-class competition.

Clearly, there is much fertile ground in the area of intra-specific competition and size-class interactions that remains to be

explored. Eventually, it may be possible to relate not only foraging efficiency and growth potential to an organism's body size, but also such factors as mortality risk and fecundity. At that point it should be possible to develop quite realistic population models based on body size (e.g. Werner and Caswell 1977) which can then be used to examine the relative effects of prey distribution and habitat structure on the equilibrium size structure and growth rate of a population.

APPENDICES

APPENDIX A

DISTRIBUTION OF BODY SIZE IN THE PREY OF FISHES

A legion of studies exist which attempt to determine the availability of prey organisms to fish in small temperate lakes. Only a very few, however, have measured quantitatively both the abundance and size of all available prey organisms and fewer still have attempted to make these measures in different habitats across the growing season. Studies which have accomplished a portion of these goals are: Wohlschlag (1950), Ball and Hayne (1952), Anderson and Hooper (1956), Gerking (1962), Keast (1965), and Phoenix (1976). Only the work of Phoenix (1976), however, gives detailed information on the distribution of available prey sizes and his information is generally limited to small cladoceran species. Given the importance of prey size to the growth (Paloheimo and Dickie 1966, Martin 1970, Kerr 1971, Wankowski and Thorpe 1979), foraging behavior (Ivlev 1961, Galbraith 1967, Ware 1972, Werner and Hall 1974) and habitat selection (Werner and Hall 1976, 1977, Werner et al. 1980) of fish, it seems crucial that fisheries biologists and ecologists have at their hands detailed descriptions of the distribution and abundance of prey sizes found in the habitats of natural lakes.

Towards this end I have quantified the size distributions of invertebrate prey found in the vegetation, bare sediments and open water of a small marl lake in southwest Michigan during the months of May through August, 1979. Size-frequency distributions of prey lengths

found in these habitats were fit to the lognormal distribution. The ability to fit the lognormal curve to these data is an extremely useful property as it allows one to describe the relative abundance of prey sizes from just two parameters, the mode (or mean) and variance; and knowing the total number of prey in any size class, the absolute abundance of each prey size can be calculated.

Prey organisms were also grouped taxonomically and body lengths converted to dry weights to examine seasonal changes in the abundance and biomass of different prey types in each habitat.

METHODS

Site

Lawrence Lake, a mesotrophic, marl lake, 4.9 ha in surface area, located 2.1 km east of Hickory Corners, Barry County, Michigan was selected for study as it contains a very simple and stable vegetational community (79% Scirpus subterminalis by weight (Rich et al. 1971)), a number of areas of discrete habitat types, and receives only slight fishing pressure. The east shore of Lawrence Lake was used as the primary study site. Here the bench is characterized by areas of barren marl sediments (85% open bottom) extending 8-12 m from shore to an average depth of .75 m. The far edge of the bench and the entire slope region, which drops steeply from 1.5 to 6 m, are covered by a dense stand of Scirpus subterminalis (82% cover), .4 to .6 m in height. Beyond the littoral zone the lake bottom slopes gradually to a maximum depth of 12.6 m located approximately 100 m from the east shore.

Prey sampling

Invertebrate prey were sampled from each of three habitats (barren marl bench, vegetated bench and slope, and open water) during the months

of May-August, 1979. Prey living in the marl sediments were sampled with a plexiglass corer (6.5 cm dia.; 8 cm deep) by a diver using mask and snorkel or SCUBA. The diver's corer has been shown to be the most successful sampling device for this type of habitat (Flannagan 1970). Five random samples were taken on each sampling date. After collection samples were removed to the laboratory and gently washed through a series of U.S. standard sieves (2.83, 0.70, 0.180 mm). Organisms retained by the two larger meshed sieves were removed by hand and preserved in 10% formalin. Contents of the smallest meshed sieve were mixed with a 20% solution of $MgSO_4$ which allowed 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). Basically, the device consists of plexiglass cylinder (21.5 cm dia.) with a #10 plankton net and quart Mason jar attached at the top. At the base of the cylinder are two sliding plates which can be closed to form a seal. A sample is then taken by opening the plates, slipping the cylinder completely over the vegetation and rapidly sliding the plates closed. Since the dominant vegetation encountered, S. subterminalis, is quite thin and flexible, the closed plates form a tight seal around the base of the vegetation. The sample is then removed to the surface by either uprooting the vegetation or cutting it at the base with a knife. At the surface the sampler is inverted and the vegetation and associated prey are washed from the plankton net into the attached jar (or into a large bucket if necessary). This sampler is quite 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 (.5-1.5 m depth) and five samples taken randomly along the slope (2-4 m depth) on each date.

After collection the vegetation samples were carefully washed into a series of sieves (2.83, 0.70, 0.180 mm). Contents of the two largest sieves were placed in white enameled pans and the live prey removed by hand and preserved in 10% formalin. Contents of the smallest sieve were separated using 20% $MgSO_4$ as with the core samples.

Open water prey were sampled using a 30 cm diameter #10 plankton net. Two vertical tows from a depth of 4 m were taken at a location in the limnetic zone approximately 60 m from shore. A depth of 4 m was chosen as it defines the usual depth of the thermocline in Lawrence Lake during the summer (Wetzel 1975). Previous work has suggested that the warmwater fish of these small lakes remain above the thermocline when feeding (Hall et al. 1979) and echosounder traces taken in Lawrence Lake on July 29, 1979 confirmed that all fish were located at depths less than 4-5 m (thermocline at 4 m (Wetzel, personal communication)). Plankton samples were subsequently preserved in 95% alcohol.

Resource sampling was conducted during the hours immediately post-dawn as many fish species have been shown to exhibit a feeding peak during these hours (Keast and Welsh 1968, Sarker 1977, Wilsmann 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 post-sunrise and was completed by 70 min post-sunrise. Resources sampled thus represent prey availabilities during this morning feeding period.

Prey samples were enumerated under a dissection microscope at 25 X

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. Subsampling was conducted by placing the sample in a scored petri dish and counting the number of prey organisms in 4 of 16 total divisions, chosen at random. Fifteen to fifty randomly chosen individuals in each prey category were measured for total body length in each sample using an ocular micrometer. 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. Length-weight regressions were also obtained for each prey taxon permitting the conversion of prey lengths to dry weights (exclusive of shells or cases).

RESULTS

Body size distributions

The distributions of prey sizes available in the vegetation, sediments and open water show a strong, numerical dominance by small prey (Tables A1-3), with the range of prey sizes being greatest in the vegetation and least in the open water. Such distributions generally conform to a normal distribution when the measure of prey size, L , is transformed to $Y = \ln L$; therefore the original distribution of L is termed lognormal (Aitchison and Brown 1957). Using a computer program developed by Gauch and Chase (1974) normal curves were fit to logarithmic transforms of prey lengths in each habitat and the fitted

Table A1. Size Distribution of Invertebrate Prey in the Vegetation of Lawrence Lake. Data are mean densities (\pm 1 SE); n = 10 samples per date.

Prey length (mm)	Prey density (#/m ³)			
	May 21	June 14	July 19	August 23
0 - 0.5	31,506 + 7,976	62,210 + 7,976	14,552 + 4,399	7,416 + 770
0.5 - 1.0	29,853 + 3,147	31,357 + 4,076	30,735 + 4,881	17,246 + 2,319
1.0 - 1.5	6,155 + 644	12,357 + 1,934	16,029 + 2,970	7,499 + 1,441
1.5 - 2.0	1,813 + 188	2,353 + 290	10,860 + 2,237	2,408 + 508
2.0 - 2.5	3,835 + 1,048	1,938 + 238	4,766 + 853	1,741 + 362
2.5 - 3.0	3,069 + 1,197	1,691 + 340	1,691 + 337	909 + 253
3.0 - 3.5	2,937 + 1,401	1,229 + 302	1,901 + 383	419 + 106
3.5 - 4.0	920 + 214	672 + 154	446 + 111	164 + 60
4.0 - 5.0	1,146 + 232	584 + 129	799 + 143	11 + 11
5.0 - 6.0	419 + 96	181 + 59	391 + 124	0
6.0 - 7.0	242 + 66	94 + 28	187 + 39	0
7.0 - 8.0	308 + 63	44 + 16	171 + 65	0
8.0 - 9.0	231 + 48	50 + 17	44 + 18	5 + 5
9.0 - 10.0	105 + 28	44 + 21	55 + 33	0
10.0 - 12.0	171 + 52	22 + 12	11 + 7	0
12.0 - 14.0	55 + 16	38 + 27	5 + 5	0
14.0 - 16.0	11 + 7	5 + 5	0	0
16.0 - 18.0	5 + 5	5 + 5	5 + 5	0
18.0 - 20.0	5 + 5	0	5 + 5	0
\bar{x} length (\pm 1 SE)	1.07 \pm .02	0.72 \pm .02	1.33 \pm .17	1.07 \pm .02

Table A2. Size Distribution of Invertebrate Prey in the Rare Sediments of Lawrence Lake. Data are mean densities (\pm 1 SE); n = 5 samples per date.

Prey length (mm)	Prey density (#/m ²)			
	May 21	June 14	July 19	August 23
0 - 0.5	301 + 1,445 +	181 + 1,445 +	963 + 4,395 +	667 + 3,882 +
0.5 - 1.0	612 + 301 +	558 + 1,686 +	978 + 6,562 +	115 + 283 +
1.0 - 1.5	135 + 1,204 +	338 + 963 +	590 + 4,334 +	1,586 + 3,817 +
1.5 - 2.0	330 + 2,288 +	221 + 1,686 +	338 + 3,431 +	675 + 385 +
2.0 - 2.5	584 + 2,408 +	472 + 1,385 +	153 + 1,324 +	123 + 668 +
2.5 - 3.0	494 + 1,385 +	526 + 602 +	244 + 361 +	114 + 330 +
3.0 - 3.5	310 + 361 +	316 + 120 +	147 + 361 +	160 + 260 +
3.5 - 4.0	241 + 421 +	74 + 421 +	221 + 415 +	226 + 373 +
4.0 - 5.0	120 + 246 +	153 + 120 +	111 + 231 +	0 + 0 +
5.0 - 6.0	117 + 60 +	74 + 60 +	158 + 60 +	60 + 60 +
6.0 - 7.0	60 + 60 +	0 + 0 +	60 + 60 +	0 + 0 +
7.0 - 8.0	0 + 60 +	0 + 0 +	0 + 0 +	0 + 0 +
8.0 - 9.0	0 + 60 +	0 + 0 +	0 + 0 +	0 + 0 +
9.0 - 10.0	0 + 60 +	0 + 0 +	0 + 0 +	0 + 0 +
10.0 - 12.0	60 + 60 +	0 + 0 +	0 + 0 +	69 + 100 +
\bar{x} length (\pm 1 SE)	2.51 \pm .12	2.04 \pm .09	1.64 \pm .05	1.55 \pm .07

Table A3. Average Size Distribution of Invertebrate Prey in the Open Water of Lawrence Lake. Data are mean densities (\pm 1SE); calculated from 8 samples taken between May and August, 1979.

<u>Prey length (mm)</u>	<u>#/liter</u>
0 - 0.1	0
0.1 - 0.2	0.08 \pm 0.08
0.2 - 0.3	3.26 \pm 1.46
0.3 - 0.4	7.92 \pm 2.81
0.4 - 0.5	2.53 \pm 1.18
0.5 - 0.6	2.14 \pm 0.68
0.6 - 0.7	3.06 \pm 0.88
0.7 - 0.8	2.73 \pm 0.83
0.8 - 0.9	1.41 \pm 0.35
0.9 - 1.0	0.69 \pm 0.29
1.0 - 1.1	1.33 \pm 0.39
1.1 - 1.2	0.43 \pm 0.16
1.2 - 1.3	0.21 \pm 0.12
1.3 - 1.4	0.06 \pm 0.03
1.4 - 1.5	0.09 \pm 0.04
1.5 - 1.6	0.03 \pm 0.01
1.6 - 1.7	0.04 \pm 0.02
1.7 - 1.8	0.01 \pm 0.01
1.8 - 1.9	0.01 \pm 0.01
> 1.9	< 0.01

Table A4. Parameters of the Normal Distribution Fit to the Logarithm to Base e of Prey Length in Three Habitats.

VEGETATION				
	<u>Modal prey size (mm)</u>	<u>Variance</u>	<u>Density at the mode (#/m³)</u>	<u>R²</u>
May 21	0.21	1.243	34,658	.90
June 14	0.28	0.668	63,059	.99
July 19	0.59	0.460	32,357	.99
August 23	0.60	0.344	19,808	.99
Seasonal average	0.18	1.562	32,794	.91

SEDIMENTS				
	<u>Modal prey size (mm)</u>	<u>Variance</u>	<u>Density at the mode (#/m²)</u>	<u>R²</u>
May 21	2.41	0.104	2,611	.68
June 14	1.20	0.474	1,693	.82
July 19	1.16	0.268	6,560	.97
August 23	1.14	0.177	6,921	.98
Seasonal average	1.13	0.387	3,672	.98

PLANKTON				
	<u>Modal prey size (mm)</u>	<u>Variance</u>	<u>Density at the mode (#/L)</u>	<u>R²</u>
Seasonal average	0.36	0.237	5.24	.76

parameters of the normal distributions are listed in Table A4. Since the method of Gauch and Chase (1974) is a regression approach one can examine the percent of the total variance explained by fitting the lognormal distribution, R^2 , to determine the goodness of fit. Examination of the R^2 's in Table A4 indicates that the distribution of prey sizes in each habitat was quite adequately described by the lognormal curve as generally greater than 90% of the variance was accounted for. Since prey weight (W) can be related to length (L) by a power function such as $L = cW^x$; this implies that prey weights are also distributed lognormally in each habitat (Aitchison and Brown 1957, Schoener and Janzen 1968).

The range of prey sizes available in the three habitats is reflected in the variances of the fitted distributions, the variance being greatest in the vegetation and least in the plankton (Table A4). These differences in variances between habitats result in large differences in the relative biomass of small and large prey and can have marked effects on the feeding preferences of fish (see Chapter 1). Figures A1-3 illustrate the fitted lognormal curves and actual prey size distributions found in each habitat averaged across the season.

Seasonal Patterns

There was a strong decline in the abundance of large prey in the vegetation habitat across the summer (Tables A1,5). This change in the vegetation prey size distribution is evident in the steady decrease in the variance of the fitted lognormal distribution from May to August (Table A4). However, the seasonal loss of large prey in this habitat is not reflected in either a change in the mean or modal prey size indicating these measures alone are inadequate for determining the

Figure A1. Distribution of Prey Sizes (mm body length) in the Vegetation Habitat Averaged Over the Season. Density is in $\#/m^3$. Fitted curve is the normal distribution of \ln prey length with mode = 0.18 and variance = 1.56.

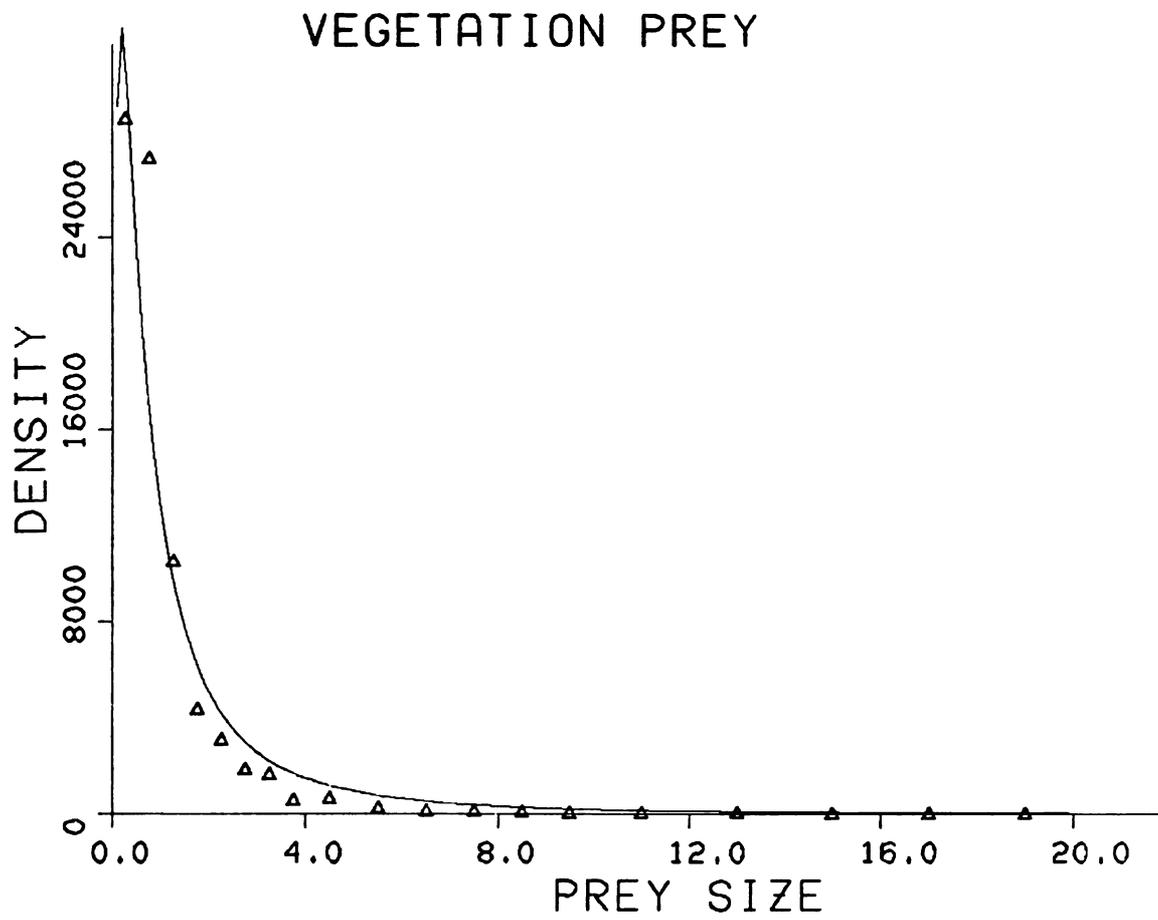


Figure A1

Figure A2. Distribution of Prey Sizes (mm body length) in the Bare Sediment Habitat Averaged Over the Season. Density is in $\#/m^2$. Fitted curve is for the normal distribution of \ln prey length with mode = 1.13 and variance = 0.39.

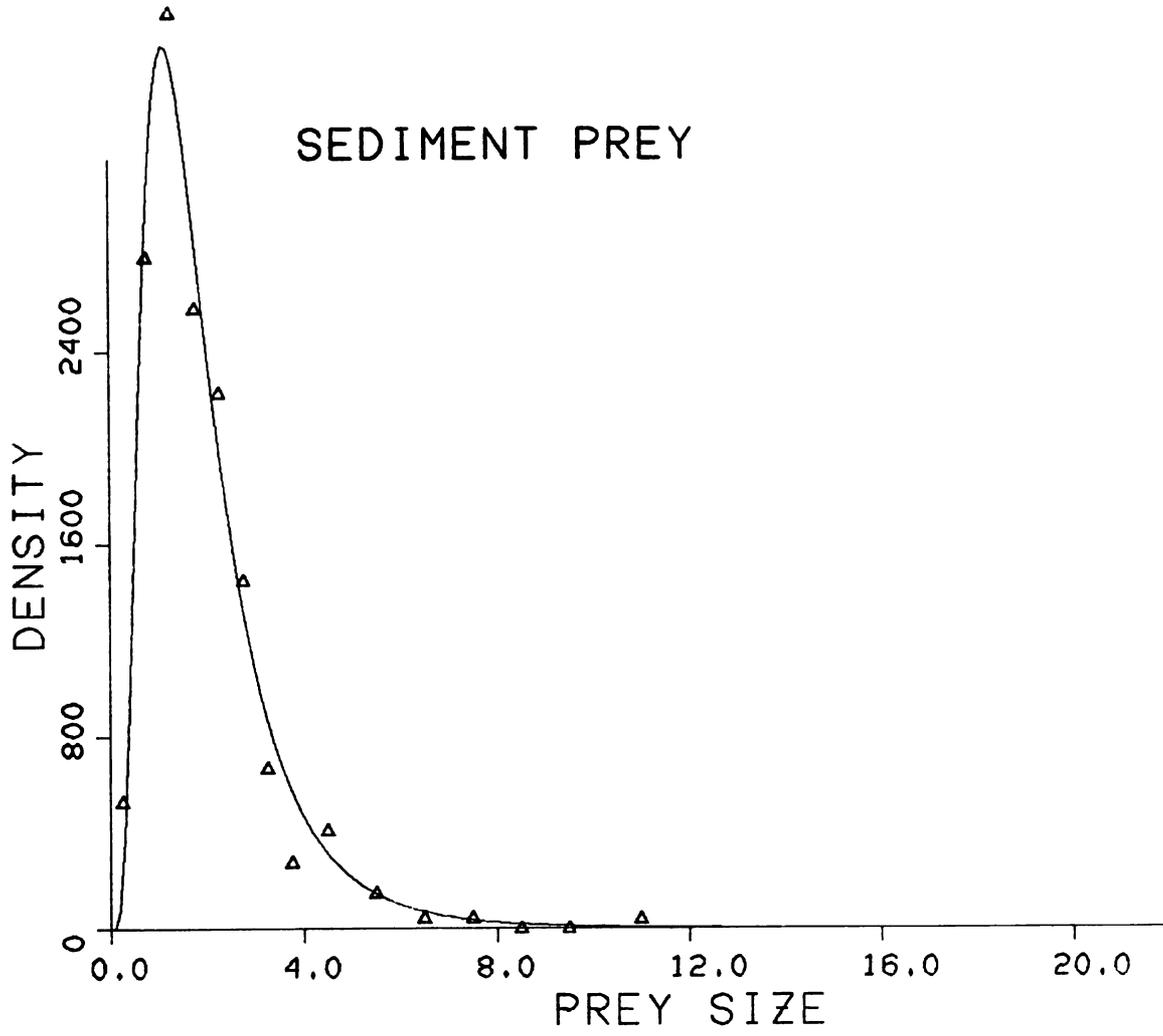


Figure A2

Figure A3. Distribution of Prey Sizes (mm body length) in the Open Water Habitat Averaged Over the Season. Density is in #/liter. Fitted curve is for the normal distribution of ln prey length with mode = 0.36 and variance = 0.24.

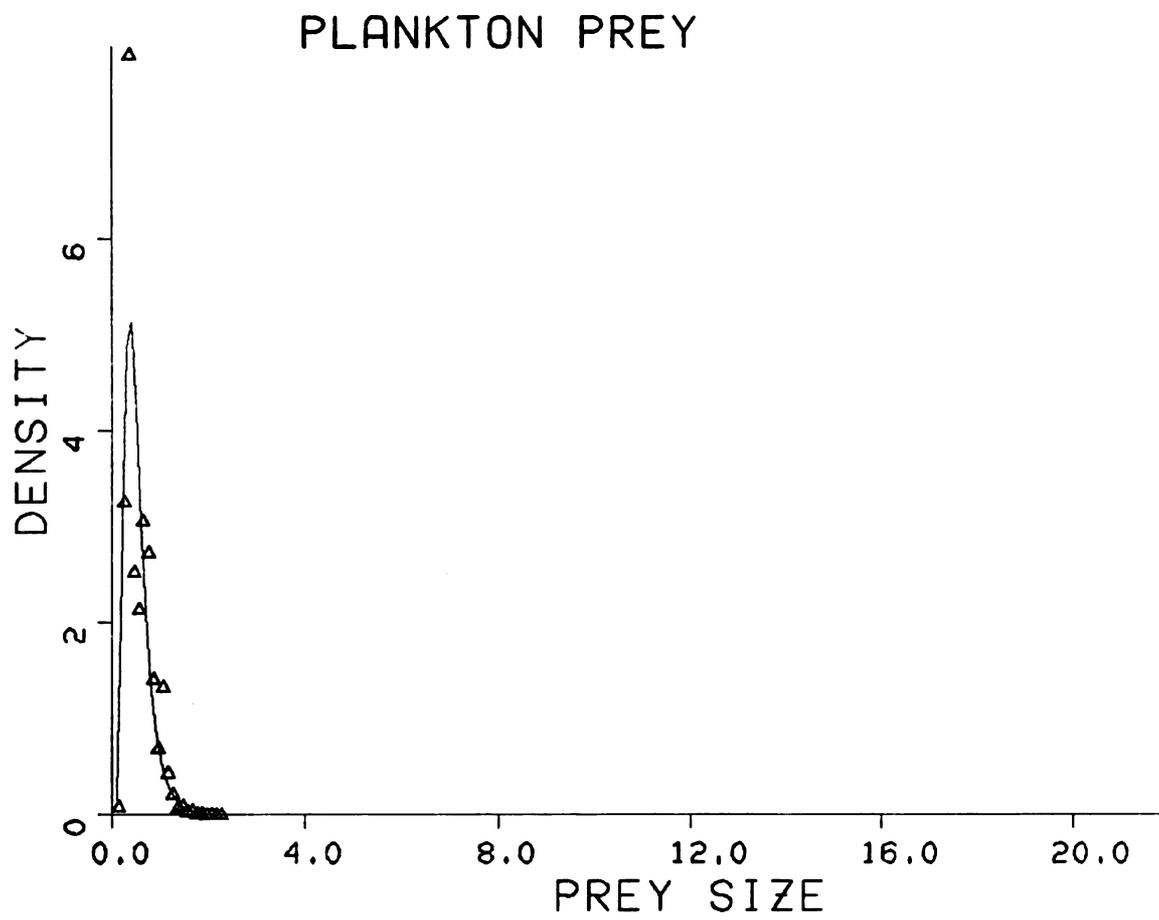


Figure A3

Table A5. Seasonal Pattern in the Density of Prey Organisms ≥ 3.0 mm Body Length in the Vegetation and Sediment Habitats. Densities are $\#/m^3$ for the vegetation and $\#/m^2$ for the sediments.

	Density of prey ≥ 3.0 mm in length			
	<u>May</u>	<u>June</u>	<u>July</u>	<u>August</u>
Vegetation	6,555	3,062	4,020	599
Sediments	2,593	1,323	1,488	1,123

availability of prey sizes to fish.

Table A6 lists the mean number and dry weight of the major prey groups found in the vegetation across the summer. The total biomass of insect prey declined from May to August, as did the biomass of amphipods and ostracods, with the sharpest reduction occurring between May and June. The decline of these prey groups was offset by the increasing biomass of gastropods, so that the total biomass of all prey in the vegetation remained fairly constant for much of the summer. Since most fish species do not possess the specialized adaptations required to feed effectively on gastropods (e.g. a crushing pharyngeal "mill" with large molariform teeth (Keast 1978, Laughlin and Werner 1980)), it is informative to examine the patterns in total prey biomass exclusive of gastropods. Table A7 compares the biomass of non-gastropod prey in the vegetation, separated into the bench and slope regions of the habitat. The total biomass of these prey declined steadily and by more than 2.5 fold from May to August. A reduction in the total volume of prey in the vegetation over this time period has also been reported by Ball and Hayne (1952) and Anderson and Hooper (1956). Note that prey biomass and prey size were generally larger in the bench region (.5-1.5 m deep) than on the slope (2-4 m deep). These differences between regions of the vegetation also exist if gastropods are included in the prey distribution (Table A8).

Prey numbers and biomass in the bare sediments (Table A9) were considerably less than those available in the vegetation (Table A6) (prey densities in $\#/m^3$ for the vegetation can be converted to $\#/m^2$ of lake bottom by multiplying by 0.5 as vegetation height was approximately 0.5 m). Differences in prey abundance between vegetated and barren

Table A6. Mean Number and Dry Weight (per m³) of Major Prey Groups

Found in the Vegetation. N = 10 samples per date.

	Vegetation Prey #/m ³ (mg dry wt.)			
	<u>May 21</u>	<u>June 14</u>	<u>July 19</u>	<u>August 23</u>
Simcephalus	4,361 (88)	4,950 (211)	2,271 (38)	2,068 (33)
Sida	236 (10)	357 (12)	10,109 (383)	3,366 (71)
Bosmina	4,224 (6)	33,814 (37)	951 (1)	**
Cydoridae	22,817 (66)	31,930 (411)	6,281 (53)	4,276 (33)
<u>Total Cladocera</u>	31,638 (170)	70,993 (411)	19,601 (482)	9,702 (142)
Copepoda	21,340 (81)	23,067 (126)	22,302 (92)	11,599 (32)
Ostracoda	11,637 (257)	6,050 (105)	4,634 (82)	1,603 (60)
Hyalella	2,728 (235)	3,399 (132)	3,465 (166)	1,958 (49)
Hydracarina	1,133 (86)	1,743 (138)	1,633 (135)	1,243 (87)
Chironomidae	6,750 (372)	5,345 (140)	21,180 (363)	5,422 (140)
Other Diptera	4,579 (108)	1,532 (27)	1,598 (83)	898 (4)
Tricoptera	473 (293)	154 (42)	451 (37)	390 (25)
Ephemeroptera	1,254 (595)	1,270 (285)	2,100 (123)	1,704 (82)
Odonata	192 (228)	121 (248)	220 (45)	231 (276)
<u>Total Insecta</u>	13,293 (1,534)	8,448 (747)	22,907 (653)	8,811 (535)
Gastropoda	562 (265)	804 (1,279)	1,174 (1,230)	1,003 (694)
<u>Total Prey</u>	82,687 (2,639)	114,669 (2,946)	82,577 (2,856)	38,593 (1,603)

** absent

Table A7. Total Dry Weight (mg/m^3) and Mean Size (mg dry wt.) of Vegetation Prey (exclusive of gastropods). Total weights are $\bar{x} \pm 1$ SE based on 5 samples/date for both the bench and slope. Prey sizes are $\bar{X} \pm 1$ SE based on > 600 measurements/date for both the bench and slope.

	Prey dry weight (mg) / m^3			\bar{x} prey size (mg dry weight)		
	<u>Bench</u>	<u>Slope</u>	<u>Combined</u>	<u>Bench</u>	<u>Slope</u>	<u>Combined</u>
May 22	3,395 \pm 580	1,351 \pm 146	2,374 \pm 442	0.047 \pm .013	0.017 \pm .002	0.029 \pm .006
June 14	1,901 \pm 431	1,432 \pm 219	1,667 \pm 241	0.017 \pm .004	0.013 \pm .002	0.015 \pm .004
July 19	1,942 \pm 244	1,310 \pm 256	1,626 \pm 197	0.021 \pm .001	0.023 \pm .006	0.020 \pm .003
August 23	1,463 \pm 215	356 \pm 49	910 \pm 211	0.033 \pm .007	0.013 \pm .001	0.024 \pm .007

Table A8. Total Dry Weight (mg/m³) and Mean Size (mg dry wt.) of All Vegetation Prey. Total weights are $\bar{X} \pm 1$ SE based on 5 samples/date for both the bench and slope. Prey sizes are $\bar{x} \pm 1$ SE based on > 600 measurements/date for both the bench and slope.

	Prey dry weight (mg) / m ³			\bar{x} prey size (mg dry weight)		
	<u>Bench</u>	<u>Slope</u>	<u>Combined</u>	<u>Bench</u>	<u>Slope</u>	<u>Combined</u>
May 22	3,729	1,548	2,639	0.052	0.018	0.032
	+ 534	+ 190	+ 451	+ .013	+ .003	+ .006
June 14	4,033	1,860	2,946	0.037	0.016	0.026
	+ 680	+ 203	+ 492	+ .006	+ .002	+ .005
July 19	3,929	1,783	2,856	0.040	0.031	0.034
	+ 939	+ 308	+ 587	+ .008	+ .009	+ .006
August 23	1,816	1,390	1,603	0.039	0.049	0.041
	+ 185	+ 195	+ 145	+ .005	+ .002	+ .008

Table A9. Mean Number and Dry Weight (per m^2) of Major Prey Groups Found in the Sediments. N = 5 samples per date.

	Sediment Prey $\#/m^2$ (mg dry wt.)			
	<u>May 21</u>	<u>June 14</u>	<u>July 19</u>	<u>August 23</u>
Cladocera	181 (1)	120 (1)	843 (9)	840 (9)
Ostracoda	783 (22)	60 (2)	1,385 (33)	181 (5)
Hyalella	120 (18)	**	181 (2)	**
Hydracarina	241 (18)	241 (18)	241 (16)	602 (34)
Chironomidae	2,769 (92)	5,538 (106)	11,378 (190)	12,522 (99)
Other Diptera	4,515 (25)	2,167 (17)	6,742 (18)	2,829 (183)
Tricoptera	**	**	**	60 (1)
Ephemeroptera	421 (296)	60 (63)	**	783 (130)
Odonata	120 (542)	**	**	**
<u>Total Insecta</u>	8,067 (542)	7,766 (129)	18,602 (208)	16,194 (417)
Gastropoda	361 (356)	181 (147)	**	60 (12)
<u>Total Prey</u>	10,595 (962)	8,669 (299)	22,876 (278)	18,361 (486)

**absent

Table A10. Total Dry Weight (mg/m²) and Mean Size (mg dry wt.) of All Sediment Prey. Total weights are $\bar{X} \pm 1$ SE based on 5 samples/date. Prey sizes are $\bar{x} \pm 1$ SE based on >140 measurements/date.

	Prey dry weight (mg) / m ²	\bar{x} prey size (mg dry weight)
May 22	962 \pm 346	0.091 \pm 0.030
June 14	299 \pm 110	0.034 \pm 0.011
July 19	278 \pm 35	0.012 \pm 0.001
August 23	486 \pm 217	0.026 \pm 0.011

habitats have also been recorded in other studies (Wohlschlag 1950, Gerking 1962) and presumably these differences reflect both a lack of micro-habitat diversity and an increased predator vulnerability for invertebrates in open areas. Prey types notably reduced or absent in the bare sediments relative to the vegetation were cladocera, copepoda, Hyaella and many insect groups.

Total biomass in the sediments was at a peak in May, declined by approximately 3 fold in June and July and then increased in August. This pattern in total biomass was paralleled by changes in the mean dry weight of prey over this same time period (Table A10).

DISCUSSION

This study represents the first attempt to quantify the total size distribution of invertebrate prey found in a natural lake. Results demonstrate that within each major habitat type the distribution of prey sizes closely matches the lognormal curve. The ability to characterize prey availabilities by a simple, two parameter distribution should prove extremely useful for general examinations of prey size selection and potential overlaps in resource utilization by different fish species or size classes (see Werner 1977 for a good example). The work of Werner (1977) represents the only other study which has attempted to determine the size distribution of prey in a freshwater system (a series of small experimental ponds). Werner also found the distribution of prey sizes (weights) to be lognormal and Schoener and Janzen (1968) and Hemmingen (1934) both report body length in terrestrial insect communities to be lognormally distributed. Thus, there is growing evidence that the body size distributions of insects and other invertebrates in both aquatic and terrestrial environments corresponds to the lognormal curve.

Whether this correspondence to the lognormal represents a common set of biological interactions or simply reflects statistical laws of large numbers, as May (1975) has shown to be the apparent case for many species-abundance relationships, remains to be determined.

The seasonal patterns in prey size and abundance found in this study can be compared to the results of other workers who have measured prey availabilities in small temperate lakes. Table All summarizes the results of those studies which have estimated the total biomass of invertebrate prey found in littoral habitats. Results most directly comparable to this study are those of Wohlschlag (1950) who examined prey abundances in a small marl lake in Indiana. His estimates of total prey biomass are considerably less than those reported here for both the vegetation and bare marl habitats. Wohlschlag was unable to measure the abundance of gastropods and cladocera using his sampling technique, but it is doubtful that the inclusion of these prey would be sufficient to make up the difference in biomass between his results and those of this study. It is probable that his method of collection, which used a standard Eckman dredge, was much less efficient at sampling vegetation prey than was the device developed and used here. There is good agreement, however, between Wohlschlag's data and mine concerning the paucity of prey biomass in the bare marl as compared to vegetated habitats.

Estimates of total prey biomass determined by Phoenix (1976) are also far below those measured in Lawrence Lake. Phoenix used a very small plexiglass cylinder (3.8 cm I.D.) to sample individual Eleocharis stems and it is quite likely that large motile prey (e.g. Coenagrionidae, Baetis) were able to escape as this cylinder was lowered

Table All. Total Biomass (mg dry wt./m²) of Invertebrate Prey Found in the Littoral Habitats of Small Lakes by Various Researchers.

	Total Prey Biomass (mg dry wt./m ²)			
	Phoenix (1976)	Wohlschlag (1959) ¹	Gerking (1962) ²	This study
	<u>Vegetation (Eleocharis)</u>	<u>Vegetation (Scirpus)</u>	<u>Vegetation (Chara)</u>	<u>Vegetation (Scirpus)</u>
		<u>Bare marl</u>		<u>Bare marl</u>
May		359	29	1319
June	281	329	30	1473
July	85	257	181	1428
August	42	332	156	801
			1320	278
			817	486

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¹ Biomass determined as wet weight; converted to dry weight by multiplying by 0.10. Gastropods not included in samples.

² Average biomass for two years (1955, 1956) sampled from 0-2 depth stratum.

over a plant. Phoenix also calculated prey biomass using "average weights for representative sizes of organisms" and suggested for this reason that his estimates of biomass are "useful only for showing general trends".

The work of Gerking (1962) represents probably the best attempt at determining the biomass of available prey in terms of employing an efficient sampling device and a large number of samples. Clearly from Table All, there is good agreement between Gerking's estimates of prey biomass (measured in a northern Indiana lake) and those determined in this study. This agreement may be superficial, however, as Gerking studied a shallow eutrophic lake whereas Lawrence Lake is mesotrophic and has a very low primary productivity (Wetzel 1975). Differences in productivity alone would suggest that prey biomass should have been much lower in Lawrence Lake as compared to Gerking's work. Again, it would appear that the sampling program employed in this present study was simply more efficient in collecting the total distribution of available prey species. Therefore, comparisons with other studies of aquatic invertebrate communities demonstrate the success of the present study in sampling the entire prey fauna and the sound basis upon which the general patterns of habitat specific prey abundances and size distributions are constructed.

The high degree of predictability in the seasonal pattern of abundance of littoral invertebrates both within and between lakes (Ball and Hayne 1952, Gerking 1962, Keast 1977) indicates that the prey data obtained for the vegetation and sediment habitats should be generalizable to other aquatic systems. Plankton abundances and size distributions, however, are extremely variable yearly within a lake and

between lakes. Therefore, comparisons of the size and abundance of plankton in Lawrence Lake with those of other lakes would not be particularly informative. The average size distribution of the plankton has been included in this study primarily to demonstrate its truncated nature with respect to large prey sizes and to provide a complete picture of prey availabilities in all the major habitats within a single lake.

The seasonal reduction in the abundance of large prey in both the vegetation and sediment habitats and the seasonal decline in the total biomass of vegetation prey (exclusive of gastropods) are striking features of the Lawrence Lake data. Other workers have reported a reduction in the total volume or biomass of littoral prey from May to August (Ball and Hayne 1952, Anderson and Hooper 1956, Phoenix 1976); but few studies have demonstrated how these changes can shift the size distributions of available prey. In Chapter 1 I have shown that these shifts in prey size distributions can dramatically effect the energetic intake and habitat use of a generalized forager, the bluegill sunfish (Lepomis macrochirus). Given the importance of prey size to the feeding efficiency and prey selection of many groups of predators (Schoener 1969, Wilson 1975, Werner 1977) it is clear that a thorough understanding of the patterns of prey sizes in aquatic communities will be crucial in interpreting resource utilization and potential competitive interactions between co-occurring fish species. This study provides initial data on these patterns of prey availability in a natural system.

APPENDIX B

CALCULATION OF PREY ENERGETIC CONTENTS

Relationships between prey length (i) and energy content ($e(i)$) were determined for prey characteristic of each of the three habitats studied. Lengths were converted to weights by the following regressions: open water habitat, $w = 0.012 i^{2.63}$; bare sediment habitat, $w = 0.003 i^{2.35}$ ($r = .98$, $n = 64$); vegetation habitat, $w = 0.005 i^{2.16}$ ($r = .93$, $n = 179$). The open water regression is for 4 species of Daphnia (Burns 1969), the bare sediment regression is for Chironomus larvae (Mittelbach unpublished data), 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, Werner and Hall unpublished data, Mittelbach unpublished data). Prey dry weights were then converted to calories using the following caloric equivalents: 5.0 cal/mg dry wt. for Daphnia (Richman 1958, Cummins and Wuycheck 1971), 5.5 cal/mg dry wt. for Chironomidae (Elliot 1976, Cummins and Wuycheck 1971), and 5.0 cal/mg dry wt. for vegetation prey (Cummins and Wuycheck 1971).

LITERATURE CITED

LITERATURE CITED

- Aitchinson, J. and J. A. C. Brown. 1957. The lognormal distribution. Cambridge University Press, New York.
- Anderson, R. O. and F. F. Hooper. 1956. Seasonal abundance and production of littoral bottom fauna in a southern Michigan lake. Transactions, American Microscopical Society 75:259-270.
- Ball, R. C. and D. W. Hayne. 1952. Effects of the removal of the fish population on the fish-food organisms of a lake. Ecology 33: 41-48.
- Belovsky, G. E. 1978. Diet optimization in a generalist herbivore: The moose. Theoretical Population Biology 14:105-134.
- Bohl, E. 1980. Diel pattern of pelagic distribution and feeding in planktivorous fish. Oecologia 44:368-375.
- Burns, C. W. 1969. Relation between filtering rate, temperature, and body size in four species of Daphnia. Limnology and Oceanography 14:693-700.
- Charnov, E. L. 1976. Optimal foraging; attack strategy of a mantid. American Naturalist 110:141-151.
- Confer, J. L., G. L. Howick, M. H. Corzette, S. L. Kramer, S. Fitzgibbon, and R. Landesberg. 1978. Visual predation by planktivores. Oikos 31:27-37.
- Covich, A. P. 1976. Analyzing shapes of foraging areas: some ecological and economic theories. Annual Review of Ecology and Systematics 7:235-257.
- Cummins, K. W. and J. C. Wuycheck. 1971. Caloric equivalents for investigations in ecological energetics. Mitteilungen, Internationale Vereinigung für Theoretische und Angewandte Limnologie. No. 18.
- Davies, N. B. 1977. Prey selection and the search strategy of the spotted flycatcher (Muscicapa striata): A field study on optimal foraging. Animal Behavior 25:1016-1033.
- Dumont, H. J., I. Van de Velde, and S. Dumont. 1975. The dry weight estimate of biomass in a selection of cladocera, copepoda and rotifera from the plankton, periphyton and benthos of continental waters. Oecologia 19:75-97.

- Eggers, D. M. 1977. The nature of food selection by planktivorous fish. *Ecology* 58:46-59.
- 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.
- Flannagan, J. F. 1970. Efficiencies of various grabs and corers in sampling freshwater benthos. *Journal, Fisheries Research Board of Canada* 27:1691-1700.
- Galbraith, M. G. 1967. Size-selective predation on Daphnia by rainbow trout and yellow perch. *Transactions, American Fisheries Society* 96:1-10.
- Gauch, H. G. and G. B. Chase. 1975. Fitting the gaussian curve in ecological applications. *Ecology* 55:1377-1381.
- Gerking, S. D. 1957. A method of sampling the littoral macrofauna and its application. *Ecology* 38:219-225.
- Gerking, S. D. 1962. Production and food utilization in a population of bluegill sunfish. *Ecological Monographs* 32:31-78.
- Glass, N. R. 1971. Computer analysis of predation energetics in the largemouth bass. In: B. C. Patten (ed.) *Systems Analysis and Simulation in Ecology*. Academic Press, New York.
- Goss-Custard, J. D. 1977. Optimal foraging and the size selection of worms by redshank (Tringa totanus). *Animal Behavior* 25:10-29.
- Hall, D. J., W. E. Cooper, and E. E. Werner. 1970. An experimental approach to the production dynamics and structure of freshwater animal communities. *Limnology and Oceanography* 15:829-928.
- Hall, D. J. and E. E. Werner. 1977. Seasonal distribution and abundance of fishes in the littoral zone of a Michigan lake. *Transactions, American Fisheries Society* 106:545-555.
- Hall, D. J., E. E. Werner, J. F. Gilliam, G. G. Mittelbach, D. Howard, C. G. Doner, J. A. Dickerman, and A. J. Stewart. 1979. Diel foraging behavior and prey selection in the golden shiner (Notemigonus crysoleucas). *Journal, Fisheries Research Board of Canada* 36:1029-1039.
- Hemmingsen, A. M. 1934. A statistical analysis of the differences in body size of related species. *Videnskabelige Meddelelser Dansk naturhistorisk Forening Kobenhavn*. 98:125-160.

- Hester, F. J. 1968. Visual contrast thresholds of the goldfish (Carassius auratus). *Vision Research* 8:1315-1336.
- Ivlev, V. W. 1961. Experimental ecology of the feeding of fishes. Yale University Press, New Haven, Connecticut.
- Keast, A. 1965. Resource subdivision amongst cohabiting fish species in a bay, Lake Opinicon, Ontario. Great Lakes Research Division, University of Michigan. Pub. No. 13.
- Keast, A. 1977. Mechanisms expanding niche width and minimizing intra-specific competition in two centrarchid fishes. *In*: M. K. Hecht, W. C. Steere and B. Wallace (eds.) *Evolutionary Biology*. Vol. 10. Plenum Press, New York and London.
- Keast, A. 1978. Feeding interrelations between age groups of pumpkin-seed sunfish (Lepomis gibbosus) and comparisons with the bluegill sunfish (L. macrochirus). *Journal, Fisheries Research Board of Canada* 35:12-27.
- Keast, A. and L. Welsh. 1968. Daily feeding periodicities, food uptake rates, and dietary changes with hour of day in some lake fishes. *Journal, Fisheries Research Board of Canada* 25:1133-1144.
- Kerr, S. R. 1971. Prediction of fish growth efficiency in nature. *Journal, Fisheries Research Board of Canada* 28:809-814.
- Krebs, J. R. 1978. Optimal foraging: Decision rules for predators. *In*: J. R. Krebs and N. B. Davies (eds.) *Behavioural Ecology*. Sinauer Associates, Inc., Sunderland.
- Krebs, J. R., J. T. Ericksen, M. I. Weber, and E. L. Charnov. 1977. Optimal prey selection in the Great Tit (Parus major). *Animal Behavior* 25:30-38.
- Laughlin, D. R. and E. E. Werner. 1980. Resource partitioning in two coexisting sunfish (Lepomis gibbosus and Lepomis megalotis peltastes). *Journal, Fisheries Research Board of Canada* (in press).
- Lynch, M. 1977. Fitness and optimal body size in zooplankton populations. *Ecology* 58:763-774.
- Martin, N. Y. 1970. Long-term effects of diet on the biology of the lake trout and the fishery in Lake Opinicon, Ontario. *Journal, Fisheries Research Board of Canada* 27:125-146.
- May, R. M. 1975. Patterns of species abundance and diversity. *In*: M. L. Cody and J. M. Diamond (eds.) *Ecology and Evolution of Communities*. Harvard University Press, Cambridge, Massachusetts.
- Neill, W. E. 1975. Experimental studies of microcrustacean competition, community composition and efficiency of resource utilization. *Ecology* 56:809-826.

- O'Brien, W. J. 1979. The predator-prey interaction of planktivorous fish and zooplankton. *American Scientist* 67:572-581.
- Paloheimo, J. E. and L. M. Dickie. 1966. Food and growth of fishes. III. Relations among food, body size, and growth efficiency. *Journal, Fisheries Research Board of Canada* 23:1209-1248.
- Pearson, N. E. 1976. Optimal foraging: some theoretical consequences of different feeding strategies. Ph.D. Thesis, University of Washington.
- Phoenix, D. R. 1976. Temporal dynamics of a natural multipredator-multiprey system. Ph.D. Thesis. University of Pennsylvania.
- Pyke, G. H., H. R. Pulliam, and E. L. Charnov. 1977. Optimal foraging: A selective review of theory and tests. *Quarterly Review of Biology* 52:137-154.
- Rich, P. H., R. G. Wetzel, and N. V. Thuy. 1971. Distribution, production and role of aquatic macrophytes in a southern Michigan marl lake. *Freshwater Biology* 1:3-21.
- Richman, S. 1958. The transformation of energy by Daphnia pulex. *Ecological Monographs* 28:273-291.
- Rosenzweig, M. L. 1974. On the optimal above ground activity of banner-tail kangaroo rats. *Journal of Mammology* 55:193-199.
- Sarker, A. L. 1977. Feeding ecology of the bluegill, Lepomis macrochirus, in two heated reservoirs of Texas. III. Time of day and patterns of feeding. *Transactions, American Fisheries Society* 106:596-601.
- Schoener, T. W. 1969. Models of optimal size for solitary predators. *American Naturalist* 103:277-313.
- Schoener, T. W. 1974. Competition and the form of habitat shift. *Theoretical Population Biology* 6:265-307.
- Schoener, T. W. 1976. Alternatives to Lotka-Volterra competition: models of intermediate complexity. *Theoretical Population Biology* 10:309-333.
- Schoener, T. W. 1978. Effects of density-restricted food encounter on some single-level competition models. *Theoretical Population Biology* 13:365-381.
- Schoener, T. W. and D. H. Janzen. 1968. Notes on environmental determinants of tropical versus temperate insect size patterns. *American Naturalist* 102:207-224.
- Sih, A. (in prep.). Optimal behavior: Can foragers balance two conflicting demands?

- Stuntz, W. E. 1975. Habitat selection and growth of bluegills. Ph.D. Thesis. University of Wisconsin.
- Swingle, H. S. and E. V. Smith. 1940. Experiments on the stocking of fish ponds. Transactions, American Wildlife Conference 5:267-276.
- Tilman, D. 1980. Resources: A graphical-mechanistic approach to competition and predation. American Naturalist (in press).
- Vinyard, G. L. and W. J. O'Brien. 1976. Effects of light and turbidity on the reactive distance of bluegill (Lepomis macrochirus). Journal, Fisheries Research Board of Canada 33:2845-2849.
- Wankowski, J. W. J. and J. E. Thorpe. 1979. The role of food particle size in the growth of juvenile Atlantic salmon (Salmo salar L.). Journal of Fisheries Biology 14:351-370.
- Ware, D. M. 1971. Predation by rainbow-trout (Salmo gairdneri): the effect of experience. Journal, Fisheries Research Board of Canada 28:1847-1852.
- Ware, D. M. 1972. Predation by rainbow trout (Salmo gairdneri): the influence of hunger, prey densities and prey size. Journal, Fisheries Research Board of Canada 29:1193-1201.
- Ware, D. M. 1975. Growth, metabolism, and optimal swimming speed of a pelagic fish. Journal, Fisheries Research Board of Canada 32:33-41.
- Wenger, A. 1972. A review of the literature concerning largemouth bass stocking techniques. Texas Parks and Wildlife Department: Technical Series No. 13, Sheldon, Texas.
- Werner, E. E. 1974. The fish size, prey size, handling time relation in several sunfishes and some implications. Journal, Fisheries Research Board of Canada 31:1531-1536.
- 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 D. J. Hall. 1976. Niche shifts in sunfishes: experimental evidence and significance. Science 191:404-406.
- Werner, E. E. and D. J. Hall. 1977. Competition and habitat shift in two sunfishes (Centrarchidae). Ecology 58:869-876.
- Werner, E. E. and D. J. Hall. 1979. Foraging efficiency and habitat switching in competing sunfishes. Ecology 60:869-876.

- Werner, E. E., G. G. Mittelbach, and D. J. Hall. 1980. Foraging profitability and the role of experience in habitat use by the bluegill sunfish. Ecology (in press).
- Werner, E. E., D. J. Hall, D. R. Laughlin, D. J. Wagner, L. A. Wilsmann, and F. C. Funk. 1977. Habitat partitioning in a freshwater fish community. Journal, Fisheries Research Board of Canada 34:360-370.
- Werner, P. A. and H. Caswell. 1977. Population growth rates and age versus stage-distribution models for teasel (Dipsacus sylvestris Huds.) Ecology 58:1103-1111.
- Werner, R. G. 1966. Ecology and movements of bluegill sunfish fry in a small northern Indiana lake. Ph.D. Thesis. Indiana University.
- Wetzel. R. G. Limnology. W. B. Saunders Company, Philadelphia.
- Wilsmann, L. A. 1979. Resource partitioning and mechanisms of co-existence of blackchin and blacknose shiners (Notropis:Cyprinidae). Ph.D. Thesis. Michigan State University.
- Wilson, D. S. 1975. The adequacy of body size as a niche difference. American Naturalist 109:769-784.
- Wohlschlag, D. E. 1950. Vegetation and invertebrate life in a marl lake. Investigations of Indiana Lakes and Streams 3:321-372.
- Wohlschlag, D. E. and R. O. Juliano. 1959. Seasonal changes in bluegill metabolism. Limnology and Oceanography 4:195-209.

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