



Original research article

# Half-saturation constants in functional responses

Christian Mulder<sup>a,\*</sup>, A. Jan Hendriks<sup>b</sup><sup>a</sup> National Institute for Public Health and the Environment, P.O. Box 1, 3720BA, Bilthoven, The Netherlands<sup>b</sup> Department of Environmental Science, Radboud University, P.O. Box 9010, 6500GL, Nijmegen, The Netherlands

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## 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

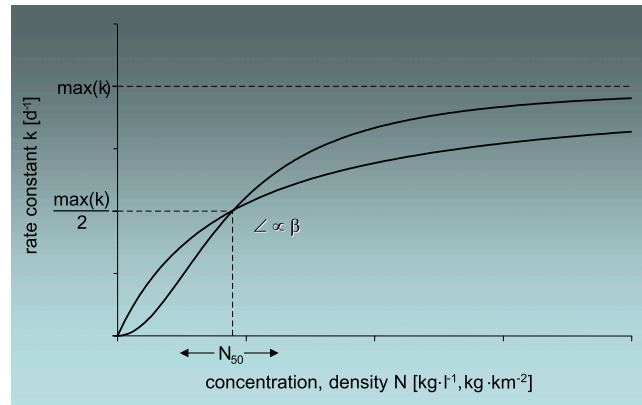
*Abbreviations:*  $k$ , intake rate constant;  $K$ , carrying capacity;  $K_m$ , half-saturation constant for nutrient absorption and food ingestion;  $L$ , predator's length;  $m$ , species' body mass;  $m_i/m_{i-1}$ , consumer-to-resource body-mass ratios;  $N$ , nutrient concentration and food density.

\* Corresponding author.

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

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**Fig. 1.** Absorption of elemental resources and ingestion of food  $k$  [ $\text{d}^{-1}$ ] 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  $\beta$  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  $\beta$ . 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.

The results will be discussed in the light of allometric regressions obtained for related parameters, in particular population density and trophic level. The meta-analysis is intended to facilitate selection of values for the half-saturation constant in ecological models where extensive empirical investigations are not possible. Furthermore, information obtained here can be used to check future observations for consistency with past studies, after adjusting species' body-size averages. In contrast to a comparable meta-analysis on Types I and II functional responses (e.g. Jeschke et al., 2004), where more attention was provided to vertebrates, we decided here to focus on plants and invertebrates (27% of the entries for vertebrates in Jeschke et al. (2004) versus 12% in the present paper). Individual data as well as regressions given in our meta-analysis may be selected to facilitate application of ecological models, especially for protection of species that have not been and will not be investigated empirically. Finally, the present study might contribute to our insight in macroecological size scaling.

## 2. Data mining

The bulk of the data was collected during the development of allometric regressions on other ecological parameters (Jeschke et al., 2004; Hendriks and Mulder, 2008, 2012). Additional values were obtained by literature searches in 'Web of Science' with the keywords: "half-saturation constant", "functional response", "feeding experiment" and "feeding trial". Taxon-specific reviews were preferred but as they were largely absent, research papers were collected. Following the interest for natural communities, the focus was on journals in the field of nature management and ecology. Therefore, this meta-analysis is not intended to be exhaustive, but we aimed only to cover different types of resources and species. Reviews on specific elemental resources (e.g., nitrogen) or species groups (e.g., invertebrates) were preferred, if available.

Half-saturation constants calculated by the authors were individually taken as originally reported. If not provided, their values were estimated from the graphs given as published in the papers by fitting a curve through the data points and taking half the concentration or density at half the maximum value. In total, 338 half-saturation constants were obtained. Data on plants refer to the absorption of elemental nutrients from experimental solutions by microalgae, macroalgae and some vascular plants. Terrestrial studies were omitted because variability of soil characteristics (like acidic or basic conditions) prevents direct comparison. Half-saturation constants for food ingestion by aquatic animals were obtained from laboratory studies. Data reported for terrestrial mammals represent empirical observations. Values referring to the same species, size or resource were averaged geometrically if taken from equivalents.

Nutrients were reported as the nitrate, ammonium, nitrogen and phosphorus concentrations in water. Food densities at half the maximum intake rate for aquatic species were mostly measured in a volume of water [ $\text{kg} \cdot \text{l}^{-1}$ ]. To obtain a consistent data set, aqueous values were discarded if expressed per unit of area. Half-saturation constants for terrestrial animals usually referred to numerical abundance [ $\text{km}^{-2}$ ] or wet biomass [ $\text{kg} \cdot \text{km}^{-2}$ ] in a region. When introduced in Section 3, these data were used without conversion. Later in the discussion, however, half-saturation constants for food were converted to allow aquatic [ $\text{kg} \cdot \text{l}^{-1}$ ] and terrestrial [ $\text{kg} \cdot \text{km}^{-2}$ ] species to be compared to each other and to other density parameters. Area units were converted to volumetric equivalents, assuming a water depth of 10 m, close to the geometric average of 5 and 100 m, as known for freshwater and marine systems (Cyr and Peters, 1996; Li, 2002). For instance, the areal density of phytoplankton communities scales to size according to  $10^7 \cdot \text{m}^{1/4}$  [ $\text{kg} \cdot \text{km}^{-2}$ ] and corresponds to a volumetric concentration of  $10^7 / 10^{10} \cdot \text{m}^{1/4}$  [ $\text{kg} \cdot \text{l}^{-1}$ ] (Hendriks and Mulder, 2012).

To allow a direct comparison of nutrient concentrations and food densities, all organisms were assumed to have the same molecular composition (Table 1). The half-saturation constants were then linked to individual body size, using ordinary regression analysis. Regressions were considered significant if  $p < 0.05$  and noteworthy if  $p < 0.2$ , keeping in mind the usual variability in cross-taxon meta-analyses. (A level of  $p = 0.2$  represents the upper value of the range commonly chosen in macroecological studies.) However, most studies include non-linear regressions with multiple independent variables, whereas the analysis here is limited to linear regressions with adult body-mass values as expected explanatory factor.

Although the half-saturation constant refers to the density of a specific resource, it was not related to the body size of the food because the body mass of an individual resource is usually not reported accurately in literature (most studies report only the "productivity", thus the total biomass). Instead, the density of the food at half the maximum consumption rate was related to the consumer's mass according to Eq. (2). However, regressions on the resource, i.e. the nutrient concentration or the prey density of "food species"  $N$ , are always expressed as a respective function of the plant or animal body mass  $m_{i-1}$  themselves (Hendriks and Mulder, 2012). To allow for comparison, the population density regressions were therefore converted to functions of consumer's body mass  $m_i$  according to

$$N = \gamma \cdot m_{i-1}^{\kappa} = \gamma \cdot \left( \frac{m_i}{m_i/m_{i-1}} \right)^{\kappa} \quad (4)$$

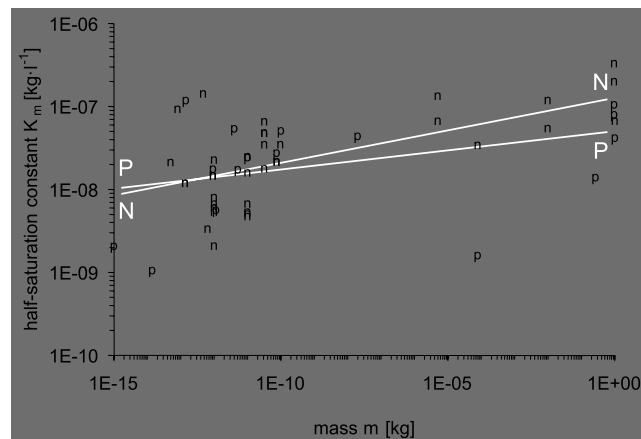
using consumer-to-resource body-mass ratios ( $m_i/m_{i-1}$ ) of  $10^4$  for phytoplanktivores, zooplanktivores, and terrestrial herbivores,  $10^2$  for piscivores, and 10 for terrestrial carnivores (Scharf et al., 2000; Shurin and Seabloom, 2005; Vezina, 1985). For instance, the maximal vegetation density versus plant mass with an intercept of  $10^7 \text{ kg} \cdot \text{km}^{-2}$  was translated to a function of ungulates' body mass with an intercept of  $10^7 / 10^{4 \cdot 0.25} \text{ kg} \cdot \text{km}^{-2} = 10^6 \text{ kg} \cdot \text{km}^{-2}$ . This corresponds to a shift of the original linear regression by four orders of magnitude to the right.

**Table 1**

Half-saturation constants for absorption of nutrients by plants and ingestion of food by animals, categorized according to resource and consumer. For each subset, the number of data ( $n$ ), the geometric average with its confidence interval ( $\mu$ , 95% C.I.), and the allometric function  $K_m = \gamma \cdot m^\kappa$  and statistical significance were provided. Values referring to the same species, size or resource were averaged geometrically if taken from equivalents. Nutrients were reported as the nitrate, ammonium, nitrogen and phosphorus concentrations in water. Food densities at half the maximum intake rate for aquatic species were mostly measured in volume. Half-saturation constants for food were converted to allow aquatic [ $\text{kg} \cdot \text{l}^{-1}$ ] and terrestrial [ $\text{kg} \cdot \text{km}^{-2}$ ] species to be compared to each other and to other density parameters. Area units were converted to volumetric equivalents, assuming a water depth of 10 m. Areal density of phytoplankton communities scaled to size according to  $10^7 \cdot \text{m}^{1/4}$  [ $\text{kg} \cdot \text{km}^{-2}$ ], which corresponds to a volumetric concentration of  $10^7 / 10^{10} \cdot \text{m}^{1/4}$  [ $\text{kg} \cdot \text{l}^{-1}$ ]. To allow a direct comparison of resources, all organisms were assumed to have the same molecular composition ( $\text{C}_{106}\text{H}_{180}\text{O}_{46}\text{N}_{16}\text{P}$  (Sterner and Elser, 2002)). As a result, 1 kg of wet matter corresponds to  $20\% \cdot 16 \cdot 14 / 2443 \text{ kg} = 0.02 \text{ kg N}$  and  $20\% \cdot 1 \cdot 31 / 2443 \text{ kg} = 0.0025 \text{ kg P}$  dry matter. The  $K_m$  values were then linked to size, using ordinary regression analysis (Significance levels as follows: \*,  $0.01 < p < 0.05$ , \*\*,  $0.001 < p < 0.01$ , \*\*\*,  $p < 0.001$ , NS,  $p > 0.05$ ).

Sources: Protista, Mollusca and Arthropoda (Hansen et al., 1997); Schizo-Phycophyta (Eppley et al., 1969; Halterman and Toetz, 1984; Hein et al., 1995; Rees, 2001; Vadstein and Olsen, 1989); Spermatophyta (Cedergreen and Madsen, 2002; Comas et al., 2002; Morris, 1980); Osteichthyes (Barnhisel and Kerfoot, 2004; Buckel and Stoner, 2000; Koski and Johnson, 2002; Miller et al., 1992; Willette et al., 1999; Wright et al., 1993); Mammalia (Baumont et al., 2000; Bergman et al., 2000; Gilg et al., 2003; Hudson and Frank, 1987; O'Donoghue et al., 1998; Pitt and Ritchie, 2002; Prins and Olff, 1998; Short, 1985; Turchin, 2003; Turchin and Batzli, 2001; Turchin and Hanski, 1997; Wilmshurst et al., 1999).

Resource	Consumer	$n$	$\mu$ (95% C.I.)	$K_m = \gamma \cdot m^\kappa$	$r^2$	$p$
Nitrogen ( $\text{kg} \cdot \text{l}^{-1}$ )	All plants	44	$3.0 \cdot 10^{-8}$ ( $2.1 \cdot 10^{-8}$ – $4.4 \cdot 10^{-8}$ )	$1.2 \cdot 10^{-7} \cdot m^{0.08}$	0.49	<.0001***
	Bacteria and microalgae	26	$1.5 \cdot 10^{-8}$ ( $9.9 \cdot 10^{-9}$ – $2.3 \cdot 10^{-8}$ )	$1.8 \cdot 10^{-7} \cdot m^{0.09}$	0.04	0.34-NS
Phosphorus ( $\text{kg} \cdot \text{l}^{-1}$ )	All plants	22	$2.5 \cdot 10^{-8}$ ( $1.4 \cdot 10^{-8}$ – $4.5 \cdot 10^{-8}$ )	$5.0 \cdot 10^{-8} \cdot m^{0.05}$	0.18	<.05*
	Bacteria and microalgae	9	$3.1 \cdot 10^{-8}$ ( $1.6 \cdot 10^{-8}$ – $6.0 \cdot 10^{-8}$ )	$6.5 \cdot 10^{-8} \cdot m^{0.03}$	0.01	0.77-NS
Algae ( $\text{kg} \cdot \text{l}^{-1}$ )	Dinoflagellata	7	$1.7 \cdot 10^{-6}$ ( $5.4 \cdot 10^{-7}$ – $5.4 \cdot 10^{-6}$ )	$8.4 \cdot 10^{-1} \cdot m^{0.52}$	0.64	0.03*
	Ciliophora	12	$6.1 \cdot 10^{-7}$ ( $4.0 \cdot 10^{-7}$ – $9.1 \cdot 10^{-7}$ )	$2.9 \cdot 10^{-6} \cdot m^{0.07}$	0.01	0.71-NS
	Rotifera	14	$5.2 \cdot 10^{-6}$ ( $2.3 \cdot 10^{-6}$ – $1.2 \cdot 10^{-5}$ )	$1.5 \cdot 10^1 \cdot m^{0.70}$	0.22	0.11-NS
	Sarcomastigophora	18	$3.3 \cdot 10^{-6}$ ( $1.9 \cdot 10^{-6}$ – $5.5 \cdot 10^{-6}$ )	$1.1 \cdot 10^0 \cdot m^{0.42}$	0.10	0.21-NS
	Mollusca	12	$7.1 \cdot 10^{-7}$ ( $3.1 \cdot 10^{-7}$ – $1.6 \cdot 10^{-6}$ )	$8.5 \cdot 10^{-2} \cdot m^{0.61}$	0.38	0.03*
	Arthropoda	37	$2.7 \cdot 10^{-6}$ ( $1.7 \cdot 10^{-6}$ – $4.4 \cdot 10^{-6}$ )	$2.2 \cdot 10^{-4} \cdot m^{0.26}$	0.09	0.08-NS
Animals ( $\text{kg} \cdot \text{l}^{-1}$ )	Osteichthyes	21	$1.7 \cdot 10^{-6}$ ( $7.8 \cdot 10^{-7}$ – $3.8 \cdot 10^{-6}$ )	$4.7 \cdot 10^{-7} \cdot m^{-0.22}$	0.15	0.09-NS
Grasses ( $\text{kg} \cdot \text{km}^{-2}$ )	Grazing Mammalia	11	$8.6 \cdot 10^4$ ( $4.5 \cdot 10^4$ – $1.7 \cdot 10^5$ )	$4.9 \cdot 10^4 \cdot m^{0.20}$	0.41	0.04*
Mammals ( $\text{kg} \cdot \text{km}^{-2}$ )	Pred Aves + carn Mammalia	7	$3.4 \cdot 10^1$ ( $5.8 \cdot 10^0$ – $2.0 \cdot 10^2$ )	$1.5 \cdot 10^1 \cdot m^{0.57}$	0.31	0.20-NS

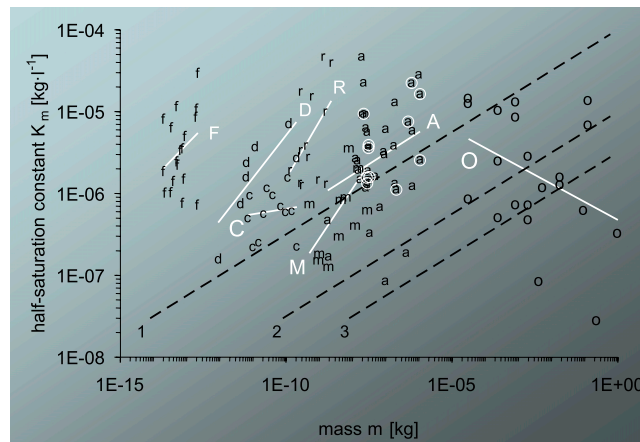


**Fig. 2.** Half-saturation constants  $K_m$  [ $\text{kg} \cdot \text{l}^{-1}$ ] versus individual plant mass  $m$  (kg) for absorption of nutrients. Data (lower case letters) and regressions (solid lines with upper case letters) thereof with N,n = nitrogen, P,p = phosphorus.

### 3. Results/discussion

#### 3.1. Absorption of nutrients by plants

On average, half-saturation constants [ $\text{kg} \cdot \text{l}^{-1}$ ] for uptake of nitrogen and phosphorus did not significantly deviate from each other ( $K_m$  values and overlapping CIs shown in Table 1). Values for both elements were largely between  $10^{-9}$  and  $10^{-7} \text{ kg} \cdot \text{l}^{-1}$  (Fig. 2). Within the same study, half-saturation constants for different species were generally within one order of magnitude (Eppley et al., 1969; Halterman and Toetz, 1984; Hein et al., 1995; Vadstein and Olsen, 1989).  $K_m$  for plants scaled weakly ( $0.05 \leq \kappa \leq 0.09$ ) but significantly to size ( $p < 0.05$ , Table 1). However, this reflects cladistic differences because nutrient absorption becomes size-independent when only microphytes were considered: the nutrient uptake by microalgae (Plantae) and bacteria (Prokarya) exhibited size scalings neither for nitrogen nor for phosphorus (Table 1). Levels for macroalgae, herbs/forbs and tree seedlings were in a comparable range, with the exception of the low phosphorus concentration of  $2 \cdot 10^{-9} \text{ kg} \cdot \text{l}^{-1}$  for kelps (Rees, 2001).



**Fig. 3.** Half-saturation constants  $K_m$  [ $\text{kg} \cdot \text{l}^{-1}$ ] versus individual animal mass  $m$  [kg] for ingestion of food by aquatic herbivorous invertebrates and piscivorous fishes. Data (lower case letters) and regressions (solid lines with upper case letters) for A,a = Arthropoda, C,c = Ciliophora, D,d = Dinoflagellata, F,f = Sarcomastigophora, M,m = Mollusca, O,o = Osteichthyes, R,r = Rotifera. In addition, maximum density for food [ $\text{kg} \cdot \text{l}^{-1}$ ] as represented by the trophic levels 1 (algae), 2 (detriti-herbivores) and 3 (carnivores) taken from Hendriks and Mulder (2012) was calculated assuming  $1 \text{ kg} \cdot \text{l}^{-1} \sim 10^{10} \text{ kg} \cdot \text{km}^{-2}$  and a consumer-to-resource body-mass ratio ( $m_{i+1}/m_i$ ) of  $10^4$  for planktivores (phyto- and zooplanktivores) and  $10^2$  for piscivores (dashed lines, from top to bottom 1, 2 and 3).

## 3.2. Consumption of food by animals

### 3.2.1. Cold-blooded animals

Half-saturation constants for ingestion of algae by different invertebrate species groups were largely within the range of  $10^{-7}$  to  $10^{-5} \text{ kg} \cdot \text{l}^{-1}$  (Fig. 3). The averages for ciliates and mollusc larvae were lower than the other means. Values for different species tested under the same experimental conditions roughly varied one order of magnitude (extensively reviewed in Hansen et al., 1997). As an indication of the intraspecific variability, values for equally-sized *Daphnia magna*, the most studied species, were within one order of magnitude (encircled 'a' in Fig. 3). The food density at half of the maximum ingestion did not increase with size if invertebrate herbivores were included into the regression (Table 1). Per species group, however,  $K_m$  scaled to mass with exponents in the range of 0.26–0.70, and significantly at 0.52 and 0.61 (Table 1). While robust trends for these groups were detected ( $p = 0.03$ ,  $r^2 = 0.38$  and  $r^2 = 0.64$ ), size scaling was not noted for ciliates ( $p = 0.71$ ,  $r^2 = 0.01$ ), a result in agreement with the highly variable body mass–metabolic rate scalings of protists in comparison to metazoans (Makarieva et al., 2008; Reiss et al., 2010).

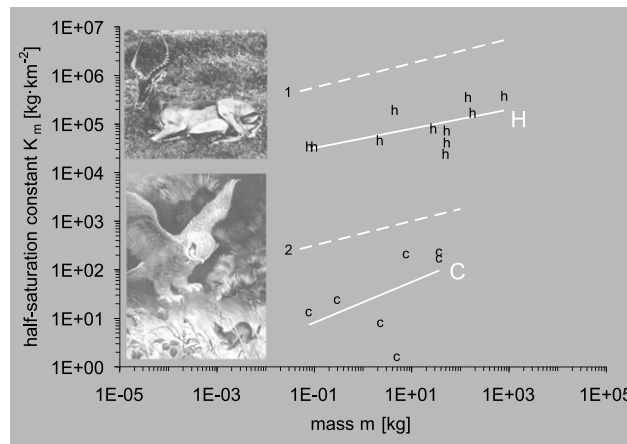
Half-saturation constants for the tilapia were not plotted with piscivorous fishes because *Oreochromis niloticus* feeds on blue-green algae (Cyanobacteria). However, the values of  $2\text{--}6 \cdot 10^{-5} \text{ kg} \cdot \text{l}^{-1}$  are in the upper edge of the range noted for herbivorous invertebrates (Northcott et al., 1991). Experiments with piscivorous fishes were mostly carried out with immature individuals. Values are in the  $10^{-7}\text{--}10^{-5} \text{ kg} \cdot \text{l}^{-1}$  range, with exception of extremely low values noted for herring and lake trout (Willette et al., 1999; Barnhisel and Kerfoot, 2004). There was no consistent difference between prey trials with zooplankton and fish as resources. In contrast to all the other body-mass regressions derived in the present study, half-saturation constants for fish decreased weakly with individual body mass.

### 3.2.2. Warm-blooded animals

Data sets for warm-blooded herbivores included mammals ranging from lemming to bison, while the carnivorous group consisted of several bird and mammals species (Fig. 4). Regression analysis indicated size dependence for both trophic levels ( $0.02 < p < 0.20$ ,  $0.31 < r^2 < 0.41$ ). Average levels for herbivorous homeotherms were significantly higher than those for carnivorous equivalents (Table 1). For both groups, variability between three species observed in the same study was less than an order of magnitude (Gilg et al., 2003; Short, 1985).

Values for herbivores applied to different species, with exception of two observations on sheep (at 53 kg in Fig. 4). The half-saturation constants reported in these studies varied a factor of 1.8 (Baumont et al., 2000; Short, 1985). All data on consumers occurring in (semi)arid terrestrial ecosystems were below the regression line (Baumont et al., 2000; Short, 1985; Wilmshurst et al., 1999). Data from experiments with artificially controlled plots were not included in the analysis because observations were between about 55 to 22,000  $\text{kg} \cdot \text{km}^{-2}$ , clearly below field levels (Hobbs et al., 2003). Browsers were excluded because functional responses were related to bite size rather than to plant density (Spalinger and Hobbs, 1992).

The low value for carnivores applied to 5 kg Arctic fox, *Alopex lagopus*, clearly more efficient than the other Arctic predators (Gilg et al., 2003). The half-saturation constant for lizard feeding on grasshoppers was not plotted because Fig. 4 is only on warm-blooded species. Still, the value of  $200 \text{ kg} \cdot \text{km}^{-2}$  noted for reptiles was in the range noted for homeotherms feeding on vertebrates (Pitt and Ritchie, 2002).



**Fig. 4.** Half-saturation constants  $K_m$  [ $\text{kg} \cdot \text{km}^{-2}$ ] versus individual animal mass  $m$  [kg] for ingestion of food by terrestrial warm-blooded animals (Aves and Mammalia). Data (lower case letters) and regressions (solid lines with upper case letters) thereof with H, h = herbivorous mammals and C, c = predatory birds + carnivorous mammals (unscaled drawings modified from Patterson, 1907; Long, 1900). In addition, maximum food density [ $\text{kg} \cdot \text{km}^{-2}$ ] as represented by the adjacent trophic levels 1 (vegetation) and 2 (herbivores) (Hendriks and Mulder, 2012) was calculated assuming a consumer-to-resource body-mass ratio  $m_{i+1}/m_i$  equal to  $10^4$  for herbivores and  $10^1 = 10$  for carnivores (dashed lines, compare with Fig. 3).

## 4. Allometry

### 4.1. Regression slopes

Although data for many species groups are scarce, some general patterns emerge from the analysis. All but two whole-taxon regressions showed that half-saturation constants increase with size, using significance levels that are common in allometric correlations ( $0.0001 < p < 0.2$ , Table 1). Values for ciliates were independent of size, possibly due to the small body-mass range covered ( $p = 0.71$ ). Fish data did not follow the pattern noted for other species. The deviation persisted even if differences between methods were excluded, because all data with  $m < 2 \cdot 10^{-3}$  kg (Fig. 3) were obtained from the same experiment where attack rate and handling time scaled to predator's length  $L$  with exponents of 4.4 and  $-3.4$  (Miller et al., 1992). Their product was inversely related to half-saturation, yielding  $K_m \propto L^{-(4.4-3.4)} = L^{-1} \propto m^{-1/3}$ , far from the almost canonical  $m^{-0.22}$  observed for fish (Table 1). However, the diet breadth for both small and large fishes was held constant during these laboratory experiments. This may explain the decrease of handling time with predator's size: under field conditions, in fact, bigger fishes tend to select larger food items, requiring more time for handling and corresponding to higher saturation constants (Pawar et al., 2012).

Previous attempts to relate  $K_m$  to size are rare. A negative slope was observed for phosphorus intake by freshwater algae (Wen et al., 1997). However, the same study reported an exponent of  $-0.30$  for the maximum intake rate  $\max(k_n)$  while the ratio  $\max(k_n)/K_m$  scaled to  $-0.32$ , supporting as exponent  $-0.30/-0.32 = 0.02$ . Another regression analysis on phytoplanktivores yielded an exponent of  $-0.03$  (Hansen et al., 1997), not different from the aforementioned exponent of 0.02.

The present analysis was largely based on the same data for invertebrates and confirmed the independency of size. However, the present analysis showed that half-saturation seems to increase with consumer size if phylogenetically smaller groups are considered. How can we understand a strong increase of half-saturation with the faunal body size? To that end, we might compare the slopes noted for  $K_m$  [ $\text{kg} \cdot \text{km}^{-2}$ ] to those noted for food density  $N$  [ $\text{kg} \cdot \text{km}^{-2}$ ]. Following the energy equivalency rule, mass values of species are expected to scale  $-1/3$  or  $-1/4$  to density values and metabolic rate constants (Damuth, 1981; Makarieva et al., 2008; Mulder et al., 2009; Peters and Wassenberg, 1983; Sechi et al., 2015; Yodzis and Innes, 1992). However,  $K_m$  strongly varied as half-saturation constants of invertebrate clades feeding on algae scaled to size between 0.07 and 0.70 (Table 1). Moreover, search and consumption rates by animals are likely to vary systematically with the dimensionality of search space, as shown by Pawar et al. (2012) who scaled search efforts and consumption rate with body size, confirming that several morphological traits constrain foraging and behavior much more than body size alone (McGill and Mittelbach, 2006).

Vegetation density at half the maximum grazing rate increased with size to the power 0.20 (Table 1) where values between 0.21 and 0.33 were noted for plant density (Duarte and Kalff, 1987; Enquist et al., 1998; Enquist and Niklas, 2002; Niklas et al., 2003). Densities of mammalian herbivores scaled to size between 0.17 and 0.44 (Damuth, 1981; Jetz, 2004; Peters and Raelson, 1984; Peters and Wassenberg, 1983; Silva et al., 1997, 2001). The slope for the density of herbivores at half the maximum grazing rate was 0.57, somewhat out of this range (Table 1). However, half-saturation constants generally increase with faunal body size in the same way as the density of their resource, suggesting that the functional response of animals is adapted to the food density that they encounter. Both half-saturation as density are relatively low for small animals and high for large animals.

Deviations may occur due to taxon-specific differences in underlying mechanisms. The wear scaling of half-saturation constants for absorption of elemental nutrients by plants cannot always be attributed to the same mechanism, because vascular plants do not necessarily imply “more” macronutrients than algae. However, theoretical models confirm the empirical observation that half-saturation constants for nutrients increase at least with algal size, due to processes like dilution (Irwin et al., 2006). Indirect support comes from the notion that minimum nutrient requirements increase with algal size too, reflecting a similar rise in the dry matter content (Shuter, 1978).

The coefficients of determination of the regression were 0.09–0.64 for aquatic herbivores, 0.41 for terrestrial herbivores and 0.31 for terrestrial carnivores (Table 1). The corresponding values on density were noted to be in the range of 0.79–0.96 for algae, of 0.25–0.74 for plants and of 0.45–0.88 for terrestrial herbivores (Boudreau and Dickie, 1992; Cyr et al., 1997; Damuth, 1981; Duarte and Kalff, 1987; Enquist et al., 1998; Enquist and Niklas, 2002; Jetz, 2004; Li, 2002; Niklas et al., 2003; Peters and Raelson, 1984; Peters and Wassenberg, 1983; Silva et al., 1997, 2001; Sprules and Stockwell, 1995). The trait ‘body size’ alone explained thus 9%–64% of the variability noted for the density at half the maximum grazing or predation rate, which remains below the range of 25%–96% noted for density variables in general.

#### 4.2. Averages and intercepts

The half-saturation constants for absorption [ $\text{kg N} \cdot \text{l}^{-1}$  and  $\text{kg P} \cdot \text{l}^{-1}$ ] were about two orders of magnitude smaller if compared to those for ingestion [ $\text{kg food} \cdot \text{l}^{-1}$ ] (Table 1, Fig. 2 versus Fig. 3). If expressed on a nutrient basis, half-saturation constants are at the same level. Nitrogen and phosphorus contents in biota seem to be typically 2% and 0.3%, respectively, so that elemental levels are expected to be 50 and 330 lower than food densities.

Per trophic level,  $K_m$  values for nutrients and food uptake generally varied within two orders of magnitude (Figs. 2–4). This variability possibly reflects different conditions between studies or divergent strategies in resource acquisition. Data on *Daphnia magna*, the most frequently studied species, indicated that differences between conditions contribute by a factor of 10 to the observed variation. Differences between species examined within the same study account for another order of magnitude variability.

Intercepts for the average density [ $\text{kg} \cdot \text{km}^{-2}$ ] of a species are variable, obviously depending on availability of sunlight, water, nutrients, and to a lesser extent to species richness (Winemiller et al., 2001). According to these authors, under optimal conditions the total number of all species in one trophic level can be used as a reference point for the half-saturation constant. This upper level reflects the total biomass within one trophic level as a function of the species’ body-size average or the total biomass of the population of dominant species. The typical values noted in a meta-analysis of empirical regressions were converted and plotted as a function of consumers’ body mass as described in the methods section. One may note that the total phytoplankton density as function of the herbivore size was at the same level as the half-saturation constants for ciliates, mollusc larvae and arthropods (dashed line 1 versus solid lines C, M, A in Fig. 3). Levels for flagellates and rotifers were substantially higher (solid lines F, D, R in Fig. 3). Such discrepancies have been observed in original data as well, calling for a species-specific analysis with actual information on consumer–resource body-mass ratios, food nutritional quality and environmental factors (Hansen et al., 1997; Jeschke et al., 2004; Mulder et al., 2009; Sechi et al., 2015; Sterner and Elser, 2002).

Maximum vegetation density was about one order of magnitude higher than the density of grass at half the grazing rate (dashed line 2 versus solid line H in Fig. 3). A similar difference was noted for smaller herbivores caught by predators (dashed line 3 versus solid line C). If the maximum density may be considered to reflect the carrying capacity  $K$  for the trophic level concerned,  $K_m/K$  ratios can be calculated to be approximately 1 for aquatic herbivores and 1/10 for terrestrial homeotherms. Interestingly, independent data on mammals indicate that these ratios fluctuate indeed around 1/10 (Turchin, 2003; Turchin and Batzli, 2001; Vasseur and McCann, 2005). The value of  $K_m$  itself, as well as its value relative to the carrying capacity  $K_m/K$  is crucial for the behavior of consumer–resource dynamics. We show that, although half-saturation constants are variable, intercepts of allometric regressions are within a realistic range and consistent with independent information.

### 5. Implications

Many ecological models that are applied to explore options or support decisions in management contain parameters that have not been determined empirically for most taxonomic groups. Often, these parameters are obtained by varying them simultaneously until the discrepancy between the predicted and observed population dynamics is minimal. Unfortunately, calibrating parameters by comparing model and field dynamics only gives indirect values, possibly influenced by other factors in the model. The credibility of these models can be increased by deriving parameters values from independent observations of the underlying processes. However, empirical studies remain too limited because of financial, practical and ethical constraints. As an alternative, one may link parameters to well-known properties of species and communities.

The present analysis focused on the half-saturation constant  $K_m$ , an important parameter in ecological processes and models on sustainable fisheries, rangeland management, pollution, and so on. Following this study, environmental models can now be supplied with realistic values in three ways. Species-specific data may be found in either the same way we collected data for this review or by using logic-based machine learning (Tamaddoni-Nezhad et al., 2012). Taxon-dependent values can be taken from the averages and with some caution from the calculated allometric regressions (Table 1). Finally,

$K_m$  can be estimated as function of size with a “physically universal exponent” (Yodzis and Innes, 1992) and an intercept that is determined by the  $K_m/K$  ratio chosen, like 1 for aquatic invertebrates and 10 for homeotherms (Hendriks and Mulder, 2008, 2012). These three approaches allow one to select an appropriate half-saturation constant value for a specific case.

Alternatively, if field calibration of the entire model is preferred, the present analysis may help to underpin and understand the value derived for the half-saturation constant. In addition to choosing a “stand-alone” value for the half-saturation constant, the present analysis allows the selection of parameter values that are consistent within an allometric framework. Just as, for instance, growth rates and age at maturity scale to size with exponents that are opposite to each other ( $-1/4$  versus  $+1/4$ ), half-saturation values need to be coherent with related parameters.

The mutual consistency of parameters is seldom checked and the present analysis allows one to do so. Such an approach narrows further the range of possible values, decreasing the variability of model. We can now also put occasional measurements of the half-saturation constant in perspective. These values are often explained in terms of physiological characteristics of the consumers, including, e.g., handling and digestion time (e.g. Jeschke et al., 2002, 2004). While these processes are undoubtedly important at the level of individuals, the present analysis shows that some mechanisms are probably of either macroecological or evolutionary nature. In the case of ciliates and microphytophages, for instance, body size explained only 1% of the variability of  $K_m$ , in contrast to dinoflagellates whose sizes predicted 64% of  $K_m$  values! On average, consumption/predation by molluscs, arthropods, fish, birds, and mammals reflects solely their size in less than 27% of the observations (Table 1).

Still, species-specific corrections in favor of a uniform exponent ( $-1/3$  or  $-1/4$ ) are systematically neglected. Obviously, simple models can be improved by relating the half-saturation constant to more species traits and community characteristics. While the body size remains an important factor, supplementary parameters may be even more important to avoid remoteness from nature. Size *per se* is not the dominant predictor determining the half-saturation constants. Future investigations may shed light on these factors, if more empirical data become available, especially on taxa with deviating metabolic trends like protists. Nevertheless, this study demonstrated that the ratio of resource and consumer's body masses is important in understanding the variability of functional responses for various species and taxonomic groups.

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