

Diel, vertical interactions between atlantic cod *Gadus morhua* and sprat *Sprattus sprattus* in a stratified water column

Niels G. Andersen*, Bo Lundgren, Stefan Neuenfeldt, Jan E. Beyer

*Corresponding author: nga@aqua.dtu.dk

Marine Ecology Progress Series 583: 195–209 (2017)

The surface-dependent cylinder model of gastric evacuation rate (GER) and the estimation of prey ingestion times and daily food rations

The model

The mechanistic, surface-dependent cylinder model advanced by Andersen & Beyer (2005a,b) is used in the present study to estimate ingestion times and food consumption rates of Atlantic cod *Gadus morhua*. Individual prey in a stomach are considered cylinders that are successively reduced by evacuation of material peeled off their curved sides. The model describes the current GER of prey i by

$$\frac{dS_{i,t}}{dt} = -\rho_{i,t} d_{i,t} \sqrt{S_{i,t}} \quad (\text{g h}^{-1}) \quad (\text{S1})$$

where $S_{i,t}$ is the current prey mass, $\rho_{i,t}$ the rate parameter and $d_{i,t} = \sqrt{S_{i,t}} l_i (\sum \sqrt{S_{i,t}} l_i)^{-1}$ the exposed part of the surface of prey i for the current prey composition in the stomach. The variable l_i is the standard (fishes and *Mysis mixta*) or total (*Saduria entomon*) prey length, which constitutes the length of the prey cylinder. The rationale behind the modeled surface contributions is described in Andersen & Beyer (2005b) and Andersen & Beyer (2008). Using length-length relationships from fresh prey (Table S1), the prey cylinder length was estimated from reduced standard length (fish) or length of pleotelson (*S. entomon*) when advanced stage of digestion did not allow for direct observation. Also, the length-length relationships were used to estimate total length of sprat *Sprattus sprattus* and herring *Clupea harengus* for comparing size ranges of ingested and trawled prey fish.

The value of $\rho_{i,t}$ depends on the prey resistance to the digestive processes, the total cod length L (cm), the temperature T (°C) and the energy density E_t (kJ g⁻¹) of the currently evacuated prey material (the chyme). Parameter values for cod (Andersen 2012) provides

$$\rho_{i,t} = \rho_{i,LTE} L^{1.30} e^{0.0837T} E_t^{-0.85} \quad (\text{S2})$$

where $\rho_{i,LTE}$ is the prey-specific, basic rate parameter that reflects the prey resistance (Table S2).

The energy density E_t of the chyme influences the digestion rate by negative feedback mechanisms from the upper intestine (Jobling 1987) and depends on the current prey composition of the evacuated material by

$$E_t = \left(\sum E_i \frac{dS_{i,t}}{dt} \right) \left(\sum \frac{dS_{i,t}}{dt} \right)^{-1} \quad (\text{S3})$$

where E_i is the prey-specific energy density (Table S2).

Table S1. Relationships between different categories of prey body length l (cm). l_T is total length, l_S standard length, l_R reduced standard length and l_P pleotelson length

Species	Length relationship	r^2	n
Sprat (<i>Sprattus sprattus</i>)	$l_S = 1.214l_R + 0.47$ $l_T = 1.138l_S + 0.43$ $l_T = 1.382l_R + 0.95$	0.980 0.988 0.971	294
Herring (<i>Clupea harengus</i>)	$l_S = 1.213l_R + 1.14$ $l_T = 1.160l_S + 0.66$ $l_T = 1.413l_R + 1.92$	0.991 0.994 0.993	147
Lesser sandeel ^a (<i>Ammodytes tobianus</i>)	$l_S = 1.181l_R + 0.20$ $l_T = 1.092l_S + 0.08$ $l_T = 1.290l_R + 0.30$	0.996 0.999 0.996	227
Sand goby ^b (<i>Pomatoschistus minutus</i>)	$l_T = 1.182l_S + 0.05$	0.991	25
<i>Saduria entomon</i>	$l_T = 1.971l_P + 2.04$	0.985	60

^a Dataset from Andersen & Beyer (2008)

^b Unpublished data by Andersen NG (fish of 3.5–6.5 cm l_T sampled in early spring in Kattegat)

Table S2. Prey-specific values of the basic gastric evacuation rate parameter $\rho_{i,LTE}$ (equation S2) and the energy density E_i (kJ g⁻¹). $E_i = al_T + b$, where l_T is total prey body length

Species	$\rho_{i,LTE} (\times 10^{-3})^a$	E_i	r^2	n
Sprat (<i>Sprattus sprattus</i>)	2.43	$-0.2224l_T + 10.22$	0.834	294
Herring (<i>Clupea harengus</i>)	2.43	$0.1178l_T + 3.38$	0.929	147
Lesser sandeel (<i>Ammodytes tobianus</i>)	2.24	4.65 ^b		30
Sand goby (<i>Pomatoschistus minutus</i>)	2.24	4.26 ^b		25
<i>Saduria entomon</i>	1.22	2.81		60
<i>Mysis mixta</i>	2.43	3.4 ^c		

^a From Andersen (2012). Sand goby is evacuated at the same rate as sandeel (Andersen 2001); *M. mixta* is assumed to be evacuated like krill and clupeids, *S. entomon* like brown shrimp *Crangon crangon* (i.e., at c. half the rate of clupeids)

^b Unpublished data by Andersen NG (gobies of 3.5–6.5 cm l_T and sandeel of 10 – 13 cm l_T sampled in early spring in Kattegat)

^c From Cummins and Wuycheck (1971)

Estimation of prey ingestion times

The period τ_i between times t_s of stomach sampling and t_i of ingestion of prey i was estimated using the cylinder model to hindcast the recovered prey mass to its original body mass, the latter being estimated from observed prey length and the relationship between prey length and fresh body mass (Table S3). Starting with the latest ingested prey, the evacuation of each individual prey i in the stomach was hindcasted by first-order numerical integration projecting its mass backwards in time in small steps Δt of 0.02 h by $S_{i,t-\Delta t} = S_{i,t} - \Delta t \frac{dS_{i,t}}{dt}$ until the estimated initial body mass S_{i,t_i} was obtained at ingestion time t_i . The prey was then ‘removed’ from the stomach and the procedure restarted until the ingestion times of all prey were estimated. The chronological order of ingestion of the individual prey was determined in advance by inverse ranking of the calculated values of $(\sqrt{S_{i,t_i}} - \sqrt{S_{i,t_s}})(\rho_{i,LTE}\sqrt{\pi l_i})^{-1}$ (Andersen & Beyer 2008).

The variance of τ_i with known prey mass S_{i,t_s} at time t_s was approximated by $V(\tau_i|S_{i,t_s}) \cong (\sigma_e \hat{\tau}_i)^2 + (2(\hat{\rho}_{i,t_i} d_{i,t_i})^{-1} \sigma_m \mu_i)^2$ (Andersen & Beyer 2008). Here, μ_i is the estimate of $\sqrt{S_{i,t_i}}$, and σ_e and σ_m are the CVs of $\hat{\rho}_{i,t_i}$ and μ_i , respectively. The values $\sigma_e = 0.077$ and $\sigma_m = 0.021$ from data on sprat in Andersen (2012) were adopted here to obtain 95 % CIs of the τ_i estimates.

Table S3. Relationship $M = al^b$ between different categories of prey body length l (cm) and mass M (g). l_T is total length, l_S standard length, l_R reduced standard length and l_P pleotelson length

Species	l category	a	b	r^2	n
Sprat (<i>Sprattus sprattus</i>)	l_T	0.0167	2.67	0.932	294
	l_S	0.0312	2.59	0.929	
	l_R	0.0716	2.49	0.918	
Herring (<i>Clupea harengus</i>)	l_T	0.0081	2.92	0.978	147
	l_S	0.0178	2.83	0.976	
	l_R	0.0635	2.63	0.976	
Lesser sandeel ^c (<i>Ammodytes tobianus</i>)	l_T	0.0017	3.29	0.991	227
	l_S	0.0025	3.26	0.990	
	l_R	0.0052	3.20	0.986	
Sand goby ^d (<i>Pomatoschistus minutus</i>)	l_T	0.0052	3.22	0.979	25
	l_S	0.0088	3.24	0.973	
<i>Saduria entomon</i>	l_T	0.0355	2.54	0.966	60
	l_P	0.2488	2.40	0.935	
<i>Mysis mixta</i> ^e	Mean $l_S = 1.5$ cm and mean $M = 0.07$ g				15

^c Dataset from Andersen & Beyer 2008

^d Unpublished data by Andersen NG (gobies of 3.5–6.5 cm l_T sampled in early spring in Kattegat)

^e Pristine individuals from cod stomachs in the present study

Estimation of daily food rations

The daily food ration C (kJ) of cod was estimated both by the mean amount of prey energy ingested by the sampled cod during the latest full feeding period (dusk-night-dawn) prior to stomach sampling as well as by the mean value of the GER of total content mass S_i in each of the sampled stomachs estimated as $\frac{dS_t}{dt} = -\sum(E_i\rho_{i,t}d_{i,t}\sqrt{S_{i,t}})$ (kJ h⁻¹) and multiplied by 24.

LITERATURE CITED

Andersen (2001) A gastric evacuation model for three predatory gadoids and implications of using pooled field data of stomach contents to estimate food rations. *J Fish Biol* 59:1198–1217

Andersen NG (2012) Influences of potential predictor variables on gastric evacuation in Atlantic cod *Gadus morhua* feeding on fish prey: parameterization of a generic model. *J Fish Biol* 80:595–612

Andersen NG, Beyer JE (2005a) Mechanistic modelling of gastric evacuation applying the square root model to describe surface-dependent evacuation in predatory gadoids. *J Fish Biol* 67:1392–1412

Andersen NG, Beyer JE (2005b) Gastric evacuation of mixed stomach contents in predatory gadoids – an expanded application of the square root model to estimate food rations. *J Fish Biol* 67:1413–1433

Andersen NG, Beyer JE (2008) Precision of ingestion time and evacuation predictors for individual prey in stomachs of predatory fishes. *Fish Res* 92:11–22

Cummins KW & Wuycheck JC (1971) Caloric Equivalents for Investigations in Ecological Energetics. *Mitt Int Verein Theor Angew Limnol* 18:1–158

Jobling M (1987) Influences of food particle size and dietary energy content on patterns of gastric evacuation in fish: test of a physiological model of gastric emptying. *J Fish Biol* 30:299–314