Nutritional status determines apparent assimilative capacity and functional response of marine predatory fish

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Supplementary material

for

Nutritional status determines apparent assimilative capacity and functional response of marine predatory fish

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Appendix S1

Estimating and testing stomach and GER allometry: deriving a general predictor of GER across predators

The cylinder model of gastric evacuation rate (GER) is at present the only model that is able to accurately predict GER of current stomach content mass irrespective of prey composition and temporal feeding pattern (Andersen, 2012). Using this model in the present study, we derive a general GER allometry and provide a common inter-specific value of the basic rate parameter that significantly facilitate the general use of the model for predatory fish because just stomach length relative to the total body length needs to be known. The mechanistic principles of the model further allow us to calculate a proxy for the maximum volume capacity S_{MAX} of any predatory fish if the mass and length of the stomach are known.

In this supplement, we examine the assumptions connected to the derivation of the general GER allometry, corroborate the derived allometry and estimate a common inter-predator basic parameter of GER. We have estimated S_{MAX} directly using only field data on stomach content of sampled cod and whiting. We therefore define a useful proxy for S_{MAX} to connect assimilative capacity with foraging strategy for a larger number of predator species.

Testing the assumptions for the derivation of general GER allometry

We examined the assumptions about isometric stomach growth and the constant ratio λ of stomach length l to total body length L for a variety of marine species. Individuals of whiting (*Merlangius merlangus*), Atlantic cod (*Gadus morhua*), saithe (*Pollachius virens*), grey gurnard (*Eutrigla gurnardus*), and haddock (*Melanogrammus aeglefinus*) were sampled and processed on board the Danish research vessel ‘Dana’ during the International Bottom trawl Survey in the North Sea (www.ices.dk) in August 2011 as well as a commercial trawler later the same year in the Danish Skagerrak. Live turbot (*Psetta maxima*) were acquired from a local gillnetter in Hirtshals, Denmark, and processed on land. The total body length L was measured, the body cavity opened, and the stomach length l measured (to nearest mm below) from *septum transversum* in front of the body cavity to the caudal end of the stomach. The stomach was then excised, cut open longitudinally, emptied, flushed with isotonic salt water, dabbed with moistened paper towel to get rid of surplus water, wrapped in aluminium-foil on board the ship, frozen, and finally weighed on land. The data are available in the accompanying Excel files.

Using nonlinear regression of a power function with free exponent and intercept, we could not for any of the predators reject a linear relationship between l and L with the regression line going through origin. The mean of the individual values of $\lambda = l/L^{-1}$ was therefore estimated by species and compared for significant difference using ANOVA followed by Tuckey HSD Post-Hoc Test. Significance was accepted for $P < 0.05$. The low values obtained from whiting and saithe differed from the other species, whereas cod, turbot and grey gurnard showed similar values like did cod, grey gurnard and haddock (Table S1.1). Data together with the fit of the linear relationship by predator species are shown in Figure S1.1.

We examined the stomach growth for isometry with data on stomach mass w (g) and stomach length l (cm) for each predator by nonlinear regression using the simple power function $w = a l^b$. The exponent b was not significantly different from the isometric value of 3 for any of the predators. The estimates of the prefactor a in the isometric relationship are provided in Table S1.1. Data together with the fit of the isometric power function by predator species are shown in Figure S1.2.

Table S1.1. Estimate by predator species of the ratio λ of stomach length l to total predator length L , the prefactor a relating stomach mass w (g) to l (cm) by $w = a l^3$, and the proxy $a \lambda$ for S_{MAX} . Values with different superscript letters are significantly different ($P < 0.05$)

Predator	L range (cm)	λ		a ($\times 10^{-3}$)		$a \lambda$ ($\times 10^{-3}$)		n
		Estimate	95% CI	Estimate	95% CI	Estimate	95% CI	
Whiting	18–46	0.233 ^a	± 0.002	5.99 ^a	± 0.16	1.39 ^a	± 0.04	73
Saithe	42–81	0.244 ^b	± 0.003	6.34 ^a	± 0.14	1.55 ^b	± 0.04	57
Turbot	18–53	0.264 ^c	± 0.003	7.95 ^b	± 0.19	2.10 ^c	± 0.06	61
Grey gurnard	15–42	0.259 ^{c, d}	± 0.002	7.40 ^c	± 0.18	1.91 ^d	± 0.05	88
Haddock	21–64	0.257 ^d	± 0.003	7.60 ^{b, c}	± 0.16	1.96 ^d	± 0.05	71
Atlantic cod	21–93	0.262 ^{c, d}	± 0.002	9.23 ^d	± 0.28	2.41 ^e	± 0.07	64

Proxy for maximum volume capacity S_{MAX} of the stomachs

The maximum stomach dilation depends on the number and size of the longitudinal folds of the stomach wall and associated structures that allow the mucosa surface to unfold and expand in pace with mass S of total stomach contents to contribute to the digestive processes in accordance with the cylinder GER model. The l -specific stomach mass described by the prefactor $a = w l^{-3}$ (Table S1.1) thus indicates how much the stomach is able to expand; i.e., the circumference and consequently the maximum lumen of a cross section of the stomach cylinder. The low values of a obtained from whiting and saithe were similar, and significantly different from the other predators. The high value for cod was different from all other species, whereas turbot and haddock provided similar intermediate values as did grey gurnard and haddock. If the relative stomach length $\lambda = l L^{-1}$ was the same for all predators, a could serve directly as a proxy for S_{MAX} . However, species-specific λ values imply that instead $a \lambda$ must be used to serve as a proxy for the total maximum volume capacity of the stomach for a given L . The l -specific stomach mass a times λ corrects for the inter-species difference in λ . It can therefore be used as a proxy for each predator to connect S_{MAX} and eventually C_{MAX} with foraging strategy. All estimates of $a \lambda$ with the exception of those for grey gurnard and haddock were different (Table S1.1). The estimates can however be arranged in three distinct groups with cod holding the highest value, turbot, grey gurnard and haddock attaining medium values, and saithe and whiting providing the lowest ones.

Empirical evidence of the derived allometry of GER

A number of values of the length scaling exponent ranging from 1.3 to 1.4 was obtained from GER data on predators in the literature and corroborate the derived interval $5/4 - 3/2$ (haddock, Jones, 1974; whiting, saithe, Andersen, 2001; cod, Andersen, 2012; turbot, Krog and

Andersen, 2009; brook trout (*Salvelinus fontinalis*), Khan *et al.*, 2016; whiting, Ross *et al.*, 2018). Lower values have been reported as well. The latter are mostly obtained from data that include different meal sizes using an exponential GER function (i.e., $\frac{dS_t}{dt} = -\rho S_t$, where S_t is the current stomach content mass and ρ the rate parameter) or different prey sizes increasing with predator size without accounting for prey energy density (e.g. dos Santos and Jobling, 1995; Koed, 2001). The exponential overestimates GER of large meals (Temming and Andersen, 1994), and prey energy density usually increases with prey size, which depresses GER (Jobling, 1986). Both of these circumstances depress the estimated effect of predator size on GER (Andersen, 2012). It should be mentioned that Temming and Herrmann (2003) obtained lower estimates of *c.* 0.90 of the length exponent from extensive datasets on cod. Their analyses of these datasets were however rather convoluted due to the complex data structure, which might have caused bias. We therefore disregard this result here.

To attain a common scaling in a consistent way, we re-estimated the intra-specific effect of body length on GER from data on whiting and saithe (Andersen, 2001) using the nonlinear regression procedure described in Krog and Andersen (2009) and Andersen (2012) for turbot and cod. Kahn *et al.* (2016) used this procedure as well on brook trout like we did on grey gurnard (unpublished data, N.G. Andersen, see data in the accompanying Excel files). The estimates of the scaling power were not significantly different (ANOVA, $P>0.05$) (Table S1.2), and we used a common value of 1.35 for all species in the following.

Table S1.2. Estimates of the exponent k relating gastric evacuation rate (GER) to total predator length L (cm) by $\frac{dS_t}{dt} = -\rho_L L^k \sqrt{S_t}$, where S_t is the current stomach content mass (g) and ρ_L the rate parameter. The methodology by Andersen (2012) was used for all estimations. None of the estimates of k were significantly different ($P>0.05$)

Predator	Data source	k		r^2	n
		Estimate	95% CI		
Whiting (<i>Merlangius merlangus</i>)	Andersen (2001)	*1.35	± 0.14	0.962	97
Atlantic cod (<i>Gadus morhua</i>)	Andersen (2012)	1.31	± 0.09	0.961	109
Saithe (<i>Pollachius virens</i>)	Andersen (2001)	*1.38	± 0.10	0.978	129
Turbot (<i>Psetta maxima</i>)	Krog and Andersen (2009)	1.41	± 0.25	0.907	77
Brook trout (<i>Salvelinus fontinalis</i>)	Kahn <i>et al.</i> (2016)	1.31	± 0.09	0.972	90
Grey gurnard (<i>Eutrigla gurnardus</i>)	Andersen (unpubl. data)	*1.33	± 0.14	0.967	74

*Estimated from unpublished data (*E. gurnardus*) or re-estimated from already published studies (all these data are available in the accompanying Excel files)

Figure S1.1. Data on the relationship between stomach length l and total body length L together with the curve described by the linear function $l = \lambda L$ for each of the examined predators. Confidence limits of λ and results from test of difference between predators are reported in Table S.1.1.

Figure S1.2. Data on the relationship between stomach length l and mass w together with the curve described by the isometric function $w = a l^3$ for each of the examined predators. Confidence limits of a and results from test of difference between predators are reported in Table S.1.1.

Generic and mechanistic GER forecasting: the common inter-predator specific predictor variable

We assume that the digestive capacity of the stomach per unit of mucosa surface area is optimized to reduce costs of development and maintenance as well as occupation of body space. In accordance with the cylinder model, l rather than L should then be the predictor of GER across predator species. We used GER data from a number of predator species fed lesser sandeel (*Ammodytes tobianus*) to examine whether the stomach length l actually is the common inter-predator specific predictor variable.

First, expanding the GER rate parameter ρ to include the effects of predator length L (cm), temperature T ($^{\circ}$ C), and prey energy density E (kJ g $^{-1}$) we describe GER in accordance with the cylinder model by

$$\frac{dS_t}{dt} = -\rho_0 L^{1.35} e^{0.080T} E^{-0.85} \sqrt{S_t} \quad (\text{g h}^{-1}) \quad (\text{S1.1})$$

where ρ_0 represents the predator-specific parameter for sandeel prey. The temperature coefficient is a generally accepted value for enzymatic processes (Schmidt-Nielsen, 1983) and is representative of GER for a suite of predatory fish as well (Andersen, 2012). It should however be noted that other constraints on GER may come into play at more extreme temperatures within a species' temperature range (see later). The exponent of E was estimated from different gadoid predators (Andersen, 2001, 2012), and the value implies that the fish are able to adjust GER of energy almost independently of prey energy density (total independence requires a value of -1). Using evacuation data from the above-mentioned five marine predators fed sandeel (*Ammodytes tobianus*) (see the accompanying Excel files), we compare the estimated values of ρ_0 (Table S1.3). Integrating GER in Equation (S1.1) from time 0 of food intake to time t of recovery of the stomach contents, we calculate a value of

$$\rho_0 = 2(\sqrt{S_0} - \sqrt{S_t})(L^{1.35} e^{0.080T} E^{-0.85} t)^{-1} \quad (\text{S1.2})$$

from evacuation data on each predator individual as the outcome of a normally distributed variable (Andersen, 2012). The predator-specific estimate of ρ_0 is then the mean of the values obtained from all individuals of that predator species. The estimates are compared statistically by ANOVA and in the case of significance followed by Tuckey HSD Post-Hoc Test for species differences. Significance is accepted for $P < 0.05$.

Second, we follow the same procedure with L replaced by stomach length l using the relationship

$$\frac{dS_t}{dt} = -\rho_0 (\lambda L)^{1.35} e^{0.08T} E^{-0.85} \sqrt{S_t} \quad (\text{S1.3})$$

and expecting that ρ_0 should be similar across predators if mucosa performance is optimized.

Using L , the estimates of ρ_0 were significantly different. Replacing L by predator-specific stomach length l (using λL) provided similar values of ρ_0 for all the predators, which corroborates the usefulness of the common, interspecific value of the evacuation rate parameter for piscivorous fish if their stomach lengths are known (Table S1.3). Data together with the evacuation curve by predator species, predicted using the common value of the stomach length-based ρ_0 , are shown in Figures S1.3–S1.5.

Table S1.3. Estimates of the predator-specific rate parameter ρ_0 obtained from data on gastric evacuation of sandeel prey using $\frac{dS_t}{dt} = -\rho_0 L^{1.35} e^{0.080T} E^{-0.85} \sqrt{S_t}$ or $\frac{dS_t}{dt} = -\rho_0 (\lambda L)^{1.35} e^{0.080T} E^{-0.85} \sqrt{S_t}$ (g h⁻¹), where L is total predator length (cm), λ relative stomach length, T temperature (°C), E prey energy density (kJ g⁻¹) and S_t current stomach content mass (g). Values with different superscript letters are significantly different ($P < 0.05$). Data sources are listed in Table S1.2, and the data used here are available in the accompanying Excel files.

Predator	L -based ρ_0 ($\times 10^{-3}$)		l -based ρ_0 ($\times 10^{-2}$)		n
	Estimate	95% CI	Estimate	95% CI	
Whiting (<i>Merlangius merlangus</i>)	1.65 ^a	± 0.04	1.18 ^a	± 0.03	149
Atlantic cod (<i>Gadus morhua</i>)	1.97 ^b	± 0.05	1.20 ^a	± 0.03	145
Saithe (<i>Pollachius virens</i>)	1.76 ^{a, c}	± 0.09	1.18 ^a	± 0.06	21
Turbot (<i>Psetta maxima</i>)	1.93 ^{b, c}	± 0.18	1.17 ^a	± 0.11	19
Grey gurnard (<i>Eutrigla gurnardus</i>)	1.99 ^b	± 0.16	1.24 ^a	± 0.09	19
All predators; common estimate	—	—	1.19	± 0.02	353

The common estimate of ρ_0 applies to predators that eat fish prey, which vary only a little in their resistance to the digestive processes (e.g. Andersen, 2012). The resistance of some invertebrate prey may however differ significantly, which should be considered if they comprise a substantial part of the predator's diet. Crustaceans constitute the most important invertebrate prey for most marine piscine predators. Values of ρ_0 for the different groups of crustaceans have been estimated (Andersen *et al.*, 2016) and can be used in the same way to estimate GER by the cylinder model.

The effect of temperature on GER described by the exponential with a coefficient of 0.08 probably does not apply for most fish experiencing extreme temperatures. An optimum temperature followed by a decline close to the upper tolerance limit has been reported for cod as well as a number of other species (e.g. Brett and Higgs, 1970; Tyler, 1970; Sweka *et al.*, 2004; Bernreuther *et al.*, 2009, Andersen 2012). A likely explanation is constraints and eventual collapse in the cardiovascular system, probably because of a mismatch in the heart between oxygen supply and demand (Lannig *et al.*, 2004; Farrell *et al.*, 2009). Using the exponential, dos Santos and Jobling (1991, 1992, 1995) further obtained values of the temperature coefficient between 0.11 and 0.13 in the temperature interval 1–14 °C. Using a segment of dos Santos and Jobling's data on temperatures in the interval 1–6 °C, Salvanes *et al.* (1995) estimated an even higher estimate of 0.23. Low temperatures thus also seem to impose a constraint upon GER (Figure S1.6). The mechanism behind has not been examined for fish. However, aquatic invertebrates and insects fail to maintain ion and water balance at low temperature (MacMillan, 2019), and this may as well be the case for fish.

Figure S1.3. Data on remaining stomach content mass S_t at postprandial time t in **whiting** fed meals of sandeel. The predicted gastric evacuation curves are provided using the integrated version of Equation (S1.3) with the common estimate 0.0119 ± 2 S.D. of l -based ρ_0 obtained from data on all predators, and the whiting-specific estimate 0.233 of λ . Predator length L , temperature T and prey energy density E are provided as well. Experiment Nos refer to the accompanying Excel files.

Figure S1.4. Data on remaining stomach content mass S_t at postprandial time t in **Atlantic cod** fed meals of sandeel. The predicted gastric evacuation curves are provided using the integrated version of Equation (S1.3) with the common estimate 0.0119 ± 2 S.D. of l -based ρ_0 obtained from data on all predators, and the cod-specific estimate 0.262 of λ . Predator length L , temperature T and prey energy density E are provided as well. Experiment Nos refer to the accompanying Excel files.

Figure S1.5. Data on remaining stomach content mass S_t at postprandial time t in other predatory fishes fed meals of sandeel. The predicted gastric evacuation curves are provided using the integrated version of Equation (S1.3) with the common estimate 0.0119 ± 2 S.D. of l -based ρ_0 obtained from data on all predators, and the predator-specific estimates of λ . Predator length L , temperature T and prey energy density E are provided as well. Experiment Nos refer to the accompanying Excel files.

Figure S1.6. The influence of temperature T on gastric evacuation rate (GER) according to a simple exponential (—) and an optimum temperature T_{opt} function (—). T_{low} and T_{up} indicate the lower and upper temperature tolerance limits of the predator. The dashed part of the grey line indicates the likely stronger effect of temperature close to the lower tolerance limit that is not described by the optimum temperature function.

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Appendix S2

Estimation of C_{MAX} , S_{max} and factorial hyperphagic scope

Estimation of C_{MAX} from S_{MAX}

Here, we derive the episodic assimilative capacity C_{MAX} (kJ d^{-1}) from field data on maximum stomach content mass S_{MAX} (g) including assumption about the diel feeding pattern and knowledge about the prey energy density.

If τ is the (equidistant) time (h) between discrete feeding events where the stomach content mass is replenished to S_{MAX} , then according to the cylinder model the mass S_τ immediately before refilling of the stomach is

$$S_\tau = (\sqrt{S_{MAX}} - \frac{1}{2}\rho\tau)^2 \quad (\text{g}) \quad (\text{S2.1})$$

where ρ is the rate parameter (Figure S2.1).

Given the prey energy density E (kJ g^{-1}), C_{MAX} is quantified by

$$\begin{aligned} C_{MAX} &= \frac{24E}{\tau} (S_{MAX} - S_\tau) = \frac{24E}{\tau} \left(S_{MAX} - \left[\sqrt{S_{MAX}} - \frac{1}{2}\rho\tau \right]^2 \right) \\ &= 24\rho E \left(\sqrt{S_{MAX}} - \frac{\rho\tau}{4} \right) = 24\rho E \sqrt{S_{MAX}} \left(1 - \frac{\rho\tau}{4\sqrt{S_{MAX}}} \right) \quad (\text{kJ d}^{-1}) \end{aligned} \quad (\text{S2.2})$$

In one extreme scenario, we assume that the predator does not feed during the following 24 h; i.e., $\tau = 24$ in Equation (S2.2). At the other extreme, we assume that the predator is feeding continuously, which implies that S_{MAX} is maintained throughout [and $\tau \rightarrow 0$ in Equation (S2.2)] and

$$C_{MAX} = 24\rho E \sqrt{S_{MAX}} \quad (\text{kJ d}^{-1}) \quad (\text{S2.3})$$

Predatory fish are typically not continuous feeders, so scenarios with one or a few feeding periods a day are the more realistic ones. However, Equation (S2.3) expresses the absolute maximum of daily consumption rate.

Estimation of S_{max} from C_{max}

To estimate the prevalence of demonstrated hyperphagia among the sampled fish, we need to derive the maximum stomach content mass S_{max} from the sustained food consumption rate C_{max} obtained in long-term laboratory experiments. We use the same feeding scenarios as used for calculation of C_{MAX} from S_{MAX} . Thus replacing the subscript ‘MAX’ by ‘max’ and reorganizing Equation (S2.2) lead to

$$S_{max} = \left(\frac{C_{max}}{24\rho E} + \frac{\rho\tau}{4} \right)^2 \quad (\text{g}) \quad (\text{S2.4})$$

Similarly, reorganization of Equation (S2.3) produces

$$S_{\max} = \left(\frac{C_{\max}}{24\rho E} \right)^2 \quad (\text{g}) \quad (\text{S2.5})$$

in the case of continuous feeding.

To quantify the sustained food consumption rate $C_{\max}$ for our two predator species we apply the relationships obtained in two long-term laboratory studies:

Using laboratory data on Atlantic cod (*Gadus morhua*) fed to satiation with capelin (*Mallotus villosus*) by Johnsen (1981) and Braaten (1984), Jobling (1988) established the relationship

$$C_{\max} = 0.223 W^{0.802} \exp(0.104T - 0.000112T^3) \quad (\text{kJ d}^{-1}) \quad (\text{S2.6})$$

where W is body mass (g) and T temperature ($^{\circ}\text{C}$). Assuming isometric growth of cod, $C_{\max}$ scales with $L^{2.41}$.

Similarly, Andersen and Riis-Vestergaard (2003) fed lesser sandeel (*Ammodytes tobianus*) to whiting (*Merlangius merlangus*) and obtained the following expression:

$$C_{\max} = 0.0074 L^{2.28} \exp(0.076T) \quad (\text{kJ d}^{-1}) \quad (\text{S2.7})$$

where L is total body length (cm) and T temperature ($^{\circ}\text{C}$). Assuming isometric growth of whiting, $C_{\max}$ scales with $W^{0.76}$

Figure S2.1. The relationship between maximum stomach content mass $S_{\max}$ (g) and maximum daily energy intake $C_{\max}$ (kJ d^{-1}), where energy density E (kJ g^{-1}) for simplicity is put to 1. Two scenarios: the predator is feeding once (blue) or twice (red) a day (vertical parts of the curves) to replace evacuated food and regain $S_{\max}$ (blue and red symbols). Reduction of the current content due to gastric evacuation is described by $S_t = (\sqrt{S_{\max}} - \frac{1}{2}\rho t)^2$ during total periods τ of 24 h and 12 h.

Factorial hyperphagic scope

We calculate the factorial hyperphagic scope $C_{MAX}C_{max}^{-1}$. In addition to the effect of body size, the estimate of C_{MAX} depends on temperature and prey energy density [Equation (S1.1)], and C_{max} on temperature [Equations (S2.6) and (S2.7)]. For cod in the Barents Sea, the scope is calculated at the average values of predator temperature and prey energy density (Figure 4) as well as for values representing their normal ranges (prey energy density, Andersen and Beyer, 2008; temperature, Righton *et al.*, 2010) (Table S2.1). Use of the different variable values does not substantially change the estimates of the scope. This can be explained by the similar effects of temperature on C_{max} and C_{MAX} in the relevant temperature interval and by gastric evacuation rate expressed in energy units being almost independent of prey energy density according to the power value -0.85 of E [Equation (S1.1)].

Table S2.1. The factorial hyperphagic scope of 20 cm and 80 cm Atlantic cod (*Gadus morhua*) calculated for nine temperature and prey energy density combinations. The grey bar shows the scenario of average temperature and energy density, whereas the other variable combinations represent their normal ranges.

Temperature (°C)	Prey energy (kJ g ⁻¹)	Factorial scope of hyperphagia $C_{MAX}C_{max}^{-1}$			
		Feeding once a day or less		Continuous feeding	
		20 cm	80 cm	20 cm	80 cm
2	4	1.47	2.76	1.57	2.91
2	6	1.59	2.98	1.67	3.09
2	8	1.68	3.14	1.75	3.23
6.4	4	1.32	2.49	1.46	2.70
6.4	6	1.45	2.71	1.55	2.86
6.4	8	1.53	2.87	1.62	2.99
10	4	1.27	2.41	1.45	2.69
10	6	1.41	2.65	1.54	2.85
10	8	1.50	2.81	1.61	2.98

A similar insensitivity of the factorial scope to temperature and prey energy density applied to whiting.

Table S2.2. The factorial hyperphagic scope of 20 cm and 40 cm whiting (*Merlangius merlangus*) calculated for six temperature and prey energy density combinations. The grey bar shows the scenario of average temperature at sampling together with the average prey energy density at large for whiting, whereas the other variable combinations represent their normal ranges.

Temperature (°C)	Prey energy (kJ g ⁻¹)	Factorial scope of hyperphagia $C_{MAX}C_{max}^{-1}$			
		Feeding once a day or less		Continuous feeding	
		20 cm	40 cm	20 cm	40 cm
6	4	1.20	1.80	1.32	1.95
6	6	1.31	1.96	1.40	2.08
6	8	1.39	2.07	1.46	2.17
11.7	4	1.15	1.74	1.34	1.99
11.7	6	1.28	1.92	1.42	2.11
11.7	8	1.37	2.05	1.48	2.20

Here, we use the average water temperature 11.7 °C at the stomach sampling stations (sampling was performed in September in two consecutive years) combined with values of prey energy density representing the normal range in the North Sea (Andersen and Beyer, 2008). The temperature at sampling represents the normal upper value for whiting in the North Sea. Therefore, we also use the normal lower value of 6 °C (Hislop *et al.*, 1991) combined with the different prey energy values (Table S2.2).

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Appendix S3

Description of stomach content data and estimation of maximum stomach content mass S_{MAX} and its allometry

Stomach content data

The three datasets on total mass S (g) of contents in individual stomachs described below are available in the accompanying Excel files. For simplification, we only include predatory fish from the body length of 20 cm onwards for which fish prey dominate the diet in all three datasets.

Atlantic cod (Gadus morhua) sampled in the Barents Sea

The dataset is described by Holt *et al.* (2019). The data have been sampled annually since 1984 with good seasonal coverage except for the second quarter of the year. Only the Norwegian data from this joint Norwegian-Russian dataset are available for the current study ($n = 153970$) and include approximately half the total dataset. Sampling is mainly carried out during scientific bottom trawl surveys, and it covers the entire size range from 4 cm and up to a total body length of 146 cm, although there are few samples of cod outside the range 10–100 cm. The temperature experienced by cod in the Barents Sea ranges from $-1\text{ }^{\circ}\text{C}$ to $10\text{ }^{\circ}\text{C}$ (Ottersen *et al.*, 1998; Righton *et al.*, 2010; Fall *et al.*, 2018). However results from individual cod with data storage tags suggest that Arctic cod generally avoid temperatures below $2\text{ }^{\circ}\text{C}$ (Righton *et al.*, 2010; Thorsteinsson *et al.*, 2012), which is corroborated by the strong negative effect of lower temperatures on gastric evacuation rate in the cod (Salvanes *et al.*, 1995). The stomachs were analysed individually for prey composition and the individual prey items weighed. Capelin (*Mallotus villosus*) is the most important fish prey, representing about 30% of total stomach content mass of 20–80 cm cod ($n = 121917$ out of which 40 outliers with stomach content mass far above 25% body mass were excluded). We truncated the dataset at 80 cm because of low number of fish by 1-cm group above this size. Liver mass data are primarily available from 40–80 cm cod ($n = 36718$ out of which 3 outliers with I_{HS} far above 35% were excluded).

Whiting (Merlangius merlangus) sampled in the North Sea

The dataset is described by Rindorf (2002). The whiting were caught by bottom trawling at five locations in the North Sea in early September 1988 and 1989. In total, stomachs from 8300 whiting ranging from 14 cm to 47 cm were collected out of which 7526 (20–47 cm fish) were used in our analyses. The stomachs were analysed individually for prey composition and the individual prey items weighed. The prey were assigned to species (fishes) or major taxa (invertebrates). The average temperature at the stations was $11.7\text{ }^{\circ}\text{C}$. Sandeel (*Ammodytidae*), clupeids and Norway pout (*Trisopterus esmarkii*) constitute the vast majority of prey mass in the stomachs of fish ≥ 20 cm in the North Sea (Hislop *et al.*, 1991).

Whiting (Merlangius merlangus) sampled in the western Baltic Sea

The dataset is described by Ross *et al.* (2016). The whiting were caught during quarterly bottom trawl surveys from May 2011 to August 2013 at a number of fixed stations according to the design applied in the Baltic International Trawl Survey (BITS) and the extended

Fehmarn Belt Survey. The stations covered spatially and temporally the habitat of whiting in the western Baltic Sea. The contents of the collected stomachs ($n = 2347$) from whiting of body lengths between 5 and 53 cm were therefore assumed to reflect the diet and stomach content mass of whiting in the area. The quarterly average temperatures experienced by the whiting ranged from 4 °C to 13 °C. The stomachs were analysed individually for prey composition and the individual prey items weighed. Clupeids constitute the vast majority of prey mass in stomachs ($n = 1469$) of fish ≥ 20 cm.

Maximum stomach content mass S_{MAX} and its allometry

For the body length range 20–80 cm L ($n = 121877$) of the large dataset on cod, we calculated the 99.9th percentiles of S by 1-cm class of L to represent the size-specific maximum mass of stomach content S_{MAX} (g). Nonlinear regression of the power function $S_{MAX} = \kappa_{MAX} L^b$ provided a value of the exponent b close to the isometric relationship of 3 (Table S3.1). Fixing b at 3, the prefactor κ_{MAX} was then estimated alone. Using lower percentiles (for example the 97.5th and 99.0th) did not significantly affect the estimate of b pointing to the robustness of this large dataset.

The number of observations in the two smaller dataset on whiting did not allow for split into 1-cm L classes, so all data on S were normalized to $L = 1$ cm by $\kappa = S L^{-3}$ and the obtained values of κ were used to obtain κ_{MAX} by the 99.9th percentile. Data on 20+ cm whiting from the North Sea ($n = 7526$) were grouped into three L classes (20-24, 25-29, >29 cm) providing three values of κ_{MAX} to obtain an estimate with confidence limits. Data on 20+ cm whiting from the small dataset in the western Baltic Sea ($n = 1469$) did not allow for calculation of more than one value (Table S3.1).

Table S3.1. Estimates of the parameters in the relationship $S_{MAX} = \kappa_{MAX} L^b$ between total body length L (cm) and maximum mass of total stomach content S_{MAX} (g). Values of κ_{MAX} with different superscripts letter are significantly different (t -test, $P < 0.05$).

Predator population	L range	$\kappa_{MAX} (\times 10^{-3})$		b		n^*
		Estimate	95% CI	Estimate	95% CI	
Atlantic cod (<i>Gadus morhua</i>)						
The Barents Sea	20–80	1.47 1.72 ^a	± 0.48 ± 0.06	3.04 3	± 0.08 (fixed)	61
Whiting (<i>Merlangius merlangus</i>)						
The North Sea	20–47	1.26 ^b	± 0.14	3	(fixed)	3
The western Baltic Sea	20–53	1.32		3	–	1

*Number of calculated 99.9th percentiles

The isometric relationship between S_{MAX} and L obtained here is in accord with the relationship between the stomach mass itself and L in Appendix S1. It is furthermore generally substantiated in a number of field studies as well as in laboratory studies on artificially induced maximum inflation of the stomach (e.g., Flowerdew and Grove, 1979; Pope *et al.*, 2001).

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Appendix S4

Maximum food consumption rate and stomach filling of well-fed and pre-starved Atlantic cod (*Gadus morhua*) in laboratory experiments

Using the results from two explorative laboratory experiments described below, we show here that the level of maximum stomach filling depends on the nutritional status of cod. In particular, the results corroborate that the maximum mass of stomach content S_{MAX} estimated from cod stomachs sampled in the Barents Sea corresponds quite well to the hyperphagic response C_{MAX} to poor nutritional condition of the fish.

In a bioenergetics study, Andersen and Riis Vestergaard (2003) estimated the sustained maximum food consumption rate C_{max} from feeding experiments on groups of saithe (*Pollachius virens*) and whiting (*Merlangius merlangus*). First, they wanted to examine whether the experimental set-up provides reliable estimates of C_{max} , but no prior information on these species was available. Therefore, they performed an explorative experiment with a group of well-nourished cod fed satiation meals of lesser sandeel (*Ammodytes tobianus*) once a day to compare the results with those of Jobling (1988) parameterized in Equation (S2.6). Second, to examine the effects of nutritional status on consumption rate and compensatory growth, they conducted a pilot experiment on another group of cod starved for 8 weeks prior to the experiment (allowed only a sub-maintenance ration once a week). Due to multiple problems with the water supply, the latter experiment was terminated long before intended, and the consumption rate appeared rather variable. The results from the latter experiment were therefore never published. However, they can be used to gain some insight into the dynamics of C_{MAX} vs C_{max} and S_{MAX} vs S_{max} for cod.

Here, we compare the daily average per capita food consumption rates of the well-fed cod to Jobling's C_{max} calculated from Equation (S2.6) (Figure 5a). Those of the pre-starved fish were similarly compared to C_{MAX} of the Barents Sea cod population obtained from the maximum mass of sampled stomach content S_{MAX} using the cylinder model of gastric evacuation rate (GER) [Equation (S2.2) with $\tau = 24$ h: one feeding event per day; prey energy density of 6 kJ g^{-1}].

Using the GER model, we further estimate the stomach filling of the pre-starved cod in the successive days of the experiment from the daily average per capita consumption rates. This is compared to the maximum mass of stomach content S_{MAX} obtained from the Barents Sea cod population (Figure 5b). The current stomach filling S_n (g) of the pre-starved cod immediately after feeding on day n is calculated as a the result of the prey mass remaining from the preceding day plus the consumption of the new meal C_n (kJ):

$$S_n = (\sqrt{S_{n-1}} - \frac{1}{2}\rho 24)^2 + C_n E^{-1} \quad (\text{g}) \quad (\text{S4.1})$$

where S_{n-1} (g) is the prey mass immediately after feeding the preceding day, ρ ($\sqrt{\text{g h}^{-1}}$) the rate parameter of the GER model for sandeel prey, and E (kJ g^{-1}) the prey energy density. At day 0, the first term at the right side of the equation attains the value of 0. We applied the same procedure to the feeding rates C_n of the well-fed cod. Their daily stomach filling was compared to S_{max} (corresponding to Jobling's C_{max}) using Equation (S2.4) with $\tau = 24$ h (one feeding event per day).

We calculated the curves that describe C_{MAX} , C_{max} , S_{MAX} , and S_{max} in Figure 5 by body size considering that fish is growing linearly in length during the experiment. Body mass by day used for C_{max} was estimated assuming isometric growth and applying Fulton's condition factor of the well-fed fish. The basic data of the experiments are compiled in Table S4.1. Details of acquisition and acclimation of fish as well as conduction of experiments are similar to those described in Andersen and Riis-Vestergaard (2003).

Table S4.1. Basic data (mean $\pm$ s.d.) of two feeding experiments on well-fed and pre-starved cod fed sandeel prey of 6.0 kJ g⁻¹ to satiation once a day at 10.1 °C. Duration of the experiments appears from Figure 5.

Experiment	Start				End			
	Length (cm)	Mass (g)	*K	Fish (n)	Length (cm)	Weight (g)	*K	Fish (n)
Well-fed	27.2 $\pm$ 1.5	218 $\pm$ 40	1.07 $\pm$ 0.06	75	30.1 $\pm$ 1.6	299 $\pm$ 52	1.09 $\pm$ 0.08	74
Pre-starved	30.7 $\pm$ 1.4	212 $\pm$ 36	0.73 $\pm$ 0.05	37	32.6 $\pm$ 1.7	309 $\pm$ 55	0.88 $\pm$ 0.06	37

* Fulton's condition factor $K = 100 WL^{-3}$, where L is total length (cm) and W is body mass (g)

The daily food intake was variable for both groups of cod (Figure 5a). After the first two days on restricted food rations, the well-fed fish consumed a large meal to fill the stomach. The same applied to the pre-starved fish after three days of restricted food rations (as a precautionary measure to avoid a sudden nutritional overload after prolonged starvation). Thus, the initial maximum food intakes represent a transition, and it cannot be compared to the calculated curves of C_{max} and C_{MAX} .

At each feeding, the fish seemed to replenish the amount of stomach content to a relatively constant level that differed significantly between the two groups (Figure 5b). Whereas that of the well-fed fish corresponds well to the level expected for fish feeding according to C_{max} (Jobling 1988), the pre-starved fish filled their stomachs to a level close to S_{MAX} estimated from the Barents Sea population. This corroborates the assumption that S_{MAX} represent a hyperphagic response to poor nutritional condition of the fish, when the prey availability allows for binge feeding. Accordingly, the factorial scope of hyperphagia amounted to 1.63 for the prey-starved laboratory fish, which is close to the value of 1.71 obtained for cod of similar size from the Barents Sea population.

The duration of hyperphagia depends on how quickly the reserves are replenished to the targeted level, which depends on the actual nutritional state, the amount of ingested energy and the strategy of allocation to reserves and structural growth (Jobling and Johansen, 1999; Gurney *et al.*, 2003). The pre-starved cod maintained hyperphagia for all 10 days of feeding to satiation, and Fulton's condition factor increased from 0.73 to 0.88, whereas that of the well-fed fish displaying sustained maximum consumption rates was relatively constant at 1.07–1.09 (Table S4.1). Assuming that a condition factor of 1.08 represents the targeted reserve level, the displayed hyperphagia of the pre-starved fish would be of substantially longer duration had the experiment not been terminated prematurely.

For comparison, the mean value of Fulton's condition factor for the sampled Barents Sea cod of 27–32 cm ($n = 9932$) was 0.84 with lower and upper 95% confidence limits of 0.65 and 1.02. Extrapolating the experimental results to the Barents Sea population, most of these cod should display hyperphagia, when the opportunity arises.

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