



Original research article

Half-saturation constants in functional responses



Christian Mulder^{a,*}, A. Jan Hendriks^b

^a National Institute for Public Health and the Environment, P.O. Box 1, 3720BA, Bilthoven, The Netherlands

^b Department of Environmental Science, Radboud University, P.O. Box 9010, 6500GL, Nijmegen, The Netherlands

ARTICLE INFO

Article history:

Received 27 August 2014

Received in revised form 10 September 2014

Accepted 11 September 2014

Available online 29 September 2014

Keywords:

Allometry

Body mass

Food consumption

Nutrient absorption

Trophic level

ABSTRACT

Intake of elemental nutrients by plants and food by animals is often considered to be a hyperbolic or sigmoid function of the resource. In these global relationships, the half-saturation constant K_m , i.e. the resource availability at which half of the maximum intake is reached, determines the outcome of models and may contribute to explain behavioral traits, life-strategies and species occurrence. As macroecological data on this parameter are rather scarce, our investigation aims (1) to provide an overview of the half-saturation constants reported in literature and (2) to explore the consistency of the data with the body size trait. First, a meta-analysis was conducted on reviews and original studies published in literature. Second, the half-saturation constants obtained for several groups were linked to body size. In total, 338 half-saturation constants were collected from bacteria to ungulates, showing that the half-saturation reflects less than expected body size. Individual body size is not the dominant predictor determining the half-saturation constant, in contrast to interacting resource and consumer's sizes which are crucial to understand the variability of functional responses.

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1. Introduction

Absorption of elemental nutrients by plants and ingestion of food by animals are two crucial ecological processes for understanding of ecosystem functioning, including the assessment of the effects of anthropogenic interferences such as overgrazing, overfishing and eutrophication. Generally, the rate of intake is considered to increase with nutrient concentration and food density, until it levels off due to some kind of saturation. This relationship has been described by a large number of mathematical equations. For instance, over 40 different functions have been proposed for consumption (e.g. Spalinger and Hobbs, 1992; Jeschke et al., 2002). By contrast, empirical support for these relationships is limited to a few taxonomic groups. Even more, the lack of data is unlikely to be reduced substantially by additional species-specific observations because of financial, practical and ethical restrictions.

Models seem to be plagued with parameter values and according to Yodzis and Innes (1992) two attitudes are prevalent, either to focus on few populations, tailoring models for detailed measurements, or to leave the parameters open, creating weak and abstract models. Ecological assessments that aim to cover a broad taxonomic diversity often contain intake functions with parameters for which only some empirical values are available. Fortunately, most absorption and ingestion experiments have been examined using one single function that relates the intake rate constant k to the nutrient

Abbreviations: k , intake rate constant; K , carrying capacity; K_m , half-saturation constant for nutrient absorption and food ingestion; L , predator's length; m , species' body mass; m_i/m_{i-1} , consumer-to-resource body-mass ratios; N , nutrient concentration and food density.

* Corresponding author.

E-mail addresses: Christian.Mulder@rivm.nl (C. Mulder), a.j.hendriks@science.ru.nl (A.J. Hendriks).

<http://dx.doi.org/10.1016/j.gecco.2014.09.006>

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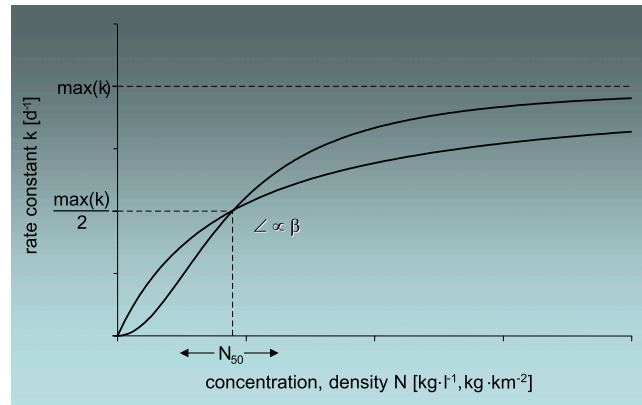


Fig. 1. Absorption of elemental resources and ingestion of food k [d^{-1}] versus nutrient concentration and food density N [$\text{kg} \cdot \text{l}^{-1}$ or $\text{kg} \cdot \text{km}^{-2}$], respectively, according to Eq. (1) with a hyperbolic ($\beta \leq 1$) and sigmoid ($\beta > 1$) response set by the half-saturation concentration or density N_{50} [$\text{kg} \cdot \text{l}^{-1}$ or $\text{kg} \cdot \text{km}^{-2}$] at which half of the maximum rate $\max(k)$ is reached.

concentration and food density N in the environment according to

$$k = \max(k) \cdot \frac{N^\beta}{N^\beta + K_m^\beta} \quad (1)$$

The aim of the present study was to provide an overview of half-saturation constants for nutrient absorption and food ingestion (K_m) and explore possible relationships to the trophic level, taxonomic group and the size of species. To achieve this, data (see 'Data mining' in Section 2) were related to species' individual mass m with regressions derived from

$$K_m = \gamma \cdot m^\kappa \quad (2)$$

equivalent to

$$\log(K_m) = \log(\gamma) + \kappa \cdot \log(m) \quad (3)$$

If resources are scarce, i.e. $N < K_m$, absorption and ingestion k rate constants [$\text{kg} \cdot \text{kg}^{-1} \cdot \text{d}^{-1}$] increase linearly with respectively the concentration of elemental nutrients and the resource density N (Fig. 1). If resources are (more) abundant, i.e. $N > K_m$, intake k levels off to the maximum value $\max(k)$ due to transport and transformation delays such as nutrient translocation in plants or food digestion in animals.

The exponent β indicates inhibition ($\beta < 1$) and facilitation ($\beta > 1$), yielding a hyperbolic and sigmoid curve, respectively. In biochemistry, the relationship describes the transport and transformation of substances, such as oxygen or glucose, without ($\beta \leq 1$) or with ($\beta > 1$) allosteric effects (Hill, 1910; Michaelis and Menten, 1913). In microbiology and plant sciences, the hyperbolic equation is used for nutrient intake (Monod, 1942). Ingestion of food by animals is described by either a Type II ($\beta = 1$) or Type III ($\beta = 2$) functional response, also reflecting independence and facilitation, e.g. due to experience in prey search or handling (Holling, 1959). The half-saturation constant K_m [$\text{kg} \cdot \text{km}^2$, $\text{kg} \cdot \text{l}^{-1}$] represents the concentration or density at which half of the maximum intake rate [$1/2 \cdot \max(k)$] is reached, independently of slope β . Low K_m values apply to plants and animals that acquire resources rapidly at low concentrations and densities, high values are noted for inefficient organisms.

For instance, half-saturation constants for nutrient absorption by phytoplankton increase along a gradient from oligotrophic oceans to eutrophic estuaries, even within the same species (e.g. Carpenter and Guillard, 1971). It suggests that adaptation of organisms to the level of resources in their environment is reflected in the value of the half-saturation constant. Only a few experiments have been carried out to obtain K_m directly. Instead, the half-saturation constant is often derived indirectly by fitting the output of ecological models as a whole to field data on population dynamics. This pragmatic approach is adequate in cases where uncertainty in the intake function is known to dominate the variability of the output. If other equations in the model also contribute, parameter values have to be derived from enrichment experiments and feeding trials, independently of field dynamics. Moreover, separation of parameter calibration with laboratory experiments and model validation with field surveys is to be preferred for good modeling practice.

A review of half-saturation constants reported in literature will stimulate such an approach. Even more, selecting appropriate values might be improved by relating half-saturation constants to well-known properties of species, such as trophic level, and functional traits, such as body size. Of the two coefficients in Eq. (1), allometric regressions for maximum rates of nutrient absorption and food ingestion $\max(k)$ have been obtained, covering different taxonomic groups (Arnot and Gobas, 2004; Gross et al., 1993; Hansen et al., 1997; Karasov and McWilliams, 2005; Kirkwood, 1983; Moloney and Field, 1989; Shipley et al., 1994; Weiner, 1992; Wen et al., 1997). Besides in the case of zooplankton (Hansen et al., 1997), other body-mass regressions for K_m have not been reported yet.

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