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Using Foraging Theory to Study Trophic Interactions

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Abstract. Foraging theory provides a potentially powerful tool for understanding the interaction between a predator population and its prey assemblage. We illustrate how foraging models developed for the bluegill (*Lepomis macrochirus* Rafinesque) and pumpkinseed sunfish (*L. gibbosus* [Linnaeus]) can be used to translate measures of prey size and abundance into estimates of energy gain to the predators. Predicted energy gains from standard optimal diet models correlate significantly with observed stomach fullnesses in the pumpkinseed and individual growth rates in the bluegill. Although mechanistic foraging models hold great promise for studying species interactions, one of their drawbacks is the time and effort needed to parameterize a model for each species of interest. Therefore, we also address the question of how well simple measures of prey abundance (e.g., total prey biomass) might work to predict relative feeding rates for fish.

We show empirically that total prey biomass poorly facilitates prediction of feeding rates or individual growth rates in a species exhibiting strong, active prey selection (e.g., bluegill feeding on zooplankton). Total prey biomass works better in facilitating prediction of feeding rates and growth rates for foragers that consume prey as encountered. However, on theoretical grounds, we show that total prey biomass should only yield good predictions of energy gains under limited conditions (e.g., prey distribution invariant among environments or encounter rates constant among prey types). These conditions are unlikely. Prey encounter rates and handling times normally scale with prey mass; therefore, feeding rates will depend on how total prey biomass is distributed among prey size classes. Further, because fish size affects components of the predator-prey interaction, biomass and other simple indices of resource availability will only be applicable to single size classes of predators. Thus, although simple models of prey availability might work under some conditions, foraging models provide the most reliable and general tools for translating prey density and size structure into predicted feeding and growth rates of predators.

Introduction

When MacArthur and Pianka (1966) first introduced (along with Emlen 1966) the ideas that have become known as optimal foraging theory, they recognized that this new theory could potentially play two major roles in ecology. First, it could lead to a better understanding of the factors governing diet choice and habitat selection in animals. Second, it could provide a tool to link measures of prey density

in the environment to the expected diets and energetic intakes of consumers feeding on those prey. Because prey assemblages consist of a variety of species, each with different behavior, morphology, and size structure, the link between prey composition and predator feeding rate is not simple. Clearly, the ability to predict the diets, habitat use, or energy gains of consumers from measures of prey abundance represents a foundation upon which a more mechanistic understanding of species interactions can be built. In fact, MacArthur and Pianka (1966) conclude their paper with a discussion of the influence of patch use on the limiting similarity of coexisting species.

In the 25 years that followed the introduction of optimal foraging theory, the development and testing of foraging models has been strongly emphasized, and much has been learned about the factors determining diet and habitat choice in animals. However, the other promise of optimal foraging theory, to potentially provide a link between prey abundance and consumer resource use and energy gain, remains largely unfulfilled. One reason for this shortcoming is that natural prey assemblages are diverse and prey species not only differ in density and size structure, but also in traits that determine their vulnerability and utility to predators. In this paper we investigate how well optimal foraging models can predict fish feeding rates and growth rates in the field. We show that for two species of sunfish, the pumpkinseed (*Lepomis gibbosus* [Linnaeus]) and the bluegill (*L. macrochirus* Rafinesque), a standard optimal diet model does very well in predicting feeding rates (pumpkinseed) and growth rates (bluegill). We then ask whether "shortcuts" to the development of foraging models might be possible in some situations; e.g., when might it be possible to use a simple measure of prey abundance in the environment (e.g., total prey biomass) to predict a fish's potential net energy gain? We show that, in general, there is no reliable way to circumvent the use of foraging models when translating prey abundances into expected feeding rates.

A General Foraging Model

The first step in developing a foraging model for any predator species is to determine which items are potential prey. This step basically relies on our skills as naturalists. We determine what types of prey a predator can potentially eat based on its morphology, body size, habitat distribution, etc. Examining a predator's diet is also instructive, but the absence of a prey type does not preclude its occurrence under different conditions. Once the domain of the prey assemblage has been defined, a predator's feeding rate is determined by the product of three important functions: the encounter rate between predator and prey, the probability that a predator attacks an encountered prey, and the probability that an attack is successful (O'Brien 1979; Greene 1983; Osenberg and Mittelbach 1989). For fish these functions are strongly related to the body size of predator and prey (e.g., Mittelbach 1981; Wright and O'Brien 1984; Bence and Murdoch 1986; Persson 1987; Osenberg and Mittelbach 1989). Thus, a model of prey selection and feeding rate for a given size of predator requires knowledge of how encounter rates, handling times, attack probabilities, and capture successes vary with size for each prey type.

We formulated foraging models for the bluegill and pumpkinseed sunfish that are extensions of the standard optimal diet model developed by Charnov (1976) and others (see Mittelbach 1981; Osenberg and Mittelbach 1989). The models are of the form:

$$E / T = \frac{\sum_{i=1}^n a_i N_i E_i P_i(a) P_i(s) - C_s}{1 + \sum_{i=1}^n a_i N_i P_i(a) P_i(s) H_i} \quad (1)$$

- where E_i = $Amb_i - C_h H_i$,
 A = the assimilable fraction of the energy content of prey size i ,
 b_i = mass of prey size i (mg),
 m = a conversion constant for prey mass to energy ($J \text{ mg}^{-1}$),
 C_h = energy costs of handling prey (in $J \text{ s}^{-1}$),
 H_i = handling time of prey size i (in s per successful attack),
 C_s = energy costs of searching (in $J \text{ s}^{-1}$),
 a_i = the average per capita encounter rate with prey of size i (in encounters per prey per predator per sec of search),
 N_i = is the average density of prey size i (i.e., aN is the total average rate of prey encounter),
 $P_i(a)$ = probability that an encountered prey is attacked, and
 $P_i(s)$ = the probability that an attacked prey is successfully consumed.

Foraging rate is equal to the total amount of assimilable food that can be collected by a fish during 1 sec of search time, minus the energy cost of foraging, divided by the total foraging time that results from 1 sec of search time.

If we assume that all encountered prey are successfully attacked ($P_i(s) = P_i(a) = 1$ for all i), Eq. 1 reduces to Holling's (1959) disk equation for multiple prey types (with the inclusion of energetic costs). However, if predators exhibit active prey choice (i.e., all P_i 's $\neq 1$), then calculating a predator's expected feeding rate requires some a priori way to determine which prey types are attacked. Optimal foraging theory provides a useful and straightforward criteria for predicting prey choice; we infer from it that a predator adjusts its attack probabilities (P_i 's) to maximize its total energy gain (E/T) (see Charnov 1976, others). We used this criteria for prey choice to predict sunfish diets and feeding rates using Eq. 1. In practice, the optimal solution to Eq. 1 is found by ranking prey by increasing profitabilities (i.e., the ratio of net energy gain per handling time) and determining the diet breadth that maximizes E/T (Charnov 1976).

Predicting Sunfish Feeding Rates

We used the foraging model described previously to predict feeding rates for bluegill and pumpkinseed sunfish in a series of small lakes near the Kellogg Biological Station in southern Michigan. In these lakes, adult bluegill feed predominantly on zooplankton (*Daphnia* sp.) and adult pumpkinseed feed predominantly on snails (see Osenberg et al. 1994; also Mittelbach 1981, 1988; Werner and Hall 1988; Osenberg and Mittelbach 1989). Prey encounter rates (a_i), handling times (H_i),

and probabilities of successful attack ($P_i(s)$) were generally determined as functions of fish size and prey size for bluegill feeding on *Daphnia* and pumpkinseed feeding on snails in a series of laboratory experiments (see Mittelbach 1981; Osenberg and Mittelbach 1989 for experimental methods and results). For bluegill, we also quantified how instantaneous encounter rates varied with prey density. The energetic costs of foraging and prey energy contents were estimated from the literature (references in Mittelbach 1981; Osenberg and Mittelbach 1989). Equation 1 was then used to predict the potential net energetic return (E/T) for a bluegill feeding on zooplankton or a pumpkinseed feeding on snails, based on the size-density distribution of these prey in the environment.

Zooplankton and snails were sampled from a series of seven lakes near the Kellogg Biological Station. Only a brief description of prey sampling methods is provided below; a full description of the lakes and sampling methods can be found elsewhere (Mittelbach 1981, 1984; Osenberg and Mittelbach 1989). Zooplankton were sampled from the epilimnion at dawn in each lake because adult bluegill in these lakes mostly feed in the epilimnion during that brief period when light is available and large *Daphnia* have not yet vertically migrated below the thermocline (Hall et al. 1979; Mittelbach 1981; Wright and Shapiro 1990). On each sampling date, we took three vertical epilimnetic tows with a 30-cm diameter, 154- μm plankton net from a depth of 4 m (roughly corresponding to the upper limit of the thermocline in all lakes except one that had a maximum depth of 4 m, which we sampled from 3.5 m). Zooplankton were collected in May and August of 1981, 1983, 1988, and 1990; not all lakes were sampled in each year. Cladocerans in the preserved samples were identified, counted, and measured for total body length. On the basis of the average density of each size class of cladocerans, we used Eq. 1 to calculate the predicted optimal foraging gain (in J s^{-1}) for a 80-mm standard length (SL) bluegill.

Adult bluegill were collected from the study lakes, and the average annual growth rate (change in mass/year) of an 80-mm bluegill was estimated for each lake and year based on back-calculation from scale annuli data (Osenberg et al. 1988; Mittelbach and Osenberg 1993). The observed growth rates were then compared to predictions of the foraging model.

Snails were collected in four lakes between 1981 and 1985. A total of 34 sampling surveys were conducted (i.e., 34 combinations of date and lake), using either a stove-pipe sampler (Osenberg and Mittelbach 1989) or a modified Gerking sampler (Mittelbach 1984). Between 6 and 16 sample cores were collected from the vegetation during each survey. Snails were sorted from the sampled vegetation, identified to species, counted, and measured. We pooled replicate samples from each survey and, using the density and size distribution of each species and the foraging model, estimated optimal foraging rates for 60, 80, 100, and 120 mm pumpkinseed.

Pumpkinseed were collected from the study lakes during 6 of the 34 surveys (Osenberg and Mittelbach 1989). We estimated the biomass of snail tissue in their stomachs based on the numbers and sizes of snails and compared these measures of snail consumption to the feeding rates predicted by the foraging model (Eq. 1).

Comparisons of Predicted Feeding Rates and Field Patterns

Predicted foraging rates for four size classes of pumpkinseed feeding on snails were strongly correlated with the biomass of snails in their stomachs (Fig. 1; $r = 0.85$, $n = 21$, $p < 0.001$). Thus, the

foraging model (Eq. 1), for which all parameters were estimated independent of the field data, appears to be a good predictor of realized feeding rates. However, because stomach capacity increases with fish size and predicted ingestion rate also generally increases with fish size, the relationship in Fig. 1 might be spurious. However, an analysis of covariance (using $\log [E/T]$ as the covariate and size class as the grouping variable) shows that predicted feeding rate explains a significant portion of the variation in stomach fullness ($F_{1,16} = 7.86$, $p = 0.013$), and that fish size has little residual effect ($F_{3,16} = 1.18$, $p = 0.35$). Thus, the optimal diet model provides a good description of the relative feeding rates of different size classes of pumpkinseed in different environments.

Bluegill growth was also highly correlated with model predictions of net energy gained from feeding on zooplankton (Fig. 2; $r = 0.59$, $n = 18$, $p < 0.01$). In determining this relationship, we used the net energy gain (E/T) calculated from the May zooplankton samples in each lake/year combination and compared these to the average observed growth of an 80-mm bluegill for the given lake and year. We restricted our analysis to the May zooplankton samples because the study lakes showed the greatest variation in zooplankton size and abundance at that time; we have hypothesized that these early season differences in zooplankton production are critical in determining the pattern of bluegill density and size-specific growth among lakes (Mittelbach and Osenberg 1993). If we use the average of the May and August E/T s to characterize the potential energetic return from each lake, the relationship between bluegill growth and predicted feeding rate remains essentially unchanged ($r = 0.65$, $n = 18$, $p < 0.01$).

Clearly, the foraging model expressed by Eq. 1 was successful in predicting fish foraging rates that correlated with observed stomach fullnesses (Fig. 1) or observed yearly growth rates (Fig. 2). We have also used the model in Eq. 1 to predict the net energy gain of juvenile bluegill feeding on benthic littoral

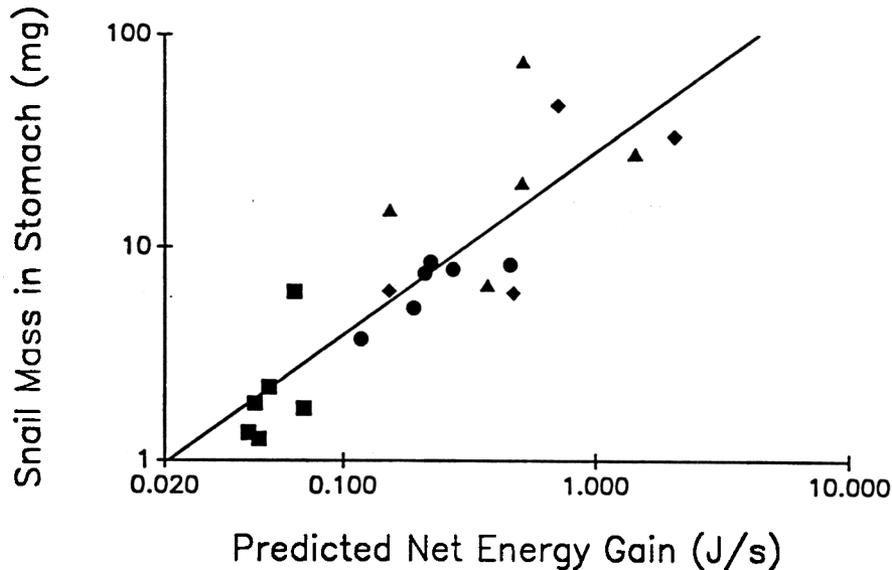


Figure 1. Total dry mass of snail tissue in pumpkinseed stomachs as a function of predicted net energy intake (calculated from Eq. 1). Data are based on means for pumpkinseed within four size classes: ■ = 50-69 mm SL, ● = 70-89 mm SL, ▲ = 90-109 mm SL, ◆ = 109-131 mm SL.

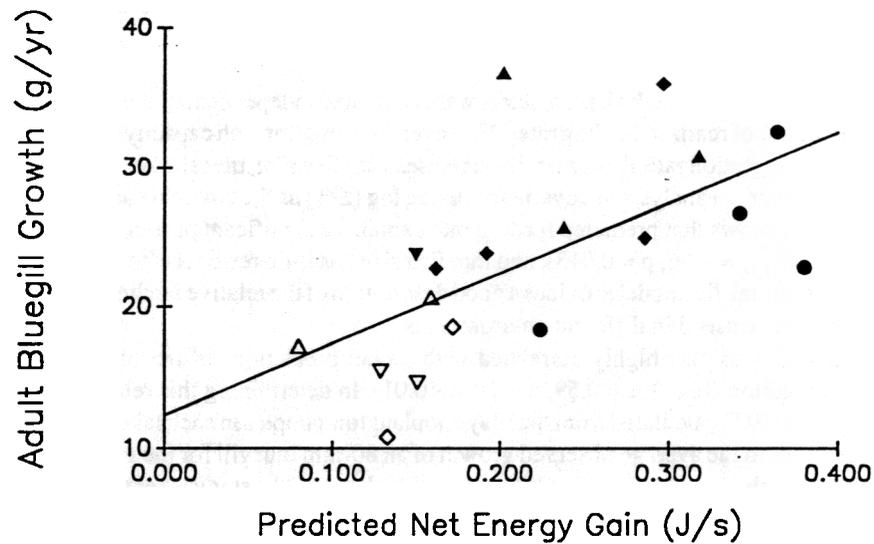


Figure 2. Adult bluegill growth as a function of the average net energy gain available from the zooplankton in May. Each point represents a specific lake/year combination, with each lake represented by a different symbol: ◆ = Lawrence Lake, ● = Three Lakes II, ▲ = Deep Lake, ▼ = Warner Lake, ◇ = Palmatier Lake, △ = Three Lakes III, ▽ = Culver Lake. Observed and predicted rates are for an 80-mm bluegill. Source: Mittelbach and Osenberg (1993).

prey in experimental enclosures (Mittelbach 1988). In this study, where small bluegill were enclosed for about 2 mo in a series of 3-m² cages, we also found a significant positive correlation between the predicted foraging gain available in an enclosure and the observed growth of the fish ($r = 0.75$, $n = 7$ cages, $p < 0.05$). Persson (1990) used a foraging model similar to Eq. 1 to predict the feeding rates of perch (*Perca fluviatilis* Linnaeus) in an experimental field study. He found that predicted E/T 's from the model were significantly correlated with perch growth, both when perch were feeding on benthic invertebrates and when perch were feeding on zooplankton.

These results suggest that standard optimal diet models can provide a useful tool to link measures of prey availability in the environment to the expected diets and energetic intakes of consumers. In many of the above comparisons, the predicted optimal diet for a fish included most of the prey types available (e.g., Mittelbach 1988; Osenberg and Mittelbach 1989; Persson 1990). Therefore, in these cases the optimality criteria of the model is not critical in predicting feeding rates; rather, it is the way in which prey encounter rates, capture successes, and handling times scale with prey size. We return to this point later in the paper.

Our enthusiasm over the success of foraging models in predicting fish energetic gains must be tempered by the fact that developing a detailed foraging model for any particular predator-prey system is an intensive effort. For example, the above studies required between 130–430 laboratory feeding trials to estimate the rates at which pumpkinseed, bluegill, or perch encountered their prey (parameter a_i in Eq. 1). One hope would be that such detailed studies of fish foraging would suggest ways in which foraging models might be simplified, or even suggest situations in which foraging models might be

circumvented and where prey abundance alone might provide a good index of fish feeding rates or growth rates in a habitat. We explore these possibilities in the following section, using data from our studies of bluegill and pumpkinseed, and Persson's (1990) studies of perch.

Prey Biomass as a Predictor of Feeding Rate

Most population models of predator-prey interactions assume that prey density provides a good measure of resource availability and, therefore predator foraging gain. However, in natural systems, the prey assemblage rarely consists of a single prey species, and few prey populations consist of single size classes. Because vulnerability of prey often depends on prey size, and because the contribution of prey to a predator's energy budget also depends on prey size, total prey *density* is unlikely to provide a good relative measure of predator foraging rates. Total prey *biomass* is likely to provide a better index because each prey type is weighted by its density and mass to estimate its contribution to the predator's energy gain. In the following text, we examine the relationship between total prey biomass found in the environment and a fish's predicted foraging gain (from Eq. 1) or its observed growth, or both, using data for the bluegill, pumpkinseed, and perch. We then turn to a more theoretical treatment of the issue to determine the conditions required for prey biomass to work as a reasonable predictor of predator foraging gains.

We used the observed density and size structure of cladocera sampled from lakes to estimate the total prey biomass and the predicted foraging gains for adult bluegill feeding on this resource. The relationship between these two measures of resource availability is weak (Fig. 3a), and the correlation is not significant ($r = 0.26$, $n = 39$, $p > 0.10$). This is rather surprising given that exactly the same information on resource density and size-structure went into calculating total prey biomass and predicted foraging gain (E/T). The lack of good correspondence between the two methods lies in the way in which different size classes are weighted in importance. The weighting of size classes in the optimal foraging model is the result of strong size selection by bluegill.

Numerous studies have shown that adult bluegill feeding on zooplankton are very size selective, feeding on the largest cladocerans available and ignoring smaller sizes classes (e.g., Mittelbach 1981; Werner et al. 1983). In these situations it is obvious that while all prey sizes contribute to the total prey biomass available in a habitat, only those sizes that are actually consumed (or are predicted to be in the diet) contribute to realized (or predicted) feeding rates. Consequently, we would expect that total prey biomass in a habitat would be a poor predictor of fish feeding rates or growth rates for any species exhibiting strong diet selection (i.e., species in which the $P_i(a)$'s in Eq. 1 are < 1 for a large number of prey types). For the bluegill, there is no correlation between average adult growth in a lake and the total biomass of cladocerans available (Fig. 4; $r = 0.09$, $n = 18$, $p > 0.50$). However, when we run these same zooplankton data through the foraging model (Eq. 1) and calculate optimal diets and associated net energy gains, there is a significant correlation between the predicted net energy gain and adult bluegill growth (Fig. 2). Thus, the bluegill/zooplankton interaction nicely illustrates how foraging models are crucial for accurately estimating fish feeding rates or energy gains when foragers exhibit active prey selection.

In contrast to bluegill, total prey biomass was a good predictor of foraging gain for pumpkinseed ($r = 0.76$, $n = 34$, $p < 0.001$ for predicted energy gain as a function of total biomass of snails in the environment; Fig. 3b). Part of the explanation for the greater comparability of the two methods for

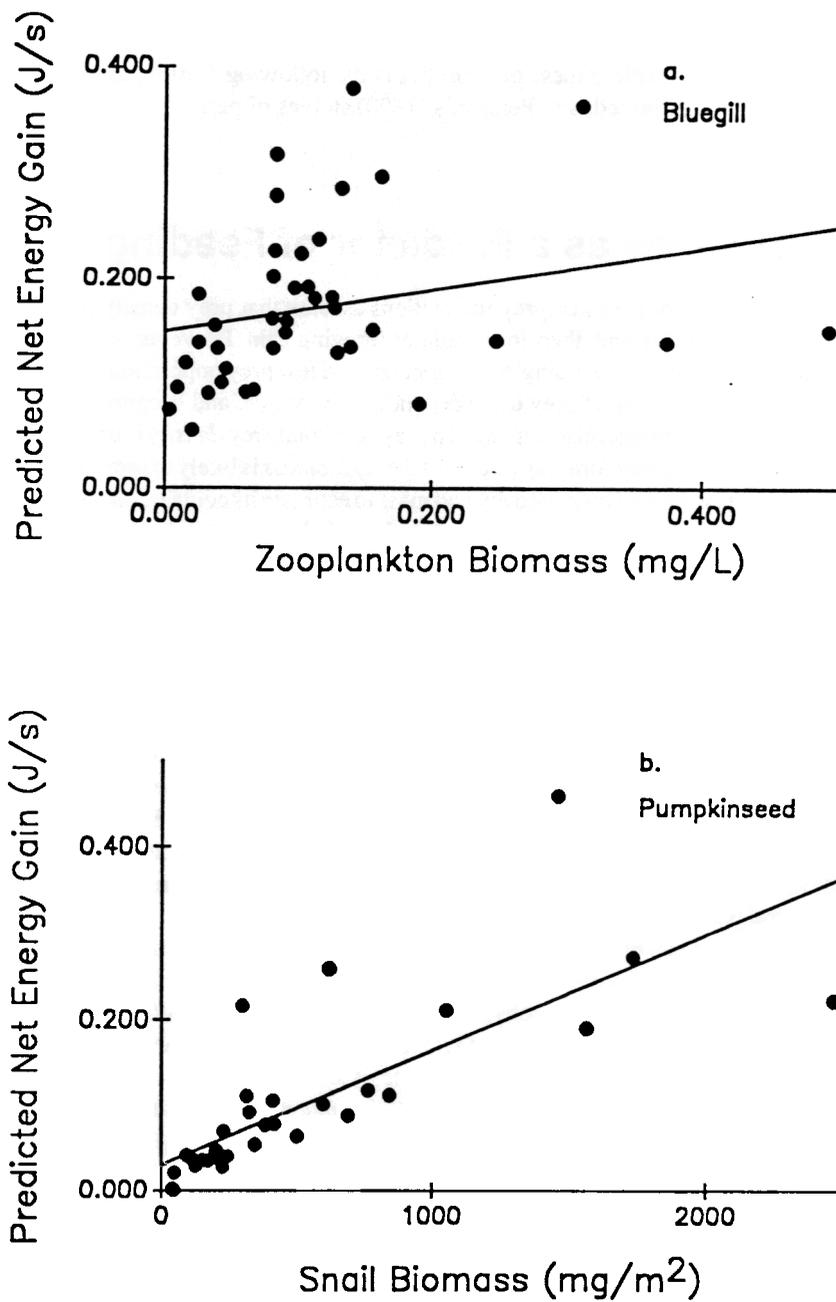


Figure 3. (a) Relationship between the total zooplankton biomass (dry mass, cladocerans only) available in a lake's epilimnion and the predicted rate of energy gained by an 80-mm bluegill feeding on those zooplankton. (b) Relationship between the total snail biomass (dry mass) available in a lake littoral zone and the predicted rate of energy gained by an 80-mm pumpkinseed feeding on those snails. Each data point in each panel represents a single lake/date combination.

pumpkinseed lies in the smaller degree of active selection exhibited by pumpkinseed. Like bluegill, pumpkinseed are size-selective predators. However, unlike bluegill, pumpkinseed diets and foraging rates can be largely predicted based upon size-specific encounter rates with prey (Osenberg and Mittelbach 1989). Although attack probabilities vary among prey types, their influence on diet composition is rather slight. Alternatively, attack probabilities for bluegill play a critical role in determining diet composition, which cannot be predicted based on encounter rates alone (Mittelbach 1981; Werner et al. 1983).

The studies of juvenile bluegill and perch provide additional examples where active prey choice is relatively unimportant in determining feeding rates. For juvenile bluegill, the biomass of benthic invertebrates was positively correlated with the predicted net foraging gain (Fig. 5, $r = 0.93$, $n = 7$, $p < 0.005$), as well as with the observed growth of bluegill ($r = 0.66$, $n = 7$, $p = 0.10$). In this case benthic prey biomass was nearly as good an index of juvenile bluegill growth as was the predicted net energy gain from the optimal diet model ($r = 0.66$ vs. $r = 0.76$). Persson (1990) also conducted an experimental cage study in which he related perch growth to predicted foraging gains (E/Ts) and total prey biomass available. He found significant positive correlations between the growth of perch feeding on zooplankton or benthic prey, and the total biomass of zooplankton or benthic prey available in the environment. In both cases model predictions of E/Ts worked better when predicting perch growth than did total prey biomass, but the difference was small (and not significant) when perch were feeding on zooplankton (Persson 1990).

The data for pumpkinseed, juvenile bluegill, and perch suggest that total prey biomass may work reasonably well in facilitating prediction of fish energetic gains under conditions where diets do not deviate strongly from those predicted from encounter rates. However, we note that the relationship

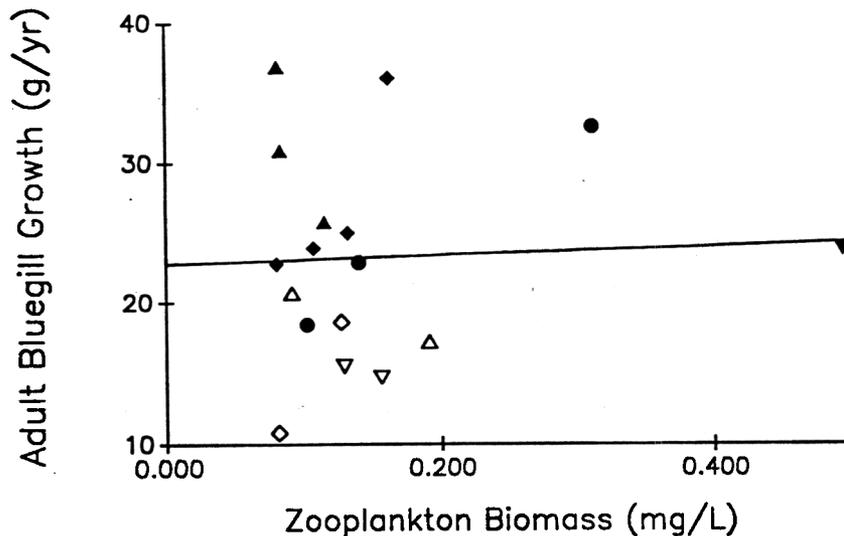


Figure 4. Observed growth of 80-mm bluegill as a function of the total zooplankton biomass (dry mass, cladocerans only) available in a lake's epilimnion in May. Symbols as in Fig. 2.

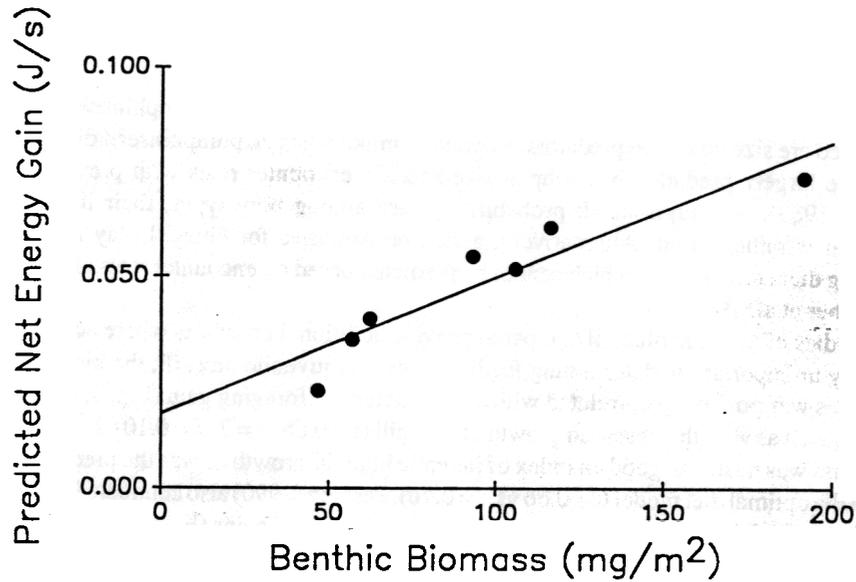


Figure 5. Relationship between the total dry biomass of benthic invertebrates available in experimental enclosures and the predicted rate of net energy gained by juvenile bluegill feeding on those benthic prey. Each data point represents a single enclosure.

between predicted net energy gain and prey biomass for the pumpkinseed exhibits considerable scatter (Fig. 3b). One might reasonably ask why there is any scatter to this relationship at all, since exactly the same prey data go into calculating total prey biomass in a habitat and into calculating the predator's potential foraging gain (e.g., both are calculated from the size-density distribution of prey available). The primary difference between the two models lies in the way weightings are assigned to each prey type. In the biomass model, each prey type's density (N_i) is weighted by its mass (b_i),

$$B = \sum_{i=1}^n (N_i b_i) \text{ or}$$

$$B = N \sum_{i=1}^n (f_i b_i) \quad (2)$$

where $N =$ the total prey density ($\sum_{i=1}^n N_i$) and

$f_i =$ the distribution of prey among the prey types (e.g., the size-structure).

In the foraging model, each prey type is weighted by its energy content (roughly its mass) as well as by specific components of the foraging process, such as encounter rate, attack probability, and capture success. Rewriting Eq. 1, but substituting $Nf_i = N_i$, allows us to assess how foraging rates (E/T) might be predicted by simply knowing prey biomass.

$$E/T = \frac{N \sum_{i=1}^n a_i f_i E_i P_i(a) P_i(s) - C_s}{1 + N \sum_{i=1}^n a_i f_i H_i P_i(a) P_i(s)} \quad (3)$$

If two environments (e.g., two different dates within a lake or two different lakes) differ only in the total density of prey, then Eq. 3 reduces to

$$E/T = \frac{Nc_1 - C_s}{1 + Nc_2} \quad (4)$$

where c_1 and c_2 are constants defined by the particular form of the foraging components and the prey size structure (see Eq. 5 and 6 below, for definitions of c_1 and c_2). In this case E/T will be a monotonic function of prey biomass (indexed by N) with no variance in the relationship. Therefore, prey biomass should work as well as E/T to predict predator foraging and growth rates, except for the nonlinearity introduced by handling times (if handling times are negligible, then Eq. 4 reduces to a linear form: $E/T = Nc_1 - C_s$). However, achieving this 1:1 relationship between foraging gains and prey biomass requires two very restrictive assumptions:

$$\sum a_i f_i E_i P_i(a) P_i(s) = c_1 \text{ for all environments, and} \quad (5)$$

$$\sum a_i f_i H_i P_i(a) P_i(s) = c_2 \text{ for all environments} \quad (6)$$

In other words, none of the components of these expressions can vary between environments. Two of these restrictions are most damning: that attack probabilities, $P_i(a)$, and prey distributions, f_i , be constant among the different environments. Indeed, one of the primary predictions of optimal foraging theory is that attack probabilities should vary as functions of prey density (i.e., overall values of E/T). The restriction on attack probabilities requires that predators be inflexible in their decision rules, which runs contrary to most empirical observations and violates the foundation of optimal foraging theory. The restriction on prey distributions requires that size structure and species composition of the prey assemblage be invariant. If prey structure changes, then the 1:1 match between biomass and E/T will be destroyed, and noise will be introduced into the relationship between biomass and E/T . That is, the same total prey biomass may yield different foraging gains to a predator, depending on how total prey biomass is distributed among prey sizes.

If we permit the prey structure to vary, some conditions still can permit 1:1 matching of the two models; however, this requires that

$$a_i E_i P_i(a) P_i(s) = c_3 \text{ for all } i \text{ and each environment, and} \quad (7)$$

$$a_i H_i P_i(a) P_i(s) = c_4 \text{ for all } i \text{ and each environment} \quad (8)$$

These conditions are unlikely. For example, they still require that attack probabilities be inflexible. More importantly, energy content (E_i) will certainly vary among different prey types (e.g., owing to size or species identity), as will encounter rates, attack probabilities, and capture successes (e.g., Osenberg and Mittelbach 1989).

Therefore, on theoretical grounds, prey biomass will give identical results to the foraging models only when predators are nonselective (all prey are consumed in proportion to their abundance) and prey structure is invariant across the different environments. Any deviation from these conditions will add noise to the relationship between biomass and predictions from the foraging model. Furthermore, if handling times are non-negligible, the relationship between biomass and predicted foraging gains will be nonlinear. As expected from these analyses, the relationships in Figs. 3 and 5 exhibit a noticeable nonlinearity (indicative of the role of handling times) and varying degrees of noise (indicative of the varying degrees of violation of the above assumptions). The fit between the two models should be (1) worst for predators with the most variable decision rule (e.g., attack probabilities vary most among prey types and environments), such as adult bluegill (Fig. 3a), and (2) better, but not perfect, for predators that exhibit less active prey choice, such as pumpkinseed (Fig. 3b), juvenile bluegill (Fig. 5), and perch (Persson 1990).

The final and compelling reason that biomass (or other simple indices of prey availability) represents a poor framework to predict predator foraging gains and growth rates arises because such simple indices completely ignore the effect of fish size on the foraging interaction. Although, under some conditions biomass might correlate well with foraging gains, the observed relationship will only be applicable to a given size class of predator. This limitation occurs because fish size influences the components of the foraging model, such as encounter rates, handling times, and capture successes (e.g., Werner 1974; Kislalioglu and Gibson 1976; O'Brien 1979; Mittelbach 1981; Hairston et al. 1982; Bence and Murdoch 1986; Wainwright 1988; Osenberg and Mittelbach 1989; Persson and Greenberg 1990). Therefore, the "constants" in Eq. 4 will depend on fish size. Only a foraging model that explicitly incorporates the effects of fish size can provide a general model applicable to a size-structured predator population.

The results for pumpkinseed feeding on snails nicely illustrate how residual effects of fish size are absent in a properly parameterized foraging model (Fig. 1). Mittelbach (1983) has also shown good correspondence between the predictions of the foraging model and observed growth rates of different size classes of bluegill. Because all fish populations (if not most predator populations, in general) are size-structured (Werner and Gilliam 1984) and because predator size has important effects on the foraging process, simple measures of prey availability are unlikely to be good predictors of energy gain to predator populations.

Conclusions

As ecologists and fisheries biologists, we are often interested in answering the question, "What is the value of a given habitat to a fish?" We want to know, for example, if fish will grow better in this

lake or that one, or how a change in the prey community (due to pollution or the introduction of a new species) will affect the growth of a resident fish population. One approach to addressing these and other questions is to relate fish feeding rates or energetic gains to the abundance of prey in the environment. If we can predict a priori the potential energetic intake or growth rate of a fish based on the abundance of prey in a habitat, we have a powerful tool for understanding and predicting the consequences of environmental change.

Optimal foraging theory was developed in part with the goal of predicting species diets, habitat use, and energetic intakes from a knowledge of resource availability and utility to the consumer. To date, however, few researchers have attempted to apply foraging theory in this regard. We reviewed four studies that have used optimal diet models to predict the growth or feeding rates of fish in the field, and we found that in each case the predictions of the foraging models were well correlated with the performance of the fish. A simpler measure of prey availability, total prey biomass, gave variable degrees of success in predicting the predator's foraging rates; in some cases prey biomasses were well correlated with predicted foraging rates or observed growth rates, while in other cases they were not (see also Noble 1975; Mills and Schiavone 1982; Mills and Forney 1988). We caution that simple indices are unlikely to provide general and robust predictors of predator foraging and growth rates. The theoretical relationship between prey biomass and foraging gain is 1:1 and linear only under very unlikely conditions. Handling time will cause the relationship to be nonlinear, and a number of factors, such as shifts in prey size-structure, the degree of flexibility in attack probabilities, and the strength of the influence of prey size on encounter rates and captures successes, will add noise to the relationship. Finally, even if these conditions are satisfied (or approximated), observed relationships between biomass and foraging gains will only hold for a single size class of predator. A more general model of foraging gains applicable to the entire predator population will require specification of how components of the foraging model scale with predator and prey size. Simple indices of resource availability, such as total prey biomass, are therefore neither robust nor general and offer only limited insight to the study of predator-prey interactions.

While optimal foraging models use the criteria of energy maximization to predict a predator's prey choice, "optimality" per se was often not a critical factor in predicting fish foraging gains in the empirical studies examined. Rather, predicted optimal diets often included many prey types from the environment, and it was the effect of prey size on encounter rates and handling times that had the largest impact on predicting fish foraging gains. Thus, while energy maximization provides a reasonable criterion for predicting prey choice, the value of using optimal foraging models to translate prey abundances into potential feeding rates may often derive more from specifying the critical components of the foraging process (e.g., prey encounter rates) than from accurately predicting optimal diets (Osenberg and Mittelbach 1989). Thus, these models can be viewed as "tools" for the community ecologist and fisheries biologist, as well as "hypotheses" for the behaviorist interested in studying how animals make foraging decisions (Werner and Mittelbach 1981).

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