

Optimal foraging and growth in bluegills

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Summary. Two models of foraging behaviour (optimal prey selection and random prey selection) were used to calculate the potential net energy intake of bluegill sunfish (*Lepomis macrochirus*) in a small Michigan lake. These predictions were then compared to the actual growth exhibited by bluegills in the lake. Predictions of net energy gain derived from optimal foraging criteria were significantly correlated with the seasonal gain in mass by the fish; both energy gain and growth were positively related to bluegill length. Predictions of net energy intake based upon non-selective foraging (i.e. prey eaten as encountered) were not significantly correlated with bluegill growth. Comparing the net energy intake of bluegills feeding optimally versus non-selectively demonstrates that optimal prey selection increases average energy gain by 4 to 10 fold. This result illustrates the strong evolutionary advantage afforded to foragers that maximize net energy intake in a natural environment. Finally, the potential usefulness of optimal foraging models to the study of species and/or size-class interactions is discussed and a heuristic example pertaining to the development of “stunted” populations in fishes is provided.

Introduction

The development of optimal foraging theory by MacArthur and Pianka (1966) and Emlen (1966) offered ecologists a fresh perspective on the study of predation. Much of the appeal of this theory lies in the fact that many optimal foraging models are quite general, simple, and potentially testable. Some have argued that these models are too simple; that they are often deterministic and therefore do not recognize the stochastic nature of foraging (Oaten 1977; Green 1980, others), or that such models fail to consider evolutionary constraints on optimization (Lewontin 1979; Gould and Lewontin 1979). These are certainly valid criticisms. Continued discussion and consideration of which these factors (e.g. Maynard Smith 1978; Werner and Mittelbach 1981; Stephens and Charnov 1982) will one hopes lead to a better understanding of predator behavior. However, the strongest judgement of the value of simple optimal foraging models is how well they explain forager behavior in the field.

To date, several studies have utilized optimal foraging models to successfully predict an organisms's diet choice and/or habitat selection in nature (Goss-Custard 1977, 1981; Belovsky 1978; Zach 1979; Mittelbach 1981a;

Werner et al. 1983a). Work with the bluegill sunfish (*Lepomis macrochirus*) has shown that within a habitat, the prey sizes selected are often quite close to those predicted by optimal foraging criteria (Mittelbach 1981a; Werner et al. 1983a). Differences between observed and optimal diets for bluegills in these studies were estimated to reduce net energy intakes by <20% of maximum. The habitat use of these fish has also been shown to match predictions based upon maximizing energy gain, but only when bluegills are large enough to be beyond the capture abilities of their predators (Mittelbach 1981a), or when predators are experimentally removed (Werner et al. 1983a). If predatory fish are present, small bluegills shift to using more protective habitats (i.e. vegetation), generally at the cost of reduced foraging gain (Werner et al. 1983b). Thus, optimal foraging models have proven useful in predicting many aspects of bluegill prey size selection and habitat use in the field, and this approach has also identified the importance of size-specific predation in mediating habitat use.

In this paper I extend these field studies of optimal foraging in bluegills by asking the following questions: 1) Are bluegill growth rates in a natural lake positively correlated with predictions of net energy intakes derived from an optimal diet model?, 2) How well do predictions of net energy intakes based upon random prey selection correlate with bluegill growth?, and 3) What is the estimated difference in seasonal energetic gain for bluegills in nature if they select prey optimally as compared to randomly?

Methods

Following the standard form developed by Schoener (1971), Pulliam (1974), Werner and Hall (1974), Charnov (1976), Pearson (1976), and others, I formulated a foraging model to predict the diets and net energy intakes of bluegill size classes in the field (Mittelbach 1981a). In this model the net rate of energy gain from habitat j (E_n/T) is described by

$$E_n/T = \frac{\sum_{i=1}^n \lambda_{ij} E_{ij} - C_s}{1 + \sum_{i=1}^n \lambda_{ij} H_{ij}} \quad (1)$$

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

Table 1. Prey encounter rate (λ_{ij}) and handling time (H_{ij}) relations for bluegills feeding in each of three laboratory habitats. The form of the regression equations describing encounter rates is $\log \lambda_{ij} = a + b_1 \log D + b_2 \log 1 + b_3 \log L$ where D = prey density, 1 = prey length, and L = fish length. Parameters are presented ± 1 SE. Prey handling times were constant below a critical ratio of prey length/fish length ($1/L_{crit}$) and then increased exponentially. Minimum handling times are $\bar{x} \pm 1$ SE. Data are from Mittelbach (1981a)

Habitat	Encounter rates					Overall significance	n
	a	b_1	b_2	b_3	R^2		
Open water	-3.374 ± 0.50	0.667 ± 0.06	0.921 ± 0.28	2.006 ± 0.29	0.79	$p < 0.001$	68
Sediments	-5.114 ± 0.30	0.719 ± 0.05	0.971 ± 0.20	0.262 ± 0.10	0.84	$p < 0.001$	58
Vegetation	-5.905 ± 0.41	0.779 ± 0.07	1.045 ± 0.22	0.694 ± 0.13	0.58	$p < 0.001$	110

	Handling times		
	Handling time (H) ($1/L \geq 1/L_{crit}$)	Minimum handling time (H) ($1/L < 1/L_{crit}$)	$1/L_{crit}$
Open water	$H = 0.536 e^{18.488 1/L}$ $r = 0.92; n = 18$	$H = 1.02 \pm 0.02$ $n = 24$	0.034
Sediments	$H = 2.364 e^{6.492 1/L}$ $r = 0.96; n = 62$	$H = 9.63 \pm 0.21$ $n = 20$	0.220
Vegetation	$H = 0.639 e^{9.966 1/L}$ $r = 0.96; n = 122$	$H = 1.02 \pm 0.02$ $n = 30$	0.045

where λ_{ij} = number of prey size i encountered per second search in habitat type j , A = assimilable fraction of the energetic content of prey, e_{ij} = energy content of prey size i found in habitat type j (J), H_{ij} = handling time of prey size i in habitat type j (s), C_h = energetic cost per unit handling time (J/s), and C_s = energetic cost per unit search time (J/s). A brief description of the methods used in parameterizing the foraging model for the bluegill is presented below. A more detailed account can be found in Mittelbach (1981a).

Prey handling times (H_{ij}) and encounter rates (λ_{ij}) were quantified in laboratory experiments using various combinations of fish size, prey size and prey density. The experiments were designed to simulate the physical structure and associated prey types found in each of three distinct habitats: the open water, bare sediments and vegetation. Prey types used in the experiments commonly occur in each habitat in nature and represent the general degree of crypsis and mobility characteristic of prey found there.

The basic format for each experiment involved dividing a 214-L aquarium into two unequal sized sections (26L and 188L) and then placing a known prey distribution in the larger section. In each experiment a single prey size and type was used. To estimate prey encounter rates and handling times in the bare sediment habitat, a layer of marl sediments (4–5 cm deep) was placed in the aquarium. Larvae of the midge, *Chironomus plumosus*, were used as prey and two sizes (19.5 ± 0.5 mm and 11.1 ± 0.3 mm body length) at three densities (50, 300, and $1,000/m^2$) were exposed to six bluegills ranging from 21–109 mm standard length (SL). Midges were introduced during the late afternoon of the day prior to an experiment as this permitted the larvae to burrow into the sediments. For each experiment a fish which had been starved for 24 h was placed into the smaller section of the aquarium and allowed to acclimate for 30–60 min. The experiment was then initiated by removing the glass partition between the aquarium sections and allowing the fish to feed. Data recorded were

handling time for each prey captured and the time between prey captures.

Experiments simulating the vegetation and open-water habitats were performed in a similar manner. In the vegetation experiments, live *Elodea* plants ($100/m^2$) were used and damselfly naiads (coenagrionidae) served as prey. Fish ranged from 21–115 mm SL (9 individuals) and prey sizes and densities were as follows: 9.51 ± 0.27 mm body length at 192, 385, and $1,538$ individuals/ m^3 ; 13.15 ± 0.33 mm body length at 192 individuals/ m^3 ; and 22.30 ± 0.28 mm body length at 38 and 192 individuals/ m^3 . For the open water, the cladoceran, *Daphnia pulex*, was used as prey in aquaria containing no environmental structure. Two prey sizes (2.20 ± 0.04 mm and 1.14 ± 0.02 mm body length) at five densities (0.1, 0.5, 2.5, 5, and 15/L) were exposed to ten bluegills ranging from 33–109 mm SL. Handling times for *Daphnia* were too short to be measured directly as the time from prey capture until the reinitiation of search. Therefore, handling times for these prey 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 (Werner 1977).

Each experimental combination of prey size, fish size, and prey density was replicated from three to six times in each habitat type. In total, over 500 feeding experiments were conducted. Multiple regression equations were fitted to the data for each habitat in order to predict encounter rates with prey as a function of prey length and density and length of fish. Handling times were a function of relative size of predator and prey and were fitted to exponential equations (Mittelbach 1981a). The statistical relationships used to predict encounter rates and handling times are given in Table 1.

The estimated energetic costs of searching for and handling prey (C_s and C_h) were calculated as functions of fish size, water temperature, and swimming speed using the data

of Wohlschlag and Juliano (1959). Swimming speeds used in calculating energetic costs were those exhibited by bluegills in the laboratory feeding experiments. The energy content of a given-sized prey from each habitat (e_{ij}) was determined by converting prey lengths to dry masses and then multiplying by the appropriate energy equivalent (Cummins and Wuycheck 1971; Mittelbach 1981a). The assimilable fraction of energy ingested (A) appears to be independent of fish size (Elliot 1976) and a value of 0.7 is appropriate for most invertebrate prey (see Ware 1975 for a general discussion, also Elliot 1976).

Equation 1 can be used to predict the average net energetic gain (E_n/T) for bluegills feeding either optimally or non-selectively. An optimal forager takes only that subset of available prey sizes which yields the highest overall energetic return. Operationally, the optimal diet and associated energy gain is determined by ranking available prey sizes from highest to lowest E_{ij}/H_{ij} and then adding prey sizes to the diet in rank order until the ratio of E_n/T is maximized. Equation 1 can also be used to calculate the energetic return of bluegills feeding non-selectively. This is done by simply taking the observed prey size distribution in a habitat and calculating the net energy gain which would result if the bluegill ate every prey it encountered. In this case, all prey sizes in the environment are eaten and the proportional representation of a given prey size in the diet is based only on the rate at which it is encountered by the predator.

To predict the average net energy gain of bluegills foraging optimally or non-selectively in a natural lake, I determined the distribution of prey sizes available in the open water, bare sediments and vegetation of Lawrence Lake, Michigan from May-August 1979. Lawrence Lake is a small, mesotrophic lake, 4.9 ha in surface area, 12.6 m maximum depth, and is located 2.1 km east of Hickory Corners in Barry County. Below I present the essentials of the prey sampling procedure; a complete description can be found in Mittelbach (1981a, b).

Vegetation-dwelling invertebrates were sampled at 3–4 wk intervals by a diver using a modified Gerking sampler (Mittelbach 1981b). Sampling was stratified with five samples taken randomly along the bench (0.5–1.5 m depth) and five samples taken randomly along the slope (2–4 m depth) on each date. Samples were carefully washed into a series of sieves (2.83-, 0.71-, 0.18 mm mesh) and the large invertebrates were separated by hand and preserved in 10% formalin. Smaller prey were separated in 20% $MgSO_4$ solution. Sediment-dwelling prey were sampled by a diver using a 6.5-cm diameter plastic corer. Five cores were taken at random from the bare sediments on the same dates when the vegetation was sampled. After collection, the benthic samples were washed into sieves and sorted in the same manner as the vegetation samples.

Open-water prey were sampled at 2–3 wk intervals using a 30-cm diameter number 10 plankton net. Two vertical tows were taken from a depth of 4 m at a location in the limnetic zone ~60 m from shore. This depth was chosen as it defines the usual depth of the thermocline in Lawrence Lake during the summer (Wetzel 1975), and previous work indicates that bluegills feed primarily above the thermocline in these small lakes (Hall et al. 1976; Mittelbach 1981a).

All resource sampling was conducted during the early morning because the bluegill, a diurnal feeder, has been shown to have a feeding peak at this time (Sarker 1977; Wilsman 1979). On average, plankton sampling began

15 min before sunrise and was completed by 10 min after sunrise. Vegetation and sediment sampling began on average 30 min after sunrise and was completed by 70 min after sunrise. Prey samples were enumerated under a dissecting microscope and organisms classified, generally to genus or family level. Fifteen to 50 randomly chosen individuals in each prey category were then measured for total body length in each sample. Prey size-frequency distributions were constructed 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 resulting prey size-frequency distributions were distinctly lognormal and are presented, along with a list of the major taxa present, in Mittelbach (1981b).

The potential net energetic gain (E_n/T) for bluegills feeding in each habitat on each sampling date was calculated by Eq. (1), using the prey-size distribution found in the habitat and the ambient water temperature. Calculations of net energy gain for fish feeding optimally or non-selectively were made for bluegills ranging in size from 15–125 mm SL. The average net energy gain for an optimal forager across the summer was determined by first calculating the fish's optimal diet and optimal habitat use on each of 7 available sampling dates. Then, because sampling dates were not evenly spaced over the summer, the values of net energetic gain for each date were interpolated to obtain an estimated relationship between net energetic gain and time. This relationship was then integrated to calculate the average energetic return for the entire summer. Unlike the optimal foraging hypothesis, no *a priori* predictions of seasonal habitat use can be made for bluegills feeding on prey non-selectively. Therefore, to compare predictions of seasonal net energetic intakes of random foragers to optimal foragers, I assumed two different patterns of habitat use for the non-selective foragers: 1) the same habitat use as predicted by the optimal foraging model, and 2) a pattern of habitat use identical to that exhibited by bluegill size classes in Lawrence Lake (see Mittelbach 1981a).

To determine how well predictions of net energetic intakes for bluegills feeding optimally or non-selectively were correlated with actual growth of the fish in Lawrence Lake, bluegills were collected by seining and angling during the summer of 1981. The growth in body mass of these fish during 1979 was determined by backcalculation from scale annuli measures using the Fraser-Lee method (Rigier 1962; Tesch 1968). Scales from 126 fish (year 2+ and older) were removed just posterior to the tip of a depressed pectoral fin and impressions made on cellulose acetate strips. Growth in length from annulus (year mark) formation in 1979 to annulus formation in 1980 was calculated for each fish, and backcalculated lengths were converted to wet masses using a length-mass (L-M) regression for Lawrence Lake bluegills: $M = 0.000021 L^{3.0822}$, $r^2 = 0.99$, $n = 58$. The gain in wet mass during 1979 was determined for 6 bluegill year classes (ages 2+ through 7+ in 1981).

Annulus formation for bluegills in southern Michigan occurs in early May (Carlander 1969), thus backcalculated growth measures represent the change in body mass from May 1979 to May 1980. Predictions of net foraging return, E_n/T , are based on prey samples collected from May-August 1979. Although predicted energy gains are available only for these four months, Gerking (1966) has shown that >80% of the yearly growth of the bluegill is completed between mid-April and the end of August in northern In-

diana lakes. Thus, the May-August measures of size-specific energetic gains encompass most of the bluegills' growing season in Lawrence Lake.

Results and discussion

The average energetic gain predicted by the optimal foraging model, and the actual growth in mass of the bluegills in Lawrence Lake, both show a positive, non-linear relationship with fish size (Fig. 1). Further, the regression between these factors is highly significant (Fig. 2), indicating that predictions of net energy intake based upon optimal foraging criteria provide a reasonable estimate of the actual energy converted to growth by the fish. Predictions of net foraging gain for bluegills feeding non-selectively (i.e. consuming prey as encountered) were also compared to bluegill growth. Assuming that random foragers use habitats in the same manner as optimal foragers, the estimated net energetic returns for randomly foraging bluegills are not significantly correlated with bluegill growth ($r^2=0.64$, $P>0.05$, $n=6$). If habitat use conforms to that actually exhibited by bluegill size classes in Lawrence Lake, the regression of growth on predicted foraging intake is also not significant ($r^2=0.41$, $P>0.05$, $n=6$). Thus, calculations of net energetic return based upon a prey encounter model are not significantly correlated with growth rates, whereas predictions of energy gain based on optimal diet choice are.

Comparing the net energy intakes of bluegills feeding optimally versus non-selectively shows the substantial advantage gained from optimal foraging (Table 2). Averaged across the season, a 125 mm bluegill increases its net foraging gain 10-fold by selecting prey optimally compared to prey consumption by random encounter. The seasonal habitat use of both forager types was assumed to be the same as that actually exhibited by bluegill size classes in Lawrence Lake. Smaller bluegills also show a substantial difference between optimal and random foraging gain (Table 2), although the magnitude of this difference is less. The fact that smaller fish pay less of a "penalty" for suboptimal foraging may partially explain why the diets of large bluegills generally show a better fit to predictions of optimal foraging theory than do those of small fish (Mittelbach 1981a; Werner et al. 1983a). However, even slight differences in growth rates between young fish can have a significant impact of their relative vulnerability to predators or probability of survival (Ricker 1979; Lasker 1981; Werner et al. 1983b). Thus, differences in energy intake between selective and non-selective feeding shown in Table 2 are likely to have a very pronounced effect on fitness at all bluegill sizes.

Both the predictions of net energy gain from the optimal foraging model, and the growth increment exhibited by the Lawrence Lake bluegills, increase with fish size (Fig. 1). However, the energy intake curve increases more rapidly with bluegill size, and in general the predicted E_n/T is too large relative to growth for small fish. This error is probably due to overestimating the potential energy gain for small bluegills in the field. Calculations of E_n/T from the optimal diet model assume that each size class of bluegill feeds in the habitat which provides the highest foraging gain. In Lawrence Lake in 1979 the optimal habitat use for all size classes of bluegills was to feed in the vegetation from May through mid-June, and then to shift to feeding on open-

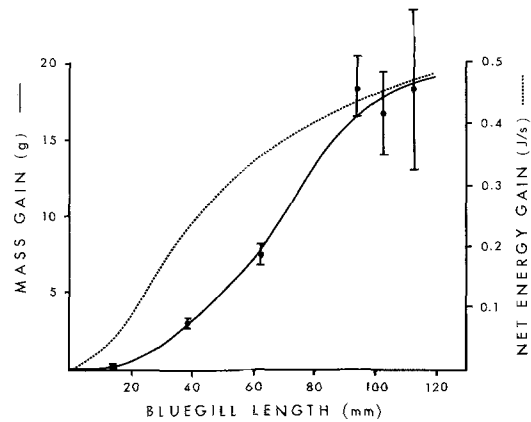


Fig. 1. Backcalculated gain in g wet mass (solid line) and predicted net energy gain in J/s (dashed line) as functions of bluegill standard length (mm). Wet mass is the mean \pm 1SE of 5 to 38 fish/year class; growth curve drawn by eye. The wet mass gain of each bluegill year class is plotted against the midpoint of the interval of mean initial and final lengths of the year class in 1979

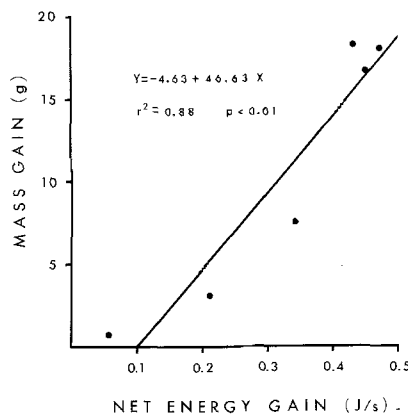


Fig. 2. Linear regression of predicted net energy gain in J/s and backcalculated gain in wet mass (g) for Lawrence Lake bluegills

Table 2. Predicted average net energy gain (J/s) for bluegills of three sizes feeding optimally or non-selectively (prey eaten as encountered). Energy intakes calculated using Eq. (1) and the distributions of prey sizes found in Lawrence Lake

Bluegill standard length (mm)	Average Net Energy Gain (J/s)	
	Optimal diet	Non-selective diet
30	0.103	0.024
75	0.214	0.049
125	0.491	0.049

water plankton from mid-June through August (see Fig. 7 in Mittelbach 1981a). Bluegills > 100 mm SL followed this pattern of habitat use quite closely, however, smaller bluegills foraged only in or near the vegetation over the entire summer. I hypothesized that the restricted habitat use of these small fish was due to a higher predation risk from piscivorous fish in the open water (Mittelbach 1981a). Results from a recent pond experiment support this hypothesis (Werner et al. 1983a, b). In the absence of predators small bluegills fed in the open water in the same manner as large bluegills, but in the presence of predators these small fish shifted to an increased use of the protective vegetation. A detailed study of the diets of bluegill size classes in Law-

rence Lake has shown that bluegills begin to make extensive use of the plankton only after reaching approximately 75 mm SL (Mittelbach 1984).

We can take into account the observed effect of predators on bluegill habitat use and calculate the optimal diets and associated energetic returns assuming bluegills ≤ 75 mm feed only in the vegetation habitat, while bluegills > 75 mm utilize both the vegetation and open water depending on relative energy gain. When this is done, the regression between net energetic intake (E_n/T) and growth is improved ($r^2 = 0.98$, $Y = -1.59 + 42.98 X$) compared to the relationship which assumes that all bluegill size classes select habitats based only on maximizing energy gain (Fig. 2). Thus, it is likely that a foraging model which incorporated both size-specific foraging efficiency and predation risk would provide more realistic estimates of net energy intakes for the bluegill. The theoretical development of such models has proven difficult, but considerable recent progress has been made (Gilliam 1982).

Although the optimal foraging model presented here erred in not including the effect of predation on habitat choice, it was still reasonably successful in translating measures of prey abundance (size and number) into estimates of net foraging gain, and these estimates were in turn positively correlated with the actual growth of bluegills in the field. This suggests that optimal foraging models may prove useful in examining such questions as: 1) how do changes in available prey size and/or number affect individual growth rates and population size structure, and 2) what are the relative energetic gains of competing species from a given prey resource? As an example, consider the situation where a population of bluegills is stocked in the absence of predators and competitors. It has commonly been observed that bluegills and many other fishes, when stocked in monoculture, invariably develop "stunted" populations dominated by small, slow growing individuals (see Wenger 1972 for a review). We can use a continuous version of Eq. (1) to examine how shifts in the available prey-size distribution may result in such "stunted" populations.

We would expect that as the number of bluegills in the population increases, and as individuals grow in size, that the total demand for prey resources will increase. In fish, such an increase in predation pressure very commonly leads to a shift in the prey-size distribution towards smaller prey due to size-selective predation (see Werner and Hall 1979; Werner et al. 1981; and Werner et al. 1983a for examples with the bluegill). Using lognormal distributions of prey sizes representative of those found in the vegetation of Lawrence Lake (Mittelbach 1981 b), such shifts in prey size can be simulated by reducing the variance of the prey distribution while holding the mean and density at the mean constant. (The number of very small prey, below the mean size, will also be reduced but this has little effect on the optimal diet or predicted energy gain). Figure 3 shows that as the abundance of large prey in the environment declines, the bluegill size which achieves maximal net energetic return also decreases. Furthermore, the net energetic intakes of large fish are reduced disproportionately relative to small fish, so that as large prey become increasingly rare bluegills reach a zero growth state ($E_n(T=0)$) at smaller and smaller sizes. Ultimately, as prey abundances decline the fish population becomes dominated by very small individuals, i.e. a "stunted" population. While Fig. 3 is largely for heuristic purposes, the prey distributions used to generate curves A-

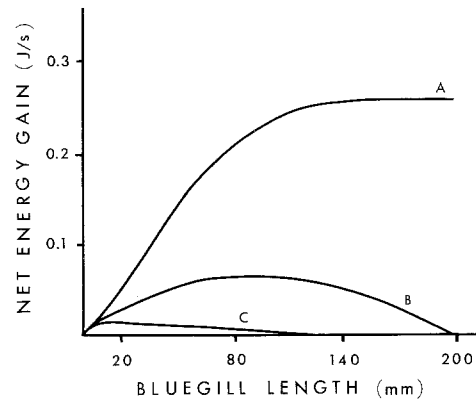


Fig. 3. Predicted net energy gain (J/s) for bluegills feeding on three different distributions of prey size in the vegetation habitat. Curves A through C represent a decreasing availability of large prey. Prey distributions are normal curves of \ln prey length (mm) with mean = 0.60, density at the mean = 20,000 individuals/m³, and variances of 0.55 (curve A), 0.45 (curve B), and 0.35 (curve C)

C are reasonable; in fact, the prey distribution underlying curve C closely approximates the distribution of prey sizes found in Lawrence Lake in late August (when resources reach their lowest level of the summer (Mittelbach 1981 a)).

The above analysis indicates that the phenomenon of stunting in many fish populations may be interpreted from a knowledge of size-specific foraging efficiencies and available prey sizes. In general, the pattern shown in Fig. 3 results from the fact that large bluegills can handle large prey in less time than small bluegills, and that searching rates also increase with fish size (Table 1 and Mittelbach 1981 a). However, when large prey become rare, the handling advantage of bigger fish is diminished and eventually becomes outweighed by increased metabolic costs. Kerr (1971), using an energetics model for brook trout (*Salvelinus fontinalis*), reached a similar conclusion: trout must have access to increasingly larger prey in order to achieve large body size. (Kerr's model, however, does not include the effects of fish size on prey handling time.) These theoretical results are consistent with empirical observations that fish in "stunted" populations generally have very small prey in their stomachs (Eschmeyer 1937) and that "stunted" fish, when transferred to richer environments, show growth rates equal to "normal" fish (Alm 1946; Burnet 1970).

One of the strengths of optimal foraging theory is that it directly links resource abundances to the predicted diets, habitat use, and energetic gains of consumers. The field study with bluegills described in this paper shows that these predictions of net energy gain can also be related to the actual growth of bluegills in the field. The demonstration of a connection between predicted and realized energy gain is important if ecologists are to have confidence in using optimal foraging models to examine questions of competition and community structure (c.f. Werner 1977). The ability of optimal foraging models to predict the resource utilization and relative energetic gains of competing species represents a potential foundation upon which more mechanistic theories of community organization may be built (Schoener 1977; Pyke et al. 1977; Werner and Mittelbach 1981). The comparisons of net energy intakes of optimal versus random foragers in Lawrence Lake also provide one of the first crude estimates of the potential evolutionary advantage afforded to optimal foragers in a natural environment.

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References

- Alm G (1946) Reasons for the occurrence of stunted populations with special regard to the perch. Reports Swedish State Inst Fresh-Water Fish Res, Drottningholm 25:146 pp
- Belovsky GE (1978) Diet optimization in a generalist herbivore: the moose. *Theor Pop Biol* 14:105–134
- Burnet AMR (1970) Seasonal growth of brown trout in two New Zealand streams. *New Zeal J Mar Freshwater Res* 4:55–62
- Carlander KD (1969) Handbook of freshwater fishery biology. Iowa State Univ Press, Ames, IA
- Charnov EL (1976) Optimal foraging: the marginal value theorem. *Theor. Pop Biol* 9:129–136
- Cummins KW, Wuycheck JC (1971) Caloric equivalent for investigations in ecological energetics. *Mitt Int Ver Limnol* 18:1–158
- Elliot JM (1976) The energetics of feeding, metabolism and growth of brown trout (*Salmo trutta* L.) in relation to body weight, water temperature and ration size. *J Anim Ecol* 45:923–948
- Emlen JM (1966) The role of time and energy in food preference. *Amer Natur* 100:611–617
- Eschmeyer RW (1937) Some characteristics of a population of stunted perch. *Papers Michigan Acad Sci Arts Letters* 22:613–628
- Gerking SD (1966) Annual growth cycle, growth potential, and growth compensation in the bluegill sunfish in northern Indiana lakes. *J Fish Res Board Can* 23:1923–1956
- Gilliam JF (1982) Habitat use and competitive bottlenecks in size-structured fish populations. PhD dissertation, Michigan State Univ
- Goss-Custard JD (1977) Optimal foraging and the size selection of worms by redshank (*Tringa totanus*). *Anim Behav* 25:10–29
- Goss-Custard JD (1981) Feeding behavior of redshank, *Tringa totanus*, and optimal foraging theory. In: Kamil AC, Sargent JM (eds), *Foraging Behavior*. Garland STPM Press, New York, NY, pp 115–133
- Gould SJ, Lewontin RC (1979) The spandrels of San Marco and the Panglossian paradigm: a critique of the adaptationist programme. *Proc R Soc London B* 205:581–598
- Green RF (1980) Bayesian birds: a simple example of Oaten's stochastic model of optimal foraging. *Theor Pop Bio* 18:244–256
- Hall DJ, Werner EE, Gilliam JF, Mittelbach GG, Howard D, Doner CG, Dickerman JA, Stewart AJ (1979) Diel foraging behavior and prey selection in the golden shiner (*Notemigonus crysoleucas*). *J Fish Res Board Can* 36:1029–1039
- Kerr SR (1971) Prediction of fish growth efficiency in nature. *J Fish Res Board Can* 28:809–814
- Lasker R (1981) Marine fish larvae: morphology, ecology and relation to fisheries. Washington Sea Grant Program, Seattle
- Lewontin RC (1979) Sociobiology as an adaptationist program. *Behav Sci* 24:5–14
- MacArthur RH, Pianka ER (1966) On optimal use of a patchy environment. *Amer Natur* 100:603–609
- Maynard Smith J (1978) Optimization theory in evolution. *Ann Rev Ecol Syst* 9:31–56
- Mittelbach GG (1981a) Foraging efficiency and body size: a study of optimal diet and habitat use by bluegills. *Ecology* 62:1370–1386
- Mittelbach GG (1981b) Patterns of invertebrate size and abundance in aquatic habitats. *Can J Fish Aquat Sci* 38:896–904
- Mittelbach GG (1984) Predation and resource partitioning in two sunfishes (Centrarchidae). *Ecology* (in press)
- Oaten A (1977) Optimal foraging in patches: a case for stochasticity. *Theor Pop Biol* 12:263–285
- Pearson NE (1976) Optimal foraging: Some theoretical consequences of different feeding strategies. PhD dissertation. Univ of Washington
- Pulliam HR (1974) On the theory of optimal diets. *Amer Natur* 108:59–74
- Pyke GH, Pulliam HR, Charnov EL (1977) Optimal foraging: a selective review of theory and tests. *Q Rev Biol* 52:137–154
- Ricker WE (1979) Growth rates and models. In: Hoar WS, Randall DJ, Brett JR (eds), *Fish physiology*. Vol VIII. Bioenergetics and growth. Academic Press, New York, NY, pp 677–743
- Regier HA (1962) Validation of the scale method for estimating age and growth of bluegills. *Trans Am Fish Soc* 91:362–374
- Sarker AL (1977) Feeding ecology of the bluegill, *Lepomis macrochirus*, in two heated reservoirs of Texas. III Time of day and patterns of feeding. *Trans Am Fish Soc* 106:596–601
- Schoener TW (1971) Theory of feeding strategies. *Ann Rev Ecol Syst* 2:369–404
- Schoener TW (1977) Competition and the niche. In: Gans C, Tinkle DW (eds), *Biology of the Reptilia*. Vol 7. Academic Press, New York, NY, pp 35–136
- Stephens DW, Charnov EL (1982) Optimal foraging: some simple stochastic models. *Behav Ecol Sociobiol* 10:251–263
- Tesch FW (1968) Age and growth. In: Ricker WE (ed), *Methods for assessment of fish production in fresh waters*. Blackwell Scientific Publications, Oxford, pp 93–123
- Ware DM (1975) Growth, metabolism, and optimal swimming speed of a pelagic fish. *J Fish Res Board Can* 32:33–41
- Wenger A (1972) A review of the literature concerning largemouth bass stocking techniques. Tech Ser 13, Texas Parks and Wildlife Dept, Sheldon, Texas
- Werner EE (1977) Species packing and niche complementarity in three sunfishes. *Amer Natur* 111:553–578
- Werner EE, Hall DJ (1974) Optimal foraging and the size selection of prey by bluegill sunfish (*Lepomis macrochirus*). *Ecology* 55:1042–1052
- Werner EE, Hall DJ (1979) Foraging efficiency and habitat switching in competing sunfishes. *Ecology* 60:256–264
- Werner EE, Mittelbach GG (1981) Optimal foraging: field tests of diet choice and habitat switching. *Amer Zool* 21:813–829
- Werner EE, Mittelbach GG, Hall DJ (1981) The role of foraging profitability and experience in habitat use by the bluegill sunfish. *Ecology* 62:116–125
- Werner EE, Mittelbach GG, Hall DJ, Gilliam JF (1983a) Experimental tests of optimal habitat use in fish: the role of relative habitat profitability. *Ecology*, in press
- Werner EE, Gilliam JF, Hall DJ, Mittelbach GG (1983b) An experimental test of the effects of predation risk on habitat use in fish. *Ecology*, in press
- Wilsmann LA (1979) Resource partitioning and mechanisms of coexistence of blackchin and blacknose shiners (*Notropis*: Cyprinidae). PhD dissertation, Michigan State Univ
- Wohlschlag DE, Juliano RO (1959) Seasonal changes in bluegill metabolism. *Limnol Oceanogr* 4:195–209
- Zach R (1979) Shell dropping: Decision making and optimal foraging in northwestern crows. *Behavior* 58:106–117