ON THE RELATION BETWEEN FEEDING RATE AND
STOMACH CONTENTS IN FISHES

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Abstract

If the fraction of a food item remaining in a fish stomach t time
units after ingestion is f(t), regardless of the other food eaten
before or during these t time units, then the feeding rate r,

\[ r = \text{amount of food eaten per unit time} \]

is related to f(t) by the formula

\[ r = \frac{\bar{W}}{\int_0^\infty f(t) dt} \]

where \( \bar{W} \) is the average stomach content. Thus, in order to estimate r
from the observed stomach contents of a sample of fish it is necessary
to experimentally determine the digestion curve f(t) and calculate its
integral

\[ A = \int_0^\infty f(t) dt \]

Feeding rate is then estimated by

\[ \hat{r} = \frac{1}{A} \text{(average stomach content)} \]

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The weight (or number) of food items in the stomachs of fishes collected at a single point in time is commonly used as a basis for estimating feeding rate. Individual items in the stomach are in varying stages of digestion, depending upon when the item was ingested, and some methods of estimating feeding rate entail a type of back-calculation to reconstruct the feeding process which produced the observed stomach contents. Thus, the time of ingestion of each remnant and its original form at the time of ingestion are reconstructed in so far as this is possible.

If we can assume that the stomach contents include the remains of all food items eaten during the preceding V units of time, and none eaten earlier than that, then if P is the reconstructed weight (or number) of items eaten during this V period, the ratio \( r = \frac{P}{V} \) is by definition the rate of feeding for this V period.

If feeding is a discrete process in the sense that individual items are ingested at discrete points in time:

\[
\begin{align*}
M_1 & \quad M_2 & \quad M_3 & \quad M_4 \\
T_1 & \quad T_2 & \quad T_3 & \quad T_4
\end{align*}
\]

then the long term average feeding rate is
\[
\begin{align*}
\bar{r} &= \frac{\bar{M}_1 + \bar{M}_2 + \bar{M}_3 + \cdots}{T_1 + T_2 + T_3 + \cdots} = \frac{\bar{M}}{\bar{T}}
\end{align*}
\]

where \( \bar{M} \) is the average meal size and \( \bar{T} \) is the average period between feedings. The ratio \( \frac{P}{V} \) therefore estimates \( \bar{M}/\bar{T} \), and if we could further assume that each meal is fully digested before the next meal is taken then

\[
\bar{M} = \frac{\text{no. or wt. of prey (reconstructed)}}{\text{no. of predators with food}}
\]

and \( \bar{M}/\bar{r} \) then estimates \( \bar{T} \), the average period between feedings.

If stomach contents cannot be sorted and/or the initial weight (or number) reconstructed then \( \bar{r} \) may be estimated from the observed weight \( \bar{W} \) of the stomach contents by

\[
\hat{r} = \frac{\bar{W}}{A}
\]

where \( A \) is the area under the digestion curve. This result can be deduced, for example, from the following model.

**Digestion model**

If an amount \( M(t) \) is ingested at time \( t \) then at time \( t+x \) the amount remaining from \( M(t) \) is

\[
M(t, x) = M(t)f(x) .
\]

The function \( f(x) \) might be assumed to have the property

\[
f(x)f(y) = f(x+y) ;
\]

\[1\] This property is not essential to the subsequent argument. Note that this property holds if and only if \( f(x) = \exp(-x/A) \).
thus, this property did hold then at time \( t+x+y \)

\[
M(t,x+y) = M(t,x)f(y) \\
= M(t)f(x)f(y) \\
= M(t)f(x+y)
\]

**Definitions**

- \( \bar{M} = \text{average meal size} \)
- \( \bar{T} = \text{average time between feedings} \)
- \( \bar{W} = \text{average amount of food in the stomach} \)

\[
A = \int_{0}^{\infty} f(x)dx
\]

**Theorem**

\[
\bar{W} = \frac{\bar{M}}{\bar{T}} A
\]

**Proof**

We assume that feeding occurs at discrete points in time, and starting with an amount \( M_0 \) in the stomach at time \( t=0 \), let the first meal of size \( M_1 \) occur at time \( T_1 \); after a waiting period of duration \( T_2 \) the second meal of size \( M_2 \) occurs at time \( T_1 + T_2 \), and so on. The graph of the function \( W(t) \) then has the form:
Over a period of \( K \) such intervals the average value of \( W(t) \) is

\[
\frac{\int_0^{T_1 + \cdots + T_K} W(t) \, dt}{T_1 + \cdots + T_K} = \frac{1}{T_1 + \cdots + T_K} \left[ M_0 \int_0^T f(x) \, dx + M_1 \int_0^{T_1} f(x) \, dx + M_2 \int_0^{T_2} f(x) \, dx + \cdots + M_{K-1} \int_0^{T_{K-1}} f(x) \, dx \right]
\]

Hence

\[
\bar{W} = \lim_{K \to \infty} \frac{\int_0^{T_1 + \cdots + T_K} W(t) \, dt}{T_1 + \cdots + T_K} = \frac{1}{T} \int_0^T f(x) \, dx = \frac{A}{T}.
\]

**Note**

In order to apply this result it is necessary to know \( A \) rather than \( V \) in

Digestion Curve: $f(t)$

In fact, \( V \) need not exist.