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Estimating the Average Food Consumption by Fish in the Field from Stomach Contents Data

by

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ABSTRACT

It is shown that a simple Bajkov type relationship exists between the amount of food consumed and the quantity of food observed in the stomach for fish whose rate of evacuation is only a function of current stomach contents. Based on this result, an unbiased estimator of the average consumption of food by a population is derived.

RÉSUMÉ

Il est démontré qu'un rapport simple de type Bajkov existe entre le total d'aliments consommé et la quantité d'aliments observé dans l'estomac de poissons desquels le taux d'évacuation est seulement une fonction de contenu stomacale courrant. Basé sur ces résultats, un estimateur impartial de la consommation moyenne d'aliments par une population est dérivé.

INTRODUCTION

Much work has been done on estimating the food consumed by fish in the field based on the amount of food observed in the stomach (e.g., Bajkov, 1935; Webster, 1942; Darnell and Meierotto, 1962; Kitchell, 1970; Daan, 1973; Elliott and Persson, 1978; Godin, 1981; Jobling, 1981). The estimators of consumption currently used are based on the fact that for most species the rate of gastric evacuation is proportional to the quantity of food in the stomach raised to a power (Elliott and Persson, 1978; Jobling, 1981). But these techniques are biased except for particular cases. For example, Elliott and Persson's (1978) method for estimating consumption is unbiased if the fish are eating at a constant rate but biased in other situations.

In this paper it is shown that if the rate of gastric evacuation is only a function of stomach contents, then the amount of food consumed by a fish during a time period is equal to a constant times the average over the period of a transform of stomach contents, plus the level of food in the stomach at the end of the period, minus the level at the beginning. This reduces to a simple Bajkov type relationship for longer time periods. If the manner of evacuation is identical for all fish in a particular population, then similar results hold for the average consumption per fish.

ESTIMATING CONSUMPTION

A Gastric Evacuation Model

An equation of the form

$$G(t) = -\alpha S(t)^p, \quad S(t) > 0,$$
$$= 0 \qquad\quad, \quad S(t) = 0, \tag{1}$$

is often used to mathematically describe the evacuation of food from the stomach by fish (Jobling, 1981). In equation (1), $G(t)$ is the rate of evacuation at time t, $S(t)$ is the amount of food in the stomach and α and p are constants.

The critical assumption underlying model (1) is that gastric evacuation is solely a function of the amount of food currently in the stomach. In particular, α and p do not depend on the meal size.

If a fish is not eating, then the rate of change in stomach contents ($dS(t)/dt$) will equal the rate of evacuation or

$$\frac{dS(t)}{dt} = -\alpha S(t)^p.$$

Hence for this situation,

$$S(t)^{1-p} = -\alpha(1-p)t + S_o^{1-p},\ p \neq 1,\ S(t) > 0,$$
$$= 0 \qquad\qquad ,\ S(t) = 0,$$

and

$$\ln S(t) = -\alpha t + \ln S_o\ ,\ p = 1,$$

where S_o is the amount of food in the fish's stomach after its last meal. That is, the $(1-p)^{th}$ power of stomach contents will be a linear function of time for $p \neq 1$ and $S(t) > 0$, and the log of stomach contents will be linear in time if $p = 1$.

In Figure 1 are plots of the time to depletion as a function of meal size for various values of p. The value of α for each curve was chosen so that a meal of size 2 is evacuated in 2 time units. For the exponential model ($p = 1$), complete evacuation does not occur, but the same percentage of any meal is evacuated in a given length of time.

Relationship Between Average Stomach Contents and Consumption

For a fish, the rate at which stomach contents is changing at time t is equal to the rate of food consumption (R(t)) minus the rate of gastric evacuation. That is:

$$\frac{dS(t)}{dt} = R(t) - \alpha S(t)^p. \qquad (2)$$

For a period starting at time 0 of T hours duration, the average amount of food consumed per hour (C_T) during this period is:

$$\frac{1}{T}\int_0^T R(t)dt. \tag{3}$$

Solving equation (2) for R(t) and substituting it into equation (3) yields,

$$C_T = \frac{\alpha}{T}\int_0^T S(t)^p dt + \frac{1}{T}\int_0^T dS(t),$$

which equals

$$\alpha \text{ avg } [S(t)^p] + [S(T) - S(0)]/T, \tag{4}$$

where avg$[S(t)^p]$ denotes the average value of $S(t)^p$ over the period.

If the amount of food in the stomach at the beginning of the period is equal to the amount at the end (i.e., $S(T) - S(0) = 0$), then:

$$C_T = \alpha \text{ avg}[S(t)^p]. \tag{5}$$

In general, as T becomes large, the second term in equation (4) goes to zero and for this case, equation (5) holds in the limit.

Estimation of Consumption by a Population

For a population of N fish whose mode of gastric evacuation is described by equation (1) with common parameters α and p, the average consumption per fish per time unit (C_{avg}) during a period of length T is, from equation (4), equal to

$$C_{avg} = \alpha \sum_{i=1}^{N} avg[S_i(t)^p]/N + [\sum_{i=1}^{N} S_i(T)/N - \sum_{i=1}^{N} S_i(0)/N]/T,$$

$$= \alpha\ avg[S_p(t)] + [\bar{S}(T) - \bar{S}(0)]/T, \qquad (6)$$

where

$S_i(t)$	is the stomach contents of the i^{th} fish at time t,
$\bar{S}(0)$, $\bar{S}(T)$	denote the average stomach contents of the population at times 0 and T, respectively,
$S_p(t)$	$= \sum_{i=1}^{N} S_i(t)^p/N$,

and

$avg[S_p(t)]$	is the average of $S_p(t)$ over the time interval.

Assuming α and p are known, then one way to estimate C_{avg} is to choose at random times between 0 and T, say $t_1, \ldots, t_m$, and then take a random sample of k fish at each time selected. The estimator,

$$\hat{avg}[S_p(t)] = \sum_{j=1}^{m} \hat{S}_p(t_j)/m, \qquad (7)$$

where

$$\hat{S}_p(t_j) = \sum_{i=1}^{k} S_i(t_j)^p/k \qquad (8)$$

is an unbiased estimator of $avg[S_p(t)]$. To estimate S(0) and S(T), random samples of fish are also taken at times 0 and T. An estimate of the average amount of food consumed per fish per time unit during the period is from equation (6) given by

$$\hat{C}_{avg} = \alpha\, a\hat{v}g[S_p(t)] + [\hat{\hat{S}}(T) - \hat{\hat{S}}(0)]/T \qquad (9)$$

where $\hat{\hat{S}}(0)$ and $\hat{\hat{S}}(T)$ denote the ordinary sample mean of the fish sampled at times 0 and T, respectively. The variance of $\hat{C}_{avg}$ for large N can be estimated by (Cochran, 1977, p. 279)

$$\alpha^2\, var(a\hat{v}g[S_p(t)]) + (var[\hat{\hat{S}}(t)] + var[\hat{\hat{S}}(0)])/T^2 \qquad (10)$$

where

$$var(a\hat{v}g[S_p(t)]) = \sum_{j=1}^{m} (\hat{S}_p(t_j) - a\hat{v}g[S_p(t)])^2/m(m-1). \qquad (11)$$

To estimate the consumption in terms of percent body weight, the average of $S_i(t_j)^p/W_i$, where W_i is the weight of the i^{th} fish, replaces equation (8), and the average of $S_i(t)/W_i$ at times 0 and T estimates the endpoints.

DISCUSSION

Relationship with some other Methods

If gastric evacuation is as in equation (1), then the average daily ration is equal to

$$24\ \alpha\ \mathrm{avg}[S_p(t)]. \qquad (12)$$

For exponential evacuation, equation (12) is the modified Bajkov formula (Eggers, 1979).

Eggers (1979) shows for p = 1 that equation (4) is valid if R(t) does not depend on S(t). But as shown, equation (6) is true even if R(t) is a function of S(t) (as is G(t)). In fact, a relationship of type (4) will hold as long as G(t) is only a function of the stomach contents at time t.

Other methods for estimating consumption from stomach contents data, such as those in Elliott and Persson (1978) and Jobling (1981), are in effect considering the problem of estimating consumption during a period for which only estimates of stomach contents at the beginning and the end of the period are available. For example, Elliott and Persson (1978) assume that gastric evacuation is exponential, and therefore, the problem is to estimate $\mathrm{avg}[S_1(t)]$ given only estimates of S(0) and S(T) (equation (4)). To do this, they assume that during this period feeding is constant, i.e., R(t) = F, which includes the case F = 0 or no feeding. Assuming constant feeding, they show that the average hourly consumption during the period is, in the same notation as above, equal to

$$\frac{[S(T) - S(0)e^{-\alpha T}]\alpha}{1-e^{\alpha T}} . \qquad (13)$$

When $R(t) = F$, the consumption as given by equation (13) is identical to the amount given by equation (4). The accuracy of their approximation will depend on how nearly constant feeding is during the time period.

Accuracy of the Consumption Estimates

The accuracy of the estimates depends on the validity of the assumptions underlying the model. In summary, they are:

1). the rate of gastric evacuation is proportional to stomach contents raised to a power (equation (2));

and

2) the parameters α and p are constant over the time period and for all fish in the target population.

Assumption 1) may be more nearly correct if different food categories are treated separately. Similarly, for Assumption 2) to hold it may be necessary to apply the model separately to subgroups of the population and to partition longer time periods into shorter intervals during which the parameters can be assumed to be constant. A further source of bias is the possible inability to randomly sample the target population. The difficulty in conducting truly "random" surveys at sea is well-known, and for large marine surveys, a systematic sample over space and time is probably the only practical method to sample the population. By proper sample design or proper weighting in the analysis, this source of bias, though not entirely eliminated, may be minimized.

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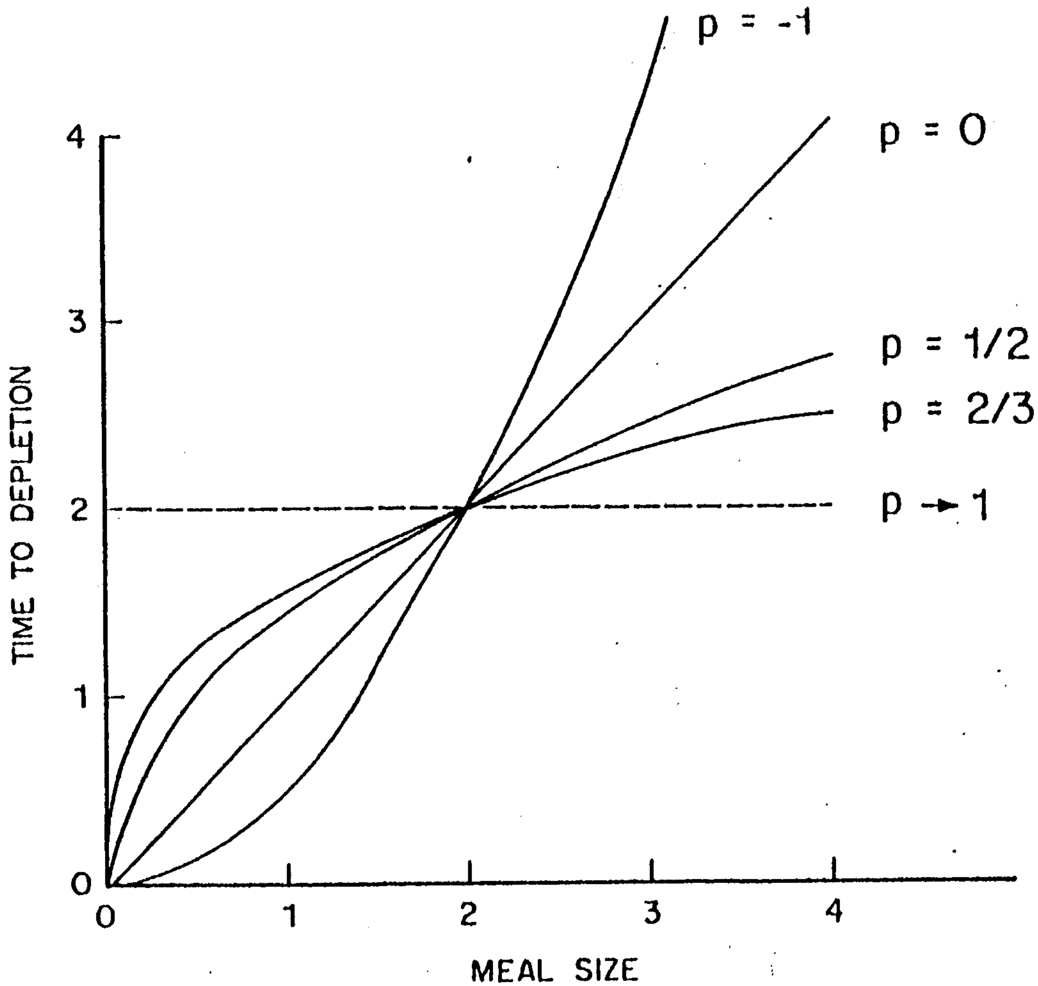
Figure 1. Time to depletion as a function of meal size for several gastric evacuation models. For each p, α is selected so that a meal of size 2 is evacuated in 2 time units. The dashed line represents the limit as p approaches 1.


p = -1
p = 0
p = 1/2
p = 2/3
p → 1
TIME TO DEPLETION
MEAL SIZE
0
1
2
3
4