Foraging Theory and Piscivorous Fish: Are Forage Fish Just Big Zooplankton?

James E. Breck

MICHIGAN DEPARTMENT OF NATURAL RESOURCES
FISHERIES DIVISION

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*Michigan Department of Natural Resources
Institute for Fisheries Research
212 Museums Annex Building
Ann Arbor, Michigan 48109-1084*

Abstract.–Insights into the dynamics of fish growth can be gained by using foraging theory to link bioenergetics models of fish and their prey. These links are critical for modeling fish daily ration and growth, prey mortality, selection among prey, and competition among predators. However, the foraging theory that is relatively well developed for planktivores does not always apply to piscivores without important modifications. Visual encounter is often limited by visual acuity for most planktivores, but probably limited by prey contrast for piscivores, so that piscivore reactive distance is much less dependent on prey size. Whereas handling time per prey may limit the capture rate for some planktivores, it is irrelevant for most piscivores, which eat relatively small numbers of large prey and are more likely to have daily ration limited by rates of digestion or prey encounter. Time for gastric evacuation or digestion should not be a part of handling time, because search can occur simultaneously with digestion. If handling time is not important for piscivores, then Holling's Type-1 functional response may be more appropriate than the Type-2. An alternate form of the functional response is presented for predators that feed on prey of uniform size and stop foraging each day when some maximum number of prey are ingested. This functional response has a negatively accelerated rise to an asymptote, similar to the Type-2 functional response, but based on a very different mechanism. Simulations with a bioenergetics model show that the variance in daily growth among individuals is likely to be greater for piscivores, which feed on a small number of large prey, than for planktivores, which feed on a large number of small prey.

The trophic linkages between fish and their prey are critical to understanding and modeling fish daily ration and growth, prey mortality, selection among prey, and competition among predators. Bioenergetics models are useful for studying the factors influencing fish growth and food consumption, and much has been learned by using single-species bioenergetics models. In typical applications, the seasonal pattern of fish growth (or consumption) is specified and the corresponding pattern of consumption (or growth) is computed; prey dynamics are not explicitly included in such calculations, but appear indirectly in the specification of diet composition (Kitchell et al. 1977; Rice et al. 1983; Hewett and Stewart 1989; Stewart and Ibarra 1991). Further insights into the dynamics of fish growth can be gained by using foraging theory to explicitly link bioenergetics-based models of fish to models of their prey (Adams and DeAngelis 1987; Trebitz 1991; Madenjian and Carpenter 1991). However, the foraging theory that is relatively well developed for

planktivores may not apply to piscivores without important modifications.

The purposes of this paper are, first, to describe some of the differences in foraging between piscivores and planktivores; second, to show that foraging models developed for planktivores are inadequate for piscivores; third, to present an alternate functional response equation for piscivores; and fourth, to demonstrate, using a bioenergetics model, that variation in growth among individuals can be related to the average number of prey consumed per day. The intention is to facilitate taking the next step and linking bioenergetics models of piscivores and their prey.

Differences between Piscivores and Planktivores

There are several differences between piscivores and planktivores that have large consequences for understanding the link between predators and their prey. Some of these differences are shown in Table 1. In the table and the discussion that follows, I am focusing on juveniles and adults, with just a few comments on larval fish.

Differences in predator mouth shape and prey body morphology affect the sizes and types of prey taken by predators. Because most piscivores swallow their prey whole, mouth gape is critical in determining the largest prey items that can be ingested (Lawrence 1958; Johnson 1969; Hambright 1991; Reimchen 1991). In contrast, planktivores can normally ingest the full range of zooplankton sizes typically present in lakes and are thus usually not gape limited (Zaret 1980). An exception is fish larvae, which are initially gape limited, but which rapidly reach a size where they can handle most zooplankton (Zaret 1980; Schael et al. 1991).

Capture success (the probability of prey capture given an attack) is often high for fish attacking prey that are small in relation to the predator's mouth size (Drenner et al. 1978; Miller et al. 1988). However, for increasing prey sizes, capture success often decreases rapidly as prey size approaches a limit set by mouth size (Miller et al. 1988). For example, Reimchen (1991) found that the success of cutthroat trout

Oncorhynchus clarki feeding on threespine sticklebacks *Gasterosteus aculeatus* in the laboratory decreased rapidly as the prey diameter approached the trout's mouth diameter. The reviews of Miller et al. (1988) and Crowder et al. (1992) also discuss the size dependence of capture success. Because the prey of most planktivores in lakes are relatively small, capture success is generally quite high over the size range typically consumed [but capture success can be low for copepods (Drenner et al. 1978)]. For piscivores, however, the size range of potential prey often includes sizes very close to the gape limitation, where capture success can be strongly dependent on the prey size/mouth size ratio (Miller et al. 1988). In general, then, capture success tends to be a more critical predation factor for piscivores than for planktivores.

The number of prey typically consumed per day is one of the most important differences between piscivores and planktivores. Whereas most piscivores consume a few large prey per day, planktivores eat many small prey (Johnson 1969; Martin 1970; Mittelbach 1981; Persson 1987; Miller et al. 1992). This difference is critical to some of the subsequent discussion of foraging and variation in growth.

Two aspects of foraging that affect the functional response of predators to prey density are the limits on underwater vision as they affect visual search, and the importance of handling time (Holling 1959, 1965).

Visual Search

Eggers' (1977) discussion of visual search indicates that vision is limited by *visual acuity* for small objects, objects with high contrast, high light levels and low turbidity. At the other extreme, vision is limited by *contrast* for large objects, objects with low contrast, low light levels and high turbidity. For intermediate conditions both visual acuity and contrast are important (Eggers 1977). These aspects of underwater vision have relevance for the construction of models of visual search by planktivores and piscivores.

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Planktivores.–Foraging models are quite well developed for visually feeding planktivores (e.g., Wright and O'Brien 1984). The maximum distance at which a fish reacts to a prey is called the reactive distance for that prey type. The reactive distance generally increases with prey size, fish size, asymptotically with light level, and with closer angular spacing of cones in the retina (Vinyard and O'Brien 1976; Eggers 1977; O'Brien 1979; Hairston et al. 1982; Breck and Gitter 1983). This provides evidence that at high light levels the visual search of planktivores is limited primarily by visual acuity, which is related to some minimum image size on the retina (Eggers 1977).

Visual search can be influenced by both retinal image size and the contrast between the prey and its background (Eggers 1977). Reactive distance decreases at low light levels or with increasing turbidity, and increases for cladoceran females containing parthenogenic eggs (which have a higher contrast than females without eggs) (Vinyard and O'Brien 1976; Eggers 1977; Tucker and Woolpy 1984).

A common model for foraging planktivores calculates the volume searched as a cylinder (sometimes with a hemispherical end), with the distance swum as the length of the cylinder, and the reactive distance as the radius (Confer and Blades 1975; Eggers 1977; Werner et al. 1983). Because the reactive distance of fish to zooplankton of similar morphology is a linear function of zooplankton length (L), the volume of the search cylinder will be related to L^2, and so will the encounter rate for prey of that size (Confer and Blades 1975; Eggers 1977; O'Brien 1979; Werner et al. 1983). Another foraging model describes fish that use a saltatory search pattern and scan successive search spheres, hemispheres, or other shapes (Werner and Hall 1974; O'Brien 1989; Browman and O'Brien 1992). For saltatory searchers the total volume scanned will be related to L^3, because each individual scan searches a fraction of a sphere and thus a volume proportional to L^3 (Werner and Hall 1974; Werner et al. 1983). In both of these foraging models, larger zooplankton are much more likely to be encountered than smaller ones of similar contrast because of the effect of visual acuity.

Piscivores.–For fish visually searching for large prey items, reactive distance is more likely to be limited by contrast than by visual acuity because the length of the visual path is affected by water clarity. Extrapolating from laboratory measurements of reactive distance for 2.6-mm *Daphnia* (Breck and Gitter 1983), a bluegill *Lepomis macrochirus* of 150-mm total length would be able to locate a 20-mm *Daphnia* (were one to exist) at a distance of 3.9 m, a 40-mm *Daphnia* at 7.8 m, and a 60-mm *Daphnia* at 11.8 m. A 150-mm largemouth bass *Micropterus salmoides* can ingest a 60-mm bluegill (Lawrence 1958). If this predator had the visual acuity measured for bluegills, it is likely that prey detection would be limited by contrast at such distances because of the water clarity of typical freshwater systems. In Wisconsin lakes, for example, the modal Secchi disk transparency is in the class 1.0-1.4 m for drainage lakes, and in the class 3.0-3.4 m for seepage lakes (Hutchinson 1957).

The importance of contrast limiting the visual search distance of piscivores is that the reactive distance to prey is expected to be independent of prey size at large distances (Eggers 1977); at least it should be a much weaker function of prey size than for planktivores. Several recent models of piscivory have made the assumption, consistent with this discussion, that encounter rates with forage fish are independent of prey size (Adams and DeAngelis 1987; Madenjian and Carpenter 1991).

Howick and O'Brien (1983) measured the reactive distance of largemouth bass to bluegill prey and found that the reactive distance was approximately proportional to bluegill length, rather than constant for all sizes. The visual acuity of the bass, as determined by this behavioral measure, was much less than has been determined for bluegills. Bluegills react to *Daphnia* at a visual angle of about 0.48°, whereas largemouth bass reacted to bluegills at a visual angle of about 2.7° (Howick and O'Brien 1983). They found that a 290-mm largemouth bass reacted to a 60-mm bluegill at a distance of about 1.2 m under bright light. It would be very worthwhile to test if the visual acuity of other piscivores is so much lower than the planktivores

Handling Time

Planktivores.–The handling time per prey item may set the upper limit on capture rate for planktivores (Eggers 1977; Persson 1987; Miller et al. 1992). Crow (1982), however, has questioned whether handling time sets the limit on daily ration for planktivores, arguing that at the maximum capture rate, they can obtain a maximum ration in much less than 1 d.

Piscivores.–For many piscivores, very few forage fish are captured each day. Johnson (1969) examined 3,551 angler-caught northern pike *Esox lucius* from Murphy Flowage, Wisconsin, and found that 95% had 0 or 1 fish in their stomach (Figure 1). The average was 0.37 fish per stomach. For the 1,290 pike collected by Diana (1979) using gill nets, the average was 1.16 fish per stomach. For 183 age-1 to age-4 largemouth bass collected in 1980 from Watts Bar Reservoir, Tennessee, the average number of fish per stomach was 0.61 (DeAngelis et al. 1984). A study in the Columbia River found that northern squawfish in July 1988 had captured juvenile salmonids, which make up 78–99% of their diet, at average rates of 0.4 to 4.4 prey·predator^{-1}·d^{-1} (Petersen and DeAngelis 1992). If handling time is defined as the average time required per prey item from encounter until search resumes (which includes the time to stalk, pursue, capture, manipulate, and swallow the prey), then handling time is not likely to be important for these piscivores, because so few prey are handled per day. Handling time will not usually set the upper limit on daily capture rate because just a few prey can make up a maximum daily ration.

Handling time might be important if a piscivore ingested a large number of prey items in a day. For example, a 54.6-cm lake trout *Salvelinus namaycush* reported by Martin (1970) contained 149 age-0 yellow perch *Perca flavescens*; their consumption would take more than 24 h in the unlikely event that the handling time exceeded 10 min per prey. Average handling time might be important for piscivores

if capture success is so very low that most of their foraging time is spent on unsuccessful encounters rather than searching. But in that case the total amount of time spent physically handling the prey items would be quite small.

What if handling time is defined to include the time for gastric evacuation or digestion of each item? The digestion rate is likely to set the upper limit on daily ration for piscivores, determining the maximum number of forage fish that can be processed per day. However, there is a problem in applying this definition of handling time to the functional response: piscivores can simultaneously digest and forage. This is obvious because some individuals are found with more than one fish in their stomachs. In the Holling Type-2 functional response, as prey density increases, the capture rate deviates from a straight line due to the increasing fraction of time that is spent handling prey. Because digestion can occur at the same time as search and prey capture, digestion alone will not cause a deviation from the straight line. Digestion rate and stomach volume may set an upper limit to the number of prey that can be captured and processed each day. But these factors considered alone would produce an abrupt limit to capture rate with increasing prey density, suggesting a Type-1 rather than a Type-2 functional response.

As the stomach fills or as the hunger level decreases, the search rate may decrease or handling time may increase (Ware 1972; Werner 1974; Kislalioglu and Gibson 1976). Making search rate and handling time depend on stomach fullness or hunger level would make the functional response much more complex. In the next section I will suggest two simple alternative functional responses for piscivores.

Foraging Models for Piscivores

Functional Response

Let *a* be the volume (m^3) of water searched each day by a fish, and *D* be the density (m^{-3}) of prey. Assume that handling time is negligible, so that *a* is independent of the number of prey caught. Then $X = aD$ is the mean number of prey encountered each day. Assume that the predator's

search is a Poisson process, a common assumption of foraging models (Gerritsen and Strickler 1977; DeAngelis et al. 1984; Petersen and DeAngelis 1992). Then the probability of encountering n prey in one day is given by the Poisson distribution:

$$P(n) = \frac{X^n e^{-X}}{n!}.$$ (1)

Let p be the probability of prey capture given an encounter, and let this be a constant, independent of prey size, predator size and hunger level, etc. Then the number of prey captured given that n are encountered will follow a binomial distribution. That is, the probability that k prey are captured given that n are encountered is:

$$P(k|n) = \binom{n}{k} p^k (1-p)^{n-k}.$$ (2)

From equation (2) it follows that the probability of capturing no prey during a day given that n prey are encountered is:

$$P(0|n) = (1-p)^n.$$ (3)

Combining equation (3) and equation (1) gives the probability of capturing no prey during a day, accounting for variation in the number encountered:

$$P(0) = \sum_{n=0}^{\infty} P(0|n)P(n)$$ (4)

$$= e^{-X} \sum_{n=0}^{\infty} \frac{(X(1-p))^n}{n!}.$$ (5)

This simplifies to:

$$P(0) = e^{-pX},$$ (6)

based on the following relationship:

$$e^z = \sum_{i=0}^{\infty} \frac{z^i}{i!}.$$ (7)

Equation (6) states that there should be an exponential decrease in the proportion of fish with empty stomachs as prey density increases.

Proceeding in a similar manner, the probabilities of capturing exactly $k=1$, $k=2$, and $k=3$ prey during a day are:

$$P(1) = pXe^{-pX},$$ (8)

$$P(2) = \frac{(pX)^2}{2} e^{-pX},$$ (9)

$$P(3) = \frac{(pX)^3}{3!} e^{-pX}.$$ (10)

In general, the probability of capturing exactly k prey during a day is given by

$$P(k) = \frac{(pX)^k}{k!} e^{-pX},$$ (11)

which is the Poisson distribution with mean equal to $pX=paD$.

Stated in biological terms, for the assumptions made here, the average number of prey captured per day by a piscivore is the product of the probability of capture given an encounter (p), the volume searched per day (a), and the prey density (D). The mean number of prey captured per day is thus expected to be directly proportional to prey density (D); a graph

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of the mean number of prey captured per day plotted against prey density should be a straight line, with an intercept of zero and a slope of pa. The term pa is equivalent to the rate of successful search in Holling's functional response.

Alternatively, the mean number captured per day can be plotted against the mean number of prey encountered (aD) (Figure 2). The mean number of prey captured per day increases linearly with aD; the line has an intercept of zero and a slope of p. At a given prey density (or a given mean number of prey encountered per day), the variation among individuals in the number captured per day is described by a Poisson distribution, where the mean (and the variance) of the distribution is paD. The separate areas below the straight line in Figure 2 indicate the contributions to the mean value of individuals capturing $k = 1, 2, 3$, or more prey per day; equation (11) is used to calculate $kP(k)$ given aD and p. As prey density increases, a larger fraction of the predators capture multiple prey.

Constraint on daily ration

Under the assumptions made so far, some individuals are expected to capture a very large number of prey, especially when the average number of prey encountered is large (the tail of the Poisson distribution goes to infinity). In reality, stomach volume and digestion rate place constraints on the maximum number of prey that can be ingested daily by a predator. The functional response described above can be modified to include this constraint.

Suppose all prey are the same size. Then there will be some maximum number of prey (k_{max}) that can be consumed in 1 d. If the predator stops attacking prey after k_{max} prey have been ingested during that day, then the fish that might have captured more than k_{max} prey will only consume k_{max}. The expected number of prey captured per day given k_{max} is then:

$$E\left(k|k_{max}\right) = \sum_{k=0}^{k_{max}-1} kP(k) + \sum_{k=k_{max}}^{\infty} k_{max}P(k). \quad (12)$$

where $P(k)$ is given by equation (11). Equation (12) can be expressed as a deviation from the expected value in the absence of a limit (i.e., a deviation from pX):

$$E\left(k|k_{max}\right) = pX - \sum_{k=k_{max}}^{\infty} \left(k - k_{max}\right)P(k). \quad (13)$$

or as a deviation from the asymptotic value (k_{max}):

$$E\left(k|k_{max}\right) = k_{max} - \sum_{k=0}^{k_{max}-1} \left(k_{max} - k\right)P(k). \quad (14)$$

Figure 3 shows the functional response of equation (14) for $p=0.1$ and $k_{max}=4$. As prey density (or encounter rate) increases, an increasing proportion of the predators are expected to obtain the maximum number of prey, and the expected number captured asymptotically approaches k_{max}. Notice that this functional response has a shape similar to a Type-2 functional response. However, the mechanism is quite different. The uppermost curved line in Figure 3 gradually approaches 4 prey as an asymptote. This gradual approach is caused not by additional handling time reducing search time (as in Holling's Type-2 functional response), but by the increasing proportion of individuals that forego additional prey because they have captured the maximum daily number.

Variation in Growth Among Individuals

As discussed above, one of the major differences between piscivores and planktivores is the number of prey consumed per day. This difference has implications for variation in growth among individual fish. The small number of large prey consumed each day by piscivores makes their growth much more vulnerable to stochastic variation in the daily ration.

To demonstrate the effect of number of prey consumed per day on growth variation, I performed eight simulations using an individual-

based bioenergetics model (Huston et al. 1988; Madenjian and Carpenter 1991) of largemouth bass growth, with bioenergetics parameters from Rice et al. (1983). The nominal average daily ration (g/d) was the same for all simulations, but the weight of the individual prey and the mean number of prey consumed per day varied inversely among the eight simulations. Each simulation followed 100 individuals for 60 d, and every fish started at the same size (55 mm total length and 1.879 g wet weight). The energy density of the fish was set at 4,185 J/g, and that of the prey was 3,348 J/g (Rice et al. 1983). On each day of the simulation the number of prey consumed was determined separately for each individual by selecting numbers from the Poisson distribution given by equation (11) (Press et al. 1986). For the eight simulations the mean of the Poisson distribution (pX) was fixed at 0.5, 1, 2, 4, 8, 16, 32, or 64 prey consumed per day. In order to keep the nominal daily ration the same, the biomass of the prey was fixed at 2, 1, 1/2, 1/4, 1/8, 1/16, 1/32, or 1/64 of a unit ration, respectively. The unit ration was set at 80% of the maximum ration for fish of the initial size growing at 27.5°C.

As the predator's simulated weight increased, length was increased according to the following weight-length equation for Michigan largemouth bass (Merna et al. 1981):

$$\log L = (\log W + 5.16885) / 3.12735;$$

W is wet weight (g), and L is total length (mm). When simulated weight decreased, length did not change (see Rice et al. 1983). The mean and standard deviation of the growth in length was determined for each of the eight simulations.

The results of the simulations show that the variation in growth increases as the prey size increases and the mean number of prey consumed per day decreases (Figure 4). This occurs even though the nominal daily ration (in g/d) is the same. This suggests that all else being equal, piscivores are expected to have greater individual variation in growth than planktivores due to chance effects of "ecological luck" in foraging.

The statistical reason for the increasing variation in growth is that the coefficient of variation (CV) of number of prey consumed per day increases as the mean decreases. For the Poisson distribution, the variance equals the mean, so as the mean number consumed decreases from 64 to 0.5 prey/d in the eight simulations, the CV increases from 12.5% to 17.7%, 25.0%, 35.4%, 50.0%, 70.7%, 100.0%, and 141.4%, respectively. Some fish will by chance receive an above average number of prey and grow more, and others will receive a below average number and grow less.

Discussion

The proposed simple model for the functional response of piscivores can be modified to include other factors. Because capture success varies with the ratio of prey size to predator size (Miller et al. 1988; Crowder et al. 1992), the probability of capture given encounter (p) could be made a function of that ratio. Both p and the search volume (a) could be made functions of hunger level or stomach fullness. Decreasing hunger can lead to increases in handling time and prey selectivity (Ware 1972; Werner 1974; Kislalioglu and Gibson 1976), and hunger may affect capture success and search rate as well. Learning can also play a role in modifying foraging parameters (Kislalioglu and Gibson 1976; Werner et al. 1981; Abrams 1990), so if multiple prey types are included in the model, p and a could depend both on prey type and the number of recent encounters with each prey type.

Expressed relative to prey density, a piscivore's relative encounter rate with forage fish is likely to increase with prey size because larger forage fish tend to swim faster than smaller forage fish. As prey move faster they are more likely to enter the perceptual field of the predator (Gerritsen and Strickler 1977). This effect could be added to the proposed functional response model by making a depend on size-dependent swimming speeds of both predator and prey. The influence of prey swimming speed on encounter rate is likely to be greater for ambush predators than for cruising predators (Gerritsen and Strickler 1977).

Optimal foraging theory, as developed for planktivores and fish feeding on benthic invertebrates, predicts that predators should rank

prey by the ratio of net energy gain to handling time (Krebs 1978; Mittelbach 1981). It is especially important for piscivores that, for each prey type, the values in the ratio be adjusted for capture probability. The ratio should be the *expected* energy return per prey item encountered (i.e., energy return times capture probability given encounter) divided by the *expected* handling time per item encountered. The expected handling time per encounter (t_h) is:

$$t_h = pt_{se} + (1 - p)t_{ue},$$

where p is the probability of capture given an encounter, t_{se} is the average time spent per *successful* encounter with a prey, and t_{ue} is the average time spent per *unsuccessful* encounter with a prey. I suggest that for piscivores, the rankings of prey types will be influenced more strongly by the capture probability given encounter (p) and the mean handling time per *unsuccessful* encounter (t_{ue}) than by the mean handling time per *successful* encounter (t_{se}). Crow (1982) suggested that capture success was the critical factor controlling diet composition. He proposed that an inverse relationship between handling time in laboratory experiments and capture success in the field could be responsible for the success that handling time has had in explaining food habits.

The Poisson distribution (or modifications of it) has proven to be useful in describing and modeling the distribution of fish per stomach (DeAngelis et al. 1984; Petersen and DeAngelis 1992). The Poisson distribution often applies in situations involving two-outcome trials (e.g., "heads" or "tails" can occur) in which the number n of trials is large, the probability p of a "success" (e.g., "heads") is small, whereas the product np is of moderate magnitude (Feller 1968). One interpretation, then, of the Poisson application to fish stomachs is that prey capture by piscivores is a rare event, that many forage fish may be encountered, but that only rarely is a prey in a condition or situation or location to be vulnerable to a piscivore. This interpretation would explain the low "encounter" rates with forage fish used by Madenjian and Carpenter (1991) to generate

observed size distributions of age-0 walleye with their individual-based model. It would be valuable to estimate a piscivore's encounter rate and capture success under field conditions to evaluate this interpretation.

The quantitative results of the simulations presented in Figure 4 depend on the bioenergetics parameters used, initial fish size, water temperature, the energy densities of predator and prey, and the size of the unit ration. These factors were held constant across all eight simulations. The qualitative pattern, however, should be quite robust. When the number of prey consumed per day varies stochastically with a distribution similar to the Poisson, the variation in growth among individuals is expected to be larger for predators that consume a few large prey than for predators that consume many small prey. If the energy density of the prey increased with prey size, the variance in growth among individuals would be enhanced for predators of large prey. On the other hand, for predators feeding on just a few prey per day, the high variance in growth rate would be reduced if search rate decreased as stomach fullness increased.

A bioenergetics model of fish growth was a useful tool for evaluating the effect of the average number of prey consumed per day on the variance in predator growth rate (Figure 4). Bioenergetics models have been used for addressing many other questions (Adams and Breck 1990). Linking bioenergetics models of predators and prey by means of foraging theory should provide additional insights into the dynamics fish growth.

Because of the differences between piscivores and planktivores, the theory developed for fish foraging on zooplankton must be modified for application to piscivores. The analysis presented here shows some ways that this might be done and some consequences for variation in growth among individuals. Forage fish are not just big zooplankton.
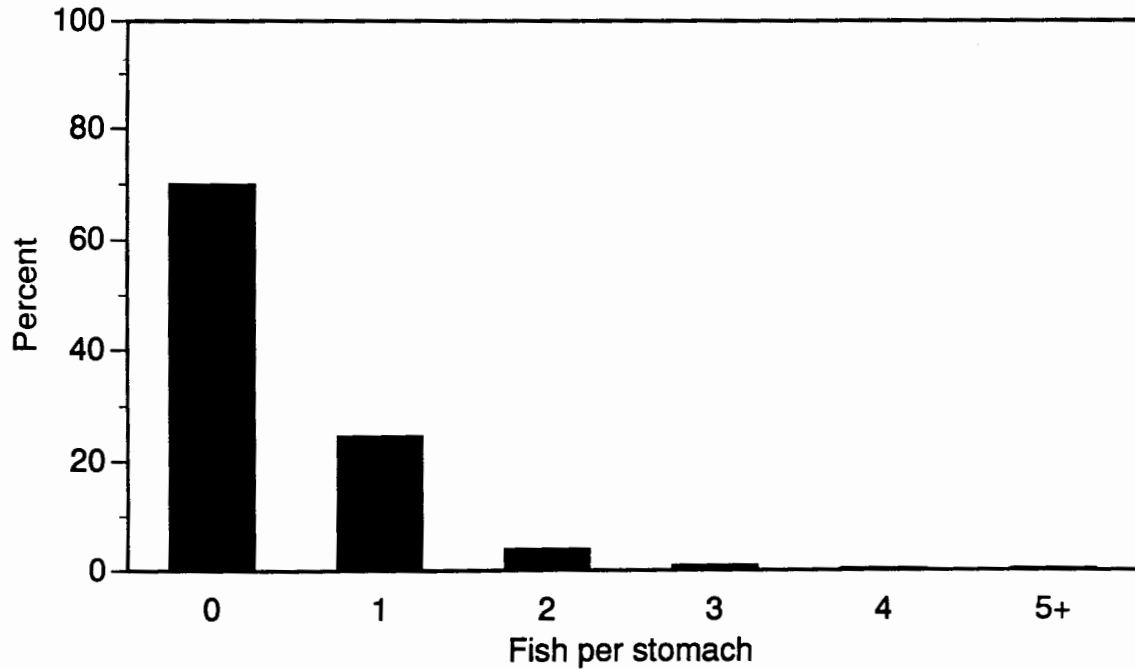
Figure 1.—The frequency distribution of number of fish per stomach for 3,551 angler-caught pike from Murphy Flowage, Wisconsin (Johnson 1969). The average is 0.37 fish per pike stomach.
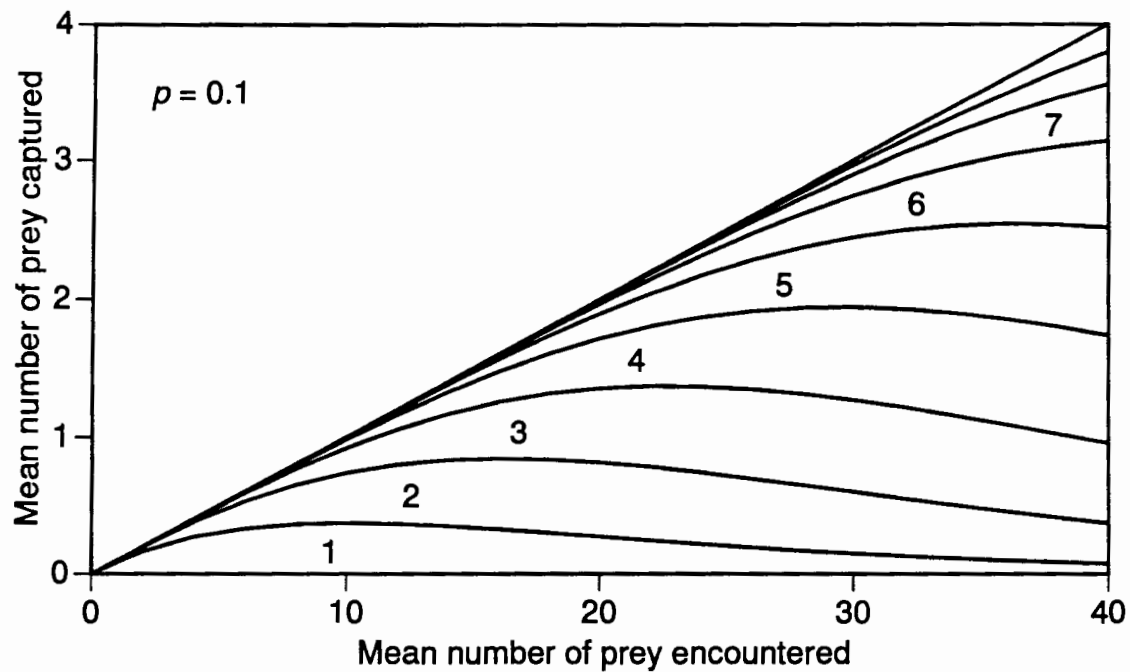

Figure 2.—A functional response for piscivores, assuming that handling time is negligible, and that the actual number encountered each day is a Poisson distribution [equation (11)] with the specified mean; p is the probability of prey capture given an encounter. The separate areas indicate the contributions to the mean value of capturing 1, 2, 3, or more prey/d.
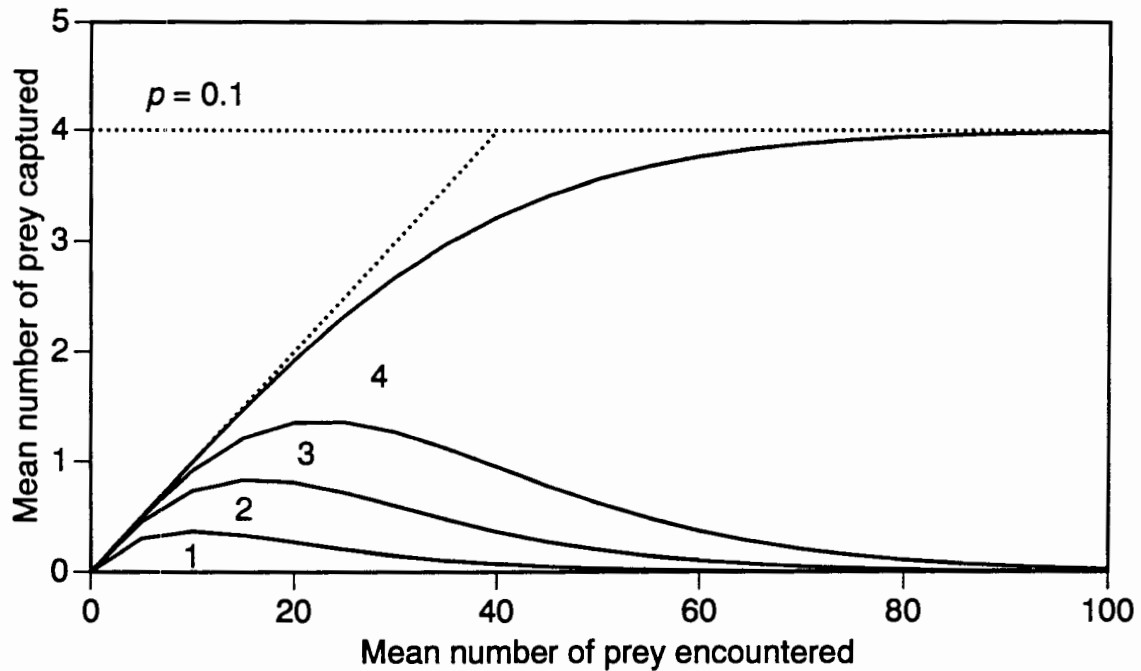
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Figure 3.—A functional response for piscivores, with the same assumptions as in Figure 2, but also assuming that foraging stops if a daily limit of 4 prey/d is reached [equation (14)]. The separate areas indicate the contributions to the mean value from capturing 1, 2, 3, or 4 prey per day.
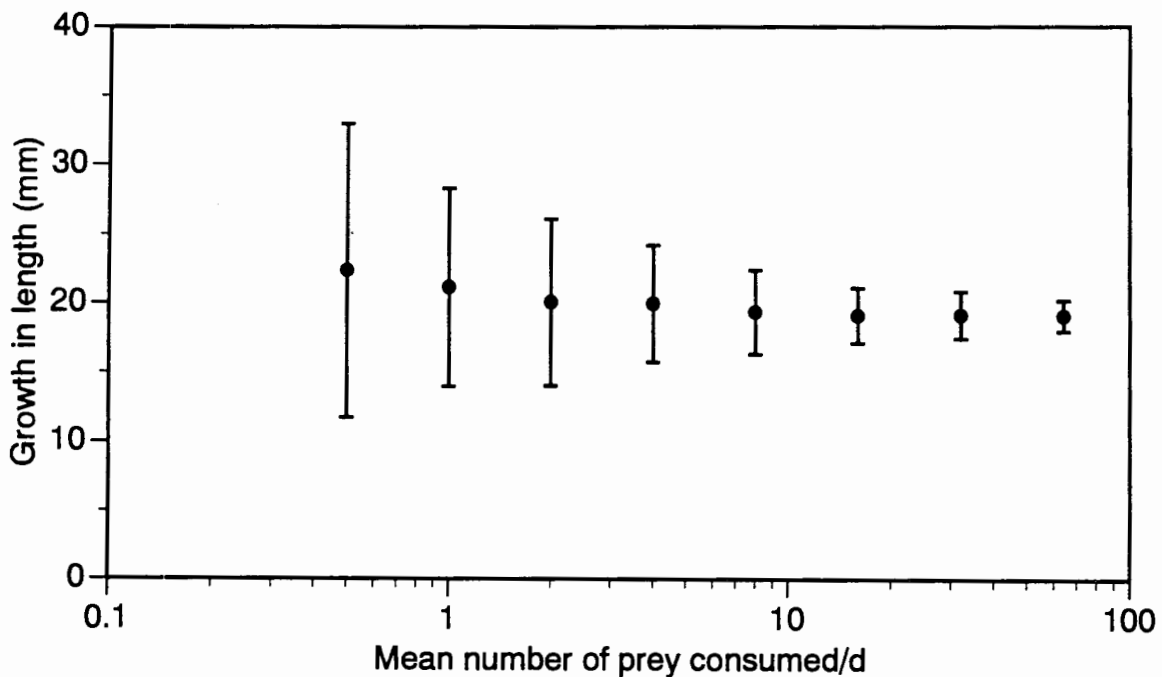

Figure 4.—Simulated 60-d growth increment (mean ±2 SD) for 100 juvenile largemouth bass with an identical starting length of 55 mm. For all groups the product of prey weight and mean number/d was the same; on each day and for each individual, the number of prey consumed that day was selected randomly from a Poisson distribution [equation (11)] with the given mean. With mean daily ration held constant, variation in growth decreases as the mean number of prey consumed/d increases.

Table 1.–Comparison of selected factors in piscivory and planktivory.

Factor	Piscivory	Planktivory
Fish gape	Critical	Important for small fish
Number of prey consumed/day	Few large prey	Many small prey
Capture success	Critical	Important for copepods, less for cladocerans
Limit to vision	Contrast?	Visual acuity
Reactive distance	Same for all prey?	Increases with prey size
Handling time[a]	Unimportant	Sometimes important

[a]Not including time for gastric evacuation or digestion.

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