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Diel pattern of food intake in whiting (*Merlangius merlangus*) investigated from the weight of partly digested food particles in the stomach and laboratory determined particle decay functions

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The daily periodicity of the food intake of North Sea whiting feeding on sandeels was investigated by means of analysing the weight of partly digested prey particles found in the stomachs. The digestion times corresponding to the weights of partly digested sandeels were estimated from the assumed weight at ingestion as derived from the length–weight relationship of the prey and a gastric evacuation model that was based on experimental data with whiting fed on sandeels. The results indicated a single feeding peak with a maximum feeding between 2200 and 2400 h and minimal food intake between 0800 and 1000 h. Additional simulation exercises were performed to investigate the precision of the back-calculation method. These simulations revealed that the scatter of individual weights around the mean weight at a given length is transformed into a corresponding scatter in the estimated times of food intake. The main conclusion from the analysis that whiting appear to feed during the night hours was found to be robust against changes of the actual parameters of the particle decay function within the range of the most likely values.

Key words: whiting, food intake, diet pattern, gastric evacuation, sandeel, North Sea.

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Introduction

Investigations into daily periodicity in feeding of fish have been generally based on the analysis of changes in total stomach content during a 24 h period. This approach gives meaningful results if small predator fish are investigated and/or environmental temperatures are high and food particles are small (Arrhenius and Hansson, 1993, 1994; del Norte Campos and Temming, 1994). In these cases, gastric evacuation times are significantly shorter than 24 h so that periods without food intake are indicated by decreasing stomach contents. In larger fish and/or at lower temperatures and with larger food particle sizes gastric evacuation is decreased, resulting in gastric evacuation times of one to several days (Daan, 1973; dos Santos and Jobling, 1992). Long gastric evacuation times thus obscure the diel patterns of mean total stomach content. The daily pattern of total stomach content is further complicated by the intake of various prey species, since the time of intake is also influenced by the diel behaviour patterns of the prey (Burrows *et al.*, 1994.

Various authors have recorded the degree of digestion of prey organisms and this information should, in principle, help to identify times of maximum food intake more precisely. However, the coarse rank scales with very few different digestion stages mostly used do not allow estimation of the ingestion times of the prey items with sufficient accuracy. Also, in most studies no additional digestion experiments were performed to establish a link between digestion times and degrees of digestion. Griffiths (1976), however, studying perch (*Perca fluviatilis*) feeding on common New Zealand bullies (*Gobiomorphus cotidianus*) introduced a metric scale for the digestion stage, which is defined as the percentage of weight of the partly digested prey relative to the weight of this prey at the time of ingestion. The weight of a prey at ingestion was back-calculated from the length of the partly digested prey by means of a length–weight relationship (established for fresh prey).

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Griffiths (1976) applied an exponential gastric evacuation model to estimate the exact times of digestion and food intake for the individual prey items found in perch stomachs. The exponential evacuation model was fitted to data on total stomach content over time from a single meal evacuation experiment. The same approach was used by Degnbol (unpubl. data), who communicated the idea to us.

In this investigation we have applied the method of Griffiths (1976) to a field situation in the North Sea, where a local population of adult whiting was almost exclusively feeding on sandeels. The concentration on such a homogeneous situation should help to avoid any confusions from differences in gastric evacuation rates and differences in the diel availability of prey items. We conducted additional gastric evacuation experiments with whiting of the same size fed on sandeels. Here, we focused on a quantitative description of the decay of individual food particles (sandeels) which is different from the description of the stomach evacuation. If stomach evacuation is studied, usually the total content of the stomachs is measured, whereas in our case the weight of individual partly digested prey organisms in the stomach is measured, excluding the detached material of the prey organisms which is still found in the stomach.

Data were analysed to test the hypothesis of the existence of a daily feeding pattern in adult whiting. Results from additional simulations will be presented here, in order to give an indication of the accuracy of the presented methodology and the sensitivity of the results with regard to the parameter values used in the particle decay model.

Materials and methods

Field data

Whiting were trawled from a 10 nmi × 10 nmi box at 57.53°N, 0.54°W during 24 h fishing in May/June 1992. A total of 23 hauls was carried out with the ICES standard GOV-trawl (towing time: 30 min) between 0200 h and 2300 h (30.5–1.6.92). From each haul 30 whiting (size class 25–29.9 cm) were sampled at random, their stomachs were removed and immediately deep frozen at −30°C.

In the laboratory the contents of each stomach were analysed separately with regard to individual food particles (only sandeels) and total stomach content weight. For each partly digested sandeel found in a stomach, the wet weight and total length were measured. When the standard length could not be determined due to advanced digestion, alternatively several partial lengths (anterior anal, posterior anal length and the length between the end of the operculum and the anus) were measured. These were converted later into standard lengths at the time of ingestion. Regression equations relating sandeel standard lengths to partial lengths were determined together with the length–weight relationship from fresh sandeels, sampled for this purpose from the same trawl catches.

Morphometric analysis of fresh sandeels

Linear functions were used to describe the relationships between standard length (TL) and partial lengths (XL). The back-calculation of the weight of a sandeel at time of ingestion (G) was done using the length–weight relationship:

$$G = k * TL^a \quad (1)$$

where G = total weight at time of ingestion, k = constant, a = exponent. Parameters k and a were estimated by means of non-linear regression using the NONLIN procedure in SPSS for Windows.

Gastric evacuation experiments

Whiting used for gastric evacuation experiments were caught by hand-lining in the harbour of Hirtshals (Denmark) and had spent two years in the experimental aquarium of the North Sea Center (Danish Institute for Fisheries Research) prior to experiments. For the experiments, 16 individuals with length 25–29.9 cm were chosen (mean length 27.5 cm, s.d. 6.48, mean wet weight 224 g, s.d. 16.48). These fish were transferred to four glass fibre tanks with diameter of 1 m. Each tank was subdivided into four compartments by perforated plastic walls in order to keep the individual fish separated from each other. Water was supplied through a pipeline from the North Sea at 10.4°C, and variations in temperature were negligible. Prior to the evacuation experiments the fish were acclimatised to the compartments and the experimental food for 11 d. The sandeels used in the experiments were sorted fresh, stored deep frozen, and thawed immediately before feeding. Each individual meal consisted of one sandeel with a weight of 7 g. Unfortunately the only sandeels available at that time were smaller than those found in the stomachs of the whiting from field samples. It has been shown, however, that the type of gastric evacuation model used in this study with values of the shape parameter b (Equation 3) in the range of 0.3 to 0.5 gives good predictions of evacuation rates for variable meal sizes (Temming and Andersen, 1994). In order to test the sensitivity of our results to the choice of the parameter b, a low (b = 0.3) and a high (b = 0.5) value were also used in the calculations. In these cases the evacuation model was fitted to the data with parameter b fixed to one of these values and only the parameter R was estimated from the data.

No food was offered within 72 h before the start of an evacuation experiment, since it was known from Jones (1974) and Bromley (1988) that evacuation of a comparable meal should be completed within this time. This procedure guaranteed just empty stomachs before the start of experiments without starvation of the fish. It can be seen from the results in Figure 5 that the evacuation time was more than 2 d, so that the stomachs were empty for less than 1 d. The occurrence of some fraction of empty stomachs is frequently observed in field data (e.g. Hislop *et al.*, 1991 for whiting); in our data set 22.3% of the investigated stomachs were empty. This implies that limited periods without food in the stomachs are part of the natural feeding pattern.

At fixed intervals after the experimental meal two to four fish were removed from their compartments for gastric lavage. Fish were anaesthetised using MS222 (Sandoz, 1:20 000) until they turned upside down. A fine silicon hose was introduced into the mouth of the anaesthetised fish. Salt water was pumped through the hose and was flushed against the oesophagus. This procedure led to spontaneous regurgitation in most of the fish. Then the hose was introduced into the oesophagus and into the stomach and all food particles were flushed into a plastic container with a bottom of fine-meshed gauze. The main bolus of the partly digested sandeel was removed from the container for weight and length determination. The weight of the loose material was determined separately.

Gastric evacuation model

The ‘‘general’’ evacuation model (Jones, 1974) was fitted to the data by means of non-linear regression techniques following the procedure described by Temming and Andersen (1994). This model includes convex, linear, exponential and intermediate curve types and the shape of the curve is determined by a parameter (b), which is also estimated from the data:

$$\frac{dS}{dt} = -R*S^b \quad (2)$$

Integration of Equation (2) results for $b \neq 1$ in:

$$S_t = [S_0^{(1-b)} - R*(1-b)*t]^{\frac{1}{1-b}} \quad (3)$$

where: S_t = residual stomach contents at time t, t = time after ingestion, S_0 = initial weight of ingested meal, b = parameter that determines the shape of the curve, R = constant, depending on: temperature, predator size, prey and predator species and others.

Temperature correction of the parameter R

Since it was not possible, due to technical restrictions, to perform the laboratory experiments (10.4°C) at exactly the same temperature as that found during the field sampling (7.9°C), a temperature correction had to be applied to the estimated particle decay functions. Following Jones (1974) it was assumed that parameter b is not influenced by temperature and the temperature correction was therefore applied to parameter R, which is assumed to increase exponentially with temperature:

$$R_{T1} = R_{T2}*e^{A*T} \quad (4)$$

This type of temperature model has successfully been used to describe experimental results by Tyler (1970) for cod with A = 0.13, Elliott (1972) for brown trout with A = 0.11, Jones (1974) for whiting, cod and haddock with A = 0.081, Kiørboe (1978) for flounder with A = 0.081, Bagge (1981) quoting Hodal (1977) for cod with A = 0.073 and dos Santos and Jobling (1992, 1995) for cod with estimates between 0.1 and 0.13. We have applied the midpoint of the range (A = 0.1) of estimates to our data. The effect of a low (0.075) or a high value (0.13) for this parameter on the results is also investigated. Tyler (1970) has shown that the exponential relationship is only valid within a limited temperature range for cod, approximately between 2 and 10°C, and that evacuation rate actually decreases if temperature exceeds 15°C. However, in our case no bias is expected since we have applied the temperature correction only between 10.4°C and 7.9°C and it is unlikely that the temperature optimum in whiting is below that of cod, which has a pronounced preference for colder water, when compared with whiting.

Back-calculation of the digestion times and times of food intake of sandeels from field stomachs

The fresh weight at time of ingestion of sandeels found in whiting stomachs in the field can be derived from its length using a length–weight relationship. The difference between the weight of the partly digested sandeel and the fresh weight of this sandeel at the time of ingestion now is a function of the total (gastric) digestion time. Therefore the digestion time can be estimated from the weight difference and the experimentally determined particle decay function.

The calculation of the digestion time for a sandeel was carried out using Equation (3) solved for t:

$$t = \frac{(S_t^{(1-b)} - S_0^{(1-b)})}{-(1-b)*R} \quad (5)$$

where t = total (gastric) digestion time (h), S_0 = fresh weight of the sandeel, S_t = rest weight of the sandeel.

From the total digestion time of a sandeel in the stomach of a whiting and the time of day when the whiting was caught (mean time of tow duration) the time

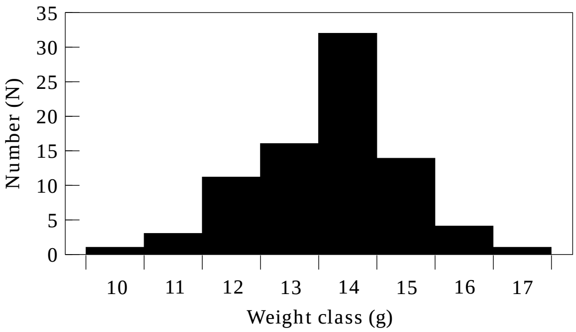


Figure 1. Variation of fresh weight for 14 cm sandeels from the trawl catches.

of day of ingestion for the sandeel was back-calculated. The (day) time at ingestion (t_i) was derived by subtracting the back-calculated digestion time (t) from the time of catch (t_c).

Simulations

Simulation 1

A simple simulation was performed in order to give an indication of the accuracy of the back-calculation method. The main problem of this method is caused by the estimation of the weight of a prey item at ingestion from the length of the partly digested prey found in the stomach. The length–weight relationship relates the length of the partly digested prey always with the mean weight of fresh prey at this length, regardless of whether this particular prey was originally heavier or lighter than average. Since the variability in the condition factor is considerable, this translates into a corresponding scatter of the back-calculated digestion times, if prey items with identical lengths but variable weights were ingested at the same time.

In order to quantify this phenomenon, an artificial data set was constructed, which consisted of 1000 sandeels of identical length (14 cm). The distribution of weights of these 1000 sandeels was derived from a sample of fresh sandeels from the trawl catches. However, since the number of specimens at this length was limited, the weight scatter was estimated from all data (length range 13–22 cm) according to:

$$W_{14} = \frac{W_{TL} * 14^{a}}{TL^{a}} \quad (6)$$

where: W_{14} = weight of a sandeel at 14 cm, W_{TL} = weight of a sandeel at length TL, a = exponent of the length–weight relationship.

With this method relative deviations of individual weights from the mean weight at any lengths are transformed into corresponding deviations at 14 cm. Figure 1 summarises the resulting weight distribution of 14 cm sandeels.

These data were used to generate an artificial set of partly digested sandeels assuming identical feeding (1300 h) and digestion times (48 h) for all 1000 sandeels. This corresponds to a situation where 1000 whiting predators have eaten one 14 cm sandeel each at exactly 1300 h and been caught 48 h later. The distribution of wet weights of partly digested sandeels after 48 h was derived from the initial distribution of fresh weights of 14 cm sandeels applying the gastric evacuation model (Equation 3, and parameters from Table 4) to the individual sandeel weights. The resulting distribution of weights of partly digested sandeels was then treated exactly in the same way as the data set that was derived from the field stomachs. The back-calculated digestion times should ideally be 48 h for all 1000 sandeels.

Simulation 2

Another simulation with the same basic design as described above was performed in order to improve the interpretation of the field data with regard to the width of the feeding interval. In a pre-exercise the uniform feeding time was varied in order to minimise the sum of the squared deviations between the simulated results and the results from the field data (as numbers of prey taken per 2-h interval). The feeding time was then fixed to the value that produced the minimum sum of squared deviations. It was then assumed that the individual times of food intake were normally distributed with pre-defined standard deviation. Eight situations were analysed with standard deviation varying from 1 to 8 h. For each situation 20 repeat runs were performed with random allocation of individual sandeel weights to the individual feeding times. For each run the back-calculated numbers of sandeels eaten per 2-h interval were compared with the results from the analysis of the field data. The sum of the squared deviations between the medians of the simulation results and the field results was taken as an indicator of the similarity between both. It was also investigated whether a feeding situation with two narrow feeding peaks at dusk and dawn could produce a pattern similar to that derived from the field data.

Results

Field data

Table 1 summarises the catch rates of whiting and sandeels from the 24 h fishing. High sandeel catches were only obtained during daytime (0957–1252 h and 1422–1707 h), but the large number of zero catches indicates the patchy distribution of these schooling species. Whiting catch rates were less variable throughout the day, but the two hauls performed at darkness gave significantly lower catch rates than the day hauls.

Table 1. Catch rates of whiting and sandeels from the 24 h fishing.

Station number	Time of day	Empty stomachs per 30 whiting (n)	Total catch of whiting n/30 min	Total catch of sandeels n/30 min
1	2.30	8	185	2
2	4.38	10	2699	0
3	6.06	6	1113	0
4	7.40	9	510	0
5	8.48	9	1400	0
6	9.57	6	1200	314
7	11.45	5	1152	504
8	12.52	7	184	696
9	6.43	No observation	1036	0
10	8.45	3	639	0
11	10.05	3	1272	0
12	11.10	10	424	0
13	13.00	9	248	0
14	14.22	6	1262	54
15	15.40	5	1919	420
16	17.07	10	3282	113
17	13.10	9	356	0
18	14.50	5	856	0
19	16.02	5	2496	9
20	17.45	14	515	0
21	19.19	6	1278	0
22	20.30	2	1362	0
23	21.43	3	1238	0
24	23.37	5	42	1

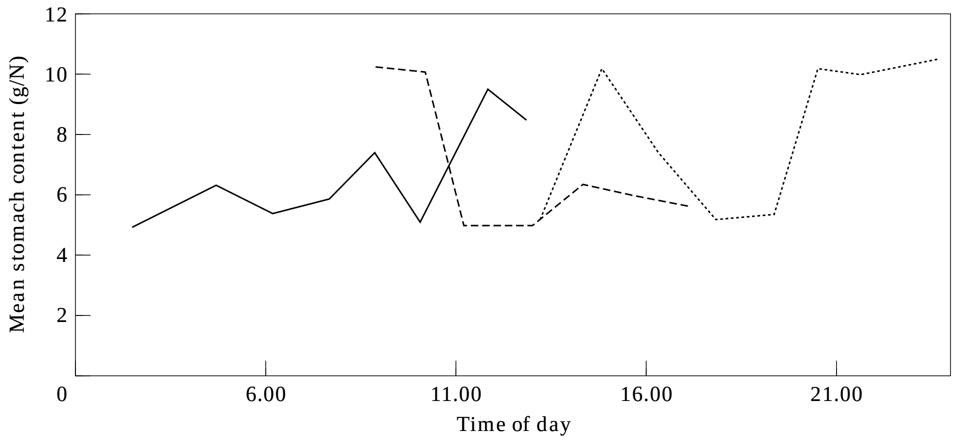


Figure 2. Mean stomach contents of whiting during 24 h fishing (—— 30.5.92, – – – 31.5.92, · · · 1.6.92).

Mean catch rate during darkness was 114 30 min^{-1} compared with a mean catch rate during daylight of 1202 30 min^{-1}. Figure 2 shows the variation of the mean stomach contents of whiting during the 24-h day. No consistent trends are apparent.

An overview of the numbers of sandeels found in whiting stomachs is given in Table 2. The majority of whiting stomachs contained only one sandeel, the maximum observed in one whiting being four. Sandeels represented 97% of the total food from all

Table 2. Frequency of sandeels found in whiting stomachs.

Number of sandeels (n)	Number of stomachs (n)	Percentage of stomachs (%)	Total number of sandeels (n)
0	154	22.3	0
1	396	57.4	396
2	123	18.8	246
3	16	2.3	48
4	1	0.1	4
Σ	690	99.9	694

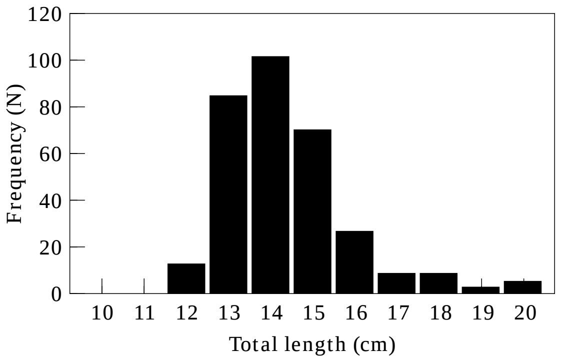


Figure 3. Length–frequency distribution of sandeels found in whiting stomachs.

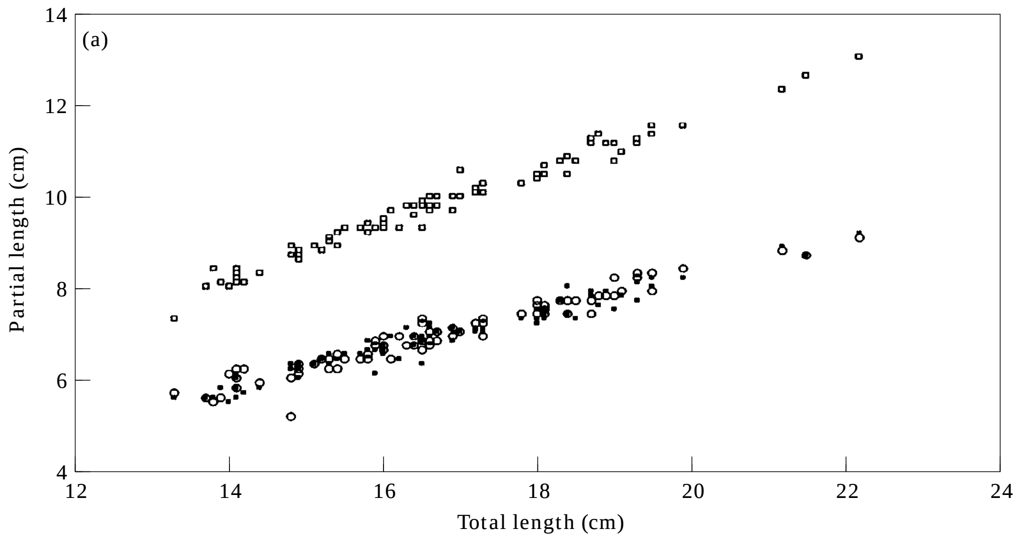
whiting stomachs investigated. The length–frequency distribution (total length, direct measurement) of sandeels found in whiting stomachs (Fig. 3) ranges from 12 to 20 cm with a single mode at 14 cm.

Table 3 and Figure 4a present the regressions of partial lengths vs. total length of fresh trawl-caught sandeels. The estimated length–weight relationship based on 82 fresh sandeels (Fig. 4b) was:

$$G_{t0} = 0.035 * TL^{2.24} \quad r^2 = 0.88 \qquad (7)$$

Gastric evacuation and particle decay functions

Parameter b of the particle decay function is estimated as 0.4 with confidence limits 0.18–0.62, thus being



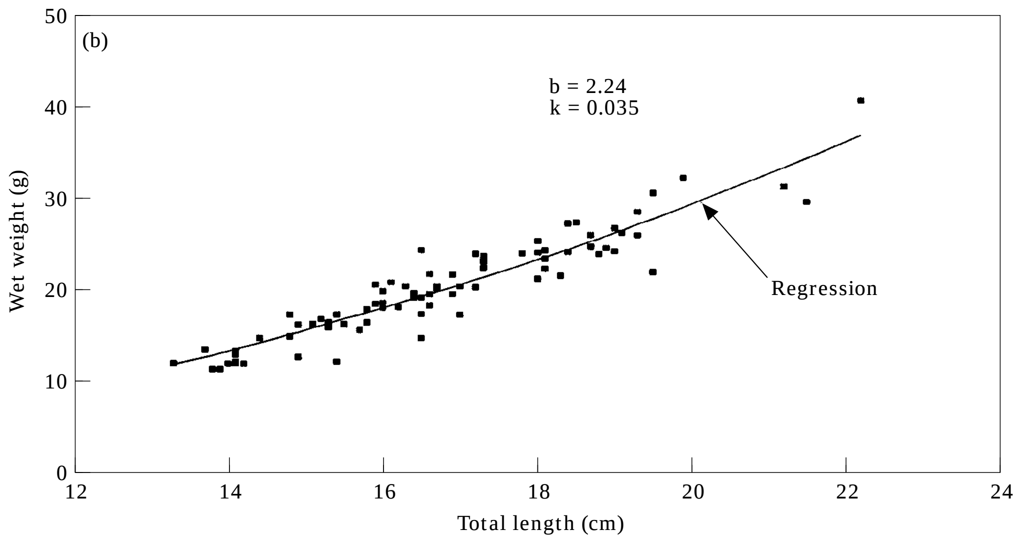


Figure 4. (a) Regression of partial length vs. total length (□ anterior anal length, ■ posterior anal length, ○ length between the end of operculum and the anus) and (b) length–weight relationship of fresh trawl-caught sandeels (n = 82).

Table 3. Results of the regressions of partial lengths vs. total length of fresh trawl-caught sandeels.

Partial length	Slope	Intercept	r^2	Number of observations
Anterior anal length	0.590	− 0.126	0.97	82
Length between the end of operculum and the anus	0.403	0.161	0.95	82
Posterior anal length	0.318	0.029	0.94	82

Table 4. Estimated parameters and asymptotic 95% confidence limits of the particle decay function and the gastric evacuation curve for the total stomach content.

	Particle decay		Total stomach content	
Number of observations (n)	31			
	R	b	R	b
Upper limit of confidence interval	0.128	0.619	0.109	0.55
Estimated parameter	0.094	0.399	0.087	0.37
Lower limit of confidence interval	0.079	0.179	0.065	0.18
Upper limit of confidence interval	0.115			
Estimated parameter	0.108	**0.3** (fixed)		
Lower limit of confidence interval	0.101			
Upper limit of confidence interval	0.088			
Estimated parameter	0.083	**0.5** (fixed)		
Lower limit of confidence interval	0.077			
r^2	0.94		0.95	

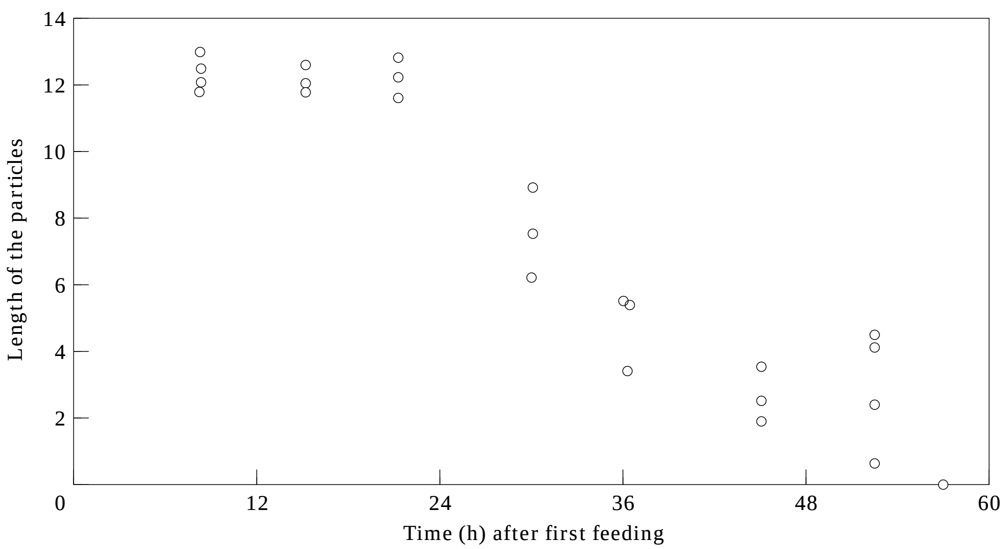


Figure 5. Decreasing length of the ingested sandeels in the gastric evacuation experiments.

significantly different from the linear (b = 0) and exponential (b = 1) evacuation patterns (Table 4). The total length of a sandeel does not change during the first 24 h of digestion (Fig. 5). The gastric evacuation curve (total stomach content) has a very similar exponent with b = 0.37 (0.18–0.55) (Table 4 and Fig. 6). Parameter estimates for R with b fixed to 0.3 and 0.5 were 0.108 and 0.083 respectively.

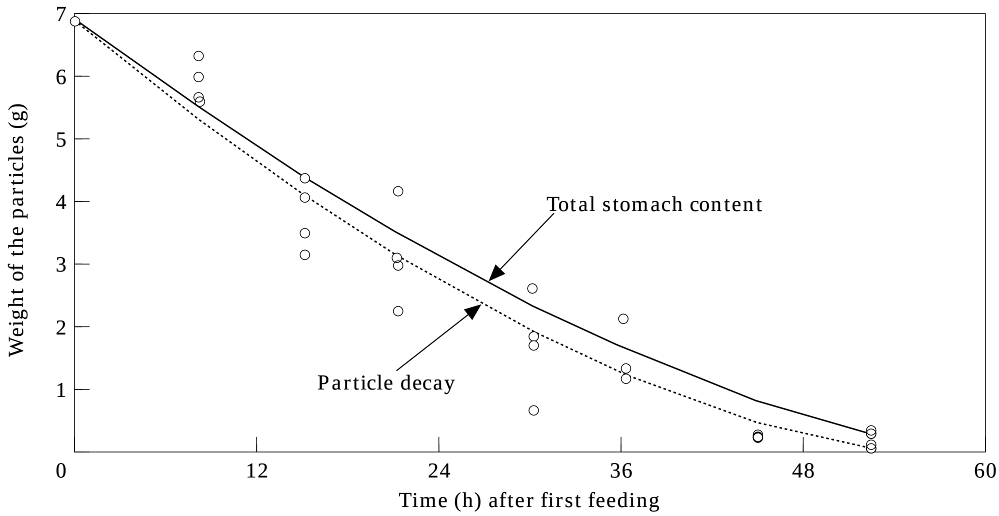


Figure 6. The relationship between the particle weight (dotted line), the total stomach content and time after ingestion for whiting fed on sandeels.

Back-calculated times of digestion and food intake

Back-calculated digestion times based on all sandeels, from which at least a partial length could be measured, vary between 6 and 76 h (midpoints of 2 h classes, Fig. 7a). This converts into a distribution of times of food intake that spreads out over the entire 24-h period (Fig. 7b). There is, however, a clear pattern in the distribution of feeding times with food being taken most frequently between 2200 and 2400 h and minimal food intake between 0800 and 1000 h. When only those sandeels were included for which the total length could be measured directly, the pattern becomes even more pronounced, with minimum and maximum falling in the same 2-h classes (Fig. 8) as described before. This general pattern of night feeding does not disappear if alternative values for either parameter A (0.075 and 0.13 instead of 0.1) or parameter b (0.3 and 0.5 instead of 0.4) are used. Changes in the parameter values result in shifts of the feeding peak of 2–4 h, while the minimum of the distribution is not shifted by more than 2 h (Fig. 9a–d).

Simulation exercises

Simulation 1

The back-calculated digestion times from the simulation exercise spread over a wide range from 36 to 66 h with a single mode at 47–49 h (Fig. 10a). The mean digestion time was 47.74 h. Ideally, all estimated digestion times should have been 48 h, since this figure was used in the simulation. When the digestion times were converted into times of food intake (Fig. 10b) the mode of the distribution was located in the time-of-day class 1400–1600 h. The scatter of the back-calculated times of food intake is considerable; ideally, all data should have fallen in the time-of-day class 1200–1400 h, since the feeding time in the simulation was 1300 h.

Simulation 2

The greatest similarity between simulated results with uniform feeding times and the field results was achieved assuming feeding at 2200 h (sum of squared deviations = 133.88, Table 5). The minimal sum of squared deviations between simulated results (as frequencies of food intake per 2-h interval) with normally distributed feeding times (mean = 2200 h) and results based on the analysis of field data was obtained with a standard deviation of the simulated feeding times of 5 h (sum of squared deviations = 40.66) (Fig. 11). This situation corresponds to 67% of the food intake occurring between 1700 and 0300 h. A total of 23 additional simulations was performed assuming two feeding peaks, each with normally distributed feeding times and small standard deviations of 1–3 h. Greatest similarity with the field results (sum of squared deviations = 52.61) was observed with feeding peaks at 2000 h (s.d. = 2 h, 75% of the food intake) and 0200 h (s.d. = 2 h, 25% of the food intake) (Table 5 and Fig. 12).

Discussion

Choice of parameter values of gastric evacuation model

The observed times of minimum and maximum food intake were shifted by no more than 2 h if either the highest (A = 0.13) or lowest estimate (A = 0.075) for the temperature model were applied in the analysis. The

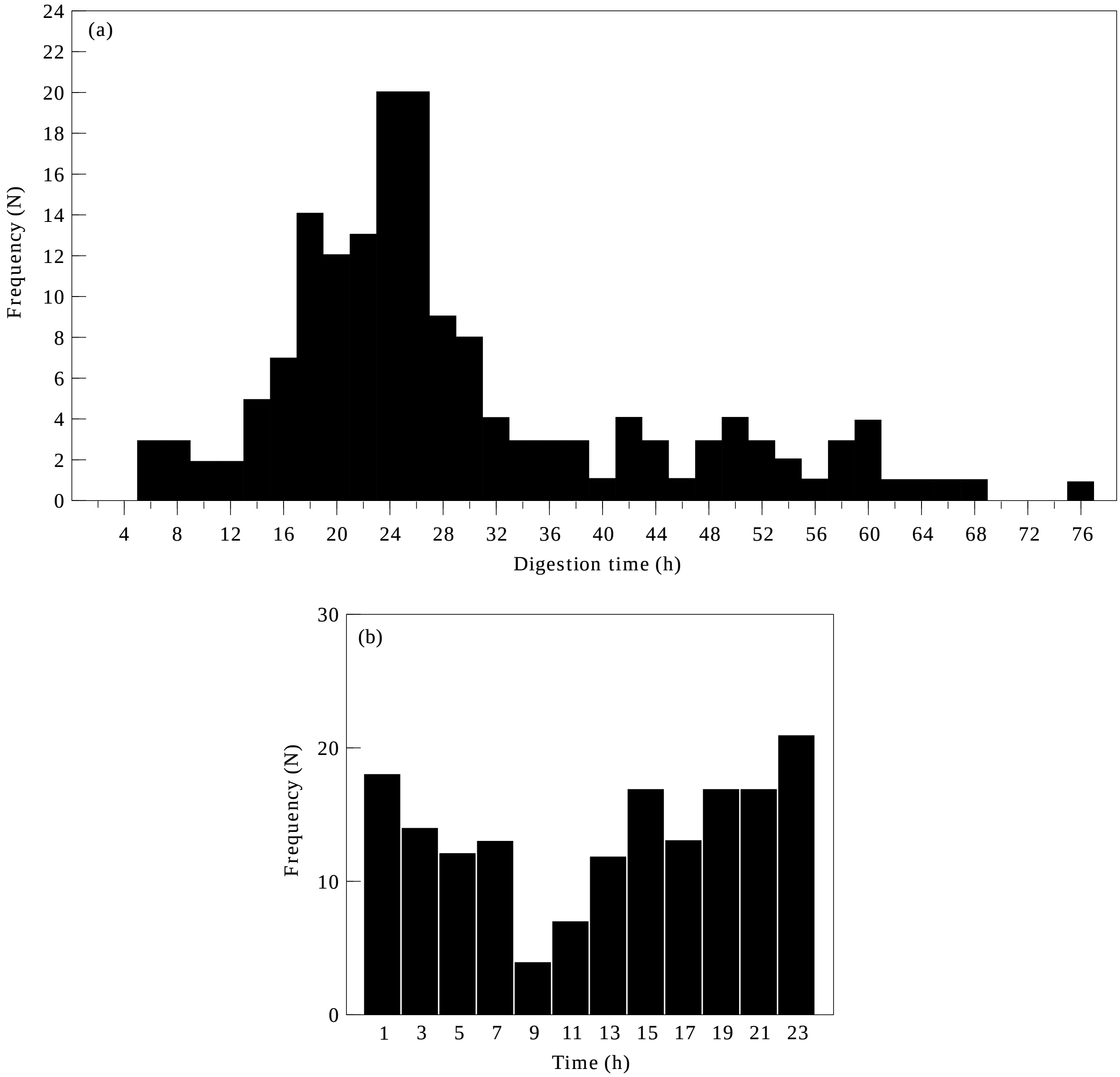


Figure 7. Distribution of (a) the back-calculated digestion times and (b) the derived times of food intake for sandeels found in whiting stomachs of trawl-caught whiting from which at least a partial length could be measured.

results were slightly more sensitive to the choice of the shape parameter b with a 4-h shift of the feeding peak to earlier evening hours (1800–2000 h), when a lower value for b (0.3) was applied. Applying b = 0.5 shifts the feeding peak by 2 h in the opposite direction. The correct estimation of this parameter is of particular importance in our study, since the precision of the extrapolation from our small experimental meal sizes to the larger meal sizes in the field depends mainly on this parameter. However, Temming and Andersen (1994) have shown that for cod, the best predictions for variable meal sizes are made with b-values in the range of 0.3 to 0.5. Our estimate (b = 0.39) fits well into this range and the effect of using the upper and lower end of the range has also been investigated. Differences in the particle numbers between experiments and field stomachs would have had a significant effect on the extrapolation to higher meal sizes, because the surface of the total food bolus is directly proportional to the number of food items. The gastric evacuation rate is known to be positively correlated to the total surface of the food bolus (Jobling, 1987). The number of food items was, however, the same in our experiments and in the field data used for the final analysis (n = 1). The overall conclusion of a feeding peak at night and minimum food intake in the late morning hours is therefore most likely

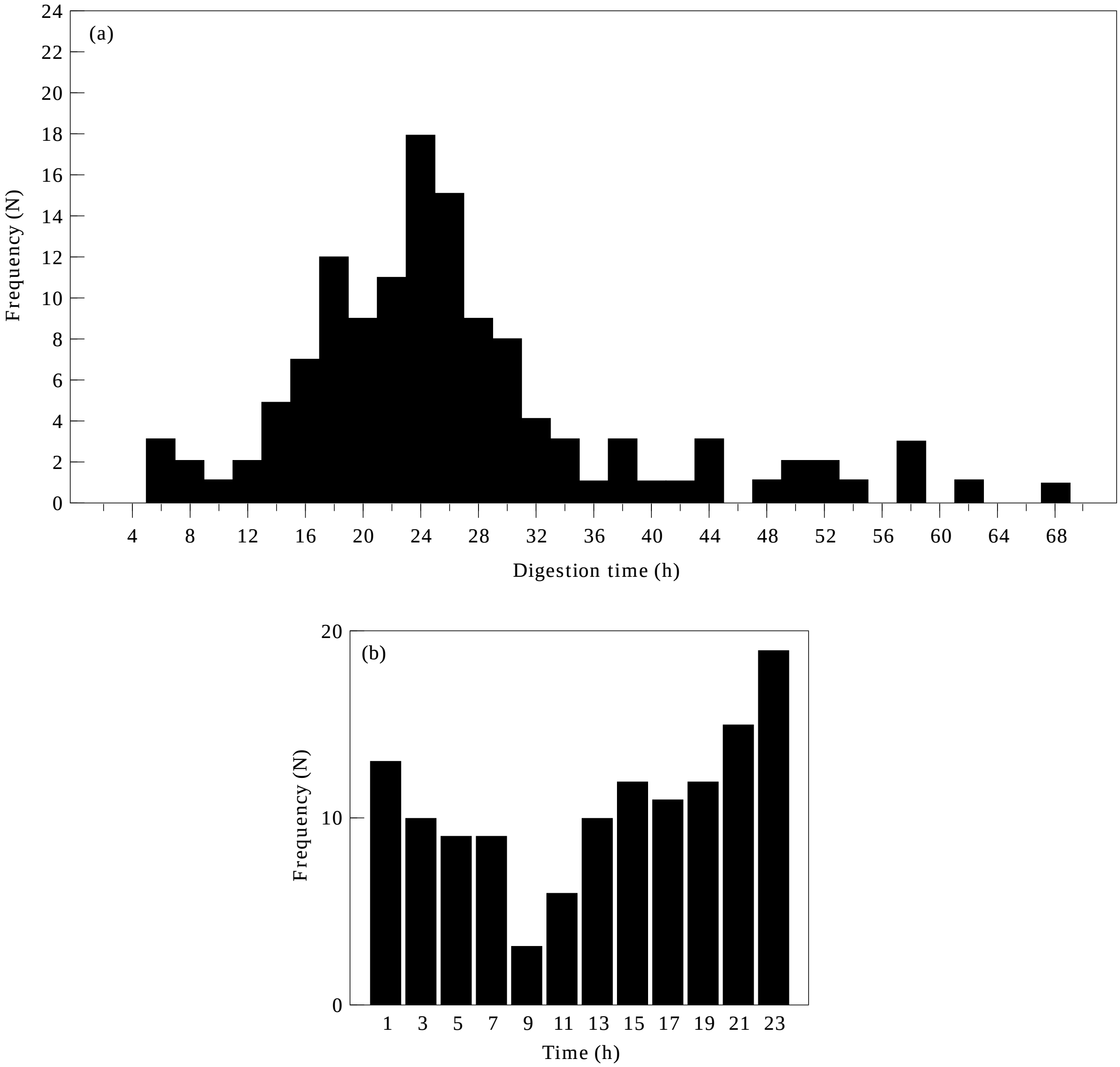


Figure 8. Distribution of (a) the back-calculated digestion times and (b) the derived times of food intake for sandeels found in stomachs of trawl-caught whiting with directly measured total length.

not to be influenced by the extrapolation to larger meal sizes.

Precision of the back-calculation method

The results of the simulation exercise clearly indicated a lack of precision of the method, resulting from the scatter of individual prey weights at a given length. The weight of a prey at the time of ingestion is derived from the length of the partly digested prey in the stomach and the length–weight relationship, which was based on the analysis of fresh trawl-caught sandeels. The length–weight relationship, however, always allocates the mean weight of the population to a particular prey length. For prey items which were in reality heavier than the average prey, the digestion time is calculated based on an underestimated fresh weight, which translates into an underestimation of the digestion time. This is illustrated in Figure 13: Line K2 represents the particle decay of a prey item that was heavier than the average weight of the distribution of prey weights (V_1) for a given length. When this heavy prey is sampled from a stomach at time t_F, its fresh weight is assumed to be the mean weight of the natural distribution at the observed prey length. The back-calculated digestion time ($t_F - t_2$) is an under-estimation of the real digestion time ($t_F - t_0$). This

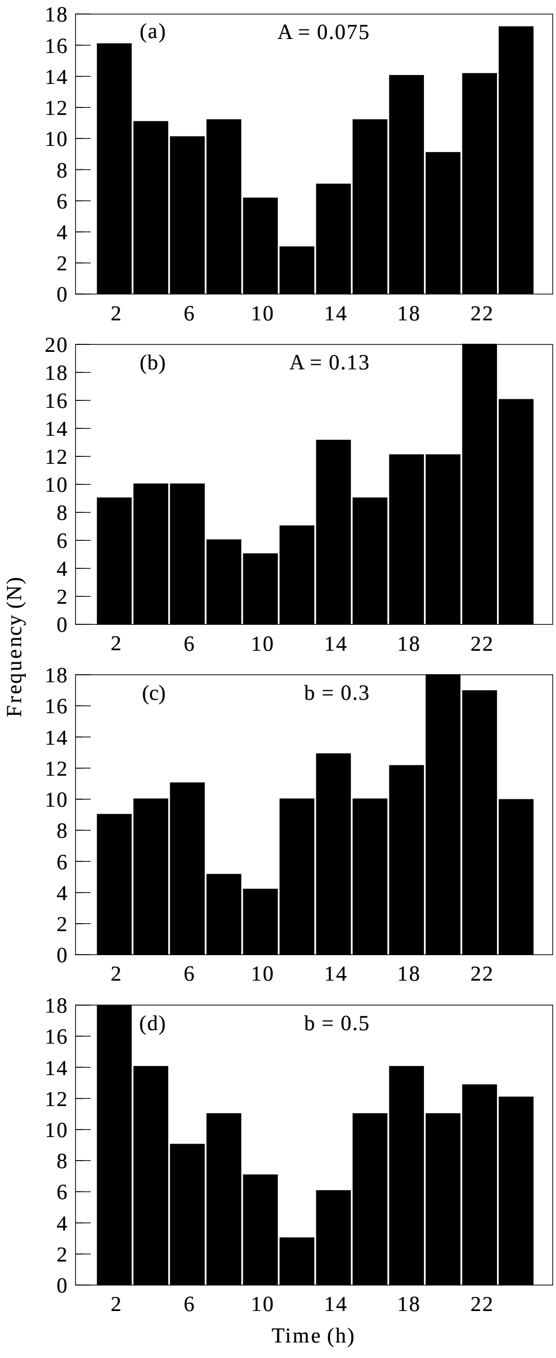


Figure 9. Back-calculated times of food intake estimated with alternative values for temperature correction parameter A (0.075 and 0.13) and parameter b (0.3 and 0.5).

translates into a corresponding error in the estimated time of food intake (t_2 instead of t_0). The opposite error occurs if the ingested prey item was lighter than the average prey at the given length (Line K3 in Fig. 13). The application of the length–weight relationship to estimate the fresh weight of the prey transforms the scatter of weights at a given length into a scatter of digestion times and times of food intake.

In our simulation exercise, however, the mode of the distribution of back-calculated digestion times matches the ''real'' digestion time that was used in the generation of the data set. The mode of the distribution of times of food intake occurred in the class next to that class where the simulated digestion was started (1300 h). This result does to some extent depend on the choice of the borders for the time classes; with a different grouping the mode actually occurred in the class that contained the starting time of the simulation. It can be concluded, nevertheless, that this method can be used as a tool to locate peaks of food intake with sufficient precision in natural populations based on stomach samples.

The additional simulations with normally distributed feeding times give some indication of the likely width of the feeding interval in the natural population. The simulated data gave the best fit with the field results if peak feeding was assumed at 2200 h with a standard deviation of 5 h. This result implies a considerable scatter of the feeding times with 67% of the whiting taking their prey between 1700 and 0300 h. Our simulations with two feeding peaks revealed that the field result could equally well be obtained with two narrow feeding peaks (each of the peaks with normally distributed feeding times and s = 2) if unequal numbers per peak were allowed.

Biological results

While Figure 2 revealed no clear pattern of the diel periodicity of food intake based on the analysis of the mean stomach content weights, the back-calculation method (Fig. 8b) clearly indicated peak feeding at night and a minimum of food intake around midday.

Generally the observation of peak feeding at night is in line with results from other authors, which were derived from the analysis of total stomach contents: Robb (1981) for 0-group gadoids (whiting, cod, haddock, saithe and Norway pout), Pattersen (1985) for adult whiting, Gordon (1977) for 0-group whiting (7–10 cm). Hall *et al.* (1995) confirmed the night feeding for haddock, which were also feeding largely on sandeels, but, contrary to these and our results their method revealed a feeding peak for whiting between 0300 and 1000 h in the morning. The result of Hall *et al.* (1995) for whiting is confirmed by data on total stomach content given by Jones (1954).

The method of Hall *et al.* (1995), is, however, neither comparable with our method nor with the total stomach content analysis. They applied a sophisticated statistical simulation model, in which the simulated feeding period was varied in order to match the various stomach content distributions that were obtained from 24 h

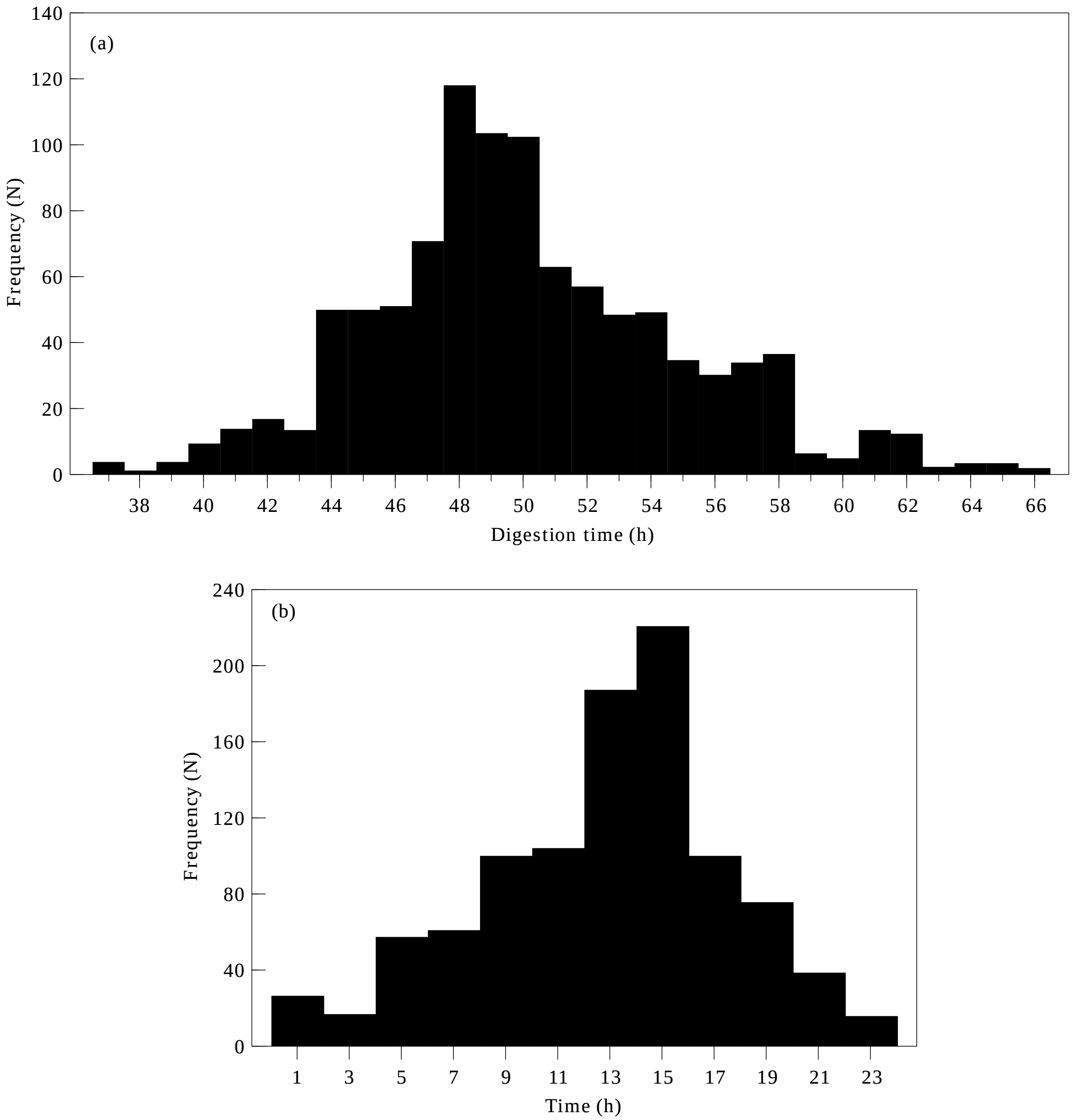


Figure 10. The (a) back-calculated digestion times and (b) times of food intake from the simulation exercise (predefined digestion = 48 h, starting time = 1300 h).

sampling. Following Bromley (1988) and Robb (1990) the model was based on a simple linear gastric evacuation. In this approach gastric evacuation rate is assumed to be independent of the amount of food in the stomach, which contradicts the results of Jones (1974), dos Santos and Jobling (1992, 1995), Temming and Andersen (1994) and the results presented in this study. Furthermore, the evacuation rate of 0.15 g h^{-1}, which was derived from data of Bromley (1988) and Robb (1990), seems to be low when compared with our results. We have extrapolated the results from our experiments to the field conditions (predator weight 100 g stomach content weights between 0 and 20 g, T = 13.2°C, prey type sandeel) described in Hall *et al.* (1995) using the gastric evacuation model from Temming and Andersen (1994) and in addition unpublished results (Temming) of

Table 5. Comparison of simulated results with back-calculated feeding times from the field.

	Times of food intake				Sum of squared deviations between the simulated results and the results from the field data				
No.	First feeding peak	Number (%)	Second feeding peak	Number (%)	Mean	Standard deviation	Minimum	Maximum	Number of datapoints
				Simulations with one feeding peak and standard deviation 0					
1	0°°	100			274.34	—	—	—	1000
2	2°°	100			432.02	—	—	—	1000
3	4°°	100			600.08	—	—	—	1000
4	6°°	100			739.30	—	—	—	1000
5	8°°	100			867.83	—	—	—	1000
6	10°°	100			829.85	—	—	—	1000
7	12°°	100			712.02	—	—	—	1000
8	14°°	100			576.67	—	—	—	1000
9	16°°	100			470.78	—	—	—	1000
10	18°°	100			307.68	—	—	—	1000
11	20°°	100			181.16	—	—	—	1000
12	22°°	100			133.88	—	—	—	1000
				Simulations with one feeding peak and standard deviation 1–8 h					
13	22°° (1)	100			127.50	7.27	114.76	143.51	20 × 1000
14	22°° (2)	100			93.37	10.53	74.51	109.45	20 × 1000
16	22°° (3)	100			67.76	13.55	40.73	81.60	20 × 1000
17	22°° (4)	100			48.11	13.02	30.36	82.21	20 × 1000
18	22°° (5)	100			40.66	8.58	28.88	53.14	20 × 1000
19	22°° (6)	100			53.52	10.95	32.82	72.08	20 × 1000
20	22°° (7)	100			69.22	13.32	41.88	90.47	20 × 1000
21	22°° (8)	100			88.84	16.02	50.36	118.41	20 × 1000
				Simulations with two feeding peaks and various standard deviations					
1	21°° (3)	50	1°° (3)	50	69.09	10.66	48.71	85.43	20 × 1000
2	21°° (3)	50	2°° (3)	50	75.65	13.99	51.99	106.00	20 × 1000
3	21°° (3)	50	3°° (3)	50	90.59	14.88	67.00	112.09	20 × 1000
4	21°° (2)	50	2°° (2)	50	92.14	14.88	66.23	122.08	20 × 1000
5	21°° (2)	50	1°° (2)	50	95.25	14.99	69.15	124.19	20 × 1000
6	21°° (2)	50	3°° (2)	50	100.48	15.39	73.75	128.39	20 × 1000
7	22°° (3)	50	2°° (3)	50	104.84	17.42	70.96	137.25	20 × 1000
8	21°° (1)	50	3°° (1)	50	113.56	10.34	101.79	131.94	20 × 1000
9	22°° (3)	50	3°° (3)	50	119.26	15.04	89.83	145.91	20 × 1000
10	21°° (1)	50	2°° (1)	50	119.53	14.68	101.78	171.46	20 × 1000
11	21°° (1)	50	1°° (1)	50	120.46	7.93	105.73	136.22	20 × 1000
12	22°° (2)	50	1°° (2)	50	130.42	16.63	92.08	162.12	20 × 1000
13	22°° (2)	50	2°° (2)	50	136.19	12.72	119.18	158.05	20 × 1000
14	22°° (2)	50	3°° (2)	50	144.56	15.27	117.10	177.17	20 × 1000
15	22°° (1)	50	3°° (1)	50	154.48	14.32	119.98	179.84	20 × 1000
16	22°° (1)	50	2°° (1)	50	157.99	14.65	136.46	186.92	20 × 1000
17	22°° (1)	50	1°° (1)	50	163.11	14.56	135.66	187.48	20 × 1000
18	23°° (2)	50	2°° (2)	50	184.12	16.79	151.28	224.57	20 × 1000
19	23°° (2)	50	3°° (2)	50	199.74	16.14	170.64	227.38	20 × 1000
20	23°° (1)	50	3°° (1)	50	224.16	10.58	203.89	242.01	20 × 1000
21	23°° (1)	50	2°° (1)	50	224.87	15.53	199.72	255.67	20 × 1000
22	21°° (3)	75	1°° (3)	25	54.12	11.71	40.43	82.81	20 × 1000
23	20°° (2)	75	2°° (2)	25	52.61	9.35	32.93	71.65	20 × 1000

gastric evacuation of whiting of different sizes to correct for differences in predator weight. Our estimates indicate that an evacuation rate of 0.15 g h^{-1} would correspond to a stomach content of only 3.5 g. For higher stomach contents the rate will increase up to 0.36 g h^{-1} at 20 g stomach content and for lower stomach contents the rate will be smaller (e.g. at 0.5 g the rate would be 0.06 g h^{-1}).

The gastric evacuation results of our study with whiting of about 200 g refer to large sandeels with high energy content. It is quite likely that the small sandeels, which were taken by the 100 g whiting analysed by Hall

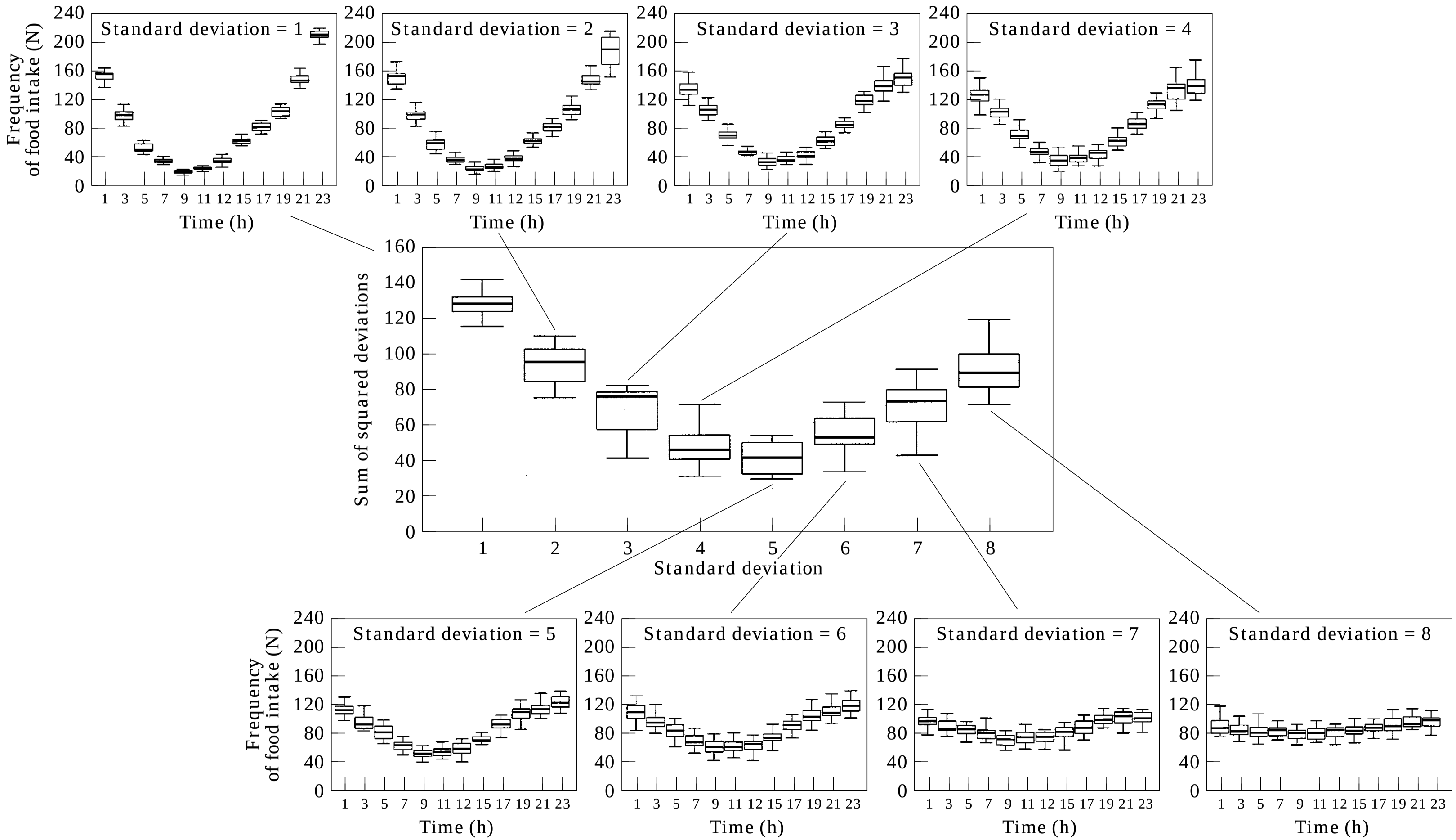


Figure 11. Back-calculated times of food intake from simulations with peak feeding at 2200 h and different standard deviations (1–8 h) in the normal distribution of times of food intake (mean 2200 h). Each simulation with a given standard deviation is repeated 20 times with random allocation of individual sandeel prey weights to times of food intake. The central graph relates the standard deviation of the simulated feeding interval with the sum of the squared deviations between the median of the simulated results and the results from the analysis of the field samples. The best fit is obtained with a standard deviation of 5 h (see also Fig. 12 and Table 5).

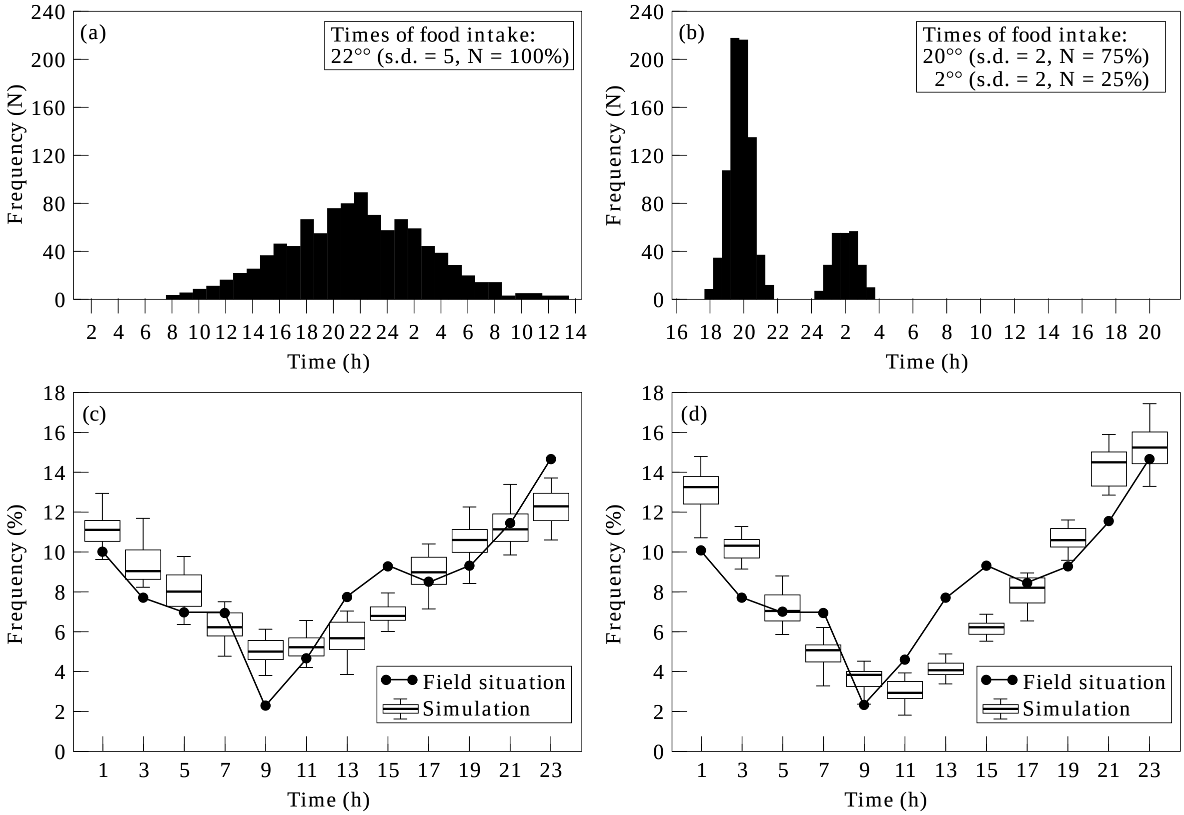


Figure 12. Back-calculated times of food intake from two simulations compared with the back-calculated times of food intake from the analysis of the field samples. In one of the simulations (c) a single feeding peak was generated at 2200 h with a standard deviation of 5 h (a). For comparison a simulation (d) is presented with two feeding peaks (2000 h, 75% of the total food intake and 0200 h, 25% of the total food intake) each with a standard deviation of 2 h (b).

et al. (1995), would have been evacuated at an even faster rate than predicted from our experiments, since evacuation rate increases with decreasing particle size and energy content (Jobling, 1987; dos Santos and Jobling, 1988). The energy content of sandeel, however, is strongly dependent on the size of sandeel as demonstrated by Hislop *et al.* (1991b).

The results from the analysis of Hall *et al.* (1995) may therefore be biased by the application of both too low an evacuation rate and the assumption that the evacuation rate is independent of the actual stomach content. This speculation is to some extent confirmed by the fact that peak feeding for small and large haddock in their investigation occurred during the night, the diet of the larger haddock also consisting to a large extent of sandeels. For haddock, however, evacuation rates were based on results from Jones (1974) and the values used were significantly higher (0.29 g h^{-1} for small and 0.62 g h^{-1} for large haddock) than those used for whiting (0.15 g h^{-1}). It is therefore possible that the low evacuation rate used in whiting has caused a corresponding shift in the estimated feeding peak. This line of argument is only correct, however, if the bias introduced by the linear gastric evacuation model is small compared with the bias that results from the low evacuation rate.

Biological interpretation of feeding pattern observed in this study

According to investigations by Patterson (1985) and Blaxter and Parrish (1958) whiting perform diel vertical migrations: during night-time whiting tend to disperse in the upper water layers, while they concentrate near the bottom during the day. Blaxter and Parrish (1958) related this behaviour pattern with the light intensity and identified a preferred light intensity of 0.17 lux, which the whiting try to maintain with their vertical migrations. This is basically confirmed by our catch rates, which are at minimum during night-time. Investigations by Patterson (1985) revealed also maximum stomach fullness during night-time, with Norway pout, sprat, sandeels and herring being the dominant prey species. With the exception of sandeels, these prey species are either generally pelagic or migrate into upper

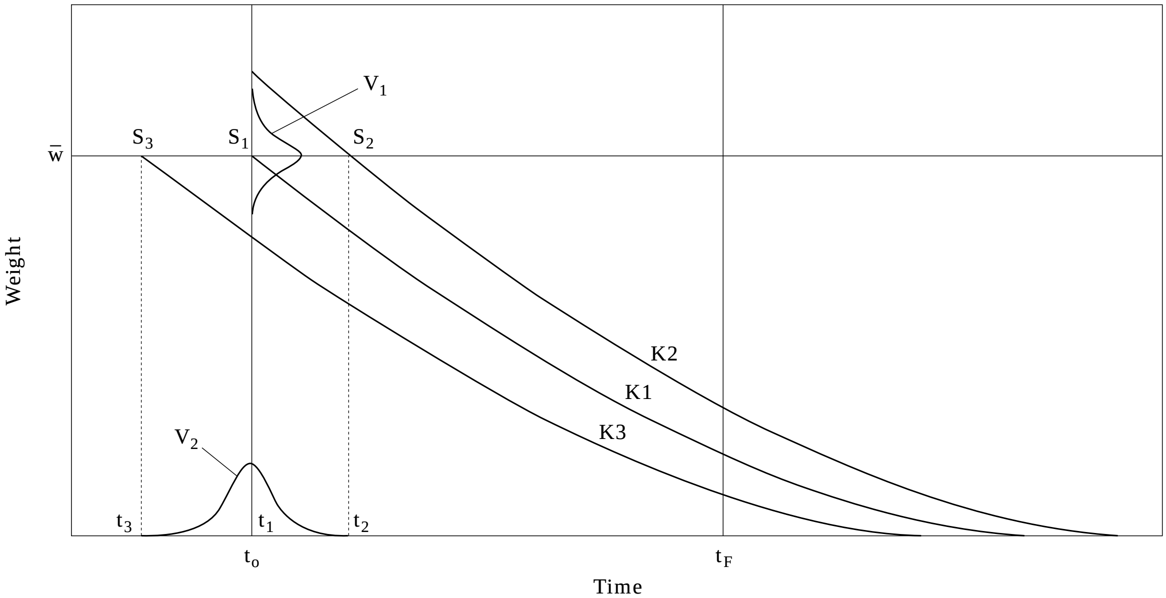


Figure 13. Illustration of the principal imprecision of the back-calculation method of times of ingestion from the wet weights of partly digested food items. The three lines indicate the decay of three particles of identical lengths ingested at time t_0. The upper line represents a particle that was heavier than average, while the middle and the lower line represent the decay of a particle of mean weight and one of less weight than average. Since in all cases the weight at ingestion is assumed to be the mean weight at this length as estimated from the length–weight relationship, the digestion time estimates will be biased if the actual weight of a food particle at ingestion deviated from the mean weight. For heavier than average particles the digestion time will be underestimated and for less than average particles the digestion time will be overestimated. These errors in digestion time are translated into corresponding errors of the estimated times of food intake.

water layers by night. Sandeels, which were the only prey found in the whiting stomachs in this investigation, are an extreme example for diel vertical migration. According to Macer (1966) and Bertelsen and Popp Madsen (1958) sandeels are only caught by the commercial fishery during the day. Reay (1986) described the migration pattern as a feeding migration into the water column by day, while sandeels bury in the substratum by night. This corresponds with our sandeel catch rates, where high catches occurred only during day-time, while night catches were always practically zero.

The opposite direction of the vertical migration routes of whiting and sandeels reduces the potential times of spatial overlap to two narrow periods during dusk and dawn, from which one would expect two feeding peaks. At the time of the year when the investigation was performed (May/June 1992), dusk and dawn occurred in the Northern North Sea at 2130 h (GMT) and 0230 h (GMT), respectively. It is unlikely, however, that two feeding peaks, which are so close together, can be separated given the limited precision of the back-calculation method.

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