A New Approach in Modelling Gastric Emptying in Fish

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Abstract: In this study, gastric emptying and factors affecting gastric emptying in fish are briefly reviewed. How stomach-sampling time affects gastric emptying curves in relation to realising the chyme in fish is presented. A new modelling approach describing gastric emptying in fishes is also given.

Key Words: Gastric emptying, models, sampling time

Balıklarda Sindirimin Modellenmesi Üzerine Yeni Bir Yaklaşım

Özet: Bu çalışmada balıklarda mide sindirimi ve mide sindirimine etki eden faktörler kısaca irdelendi. Aynı zamanda örnekleme zamanının sindirim eğrisine nasıl etki ettiği gösterildi. Balıklarda mide sindirimini matematiksel olarak modelleyen yeni bir yaklaşımda bulunuldu.

Anahtar Sözcükler: Mide sindirimi, modeller, örnekleme zamanı

Introduction

Current approaches to fisheries assessment include studies of the interaction between predators and their prey. Predation is a major component of natural mortality for most fish stocks and information is urgently needed on feeding rates for multispecies fishery assessment.

Food consumption rates of fish, and factors which govern feeding rates are of interest in studies of fish production, the ecology of fish populations and even the behaviour of fish (1). With the current interest in multispecies fisheries management and total ecosystem management, it is essential to understand the role of fish predators within the ecosystem (2,3). As a part of this, it is necessary to quantify the feeding habits and daily ration of major species.

There are two fundamental problems to be addressed to allow understanding of the interaction between a predator and its food resources. These are how much and how often the predator eats prey of a specified type. The answers to these questions will be provided by the determination of a combination of intrinsic factors (e.g., size of animals, gastric evacuation rates and metabolic rates) and extrinsic factors, such as food type and availability, as well as the effect of temperature, disease, oxygen levels, salinity and light (4).

The quantity of food consumed by fish has typically been estimated on a daily basis. Most researchers have surveyed the quantities of food found in the stomach of the individual during a 24-h period. Determination of food intake from stomach contents requires estimates of gastric emptying rates.

The rate at which food passes from the stomach or gastric emptying rate (GER; as mass or energy per unit time) has been intensively studied in a variety of vertebrates and invertebrates. In addition to the estimation of GER, the time (h) for total clearance of the stomach, gastric emptying time (GET), has also been recorded (usually in hours).

In this study, therefore, recent progress made in gastric emptying studies, factors affecting GET and

models describing the gastric emptying rates and times will be once briefly reviewed and a new modelling approach to gastric emptying in fishes will be presented.

Gastric Emptying in Fish

The importance of the rate of gastric evacuation is simply based on the assumption that over longer time periods the rate at which food is evacuated from the stomach is equal to the rate at which food is ingested. However, in many species during a given feeding time, food intake is faster than the emptying rate and feeding is followed by a non-feeding period as emptying proceeds. Emptying rate data are then used to estimate the rate of food consumption (5-10). Such studies eventually provide important information on inter-specific feeding interactions, such as competition and predation. Data on digestion rate is also useful for determining maintenance and maximum daily rations, and it is essential in order to elucidate energy transfer and food conversion efficiency for the species being examined if the energy content of foods is known within the trophic level.

The study of digestion in fish goes back to the beginning of the late 1800s (11). Earlier, attention had been concentrated on the structure and function of the alimentary canal of fish. Later, many researchers focused their attention on the gastric emptying process including studies on stomachless fish such as *Blennius pholis* L. (12) and *Ptychocheilus oregonesis* (13).

There are several established methods for studying gastric emptying. These include serial slaughter (13), X-radiography (14), gastric lavage technique (15), radio isotopic methods (16) and the use of emetics (17,18).

Numerous studies have also been conducted on a variety of fish species to see the factors affecting gastric emptying. They all have shown that the GER is influenced by a number of factors. These factors have been intensively reviewed by Kapoor et al., (1), Fänge and Grove (19), and Smith et al. (20). Among these factors, temperature (21,22), fish size (20-22), meal size (5,12,21,22) and food quality (18) have been of major importance.

Digestive Function of the Stomach and Model Development

Grove and co-workers (9,12,13,15,18) have carried out quantitative studies on gastrointestinal processing

rates in flatfish and their findings will serve as a null hypothesis for this study.

The major functions of the vertebrate stomach are to receive the ingested food items, to kill them and start the digestion process. Mathematically, it is possible to construct a simple, predictive, quantitative model of the process of gastric emptying in fish. During the main phase, in which the digestible nutrients are processed, the digestion rate at any moment should depend on the detection of food in the stomach. This stimulates the release of gastric secretions acting on the stomach content. To model this, a number of simplifying assumptions can be made:

1) **The stimulus:** In many post-juvenile fish, maximum stomach volume (S_{max}) is directly proportional to body weight ($S_{max} = a\ W$, where W is the body weight in g and S_{max} is in ml). Stomach content (S g) cannot exceed S_{max} for most foods. Changes in stomach contents (S) induce stretch in the stomach wall, which is detected as a linear stretch of branches of sensory cells in the gut wall, which can orient in any direction. The stimulus should therefore be given by

$$Stimulus = a'\ (S/W)^{1/3}$$

2) **The response:** Despite the action of the muscular coats (mainly promoting mixing of the gastric contents) the limit to the digestion rate is the secretory activity (acid, pepsin and mucus) of the gastric epithelium. Given the limited degree of epithelial folding of the epithelium, and the uniform distribution in a stated species of oxynticopeptic cells by area in fish of different sizes, the secretory (response) rate of fish at a stated temperature must (following from assumption (1) above) be related to stomach surface area. Secretory rate (E) could therefore be given as

$$E = b\ W^{2/3}.$$

3) **The effective food surface:** Digestive secretions released as a result of assumptions (1) and (2) given above act on the surface area of the food bolus. It can be simply imagined a fish chooses similar-shaped single items of food in relation to its body weight, or conglomerates multiple items of food taken over a short time period into a bolus of food, which is compacted in the stomach. Therefore, the food mass can only be digested at its surface and it is described by the area formula

$$A = c\ S^{2/3}.$$

The digestion rate (dS/dt; GER) at a given temperature is therefore likely to be a combination of stimuli, linked to response but modified by effective surface. Using these equations the following is derived

$$\frac{ds}{dt} = - K\left(\frac{S}{W}\right)^{1/3} \cdot W^{2/3} \cdot S^{2/3} \qquad (1)$$

where the constant K combines the constants of proportionality in the earlier equations. This can be simplified as

$$\frac{ds}{dt} = - KW^{1/3}S \qquad (2)$$

At a given temperature, the digestion rate of a given mass of food increases with fish size. It is also clear since

$$\frac{1}{S} \, ds = - K \cdot W^{1/3} \cdot dt \qquad (3)$$

That, for a given fish size, the emptying of a single meal will follow an exponential curve with time

$$S_t = S_o e^{(-Dt)} \qquad (4)$$

where S_t is the residuum of the initial meal (S_o, g) at a stated time (t hours) after feeding, and $D = K \, W^{1/3}$.

This basic formula is unlikely to apply in practice unless the ingested food is of such low nutrient content that gastric emptying proceeds without an inhibitory feedback from the release of intestinal hormones mentioned earlier. It is much more likely that this basic emptying curve is modified; emptying may be constrained into a series of pulses so that the anterior intestine is not overloaded with excess chyme, which would decrease the efficiency of intestinal digestion. Alternatively, the inhibitory feedback may be more continuous, simply causing a decrease in emptying rate from that predicted by the exponential model. In this model, the stomach reserves to itself the role of food reservoir and supplies the intestine with chyme at a suitable rate for processing.

The next step in developing the model is to introduce appropriate restrictions of gastric emptying. A simple model assumes that intermittent feedback from the intestinal hormones simply interrupts this exponential emptying rate at intervals. It appears reasonable to assume that pulses of chyme are released, of an equal size, that maximise the intestinal digestion rate without over-loading the capacity to release bile, pancreatic and intestinal secretions. Such a model is developed in Figure

1. In this example, the original meal is emptied in five pulses (P). In addition, the last part of the meal, which would typically comprise indigestible residues, is emptied rapidly (linearly) by true peristalsis (F: the house keeping of the gut); this ensures that (unlike an exponential curve) the stomach empties in a finite time. Examination of Figure 1 shows that if sporadic observations from a fish (or individuals from a synchronously fed group of fish) are taken, then an emptying curve will be obtained which varies according to when samples are taken in relation to the occurrence of the pulses of emptying. Observations on curve 1 happen to fall at times when a pulse is just completed, curve 2 values are obtained in mid-pause and curve 3 values apply at the end of pauses. Of course, other combinations of sampling occurrences are possible. It is clear that the pulsed emptying curve is no longer exponential.
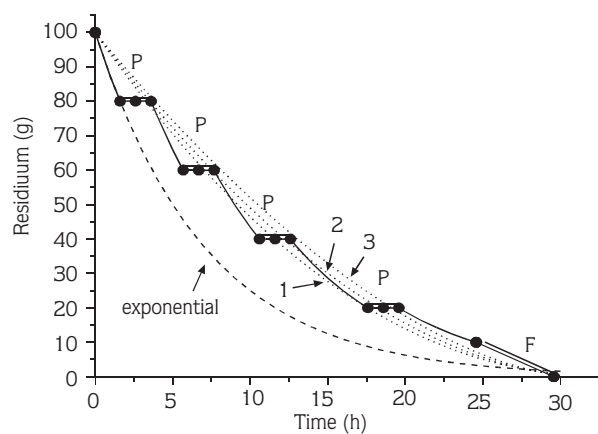

Figure 1. The effect of stomach sampling time on gastric emptying curves in relation to the releasing pulses of chyme in fish.

It is common in the literature to find that collected data are reasonably well described by a power equation

$$\frac{ds}{dt} = - KS^b \qquad (5)$$

which, on integration, gives a linear relationship

$$S_t^a = S_0^a - aK \cdot t \qquad (6)$$

where $a = 1 - b$.

In effect, the simplifying assumption was made that gastric emptying approximates a monotonic curve of the form

$$S_t = \left[S_0^a - aK \cdot t \right]^{\left(\frac{1}{a} \right)} \tag{7}$$

Curves 1 to 3 in Figure 1 were therefore fitted using a search routine (written on the spreadsheet QuattroPro) to select the best power function (a). In this example, the best fits (judged by minimising the sum of the squares of the deviations of the fitted curve (equation 6) from the observed values) were 0.466 (curve 1), 0.523 (curve 2) and 0.594 (curve 3). These values happen to be close to the value of 0.5 suggested by Jobling (23, his square root model), although based on a very different derivation. Jobling achieved this predicted value for "a" simply by assuming that the perimeter stretch of a tube of fixed length is proportional to the square root of the enclosed volume. This latter model does not easily represent the known sequence by which the stomach and intestine of a fish process food. It is, however, clear that the results obtained by fitting the power curve to the emptying process of fish of known size, fed a stated meal at a stated temperature need not necessarily fit a convenient power function. The value of "a" may vary according to the times samples are taken, the frequency and duration of pauses in emptying, the size of the fish, the temperature and even individual variations in gastrointestinal processing rates.

Figure 2 examines the consequence of feeding sub-maximal meals to a fish of known size at a stated temperature. If a reduced meal is given, it can be expected to follow the curve for a maximum meal, but start at a lower point on the trajectory. Reducing the meal by 40% or 60% of the maximum decreases the
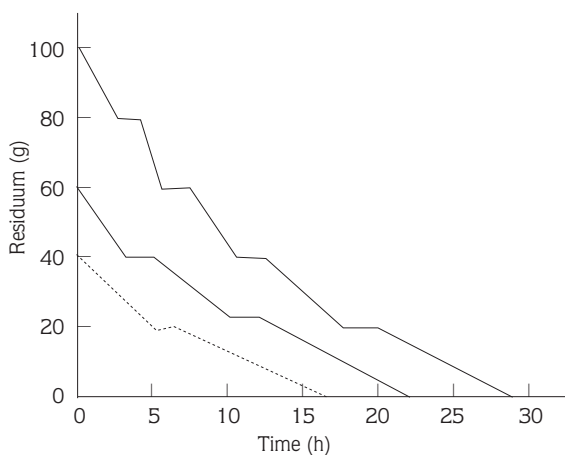

Figure 2.   The consequence of feeding sub-maximal meals to a fish of known size.

initial GER; GETs, however, are reduced by only 26% and 43%, respectively.

Nevertheless, careful experimentation can derive population averages for a species under stated conditions, where appropriate values of "a" and "K" are obtained. They enable the likely course of gastric emptying to be predicted. Such prediction can then be used to suggest the shape of the "return of appetite" curve for fish in captivity or for converting sequential field observations on stomach contents into estimates of feeding rates.

Grove et al. (17) extended Jobling's power model to include changes in the rate of gastric emptying when several assumptions of the above model are relaxed. Equation (6) was taken to describe the digestion of a single item of food of a standard shape and nutrient quality. Three further conditions were examined:

1) The consequences of eating several of the standard food items in a meal, where the items are conglomerated into a bolus subject to gastric digestion on the surface.

2) The consequences of the items remaining separate, thereby retaining a larger surface area than in condition (1), with no limitation of available gastric secretions.

3) Conditions as in condition (2) but where available gastric secretion is limited, and food items must share the available secretions.

The overall emptying rates of combined stomach contents, when "n" food items of similar size are ingested by a fish, given as aK in the linear form of the basic model (Equation 6), became

GER:

Condition 1: aK (unchanged)

Condition 2: $aK.n^a$ (increased)

Condition 3: $aK.n^{-1}$ (decreased)

and the gastric emptying times for a meal size S_o, originally given as

$$\frac{1}{aK} S_0 \tag{8}$$

became

$$\frac{1}{aK} (nS_0)^a \ \ldots \ldots \ \frac{1}{aK} n^{-a}(nS_0)^a \ldots \ldots \frac{1}{aK} n^b (nS_0)^a \tag{9}$$

for conditions 1, 2 and 3, respectively. This model predicts that as meal size increases, the GET (in comparison with the basic model) should

GET:

increase (condition 1)

remain unchanged (condition 2)

increase (condition 3)

The digestion rate of a single item, given as aK in the basic model, should become

$$aKn^{-a}, \quad aK, \quad aKn^{-1} \qquad (10)$$

So that the individual item digestion rates should

decrease (condition 1)

remain unchanged (condition 2)

decrease (condition 3)

This model has been tested for a number of diets in different fish species. Condition 1 (fusion of multiple items into a single bolus) was detected in *Limanda* (15), whilst competition for gastric juices (condition 3) and condition 2 were found in *Scophthalmus* (17) and in *Merlangius merlangus* (22,24), respectively.

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