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

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Marine predatory fish face unpredictable prey environments ranging from abundance to scarcity of food. Dimensioning their assimilative system to accommodate gorging and fasting is therefore a central life history choice. Assimilative capacity experiments typically operate with sustained feeding to satiation and therefore ignore the fluctuations in natural feeding opportunities. A more relevant description of the adaptive response is the episodic capacity associated with binge feeding (hyperphagia). We develop the theoretical foundation to define episodic and sustained capacity and its allometry. Extensive empirical evidence on marine piscivorous fish at higher latitudes confirms that the episodic capacity scales almost linearly with predator body mass (exponent approximately 0.95) producing an increasing factorial hyperphagic scope (exponent approximately 0.20). Our synthesis overturns the reigning steady state perspective on assimilative capacity. The fish can utilize an episodic capacity typically twice the size of the sustained capacity resulting in local dynamics of functional responses with profound implications for scaling-up to ecosystem level.

**Keywords:** allometry, binge feeding, digestive capacity, foraging strategy, higher latitudes, hyperphagia, piscivorous fish, stomach contents

**Introduction**

The capacity to assimilate ingested and digested food is a fundamental trait in the life history of predators. It determines the upper limit of the predators’ functional response (i.e. per capita daily energy intake as a function of prey density). It therefore determines the potential for growth and reproduction (Allen et al., 2016) and limits the predators’ ability to inflict predation mortality. Accounting correctly for the assimilative capacity is thus a crucial element of any formulation of predator-prey dynamics and the resulting predation mortality (e.g. Jeschke et al., 2002; Rall et al., 2012; Li et al., 2018).

The assimilative capacity of predatory fish is usually described by the sustained maximum daily energy intake $C_{max}$ obtained from long-term laboratory trials on *ad libitum* feeding of the fish (e.g. Armstrong and Schindler, 2011). However, they typically live in a
heterogeneous environment with unpredictable variations in prey availability. Spatial and temporal variability in feeding opportunity produces hot spots and moments of intense foraging (e.g. Mello and Rose, 2005; Temming et al., 2007), while periods of famine challenge the predator’s ability to maintain a positive energy balance (e.g. Arrington et al., 2002). Following the theory of quantitative evolutionary design (Diamond, 2002), dimensioning of the assimilative system should emerge as an adaptive response to the trade-off between system failure (suboptimal exploitations of episodes of food abundance) and maintenance costs that penalize excess capacity. The implication is that predatory fish develop an excess assimilative capacity relative to the average feeding situation in order to handle the fluctuations in feeding opportunity. This prediction is corroborated by laboratory studies on compensatory growth following periods of food deprivation showing that the fish are able to feed at levels far above the laboratory-based $C_{\text{max}}$ (Miglavs and Jobling, 1989; Hayward et al., 1997). The focus on sustained maximum energy intake therefore represents an incomplete description of the assimilative capacity of predators.

The functional response needs to be elaborated to account for the fact that starving predators of poor nutritional status under favourable feeding conditions can operate with daily food intakes much higher than $C_{\text{max}}$. The realization that the prey environment is fluctuating and not static challenges the scaling of local observations of functional response to characterize predator-prey interactions at population, community and ecosystem levels (e.g. Englund and Leonardsson, 2008). Adequate scaling is a prerequisite for obtaining reliable estimates of trophic interactions to inform ecosystem and fisheries models used for management of marine fisheries (Levin, 1992). Much attention has therefore been devoted to the problems associated with the scaling from local predator-prey interactions to larger areas corresponding to the level of interests (Hunsicker et al., 2011). However, direct observations of maximum energy intake in local predator-prey environments are lacking or difficult to obtain. This may explain the missing focus on the episodic assimilative capacity under hyperphagia (binge feeding) in natural settings.

Here, we focus on estimating the episodic assimilative capacity $C_{\text{MAX}}$ based on integrating the instantaneous rate of energy leaving the stomach. The maximum digestion and absorption rates under hyperphagia determine $C_{\text{MAX}}$ (Ali et al., 2003). Negative feedback mechanisms from the intestine control gastric evacuation rate (GER), which enables digestion and absorption of food in the intestine to keep up with the amount evacuated from the stomach (Jobling, 1987). Therefore we can estimate $C_{\text{MAX}}$ via maximum GER. Using a GER model, we thus transform data on field sampled stomach contents into an in situ proxy for $C_{\text{MAX}}$.

We propose and substantiate a new concept of assimilative capacity of predatory fish based on both sustained and episodic assimilative capacity. We apply the concept to marine piscivorous fishes in natural settings at higher latitudes and estimate the ratio of episodic to sustained assimilative capacity. We explore and discuss the adaptive background for the dimensioning and dynamics of the assimilative system including allometric aspects and foraging strategies.

**Material and methods**

**Outline of the concept of assimilative capacity**

The hyperphagic response to food deprivation is always close to the maximum possible rate at which the gut can process the food when the prey density allows (Ali et al., 2003). The duration of hyperphagia on the other hand depends on the level of growth depression and reserve depletion (Russell and Wootton, 1992; Bull and Metcalfe, 1997; Xie et al., 2001). Energy reserves are attempted to be maintained within a narrow range by endocrine signals from energy storing tissues that regulate feeding and energy expenditure, and duration of
hyperphagia seems to be closely coupled to restoration of targeted reserves after a period of food deprivation where lipid rather than protein is catabolized (Won and Borski, 2013). This is in accord with two physiologically based models of compensatory growth (Broekhuizen et al., 1994; Jobling and Johansen, 1999) in which hyperphagia subsides when the targeted lipid level is reached and homeostasis restored. The actual mechanisms involved in appetite control of fish in general have, however, been widely discussed (e.g. Volkoff, 2016).

Thus, predatory fish of poor nutritional status with depleted reserves always seem to operate with the episodic assimilative capacity $C_{\text{MAX}}$ being limited only by the maximum digestive and absorptive rate to achieve the targeted reserves. In contrast, when the reserves are replenished, appetite control ensures that the sustained maximum energy intake $C_{\text{max}}$ forms the upper limit. In accordance with Jeschke et al. (2002), who suggest that most predators are digestion limited, we use the following version of type II functional response to explain the principle of the new concept of assimilative capacity:

If the energy reserves are below the targeted level, then the daily energy intake $C(x)$ is described by

$$C(x) = \frac{x}{x+C_{\text{MAX}}}C_{\text{MAX}}$$

where $x$ is a measure of daily feeding opportunity considered proportional to encountered prey.

If the energy reserves are at the targeted level, then the predator becomes satiated by appetite control already at $C_{\text{max}}$, which generates a cut-off on the response curve (Figure 1).

We express the absolute hyperphagic scope by $(C_{\text{MAX}} - C_{\text{max}})$, and the factorial scope by $C_{\text{MAX}}C_{\text{max}}^{-1}$.

**Figure 1.** The type II functional response curve of a starved predator with depleted reserves using its episodic assimilative capacity $C_{\text{MAX}}$ and hence displaying hyperphagia. A well-fed predator with full reserves is following this response curve until a cut-off at the sustained capacity $C_{\text{max}}$, which then forms the upper response limit at higher prey encounter rates due to appetite regulation for maintenance of homeostasis. The absolute hyperphagic scope $(C_{\text{MAX}} - C_{\text{max}})$ (yellow area) is increasingly being utilised by the starved predator with increasing prey encounter rate above the point of cut-off (green area).
Gastric evacuation dynamics constitute our key to quantify \( C_{\text{MAX}} \), so we first elaborate on current GER modelling for this purpose by deriving a general GER allometry. Then we estimate \( C_{\text{MAX}} \) from the maximum stomach content mass \( S_{\text{MAX}} \) displayed in three data sets on stomach contents from Atlantic cod (\textit{Gadus morhua}) and whiting (\textit{Merlangius merlangus}) sampled in the wild. The hyperphagic scope obtained from the natural settings is compared to the results from laboratory experiments on \textit{ad libitum} feeding of pre-starved and well-fed cod. Additional information about liver mass in the data set on wild cod allowed us to examine the relationship between nutritional status and hyperphagia and the prevalence of predisposition to hyperphagia.

**General GER modelling with allometry**

The mechanistic cylinder model by Andersen and Beyer (2005a) is able to accurately predict GER of current stomach contents irrespective of prey composition and feeding pattern (Andersen and Beyer, 2005b, 2007). We expand the applicability of this model to predatory fish at large by deducing a general allometric relationship, examining empirical evidence and showing that measurement of stomach length is sufficient to predict GER.

Total stomach content at time \( t \) is viewed as a cylinder of mass \( S_t \) (of density 1), stomach length \( l \) and radius \( r_t \). The surface of its curved side \( A_t \) is successively peeled off during digestion and evacuated. Thus, GER expressed by \(- \frac{dS_t}{dt}\) is equal to \( \delta A_t \), where \( \delta \) is the rate at which \( r_t \) is reduced, and \( A_t \propto \sqrt{t} \) (Figure 2). Here we can consider \( l \propto \text{body length} \) \( L \) so \( A_t \propto \sqrt{L} \). Furthermore, the stomach is assumed to grow isometrically, so the digestive capacity of the stomach in terms of hydrochloric acid and pepsin production rates per unit of mucosa surface area in contact with the prey is proportional to \( L \) provided that the activity per unit mass of glands is constant (Diamond, 2002). In this case, \( \delta \propto L \) and consequently \( \frac{dS_t}{dt} \propto L \sqrt{L} = L^{3/2} \). Alternatively, assuming that the gland activity per unit mass of stomach has some fractal nature of the scaling exponent, the mass scaling of the enzyme production rate is \( L^3/4 \) (West et al., 1997). This implies that the area-specific enzyme production rate scales with \( L^3/4 \), resulting in \( \frac{dS_t}{dt} \propto L^{3/4} \sqrt{L} = L^{5/4} \).

Since \( A_t \propto \sqrt{S_t} \) (Figure 2), we then describe predator-specific GER by

\[
\frac{dS_t}{dt} = -\rho \sqrt{S_t} \quad \text{with} \quad \rho \propto L^k; \quad \frac{3}{4} \leq k \leq \frac{3}{2},
\]

where the rate parameter \( \rho \) is expanded to include the effects of \( L \), temperature \( T \) (°C), prey energy density \( E \) (kJ g\(^{-1}\)) and prey-specific resistance to the digestive processes. The latter can be considered similar among prey fishes (Andersen, 2012).

We examine the assumptions about an intraspecific constant value of \( \lambda = l \ L^{-1} \) and isometric stomach growth using an assortment of predatory fish sampled in the North Sea (Supplementary Appendix S1). We further compare the derived range of the exponent \( k \) to empirical estimates reported for a number of marine and freshwater species, re-estimate these exponents using the same statistical procedure on all the reported GER data, and estimate a common interspecific value.

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, which we document using available data on five predatory fish.
species fed the same prey type. We therefore expand $\rho$ to also include the effect of the predator-specific value of $\lambda$.

![Figure 2. Cylinder abstraction of total prey mass in a stomach. The cylinder length $l$ is the length of the stomach. The current prey mass (= volume) at time $t$ is denoted $S_t$ and the area of the curved side $A_t$. The rate of decrease of the current radius $r_t$ due to the digestive processes and evacuation of the curved cylinder surface is specified by $\delta$. The relationships between $A_t$, $S_t$ and $l$ are indicated. The gastric evacuation rate is expressed by the decrease in prey mass per time unit ($\frac{dS_t}{dt}$).](image)

**Allometry of episodic assimilative capacity $C_{\text{MAX}}$**

Assuming that both the maximum stomach content mass $S_{\text{MAX}}$ and predator body mass $W$ scale with $L^3$, it follows that $C_{\text{MAX}} \propto -\frac{dS_{\text{MAX}}}{dt} = \rho \sqrt{S_{\text{MAX}}} \propto L^{k+\frac{3}{2}} \propto W^{\frac{k+1}{2}}$ if the predator feeds continuously. Thus,

$$C_{\text{MAX}} \propto W^p ; \quad 1^{1/2} < p < 1,$$

which is substantially higher than the generally used theoretical and empirical body mass scaling of $\sim \frac{3}{4}$ for $C_{\text{MAX}}$ (e.g. West et al., 1997; Fish Bioenergetics 3.0, 1997).

If the predator feeds on discrete meals every $\tau$ hours, then

$$C_{\text{MAX}} \propto \rho \left( \sqrt{S_{\text{MAX}}} - \frac{\rho \tau}{4} \right) = \rho \sqrt{S_{\text{MAX}}} \left( 1 - \frac{\rho \tau}{4 \sqrt{S_{\text{MAX}}}} \right)$$

(Supplementary Appendix S2) with the same allometric exponent $p$ as in Equation (3) if $k = \frac{3}{2}$. For $\frac{3}{4} \leq k < \frac{3}{2}$ the value of the allometric exponent obtained by least squares fit to calculated values of $C_{\text{MAX}}$ by 1-cm $L$ class of the predator is slightly higher (less than 1%) than $p$ defined in Equation (3) because $\rho \ll \sqrt{S_{\text{MAX}}}$.

**Estimation of $C_{\text{MAX}}$ and hyperphagic scope**

We estimate $S_{\text{MAX}}$ and its allometry from a large data set on cod sampled in the Barents Sea ($n = 121877$) using the 99.9th percentile of $S$ by 1-cm $L$ class (Figure 3). In addition, using data on $S$ normalized to $L = 1$ cm by $\kappa = S L^{-3}$, we estimate $S_{\text{MAX}}$ from two smaller sets on
whiting obtained from the North Sea (n = 7526) and the western Baltic Sea (n = 1469) (Supplementary Appendix S3). We further compare the estimated value of $S_{\text{MAX}}$ for Barents Sea cod to the estimated stomach filling of pre-starved cod of c. 30 cm $L$ fed to satiation in a laboratory experiment by Andersen & Riis-Vestergaard (2003) (Supplementary Appendix S4).

![Figure 3](image)

**Figure 3.** (a) Total prey mass $S$ (blue open circles) in 121877 individual stomachs of Atlantic cod by 1-cm length class between 20 cm and 80 cm total body length $L$ from the Barents Sea. The estimated $S_{\text{MAX}}$ (solid line) and its 95% CLs (broken lines) corresponding to the episodic assimilative capacity $C_{\text{MAX}}$ are obtained from all stomachs using the 99.9th percentile by $L$ class (red circles). $S_{\text{max}}$ corresponding to the sustained capacity $C_{\text{max}}$ is calculated from laboratory estimates (Jobling 1988), using the gastric evacuation rate model and assuming one feeding event per day (solid line) or continuous feeding (broken and dotted line). The percentages represent the allometric increase in the prevalence of stomachs with $S > S_{\text{max}}$ that are located in the yellow shading. (b) Distribution of $S$ for cod of 50 cm $L$ (n = 2379). The stomachs are binned into classes of increasing $S$-width. Black column represents the number of empty stomachs. The other elements are explained in (a).

Using the cylinder model we estimate $C_{\text{MAX}}$ from $S_{\text{MAX}}$ in the two extreme scenarios of no feeding for the next 24 h (i.e. $\tau = 24$) or maintaining $S_{\text{MAX}}$ by continuous feeding (i.e. $\tau = 0$) (Supplementary Appendix S2). The GER depends on temperature and prey energy density. We use average values of predator temperature and prey energy density together with the two feeding assumptions.
We further estimate the stomach content mass $S_{\text{max}}$ from $C_{\text{max}}$ of cod and whiting obtained from laboratory experiments (Jobling, 1988; Andersen and Riis-Vestergaard, 2003) (Supplementary Appendix S2). The frequency of individuals with $S > S_{\text{max}}$ in the wild provides an estimate of the prevalence of displayed hyperphagia. We finally calculate the factorial hyperphagic scope and its allometry, and examine its sensitivity to temperature and prey energy density within their normal ranges (Supplementary Appendix S2).

**C_{\text{MAX}} and foraging strategy**

We need a proxy for $S_{\text{MAX}}$ to connect $C_{\text{MAX}}$ with foraging strategy for a wider range of predator species. The maximum stomach dilation depends on the number and size of the longitudinal folds of the stomach wall that allow the mucosa surface to unfold and expand in pace with the mass $S$ of contents to contribute to the digestive processes in accordance with the cylinder GER model. The $l$-specific mass of the stomach itself described by the prefactor $a = w l^{-3}$ thus indicates how much the stomach is able to expand; i.e. the maximum circumference of a cross section of the stomach cylinder. If $\lambda = LL^{-1}$ was the same for all predator species, $a$ could be applied directly as proxy for $S_{\text{MAX}}$. However, species-specific $\lambda$ values imply that instead $a \lambda$ must be used to serve as proxy, which we calculate for a variety of predator species (Supplementary Appendix S1).

**Nutritional status and predisposition to hyperphagia**

A large part of the data set on cod includes information about body and liver masses ($n = 36715$) enabling us to calculate the hepatosomatic index $I_{\text{HS}}$ (ratio of liver mass to body mass). This index indicates the lipid level and nutritional status of cod as well as gadoid predators in general (e.g. Marshall et al., 1999; Cantafaro et al., 2017) and allows us to assess the prevalence of predisposition to hyperphagia.

Cod with $S < S_{\text{max}}$ should represent a mixture of the two states of nutritional status: predators with high nutritional status operating with $C_{\text{max}}$ as the upper limit and predators with depleted reserves that would have displayed hyperphagia if plentiful prey had been available at some time prior to stomach sampling. Relating $I_{\text{HS}}$ to $S$, we estimate the nutritional status of cod clearly displaying hyperphagia by their $S$ being situated at least halfway between $S_{\text{max}}$ and $S_{\text{MAX}}$. We let the upper limit of the $I_{\text{HS}}$-values for these cod define the upper limit for predisposition to hyperphagia to estimate the fraction of cod with $S < S_{\text{max}}$ that would have displayed hyperphagia if better feeding opportunities had been available.

**Results**

The episodic assimilative capacity $C_{\text{MAX}}$ can be considered proportional to $\rho$ multiplied by $\sqrt{S_{\text{MAX}}}$, and each factor contributes to allometry.

First, the results we obtained from a number of marine species confirm that stomach length is proportional to body length within a species (constant intraspecific ratio $\lambda$ of $l$ to $L$) and stomach growth is isometric, which is used in the theoretical derivation of $\rho$ allometry (Supplementary Appendix S1). Further, the scaling exponent of $\rho$ with $L$ obtained from GER experiments on a variety of predatory fish reported in the literature ranges from 1.3 to 1.4, which matches the interval of 1.25–1.50 derived theoretically by the cylinder model. Use of the same statistical procedure on all GER data from the reported species provided a similar narrow range of estimates with a common exponent of 1.35 (Supplementary Table S1.2).

The relative stomach length $\lambda$ was statistically different among the predators. Low values obtained from whiting and saithe (Pollachius virens) differed from the other species, whereas
cod, turbot (*Psetta maxima*) and grey gurnard (*Eutrigla gurnardus*) did not show statistically different values, and neither did cod, grey gurnard and haddock (*Melanogrammus aeglefinus*) (Supplementary Table S1.1). Expressing the effect of predator size on GER by $l$ rather than $L$, the estimated values of the basic rate parameter $\rho_0$ in the expression

$$
\rho = \rho_0 E^{-0.85} (\lambda L)^{3.35} e^{0.087} T \sqrt{g \ h^{-1}}
$$

was similar among all the predator species (Supplementary Table S1.1). Here it is only $\lambda$ that is predator specific since the exponent of $E$ and coefficient of $T$ are considered generic (Andersen 2012). It should however be noticed that the simple exponential fails to describe the effect of extreme temperatures on GER (Supplementary Appendix S1). The similar values of $\rho_0$ support the assumption about optimization of the gastric mucosa performance and point to the usefulness of the mechanistic cylinder model as a generic tool for estimation of $C_{\text{MAX}}$ from field data on $S_{\text{MAX}}$ across marine predatory fishes at higher latitudes. The common estimate $1.19 \pm 0.02 \times 10^{-2}$ (estimate $\pm$ 95% C.I.) of $\rho_0$ was obtained from GER data on all the predator species.

Second, the scaling of maximum mass of stomach contents $S_{\text{MAX}}$ (g) with body length $L$ (cm) for cod from the Barents Sea was described by an exponent close to 3, which is generally supported in the literature (Supplementary Appendix S3). The estimate $1.72 \pm 0.06 \times 10^{-3}$ (g cm$^{-3}$) (estimate $\pm$ 95% C.I.) of $k_{\text{MAX}}$ (corresponding to 17.2% body mass) was then obtained for the relationship $S_{\text{MAX}} = k_{\text{MAX}} L^3$. The value $1.26 \pm 0.14 \times 10^{-3}$ estimated from data on whiting sampled in the North Sea was significantly lower. The small data set on whiting from the western Baltic Sea provided an estimate of $1.32 \times 10^{-3}$ (without confidence interval) that supports the estimate obtained from the North Sea (Supplementary Appendix S3). We did not treat the Baltic Sea population further here.

We finally quantify the episodic capacity $C_{\text{MAX}}$ inserting Equation (5) into $24\rho E\sqrt{S_{\text{MAX}}} \varphi$, where \( \varphi = (1 - \frac{p_t}{4\sqrt{S_{\text{MAX}}}}) \) is the correction for feeding on discrete meals every $\tau$ hours as compared to continuous feeding with $\varphi = 1$. This provides

$$
C_{\text{MAX}} = 24\rho_0 E^{0.155} \lambda^{1.35} L^{2.85} e^{0.087} \sqrt{k_{\text{MAX}}} \varphi \sqrt{S_{\text{MAX}}} \quad (\text{kJ d}^{-1})
$$

where $S_{\text{MAX}}$ has been substituted by $k_{\text{MAX}} L^3$. Combining the scalings of $\rho$ and $\sqrt{S_{\text{MAX}}}$ and assuming isometric body growth thus leads to

$$
C_{\text{MAX}} \propto L^{2.85} \propto W^{0.95}
$$

The maximum sustained food intake $C_{\text{max}}$ is usually assumed to scale with $W^{0.75} \propto L^{2.25}$. Thus, the factorial hyperphagic scope increases with increasing predator size with the scaling

$$
C_{\text{MAX}} C_{\text{max}}^{-1} \propto L^{0.60} \propto W^{0.20}
$$

In this study, we used $C_{\text{max}}$ obtained empirically from feeding trials on cod and whiting in the laboratory (Jobling, 1988; Andersen and Riis-Vestergaard, 2003) with estimated allometric scaling of $L^{2.41}$ and $L^{2.28}$ for the two species. This provides a scaling of the factorial scope of $L^{0.44}$ and $L^{0.57}$. The
The scaling exponents in Equations (7) and (8) refer to continuous feeding. If feeding of the sampled fish would not have taken place within the next 24 hours, the scaling exponent of \( C_{\text{MAX}} \) obtained from \( S_{\text{MAX}} \) in stomachs sampled in the field does not deviate significantly from 0.95 [Equation (4)]. The same applies to \( S_{\text{max}} \) estimated from laboratory-based \( C_{\text{max}} \) [Supplementary Equation (S2.4)]. The factorial hyperphagic scope increased accordingly from 1.45 (1.55) to 2.71 (2.86) for cod, and from 1.28 (1.42) to 1.92 (2.11) for whiting (continuous feeding in brackets) (Figure 4).

![Figure 4](image)

**Figure 4.** The relationship between assimilative capacity and body size of (a) Atlantic cod from the Barents Sea \((n = 121877)\) and (b) whiting from the North Sea \((n = 7526)\). The episodic capacity \( C_{\text{MAX}} \) is estimated from field data on maximum stomach content \( S_{\text{MAX}} \) using the gastric evacuation rate model and assuming one feeding event per day (estimate and lower 95% CL, orange lines) or continuous feeding (estimate and upper 95% CL, blue lines). The sustained capacity \( C_{\text{max}} \) is estimated from feeding trials (cod, Jobling 1988; whiting, Andersen & Riis-Vestergaard 2003). The yellow shading represents the absolute hyperphagic scope \((C_{\text{MAX}} - C_{\text{max}})\) and the red numbers indicate the allometry of the factorial scope \((C_{\text{MAX}}/C_{\text{max}})\).

The effect of temperature is almost the same for GER and \( C_{\text{max}} \), and prey energy density only slightly affects the evacuated amount of energy. The factorial hyperphagic scope is therefore quite insensitive to differences in temperature and energy density (Supplementary Appendix S2).

It supports our concept of assimilative capacity that the pre-starved cod, fed to satiation in the laboratory experiment, filled their stomachs to a level close to \( S_{\text{MAX}} \) estimated from Barents Sea cod of similar size, and the level of the well-nourished cod closely matched \( C_{\text{max}} \) calculated from the results of Jobling (1988) (Figure 5). The factorial scope consequently amounted to 1.63 for the pre-starved laboratory fish, which is close to the value of 1.71 obtained for cod of similar size from the Barents Sea population.

The \( l \)-specific stomach mass \( a = w l^{-3} \) and the ratio \( \lambda \) of \( l \) to body length \( L \) both differed among predator species. Therefore, \( a\lambda \) was used as the proxy for the maximum volume capacity of the stomach \( S_{\text{MAX}} \) for a given predator size. All estimates of \( a\lambda \) with the exception of those for grey gurnard and haddock were different (Supplementary 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 estimates, and saithe and whiting providing the lowest ones.
Figure 5. Experiments at 10 °C on two groups of cod (length ~30 cm) fed satiation meals of sandeel (energy density, 6 kJ g⁻¹). The cod were either fed to satiation (blue symbols) or pre-starved (red symbols) for a longer period prior to day 0 of the experiment. The fish were fed restricted rations the first two (well-fed fish) or three days (starved fish) of the experiment. (a) The daily food intake of the two groups and the corresponding sustained assimilative capacity $C_{\text{max}}$ (blue broken line) obtained from Jobling (1988) and episodic capacity $C_{\text{MAX}}$ (red broken line) obtained from field data on maximum stomach content $S_{\text{MAX}}$ using the gastric evacuation rate (GER) model. (b) The mass of stomach content each day immediately after feeding as the result of the prey mass remaining from the preceding day plus the consumption of the new meal for the two groups. The corresponding values of $S_{\text{max}}$ (blue broken line) are obtained from Jobling’s (1988) $C_{\text{max}}$ function using the GER model whereas $S_{\text{MAX}}$ (red broken line) comes directly from field data on cod.

The prevalence of Barents Sea cod displaying hyperphagia with $S > S_{\text{max}}$ increased with fish size from 4% (5%) to 16% (21%) (continuous feeding in brackets) (Figure 3). Median and range of the values of $I_{\text{HS}}$ for cod containing prey masses $< S_{\text{max}}$ are also representative for cod displaying hyperphagia (Figure 6). Therefore the overall nutritional status of the sampled cod with hyperphagic response does not seem to be different from the status of those with stomach content mass $< S_{\text{max}}$.

Discussion
Scope, prevalence and duration of hyperphagia together define the importance of $C_{\text{MAX}}$ for subsistence of individual species as well as for predator-prey interactions. These different aspects of hyperphagia have not been studied in natural settings (Ali et al., 2003). Based on our results, and including related information, we discuss $C_{\text{MAX}}$ as the adaptive response to cope with variability in foraging opportunity and modulated by reserve dynamics, predator avoidance and foraging strategy.

Allometry and dimensioning of hyperphagia
The factorial hyperphagic scope increased with body size from 1.4 to 2.7 for cod and from 1.3 to 1.9 for whiting. The same trend should be expected from the other examined predators cf. the general allometry of GER and isometry of $S_{\text{MAX}}$. The factorial scope after food deprivation in laboratory experiments was 1.5, 2, and >2 for Arctic char (Salvelinus alpinus), three-spined stickleback (Gasterosteus aculeatus), and hybrid sunfish (Lepomis cyanellus × L. macrochirus) (Ali et al., 2003), which is in the same range as our findings for wild fish.
Further, the factorial scope we obtained from the laboratory experiment on pre-starved cod compared well with the field estimate from the Barents Sea.

**Figure 6.** The relationship between total body length $L$ and hepatosomatic index $I_{HS}$ of wild Atlantic cod from the Barents Sea. The cod were split into two groups by prey mass $S$ in the stomach. Fish in one group (blue open circles) contained $S < S_{\text{max}}$ where $S_{\text{max}}$ corresponds to the sustained assimilative capacity $C_{\text{max}} (n = 27074)$. Those in the other group (yellow circles) displayed significant hyperphagia with the lower limit of $S$ lying halfway between $S_{\text{max}}$ and $S_{\text{MAX}} (n = 710)$. $S_{\text{MAX}}$ corresponds to the episodic assimilative capacity $C_{\text{MAX}}$. Lines represent 2.5th, 50th and 97.5th percentiles for fish with $S < S_{\text{max}}$. Jobling (1988) reported a lower limit of $I_{HS}$ for farmed cod (red circle).

Essington *et al.* (2000) and Armstrong and Schindler (2011) attribute excess assimilative capacity to an adaptive response to variability in foraging opportunity in accordance with Diamond (2002). The increase in factorial hyperphagic scope with body size should then indicate that the variability in foraging opportunity increases when the fish are growing larger. This may partly be explained by the fitness optimization strategy being reversed during the ontogenetic development as found by Rosland and Giske (1994): juveniles are benefitting most by maximizing growth rate to minimize time until reproductive size, and adults by minimizing predation mortality rate to maximize the number of offspring. Put differently, small fish take advantage of any foraging opportunity, whereas the larger ones are less risk taking and then miss foraging opportunities.

The allometry of the factorial hyperphagic scope may further reflect the general trend that energy density increases with body size (Pedersen and Hislop, 2001; Ali *et al.*, 2003). Juveniles are lean as they do not accrue lipid but use almost all the obtained net energy to increase their structural size. They therefore do not benefit from $C_{\text{MAX}}$ being substantially larger than $C_{\text{max}}$ to replete lipid reserves. In contrast, adults accumulate reserves presumably to secure adequate energy for periods of starvation and in connection with spawning (e.g. Martin *et al.*, 2017). Therefore they need a higher factorial hyperphagic scope to take advantage of favourable feeding conditions. The higher scope for large fish also fits in with accumulation of lipid reserves being hyperallometric (body mass exponent >1) and maintenance costs hypoallometric (exponent <1), so that they are able to subsist longer on their reserves alone as compared to their smaller conspecifics (Schultz and Conover, 1999; Byström *et al.*, 2006).
Prevalence and importance of hyperphagia

The prevalence of cod demonstrating hyperphagia increased with body size from 4% to 16%. Largemouth bass (*Micropterus salmoides*) relying on rare prey-encounters in three small lakes likewise seem to practise hyperphagia as c. 13% of the fish displayed stomach contents above the level corresponding to $C_{\text{max}}$ (Essington et al., 2000).

However, these estimates of prevalence of hyperphagic response do not include fish that would have exerted hyperphagia if plentiful prey had been available. The predisposition to hyperphagia depends on the nutritional status, and hyperphagia does not subside until the targeted lipid level has been reached. The range of lipid levels indicated by $I_{\text{HS}}$ did not differ between the individuals displaying hyperphagia and the other individuals in the sampled cod population. This suggests that more or less all individuals in this large population hold the predisposition to hyperphagia, and that the lipid level probably seldom reaches the high values observed in farmed fish and fish used in laboratory experiments to estimate sustained maximum consumption rate $C_{\text{max}}$ (e.g. Jobling, 1988; Grant et al., 1998; Andersen and Riis-Vestergaard, 2003). For example, the value of $I_{\text{HS}}$ for farmed cod exceeded 12% (Jobling, 1988), which is more than we find for wild populations, and far above the median value. High lipid values obtained in laboratory experiments are probably due to sustained abundance of food as well as low swimming activity costs (Andersen and Riis-Vestergaard, 2004). Altogether, it can be questioned if the sustained assimilative capacity $C_{\text{max}}$ obtained from laboratory experiments is useful to define the upper limit of the assimilative capacity of predatory fish experiencing scarcity as well as abundance of food.

In recent decades, a focus has been on the importance of small-scale hot spot predation episodes on large-scale predation mortality of fish caused by a number of marine piscivorous fishes (e.g. Temming et al., 2004; Floeter et al., 2005; Trenkel et al., 2005). Temming et al. (2004) explored a local episode of short duration in the North Sea where aggregated whiting gorged on large aggregations of newly settled juvenile cod. The predator removed more than 50 million juveniles in five days, which corresponds to around 3 percent of the average size of an incoming year class at that life stage. A limited number of hot spots of similar magnitude should then wipe out an entire incoming year class, which emphasises the potential importance of high-intensity predation events. The episodic assimilative capacity $C_{\text{MAX}}$ in natural predator populations is thus probably a more general phenomenon, and the use of $C_{\text{max}}$ to describe the functional response in such important predator-prey interactions may heavily underestimate the role of predators, for example in food web models.

Foraging strategy and assimilative capacity

It has been suggested that foraging strategy is closely related to physiology, morphology, and life history traits (Huey and Pianka, 1981). Predators’ foraging mode may be classified within a continuum ranging from sit-and wait (ambush) to active foragers. An important physiological characteristic associated with these strategies is how the predators allocate their metabolic capacity to digestion and locomotion (Bennet and Hicks, 2001). In accordance with the suggestions of Secor (2001), the ambush-foraging southern catfish (*Silurus meridionalis*) allocates most of its metabolic scope to digestion, and its locomotory capacity decreases profoundly during digestion of a large meal (Fu et al., 2009). In contrast crucian carp, (*Carassius auratus*) is foraging during digestion and allocates less of its metabolic capacity to digestion, which allows it to maintain a high capacity for swimming after feeding so that it is able to efficiently search for food and digest at the same time (Fu et al., 2009). In this connection, it is intriguing that the exponent 0.95 of the body mass scaling we find for the episodic assimilative capacity is similar to values close to 1 for maximum metabolic rate (MMR) during exercise (e.g. Brett, 1965; Glazier, 2009). Species-specific combinations of
costs of assimilation and locomotion competing for the aerobic scope (the difference between MMR and general standard metabolic rate SMR) may thus dimension MMR (cf. Norin and Clark, 2016).

The present study substantiates the relationship between foraging mode and assimilative capacity. Among the examined gadoid predators, we found that the stomach mass (which we relate to $S_{\text{MAX}}$) of the ambush-like predator cod was larger compared to that of its more active relatives, whiting and saithe, indicative of a higher digestive capacity of the former. The stomach mass of other predators examined here was of intermediate size in accord with their active but more sluggish foraging mode compared to whiting and saithe. The difference between cod and whiting in the direct estimates of $S_{\text{MAX}}$ obtained from sampled stomach contents, points to the same relationship.

Maintenance costs of the assimilative apparatus is probably not the only variable that puts a limit on assimilative capacity. Wasted space for a large assimilative system that jeopardizes body shape and swimming performance of active predatory fish would likely be penalized in accord with Diamond (2002). This aspect might therefore have contributed to the smaller stomach of saithe and whiting. The corresponding lower assimilative capacity is then presumably negated by more frequent prey encounter and lower variability in foraging opportunity because of higher capacity for swimming and prey searching.

**Conclusion**

Predatory fish are experiencing episodes of gorging and fasting and long periods of empty stomachs on a regular basis, which challenge their ability to obtain positive energy balance. These episodes appear important not only in small freshwater bodies but also in large marine systems where small-scale predation hot spots may be a significant structuring force in population and food web dynamics.

As an adaptive response to cope with the variability in foraging opportunity and to take advantage of episodes of abundant food, predators need an excess assimilative capacity relative to the average food intake. We consider the episodic capacity $C_{\text{MAX}}$ associated with hyperphagia the adaptive response rather than the commonly applied sustained capacity $C_{\text{max}}$ obtained from long-term feeding to satiation in laboratory experiments. According to our concept of assimilative capacity dynamics, $C_{\text{max}}$ is the response of well-fed fish.

The maximum gastric evacuation rate GER eventually determines $C_{\text{MAX}}$ and hence the capacity for hyperphagia and repletion of lipid stores. We demonstrate a consistent way of estimating $C_{\text{MAX}}$ from field data on $S_{\text{MAX}}$ using a generic GER model. The results from laboratory experiments on pre-starved cod reflect the field-based estimates of $C_{\text{MAX}}$ and thus provide an alternative way of estimating the episodic assimilative capacity.

The factorial hyperphagic scope increases with body size because of a higher allometric exponent for $C_{\text{MAX}}$. This increase in scope may be explained by a shift in the trade-off between maximizing food intake and minimizing predation mortality during ontogeny. The increased capacity to accumulate reserves as well as the higher energy density of large fish further supports the high allometry of hyperphagia. Superimposed in the body size-related difference in $C_{\text{MAX}}$ is the interspecific difference in foraging strategy with ambush predators holding a higher digestive capacity and larger stomach as compared to species that are more active in their prey search.

The nutritional status of cod in the Barents Sea indicates that the episodic rather than the sustained assimilative capacity is the norm. If this is a general phenomenon among predatory fish, then functional response models should be changed to allow for stronger top-down control on prey than hitherto implemented.
The theoretical framework of assimilative capacity presented here should prove useful in empirical studies on feeding of predatory fish under field conditions and contribute to a better understanding and description of their functional response. An important task in relation to multispecies and ecosystem models is to examine how the framework eventually translates information from sampled stomachs into aggregated feeding rates at the population level of the predator. In particular, the apparent importance of small-scale hot spot episodes of intense feeding calls for a closer examination of their prevalence and extent in combination with how the fish utilize the episodic assimilative capacity in terms of feeding dynamics in present and future dedicated field studies. Needed here for interpretation are more field studies on the nutritional status of different relevant fish species and laboratory studies that relate the amount of stomach content and feeding rate to the nutritional status.

**Authors’ contributions**
NGA was responsible for the rationale and design of the study and wrote the first draft of the manuscript. BB and STN compiled the field data. NGA, STN and BB processed the data. NGA and STN did the statistical analyses. JEB and KHA improved different parts of the draft. All authors provided feedback on the final manuscript draft.

**Supplementary material**
Supplementary material is available at the ICESJMS online version of the manuscript.

**Data availability**
The data supporting the results are archived in ICES’ Data Centre.

**References**


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