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THE POWER OF SIZE. 2. RATE CONSTANTS AND EQUILIBRIUM RATIOS FOR ACCUMULATION OF INORGANIC SUBSTANCES RELATED TO SPECIES WEIGHT

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Abstract—Most of the thousands of substances and species that risk assessment has to deal with are not investigated empirically because of financial, practical, and ethical constraints. To facilitate extrapolation, we have developed a model for concentration kinetics of inorganic substances as a function of the exposure concentration of the chemical and the weight and trophic level of the species. The ecological parameters and the resistances that substances encounter during diffusion in water layers were obtained from previous reviews. The other chemical parameters (the resistances for permeation of lipid layers) were calibrated in the present study on 1,062 rate constants for absorption from water, for assimilation from food, and for elimination. Data on all elements and species were collected, but most applied to aquatic species, in particular mollusks and fish, and to transition metals, in particular group IIB (Zn, Cd, Hg). Their ratio was validated on 92 regressions and nine geometric averages, representing thousands of (near-)equilibrium accumulation ratios from laboratory and field studies. Rate constants for absorption and elimination decreased with species weight at an exponent of about −0.25, known from ecological allometry. On average, uptake-rate constants decreased with about the reciprocal square root of the exposure concentration. About 71 and 30% of the variation in absorption and elimination was explained by the model, respectively. The efficiency for assimilation of elements from food appeared to be determined mainly by the food digestibility and the distribution over egested and digested fractions. (Near-)equilibrium accumulation and magnification ratios also decreased with the reciprocal square root of the exposure concentration. The level of the organism–solids concentrations ratios roughly varied between one and two orders of magnitude, depending on the number of elements and species groups investigated. Metal concentrations did not increase at higher trophic levels, with the exception of (methyl-)mercury. Organism–solids concentration ratios for terrestrial species tended to be somewhat lower than those for their aquatic equivalents. Food web accumulation, expressed as organism–organic solids and organism–food concentrations ratios, can therefore be only partly explained by ecological variables. The model is believed to facilitate various types of scientific interpretation as well as environmental risk assessment.

Keywords—Uptake Elimination Bioaccumulation Body weight

INTRODUCTION

Because of ethical, financial, and practical constraints, environmental management is in need of simple models for concentration kinetics that can be applied to many substances and species without extensive empirical studies [1]. So far, parameters of traditional first-order models have been calibrated for a few inorganic substances and species only. To allow risk evaluation for other elements and organisms, concentration kinetics may be linked to species weight. Previous work in this area has yielded correlations for this purpose, but only for one substance and individuals of one or a few species (e.g. [2,3]).

In the present study, concentration kinetics was related to several substances and species simultaneously. The aim was to explain differences observed between substances, species, and conditions. Following this objective, we applied average parameters that cover most species and substances. Deviations are discussed if substantial. In the present paper, we confined ourselves to inorganic microcontaminants and micronutrients in general, where possible. By necessity, however, the focus will be on metals for which most information is available.

Modifying fugacity theory for organic substances, we considered rate constants for influx and efflux to be a function of the exposure concentration of the substance and of the weight and trophic level of the species. The ecological parameters were taken from a review on allometric regressions on delays in water, food, and biomass flows and on food digestibilities [4]. The chemical parameters (the resistances for diffusion through water and permeation through membranes) were obtained in the present and in a related study by fitting rate constants on rate constants collected in a literature review [1]. To validate the estimations, the quotient of the rate constants for influx and efflux were compared to equilibrium accumulation ratios from laboratory and field studies. A similar approach for organic xenobiotics was described in another paper [1]. The two studies support extrapolation of information on well-known substances, species, and conditions to those that are less well investigated.

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METHODS

Data collection

Data on absorption, assimilation, and elimination rate constants published before 1994 were compiled from largely original publications obtained via reviews and on-line searches. Since 1994, all scientific journals on environmental chemistry and toxicology were scanned for this information. We used absorption, assimilation, uptake, elimination, excretion, clearance, depuration, and half-life as keywords. The literature search yielded 206, 459, and 397 rate constants for absorption, assimilation, and elimination, respectively, which have in part been published by us elsewhere [5]. Rate constants were found for algae, invertebrates, fish, and mammals. Data applied to aquatic, marine, and terrestrial species. Rate constants for mac-

rophytes were not found, but these may be available in specific physiological literature not searched here.

Thousands of laboratory and field data on (near-)equilibrium bioconcentration and biomagnification ratios, collected in 92 regressions and nine geometric averages, were taken from literature reviews and monitoring programs in the Rhine–Meuse delta (The Netherlands). If not given by the authors, log–log regressions were derived from the individual data. Studies that were carried out at one exposure level only were included as the geometric average of the accumulation ratios measured.

If reported, the wet weight (w) of the organisms was taken from the original study. If weight was not given, the size of adults was used. Adult weight was obtained from other studies or estimated from weight–length correlations. Many authors did not explicitly describe the units of their data. Rate constants were considered to apply to wet weight unless units explicitly or implicitly (e.g., as derived from values for equilibrium accumulation ratios in the same or a closely related paper) referred to dry weight. Where needed, dry and wet weight concentrations were converted using the allometric relationship (data not shown): $\log(p_s) = -0.70[-0.82 - -0.58] + 0.030\ [0.0093 - 0.050]\cdot\log(w)$ with $n = 49$, $r^2 = 0.16$. Values between brackets represent the 95% confidence intervals. The coefficient of determination r^2 indicates that variability of the actual dry weight content is high. On average, however, the regression will be closer to the actual level than an overall mean.

Data treatment

To allow for sufficient data, some values had to be adapted. Exposure concentrations were not reported for about 10% of the absorption data. These were not used for calibration. In a few assays on algae, kinetic data were expressed as a function of free metal concentrations. These levels were transformed to total metal concentrations with the ratios given in the original papers because most scientific and management publications still use total concentrations without providing characteristics (e.g., pH) needed for conversion. Exposure levels in dietary studies were usually reported as the radioactivity of labeled elements and could not be converted to concentrations. A few rate constants for absorption from water by terrestrial and benthic organisms were obtained in studies where uptake from soil or sediment might have contributed to the internal concentrations. In these cases, absorption rate constants represent a minimum value, as discussed in the text. Different species of metals as well as of plants and animals were categorized in the same group if data were scarce and similar. For instance, elimination rate constants for mercury and methylmercury were used for one regression. The same was done for concentration ratios of Cu in field insects and crustaceans.

If only half-lives ($t_{½}$) were reported, elimination rate constants were calculated as $\ln(2)/t_{½}$. If elimination was very slow, it was usually reported as a minimum half life $t_{½}$, typically as $t_{½} > 730$ d. These values were ignored if sufficient data were available for the substance and species group concerned. If not, the half-life was arbitrarily set at $2\cdot t_{½}$, for example, $2\cdot 730 = 1{,}460$, and included in the set of elimination rate constants as $\ln(2)/(2\cdot t_{½})$. Occasionally, no depuration experiments were carried out, and the efflux rate constant was calculated as the absorption rate constant divided by the (near-)equilibrium accumulation ratio. If elimination was fitted to a two-compartment model, the rate constant for the slowest phase or the geometric average for both phases was selected, depending on which approximation proved to be most correct. Minimum half-lives and two-compartment data were included only if no other clearance data were available for the substances and species concerned. In some studies, efflux rate constants were corrected for growth. In all studies, shedding of biomass (defoliation, sloughing, and so on) appeared not to be taken into account. Nearly all papers did not specify the importance of surface adsorption. To allow for a consistent approach, rate constants were regarded to be adjusted for growth if explicitly mentioned by the author. Data were considered not to be corrected for shedding of biomass. Surface adsorption was not accounted for by the model.

Concentration ratios from lab and field studies were taken from reviews and databases. If available, regressions given in the publications were used. If not available, individual data were fitted to log–log regressions. To allow for comparison, correlations from two studies had to be transformed to logarithmic regressions. Six exponential regressions for plants [6] were converted to log–log regressions by fitting on the original function. Three linear correlations for invertebrates [7] were transformed to log–log regressions by a graphical fit through the plotted data because their number was too large to allow numerical regression. Concentration ratios from laboratory accumulation studies were selected if exposure lasted sufficiently long to reach at least half the equilibrium concentration. Experiments were included if organisms were exposed for a periods of $-\ln(0.5)$ divided by the elimination rate constant, as calibrated on the kinetic data. Residues in field organisms were compared to sediment and soil concentrations measured in the same sample or to suspended solids concentrations monitored at the nearest upstream monitoring location in the same or previous year (for details, see, e.g., [8,9]). Field levels for fish were measured in muscle, whereas lab and field residues for birds and mammals were determined in various organs, in particular liver and kidney. To allow for comparison, ratios between muscle, liver, kidney, and whole body concentrations were obtained from studies in which various organs have been analyzed simultaneously. As the contribution of muscle, liver, and kidney to the total body burden depends on size of the organ, we assumed allometric proportions [10]. Roughly speaking, liver and kidney residues are a factor of 1 to 10 higher than whole body levels for most elements. Yet concentrations of Cd and Pb in liver or kidney may differ up to two orders of magnitude [11–14]. Values for muscles are between 70 and 90% of the fish body burdens [12].

Rate constants were fitted to the nonlinear equations using Microsoft® Solver 7.0 [15]. Following a common procedure, the sum of the squared differences between the logarithmic measured and estimated values, $\Sigma(\log(\text{measured}) - \log(\text{estimated}))^2/n$, was minimized. As equations were calibrated on all data simultaneously, the total was corrected for the number of data n available for absorption, assimilation, and elimination. Clear outliers were included in the analysis to represent possible extreme conditions encountered in the field, although they reinforce the impression that data variability is high and model reliability low. Possible explanations for the deviation were discussed.

RESULTS

Specification of equations

The concentration of substances in C_i is usually considered to be a function of the concentration in water $C_{0,w}$ and, for

animals, in food C_{i-1}, with adjacent rate constants for absorption from water $k_{0,x,in}$, for assimilation from food $k_{1,x,in}$, and for elimination by four routes of efflux, ${}^3\Sigma_0 k_{j,x,out}$ as specified below [1] as

$$\frac{dC_i}{dt} = k_{0,x,in} \cdot C_{0,w} + k_{1,x,in} \cdot C_{i-1} - \sum_{j=0}^{j=3} k_{j,x,out} \cdot C_i \qquad (1)$$

Unfortunately, the rate constants for inorganic substances have not been related to element characteristics in a comparable way, as exchange of organic substances has been linked to the octanol–water partitioning. Yet there appeared to be some consensus about the mechanisms that govern influx and efflux. Here we briefly recapitulated the conclusions from reviews to derive the appropriate equations [16–24].

Membranes consist of lipid layers with proteins embedded in them. Transport through lipids, like common for organic substances, is limited to hydrophobic alkylmetals such as methylmercury, tributyltin, tetramethyllead, and possibly uncharged compounds such as cadmium sulfate complexes [25]. Most ions are extremely hydrophilic and are taken up via two types of proteins called channels or pumps if they span the whole membrane and carriers if they shuttle between both sides. Anions, such as chromate and arsenate, cross membranes through large and nonselective channels as analogues of phosphate and sulfate. Some monovalent cations, such as sodium and potassium, are conducted through channels that become saturated at about 1 $mol \cdot L^{-1}$ [24]. In addition, sodium, potassium, and calcium may be taken up actively by pumps [17,21]. Alkaline earth and transition metals are bound to specific sites on carriers that transport them through membranes with a saturation level of approximately 1 $\mu mol \cdot L^{-1}$ [24]. Transport by carriers is selective but not exclusive: Several metals may share the same protein [20]. Nonessential cations like lead and cadmium are transported by proteins for essential analogues such as calcium and zinc. Rare earth metals and aluminum were found on cell surfaces only and were not transported into the cytoplasm [22].

After entering the cells, metals may be sequestered in vacuoles or granules. In addition, metals may bind to low molecular proteins: phytochelatins in plants and metallothionein in animals and some plants [19]. Metals may also be bound in soft tissues with high molecular proteins and polysaccharides or incorporated in hard tissues with a support and cover function, such as shells, chitin, bones, feathers, and fur [21]. Akylmetals may be transformed to inorganic forms as noted for methylmercury in some fish and many mammals [19,26]. Nonessential metals may replace nonessential elements, causing toxic effects that are similar to deficiency symptoms.

In general, control of metal concentrations by higher species, such as decapods and fish, was stronger than that by lower organisms such as ascidians and barnacles [19,23]. Levels of some essential metals, such as zinc and to a lesser extent copper, were considered to be regulated, whereas residues of nonessential metals, such as cadmium and lead, are not [18]. On the one hand, concentration kinetics of cadmium, copper, and lead but not zinc in dead Chironomus larvae exposed to contaminated water were equal to those accumulated by living midges [27,28]. On the other hand, cadmium absorption by intact wheat roots was significantly faster than that by dead or cold individuals [29].

Literature thus indicates that mechanisms for various metals, species, and exposure concentrations may be different. Nevertheless, rate constants for metal influx appeared to be independent of exposure concentrations if transport proteins are abundant relative to metals. Such a case was reported for cadmium, copper, cobalt, and zinc absorption by *Mytilus edulis* [30,31]. If transport proteins are scarce, rate constants for metal uptake seemed to decrease with exposure concentrations because more proteins are occupied with metals. This was noted for absorption of free zinc by algae [32]. Complete saturation, however, may not be reached because of alternative transport pathways or leakage of membranes at toxic levels. Even more, in the field intermetal competition for the same transport protein may be more important than intrametal variability.

It is evident that specification of all mechanisms per metal and species would yield a model with too many parameters to calibrate. Instead, the overall pattern emerging will be simulated by modifying a model for organic substances to include basic features for metals. The formulas have been extensively described in a related paper [1]. In the present paper, the adaptations for metals will be discussed. According to classical kinetic theory, influx rate constants are basically of the form [1]

$$\text{influx rate constant} = \frac{\text{organism weight}^{-\kappa}}{\text{water layer resistance} + \text{lipid layer resistance} + \text{flow delay}} \qquad (2)$$

whereas efflux rate constants are generally described as

$$\text{efflux rate constant} = 1/\text{accumulation ratio} \times \frac{\text{organism weight}^{-\kappa}}{\text{water layer resistance} + \text{lipid layer resistance} + \text{flow delay}} \qquad (3)$$

All resistances and delays scale to species weight w with exponent $-\kappa$. Resistances encountered during diffusion through water layers $\rho_{H_2O,j}$ ($d \cdot hg^{-\kappa}$) were considered to be independent of both organic and inorganic substances, as motivated below. Whereas lipid resistances for organic contaminants were adequately described as independent of the exposure level, the literature reviewed above indicated that metal uptake may be limited by protein carriers in the membrane. This was incorporated in the model by defining lipid layer resistance for influx as a function of the exposure concentration, as $\rho_{CH_2,0,in} \cdot C_0^{\kappa\rho}$ for water and $\rho_{CH_2,1,in} \cdot C_1^{\kappa\rho}$ for food.

The affinity of organic substances for body components could be satisfactorily related to the octanol–water partition ratio (K_{ow}). Unfortunately, there is no widely applicable equivalent for inorganic contaminants. Since metals tend to accumulate in dry biomass, affinity may be described by the distribution of inorganic substances over dry tissues and water, abbreviated as K_{tw}. Both K_{ow} and K_{tw} serve only as a surrogate parameter for the overall partitioning between fatty or dry biological matter and water. While K_{ow} does not cover variability between iso-lipophilic compounds with different chemical structures and between different types of lipids, K_{tw} cannot simulate variability between partitioning of (species of) metals and between tissues, as long as this has not been quantified empirically.

As summarized in Equations 2 and 3, exchange of inorganic contaminants may be limited by flow delays too. The flux of water, food, and biomass through organisms was correlated to species weight in allometric regressions with coefficients γ_0,

$q_{T:c}\cdot\gamma_1$, and γ_2 ($kg^{\kappa}\cdot d^{-1}$), respectively. The corresponding delays are represented by $1/\gamma_0$, dry feces $1/(p_{s,i-1}\cdot K_{tw}\cdot(1-p_1)\cdot q_{T:c}\cdot\gamma_1)$, and biomass $1/\gamma_2$ ($d\cdot kg^{-\kappa}$) and are equal to those used for organic substances after replacing $p_{CH_2,i-1}\cdot K_{ow}$ by $p_{s,i-1}\cdot K_{tw}$ [1].

The models for inorganic and organic substances are thus similar, with the exception of the lipid layer resistance for influx and the affinity for body components. Keeping in mind these adaptations, the equations for each flux of inorganic substances can be easily derived from the organic model [1]. The rate constant for absorption from water $k_{0,x,in}$ (per $\mu g\cdot kg^{-1}$ wet wt/$\mu g\cdot L^{-1}\cdot d^{-1}$) equals

$$k_{0,x,in} = \frac{w^{-\kappa}}{\rho_{H_2O,0} + \rho_{CH_2,0,in}\cdot C_0^{\kappa_\rho} + \frac{1}{\gamma_0}} \quad (4)$$

while the fraction assimilated from food as $p_{1,x}$ (/) can be described by

$$p_{1,x} = \frac{p_1/K_{e:d}}{(1-p_1)\cdot q_{T:c}\cdot\gamma_1}\cdot\frac{1}{p_{s,i-1}\cdot K_{tw}} \times \frac{1}{\rho_{H_2O,1} + \frac{\rho_{CH_2,1,in}\cdot C_{i-1}^{\kappa_\rho}}{q_{T:c}} + \frac{1}{p_{s,i-1}\cdot K_{tw}\cdot(1-p_1)\cdot q_{T:c}\cdot\gamma_1}} \quad (5)$$

The water layer resistance for absorption in Equation 4 $\rho_{H_2O,1}$ were calibrated to have a different value [1]. As mentioned above, the resistance in the lipid layer is considered to be a power function of the concentration in water C_0 and in food C_{i-1} with coefficients $\rho_{CH_2,0,in}$ (water) and $\rho_{CH_2,1,in}$ (food) and exponent κ_ρ. The increase of the contaminant assimilation efficiency $p_{1,x}$ with higher food digestibility p_1 is reflected by $p_1/((1-p_1)\cdot q_{T:c}\cdot\gamma_1)$. Contaminants are taken up from the digested p_1 and not from the egested $1-p_1$ fraction (for evidence on organic substances, see [1]). However, some inorganic elements tend to accumulate disproportionally in nondigestible organelles and tissues rather than in digestible components of cells and organisms. This is accounted for by introducing an additional adaptation to the organic model: the distribution of elements over egested and digested components $K_{e:d}$. For a few elements and species groups, its value may be approximated from quantitative studies on the distribution of polar and nonpolar fractions [33–36]. For others, it may be estimated from qualitative information of the food species composition.

Analogously, rate constants can be formulated for excretion with water $k_{0,x,out}$ ($kg^{-1}/kg^{-1}\cdot d^{-1} = d^{-1}$)

$$k_{0,x,out} = \frac{1}{p_{s,i}\cdot K_{tw}}\cdot\frac{w^{-\kappa}}{\rho_{H_2O,0} + \rho_{CH_2,out} + \frac{1}{\gamma_0}} \quad (6)$$

and for egestion with food $k_{1,x,out}$ ($kg^{-1}/kg^{-1}\cdot d^{-1}=d^{-1}$)

$$k_{1,x,out} = \frac{1}{p_{s,i}\cdot K_{tw}}\cdot\frac{w^{-\kappa}}{\rho_{H_2O,1} + \frac{\rho_{CH_2,out}}{q_{T:c}} + \frac{1}{p_{s,i-1}\cdot K_{tw}\cdot(1-p_1)\cdot q_{T:c}\cdot\gamma_1}} \quad (7)$$

Excretion and egestion rate constants are thus a function of the accumulation ratio $1/(p_{s,i}\cdot K_{tw})$, the water $\rho_{H_2O,i}$ and lipid $\rho_{CH_2,out}$ layer resistances, and the flow delays $1/\gamma_i$. Note that the water resistances for influx are similar to those for efflux because these act in both directions. In contrast to influx, the lipid layer resistance for efflux $\rho_{CH_2,out}$ was considered to be independent of the external concentration because exposure levels were reported to have no impact on depuration rates [32,37].

The rate constant for dilution with biomass $k_{2,x,out}$ $kg^{-1}/kg^{-1}\cdot d^{-1} = d^{-1}$) is defined as

$$k_{2,x,out} = \frac{w^{-\kappa}}{\frac{1}{q_{T:c}\cdot\gamma_2}} = q_{T:c}\cdot\gamma_2\cdot w^{-\kappa} \quad (8)$$

The corresponding flow delays for water $1/\gamma_0$, dry feces $1/(p_{s,i-1}\cdot K_{tw}\cdot(1-p_1)\cdot q_{T:c}\cdot\gamma_1)$ were declared above and elsewhere [1].

If the exponent κ_ρ equals 0, influx and efflux rate constants are both independent of the external concentration, indicating that the organism does not control the internal concentration C_i. If the exponent κ_ρ equals 1 and exposure is low, control is absent too. If the exponent κ_ρ equals 1 and exposure is high, rate constants for uptake but not elimination decrease linearly with external concentrations. The internal concentration is completely regulated by the organism. It may reflect a limitation of receptor sites in the membrane proteins or in the organism itself, analogously to the Michaelis–Menten kinetics for enzymes or the Langmuir kinetics for sorption [38,39]. If the exponent κ_ρ is between 0 and 1 and exposure is high, internal concentrations are partially controlled. In this case, the equations may be considered to reflect competition between metals with accumulation as a function of the available fraction for receptors analogous to the Freundlich kinetics for sorption.

Excretion, egestion and dilution together provide a minimum efflux rate constant ${}^2\Sigma_0 k_{j,x,out}$. Where necessary, one may add an extra pathway $k_{3,x,out}$ to reflect specific transport or transformation, analogously to the metabolism of organic substances [1]. For inorganic substances, excess elimination may be provided (e.g., by dealkylation of alkylmetals or by preferential transport to tissues to be shed [19,26,40]).

Calibration in general

Using allometric regressions on purely ecological data, water turnover γ_0 was fitted to be 200 for aquatic and at least 0.2 $kg^{\kappa}\cdot d^{-1}$ for terrestrial species [4]. However, calibration of rate constants for organic substances showed that 200 $kg^{\kappa}\cdot d^{-1}$ is an appropriate value for laboratory experiments with terrestrial species too. For cold-blooded organisms, the food ingestion γ_1 and (re)production γ_2 coefficients were derived to be 0.005 and 0.0006 kg^{κ}/d, respectively. In warm-blooded species, these metabolic rates were generally about $q_{T:c} = 10$ times faster compared with cold-blooded organisms. The fraction food assimilated equaled about 0.2, 0.4, and 0.8 for detritivores, herbivores, and grani-carnivores, respectively. On average, about 20% of the total production was shed; the rest was lost by the population when individuals die.

The absorption $\rho_{H_2O,0}$ and assimilation $\rho_{H_2O,1}$ resistances of 2.7×10^{-3} and 1.5×10^{-5} $d\cdot kg^{-\kappa}$ obtained for exchange of organic compounds [1] were used for inorganic substances too. Values were tentatively considered to be equal since atomic weight and volume of metals is at the lower end of the range for organic xenobiotics. As diffusion constants scale to molecular weight and volume with exponents of about 0.6 to 0.7 [41,42], diffusion constants will be within an order of magnitude. In the present study, the lipid resistance parameters $\rho_{CH_2,0,in}$, $\rho_{CH_2,1,in}$, $\rho_{CH_2,out}$, κ_ρ, and the tissue–water partition ratio of Equations 4 to 8 were calibrated on measured rate constants while all other parameters were kept on the default values from studies [1,4]. Equation 5 was fitted to the assimilation

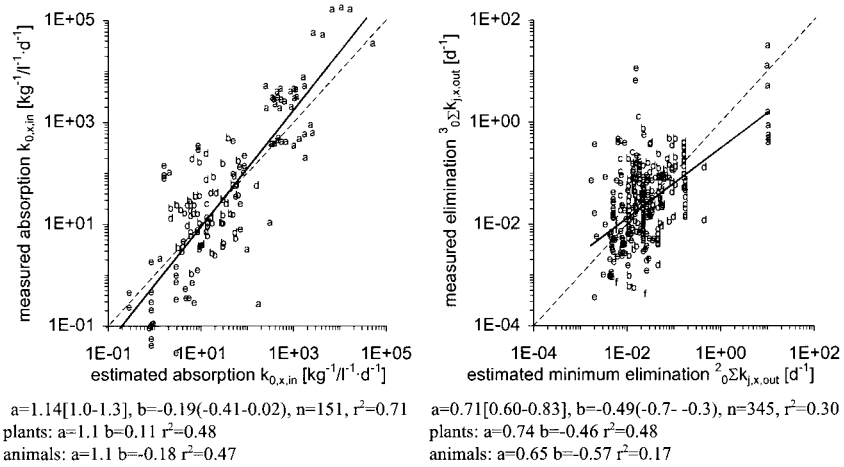


Fig. 1. Rate constants for absorption of metals from water $k_{0,x,in}$ ($\mu g \cdot kg^{-1}$ wet wt/$\mu g \cdot L^{-1} \cdot d^{-1}$) and for elimination of metals and alkylmetals $^{3}_{0}k_{j,x,out}$ (d^{-1}) measured in experiments versus estimated by the model. Regression of estimated and measured rate constants log(y) = a·log(x) + b (solid lines) and level at which estimated and measured constants match exactly (dashed lines). a = Phycophyta and Tracheophyta (algae and vascular plants), b = Mollusca (mollusks), c = Annelida (worms), d = Arthropoda (arthropods), e = Pisces (fish), f = Aves and Mammalia (birds and mammals).

data set using the slope κ_ρ obtained for absorption because food residues were reported in 5% of the studies only. In the majority of publications, radiolabeled levels were not converted to food residues. The distribution of substances over egested and digested food components $K_{e:d}$ was taken from literature or estimated from assimilation efficiencies.

Measured and estimated rate constants were generally within one order of magnitude, though larger deviations were noted too (Fig. 1). Absorption by fish tended to be slower than estimated by the model, with the exception of data on methylmercury or Hg and Pb. Deviations for elimination were evenly distributed among species, with a possible underestimation of depuration by annelids. The variation explained by the model was about 71% for absorption and 30% for elimination. Values for algae and animals were largely similar, indicating that, on average, the model applied well to both. Yet the low coefficient of determination r^2 for elimination by animals indicates that variability in the data set on animals is higher. Obviously, the fit can be additionally improved by selecting species- and element-specific parameter values, but the data set was too small to allow additional subdivision. Differences between species and elements were therefore qualitatively discussed. Discrepancies between measured and calculated were considered substantial if larger than 5 (see motivation in [1]).

Calibration of absorption rate constants

Metals. A preliminary analysis showed that the measured absorption rate constant divided by weight to the allometric power exponent ($^{3}\Sigma_0 k_{j,x,out}/w^{-\kappa}$) scaled to the water concentration $C_{0,w}$ with an exponent κ_ρ of 0.18 to 0.23 for nonessential metals (Ag, Cd, Hg) and of 0.73 to 0.78 for essential metals (Mn, Zn). The overall calibration (Table 1) also indicated that absorption rate constants decreased with increasing water concentrations ($\kappa_\rho < 0$). This trend was confirmed in individual studies with algae but not with mussels, possibly because of the small range of rate constants tested [31,32,43–45].

Rate constants for uptake of metals from water by aquatic organisms also clearly decreased with weight ($\kappa < 0$; Fig. 2). Rate constants for absorption of Cr were within a factor of 5 from the value estimated by the model panel 1 of Fig. 2), with the exception of five overestimations for Cr^{3+} in blue mussel, *Mytilus edulis*, and for Cr by rainbow trout, *Oncorhynchus mykiss*, muscles [12,45]. Of the 19 absorption rate constants, 16 were (slightly) lower than calculated by the model. Absorption of Cr^{6+} from drinking water by rat, *Rattus norvegicus* (not plotted in panel 1 of Fig. 2), was 0.00048 $kg^{-1}/L^{-1} \cdot d^{-1}$, at least 100 times slower than uptake by equally sized fish [46]. The corresponding water absorption efficiency was 0.6%,

Table 1. Factors used in the equations with typical or default values for parameters. Only those that are specific for inorganic substances are listed. Others are given in the text and listed elsewhere [1][a]

Symbol	Description	Unit	Typical or default value [95% CI]
K_{sw}	Dry solids–water partition ratio	$\mu g \cdot kg^{-1}$ dry wt/$\mu g \cdot L^{-1}$	$10^{5.1}$–$10^{2.3}$(Cd), $10^{4.7}$–$10^{3.0}$(Cu), $10^{5.2}$–$10^{2.2}$(Hg), $10^{3.9}$–$10^{2.1}$(Ni), $10^{5.8}$–$10^{3.3}$(Pb), $10^{5.04}$–$10^{2.2}$(Zn)[b]
K_{tw}	Dry tissue–water partition ratio	$\mu g \cdot kg^{-1}$ dry wt/$\mu g \cdot L^{-1}$	8.0 [5.3–11]·10^3
κ_ρ	Lipid layer resistance exponent		0.41 [0.28–0.53]
$p_{s,i}$	Dry fraction of organism (i), food (i–l)	kg dry wt/kg wet wt	0.20 [0.15–0.26]·$w^{0.03\ [0.01–0.05]}$
$K_{e:d}$	Distribution of substances over egested and digested food components		Ag, Cd, Co, Cu, Ni, Zn: 1 (i = 2) or 5 (i > 2). Pb, Hg: 5. Am, Cr: 10. nonmetals: 1
$\rho_{CH_2j,in}$	Lipid layer permeation influx resistance	$d \cdot kg^{-\kappa} \cdot (\mu g \cdot kg)^{-\kappa\rho}$	0.21 [0.10–0.32] (j = 0), 0.006 (j = 1)
$\rho_{CH_2,out}$	Lipid layer permeation efflux resistance	$d \cdot kg^{-1}$	0.30

[a] All data on a wet-weight basis unless indicated.
[b] For suspended solids and soils, respectively.

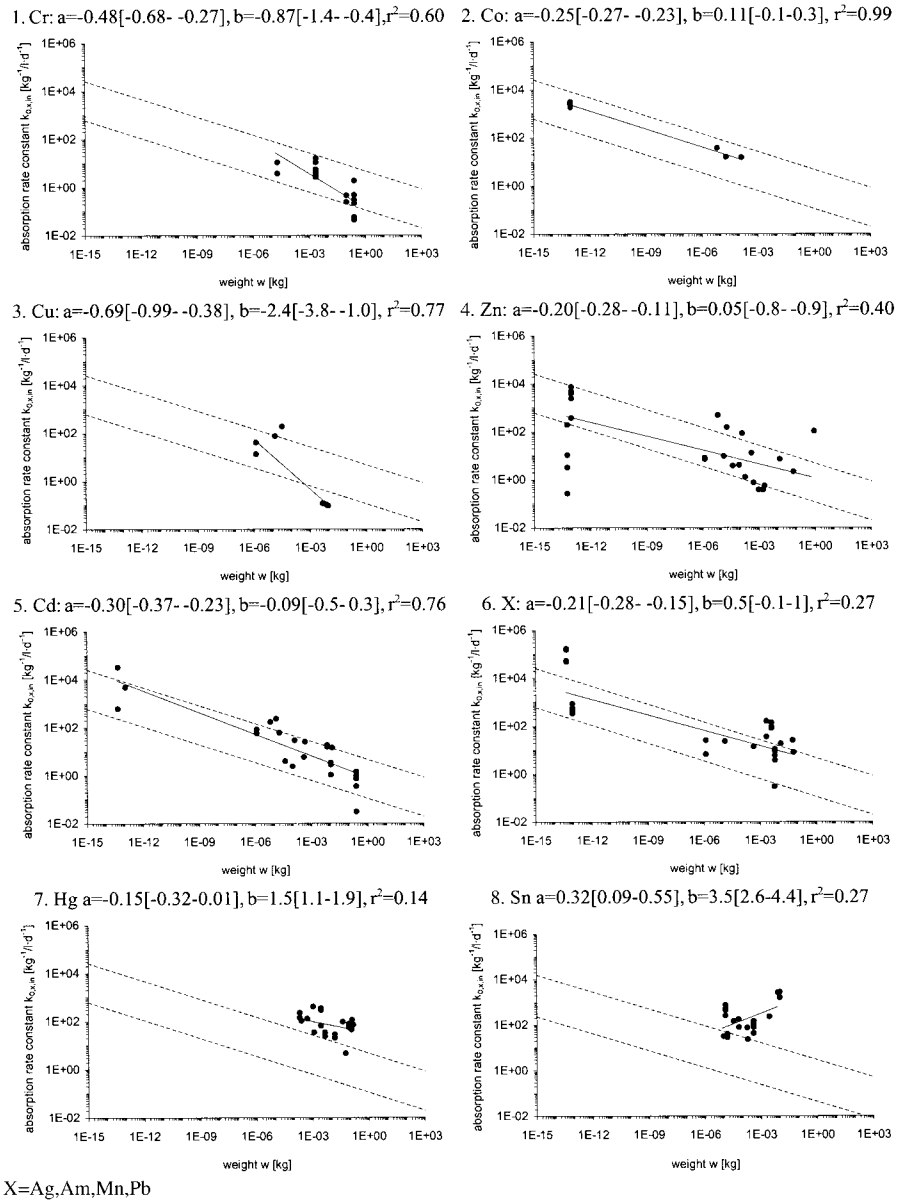


Fig. 2. Rate constants $k_{0,x,in}$ ($\mu g \cdot kg^{-1}$ wet wt/$\mu g \cdot L^{-1} \cdot d^{-1}$) for absorption of metals from water by aquatic organisms versus weight w. Laboratory measurements (closed circles), regressions log(y) = a·log(x) + b (solid lines) and model estimations for exposure to 1 (lower dashed line) and 10^4 $\mu g/L$ (upper dashed line).

about 10 times lower than the oral assimilation efficiency of 5% [47].

Though the regression for Co is nearly perfect, rate constants for *Chlorella salina* [43] were two to eight times higher than expected from the exposure concentration (panel 2 of Fig. 2). Data for Cu deviated largely more than a factor of 5 from the value estimated by the model (panel 3 of Fig. 2). Absorption of Cu by the fish *Lepomis gibbosus* was overestimated, whereas intake of Cu by the midge *Chironomus riparius* was underestimated, possibly because of additional intake via sediment [48]. Although Zn uptake followed the average trend predicted by the model, numerous deviations occurred (panel 4 of Fig. 2). Rate constants for the algae *Selenastrum capricornutum*, converted back from free ion concentrations, were overestimated. while values of equally sized *Chlorella salina* were underestimated [32,43]. Elimination data for Zn were equally distributed around the expected values.

Measured and estimated values for Cd were within a factor of 5 of each other for 22 out of 28 data (panel 5 of Fig. 2). Deviations applied to mollusks, chironomids, and fish. Initial rates for adsorption or absorption by wheat roots and rye grass, not plotted because of uncertainty about exposure levels and growth dilution, varied between 600 and 2,400 $kg^{-1}/L^{-1} \cdot d^{-1}$ within the range noted for algae [29,49].

Absorption of Mn, Ag, Pb, and Am was measured in a few species only (panel 6 of Fig. 2). The patterns were, on average, similar to that of the relatively well studied metals (panels 1–5 of Fig. 2). Uptake of Pb by fish and of Mn by the algae *Thalassiosira pseudonana* but not by the algae *Chlorella salina* was substantially underestimated [43,44,50]. The efficiency of Pb absorption by mammals from drinking water (not plotted in panel 6 of Fig. 2) equaled 10%, about equally efficient as assimilation from food [47].

Alkylmetals. Alkylmetals and nonmetals were not used during calibration because uptake mechanisms for these substances may be different. Rate constants for Hg and methyl-

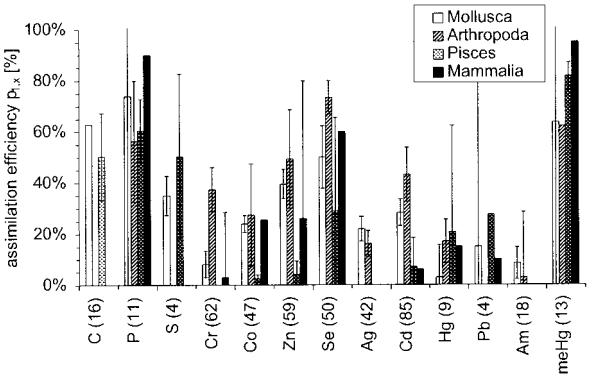


Fig. 3. Efficiencies $p_{1,x}$ (%) for dietary assimilation of inorganic substances by mollusks (white bars), arthropods (shaded bars), and fish (dotted bars) and for oral assimilation of inorganic substances by mammals (dark bars). Geometric means with the 95% confidence interval and the number of data *n* per substance between brackets.

mercury were about equal to each other and above the level expected from the model for inorganic metals (panel 7 of Fig. 2). The lower and upper dashed line can also be interpreted as the absorption calculated for organic substances with an octanol–water partition ratio of about 7 and 330, respectively [1]. The rate constants measured for methylmercury were clearly above these levels (panel 7 of Fig. 2), though K_{ow} values for methylmercury or Hg were in the range of 2.5 for $HgCH_3Cl$ and 0.6 for $HgCl_2$ [51,52]. It indicates that methylmercury or Hg accumulation is not similar to that of other inorganic or organic substances.

Rate constants for organotins were 10 to 1,000 times above the range calculated for metals (panel 8 of Fig. 2). Yet the level measured for tributyltin and triphenyltin can be explained well by application of the model for organic substances with their K_{ow} values of 1.5×10^3 and 1.3×10^4, respectively [1]. Rate constants for various mussel species were substantially higher than those for other species [53,54]. If the mollusk data were excluded, absorption scaled to -0.23, instead of the 0.32 observed for the whole set (panel 8 of Fig. 2).

Nonmetals. Uptake of Se by the mussel *Mytilus edulis* was within 3.3 to 8.2 $kg^{-1}/L^{-1}\cdot d^{-1}$, which is slower than the range of 30 to 63 $kg^{-1}/L^{-1}\cdot d^{-1}$ calculated from the metal model. The rate constant for absorption of As by *Eisenia andrei* was 11 $kg^{-1}/L^{-1}\cdot d^{-1}$, while the model predicted 13 kg/L/d.

One may conclude that the rate constant for absorption of metals $k_{0,x,in}$ by aquatic organisms from water depended on the water concentration $C_{0,w}$ of the substance and the weight w of the species. Deviations for various metals and species were usually less than a factor of 5. Uptake of large (alkyl)metals ($M \geq 201$ $g\cdot mol^{-1}$: Hg, methylmercury, Pb, tributyltin, triphenyltin) was much faster than that of the other metals ($M \leq 112$ $g\cdot mol^{-1}$). A few data on other species indicated that uptake of metals by terrestrial plants was faster than expected from their weight, whereas intake by mammals from drinking water may be equally or less efficient than assimilation from food.

Calibration of assimilation efficiencies

Metals. Average efficiencies for assimilation of Co, Cd, Ag, and Zn by mollusks and arthropods were between 15 and 50% (Fig. 3). Values for Cr, Hg, Pb, and Am were usually below this range. For these species, uptake of small positive ions ($M \leq 112$ $g\cdot mol^{-1}$) appeared thus more efficient than that of negative or large positive ($M \geq 201$ $g\cdot mol^{-1}$) ions. There was no consistent difference between detritivorous, herbivorous, and carnivorous invertebrates in our data set (see also [55]). Average efficiencies for assimilation of Co, Zn, and Cd by carnivorous fish were significantly lower than those for the largely detriti-herbivorous invertebrates. Yet data largely referred to fish feeding on crustaceans [34]. Uptake from artificial diets from vegetable origin was higher [56,57]. Efficiencies for Hg and Pb assimilation by various species groups were variable. Average oral efficiencies for mammals were usually at or above the level of dietary uptake by fish.

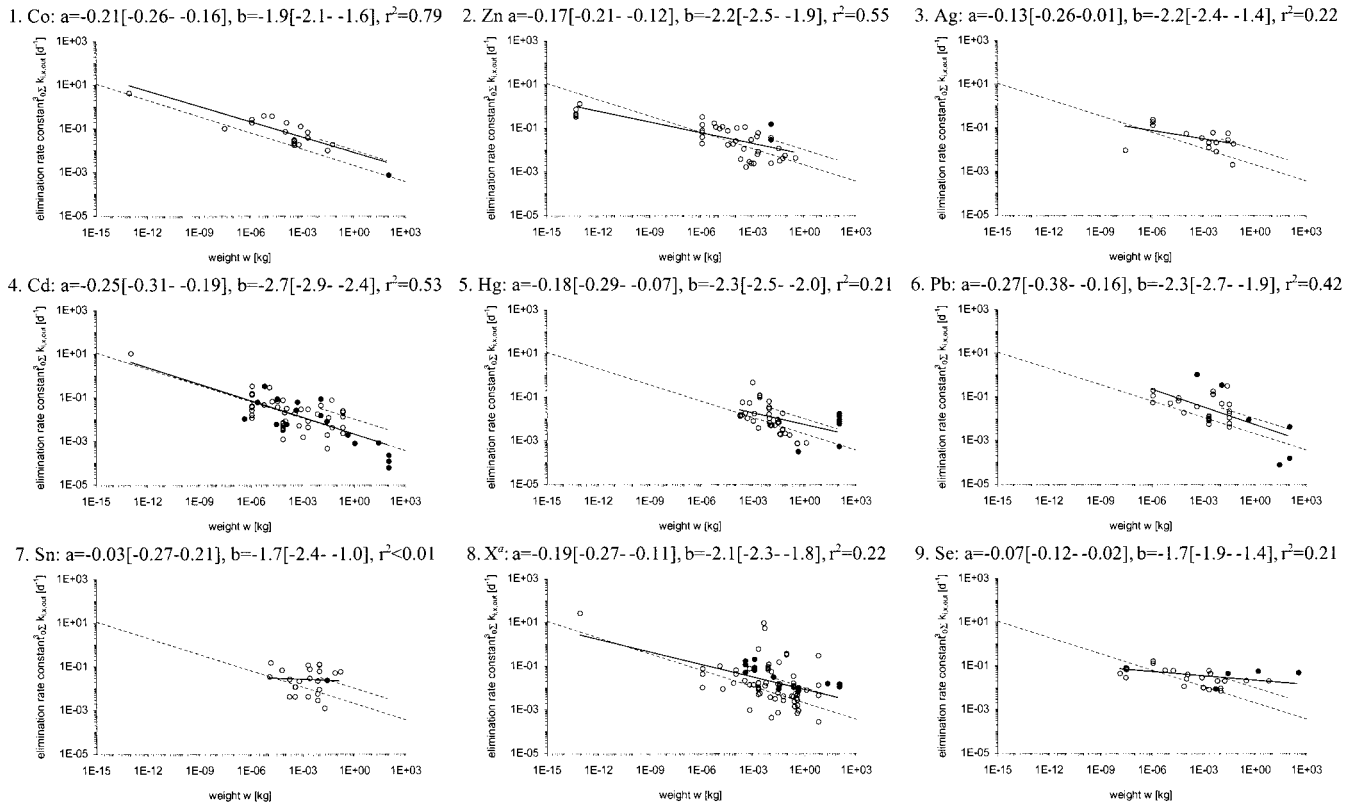
Alkylmetals and nonmetals. Values for methylmercury were similar to assimilation efficiencies for persistent, hydrophobic organochlorines and to food (or fat) digestibility. The essential nonmetals C, P, S, and Se were taken up equally or more efficient than food itself. Oral efficiencies for the nonmetals As, Cl, and F were also high [47].

Confidence intervals for metals, alkylmetals, and nonmetals were large, indicating that experiments were difficult and yielded inconsistent results [22]. Variability was usually attributed to food quantity and, especially, food quality [30,55]. Differences between elements were associated with their affinity for digestible (≈polar, cytosol) and nondigestible (≈nonpolar, membrane) food components [34–36,58]. Differences between food types appeared to depend on the fractions of these components present. Assimilation was often lower if suspended matter was poor in algae [36]. Efficiency was inconsistently influenced by differences in organic and mineral characteristics of sediments [59]. Yet variability was usually smaller than a factor of 2. Metal content only had a minor effect on assimilation by *Mytilus edulis* within the small ranges tested [30].

In vegetable diets, the nonmetals C, P, S, and Se as well as the metals Cd, Co, Zn, and to a lesser extent Ag were about equally divided over the nonpolar membrane fraction and the polar cytosol fraction ($K_{e:d}$) equaled approximately 1 [33–36]. Values for Hg and Pb may be set at 5 because assimilation efficiencies tended to be lower (Fig. 3). The partitioning of Am and Cr over nondigestible and digestible plant food was roughly 10.

For animal diets, data were available for assimilation of a few metals and nonmetals from zooplankton by fish only [34]. The distribution $K_{e:d}$ of Cd, Co, and Zn equaled about 30, corresponding to assimilation efficiencies of about 3%. However, efficiencies for assimilation of crustaceans by invertebrates and of light food by fish is substantially higher, up to the level of the food digestibility (e.g., [57,60]). In view of this variability, $K_{e:d}$ was tentatively set at 5, as an geometric mean between 1 and 30. Based on a few vertebrate data if available, Cr, Pb, Hg, and Am were set at the value for vegetable food, whereas Cu and Ni were preliminary considered to be distributed as Zn (Fig. 3). The correctness of these extrapolations was tested during validation.

Efficiencies for assimilation of metals and nonmetals $p_{1,x}$ were highly variable, largely depending on food type. In most cases, elements appeared to be more or less evenly distributed over digestible and nondigestible tissues. As a result, their assimilation was usually about equally efficient as the digestibility of food p_1 itself. Assimilation efficiencies for some metals, such as Cr and Am, and some animal food types, such as crustaceans with exoskeletons, were lower. Uptake of methylmercury was more efficient than assimilation of food itself.



[a]Am, Ce, Cr, Cs, Cu, Fe, La, Mn, Nd, Ni, Pu, Po, Pr, Rb, Sm, Sr, Tl, V

Fig. 4. Rate constants ${}^3\Sigma_0 k_{j,x,out}$ (d^{-1}) for elimination of inorganic substances versus weight w. Laboratory measurements for aquatic (open circles) and terrestrial (closed circles) species, regressions log(y) = a·log(x) + b (solid lines) and model estimations for cold-blooded (lower dashed line) and warm-blooded (upper dashed line) organisms.

Calibration of elimination rate constants

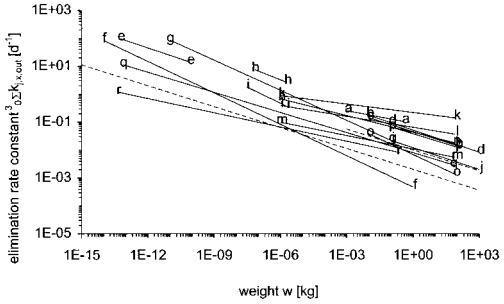
The sum of excretion (Eqn. 6), egestion (Eqn. 7), and dilution (Eqn. 8) ${}^3\Sigma_0 k_{j,x,out}$ was fitted on metal and alkylmetal data by varying the lipid resistance $\rho_{CH_2,out}$ and the tissue–water partition ratio. According to the regressions (Fig. 4), rate constants for elimination decreased with weight ($\kappa < 0$) as expected from the model. Filling in the parameter values obtained in the calibration (Table 1) into Equations 6 to 8 yielded elimination rate constants of about $0.002/w^{\kappa}$ for cold-blooded and $0.01/w^{\kappa}$ for warm-blooded organisms, respectively (Fig. 4). Using different values of 0.2 and 200 kg^{κ}/d for the water flux coefficient γ_0 did not yield different elimination rate constants for aquatic and terrestrial species.

Metals. All measurements for Co were within a factor 5 of the estimates, with the exception of two values for mollusks and one for man (panel 1 of Fig. 4). Elimination of Zn (panel 2 of Fig. 4) was overestimated in 25 of the 43 cases. Deviations of more than a factor of 5 were noted in 10 cases, five of them referring to fish liver [61]. Another five applied to growth-corrected data for algae, whereas the model included production dilution as well [32,43]. The two values for the worms *Allolobophora tuberculata* and *Enchytraeus crypticus* indicated that elimination by terrestrial species was not slower than that by aquatic species, as expected from the model. Data for Ag nicely corresponded to the model estimations (panel 3 of Fig. 4), with the exception of an extremely low rate constant for *Semibalanus balanoides* [62]. If this value is omitted, the slope became −0.25, and the correlation coefficient improved to 0.60.

For Cd, 27 out of 62 measurements deviated more than a factor of 5 from the estimated values (panel 4 of Fig. 4). Of these outliers, eight apply to the barnacle *Balanus amphitrite* [60]. Another seven overestimations referred to elimination from by mammals [26,63,64]. According to the model, however, warm-blooded animals were expected to have higher elimination rates than equally sized cold-blooded species because lipid membrane resistance for food and contaminants $\rho_{CH_2,out}/q_T$ was decreased. Measured values were perhaps low because of the use of non-(re)producing adults, as common in mammalian studies. Cadmium data confirmed that there was no substantial difference between aquatic and terrestrial species or between detriti-herbivores and carnivores, as predicted by the model.

Both Hg and methylmercury are plotted in the same graph (panel 5 of Fig. 4) because their rate constants were similar for individuals of the same species and (nearly) equal weight. Elimination of inorganic Hg was 0.7 to 2 times faster than that of methylmercury for the invertebrates, fish, and mammals for which data are available [19,26,65,66]. The 7 out of 44 rate constants that deviate by more than a factor of 5 were evenly distributed among species.

The elimination of Pb was correlated to weight (panel 6 of Fig. 4). All measurements for terrestrial annelids and fish were substantially underestimated by the model [50,67–69]. Elimination data for fish were obtained from accumulation experiments with 8% ionic lead only [50]. The rate constants for Pb in this study were in the same range as the only value reported for tetramethyllead [67]. Depuration of Pb by mammals was overestimated in some studies [26]. Elimination of (alkyl)tins was within the range expected by the model, but



a-d=N, e-i=P, j=S, k=^{59}Fe, l=^{60}Co, m=^{65}Zn, n=^{90}Sr, o=^{131}I, p=$^{134-137}$Cs [2, 10, 81, 82, 83, 84, 85, 86, 87].

Fig. 5. Rate constants $^3\Sigma_0 k_{j,x,out}$ (d^{-1}) for elimination of inorganic substances versus weight w. Literature regressions (solid lines) and model estimations for cold-blooded (lower dashed line) and warm-blooded organisms (upper dashed line).

the variability is too high to recognize a correlation to weight (panel 7 of Fig. 4). Rate constants for depuration of inorganic tin from vertebrates are similar to those for organic tin [37,63].

A correlation to weight can be recognized for the other metals despite variability among the large number of metals and species included (panel 8 of Fig. 4). Most data apply to Mn and Cs, each correlating well to size with slopes of −0.24 and −0.40, respectively (separate regressions not shown). In some cases, depuration of Cr, Cu, and other metals from fish (gills) was 10 to 100 times faster than estimated by the model (e.g., [48,57,70]).

With the exception of organotin, slopes were in the range of −0.13 and −0.27, while most 95% confidence intervals covered −0.25. The corresponding intercepts were also remarkably similar, that is, between −2.4 and −1.9. It suggests that affinity of different metals for biological matter is, on average, comparable.

Nonmetals. The measured rate constants for Se were within a factor of 5 from the estimated values for 23 out of 30 values (panel 9 of Fig. 4). Elimination appeared only weakly related to weight. Outliers applied to some small crustaceans, also known for a slow elimination of Co and Ag and to fish for the actual weight, were not reported [62,71,72]. The rate constants for depuration of As (not shown) by mussels and worms were within a factor 5 of the model predictions, but elimination from fish and man was much faster than expected [19,37,63,69].

The regressions obtained in the present investigation were compared to those reported in other studies. Intraspecific correlations for elimination of Zn, Cu, and methylmercury scaled to weight with exponents of −0.42, −1.8, and −0.58 [48,73,74]. Slopes for interspecific regressions reported in the literature (Fig. 5) were similar to those obtained in the present study (Fig. 4). Differences between intercepts may be partly attributed to the use of average conversion factors. Intercepts for essential macronutrients (N, P), however, appeared slightly higher than those for micronutrients (e.g., Co, Zn) and the average level expected from the model. The same held for elimination of ^{59}Fe, ^{60}Co, ^{65}Zn, ^{90}Sr, ^{131}I, and $^{134-137}$Cs ([2]; Fig. 5). Higher intercepts may indicate disintegration of the isotopes.

Analogously to absorption, rate constants for elimination of elements decreased with species weight. The regressions for metals were within a range of a factor of about 10, usually near the average calculated by the model (Figs. 4 and 5). Elimination of alkylmetals and selenium was similar to that of metals. It suggests that affinity of inorganic substances for biological matter is, on average, remarkably similar.

Validation on laboratory and field bioaccumulation ratios

One may test the validity of the model as calibrated on the rate constants by comparing the ratio of influx $k_{j,x,in}$ and efflux $^3\Sigma_0 k_{j,x,out}$ to the independent data on accumulation ratios (Table 2 and Fig. 6). Unfortunately, accumulation was often expressed as an organism–solids concentration ratio, without specifying the actual solids–water partitioning. To allow for comparison, organism–water concentration ratios calculated by the model were converted using average solids–water partition ratios (K_{sw}) obtained in The Netherlands ([75,76]; see Table 1). Obviously, these values served only as a tentative approximation of the actual partitioning, especially for soils with completely different characteristics.

The accumulation ratios calculated by the model for the herbivorous and detritivorous food chain applied to mollusks and annelids, respectively (panels 1–7 of Fig. 6). Curves for other phylogenetic groups in the same food chain were not plotted because these were nearly identical. For instance, predictions for algae, mussels, and fish were comparable. Accumulation in the land food chain was calculated for high (≈freshly deposited floodplain soil) and low (≈average terrestrial soil) K_{sw}.

Accumulation in aquatic and terrestrial species was estimated using a water turnover of 200 and 0.2 kg/d, respectively. Cold-blooded animals were considered to be exposed to water. In addition, herbivores were considered to feed on microphytes or macrophytes. Detritivores were supposed to ingest both organic and mineral particles because solids–water partition ratio do not distinguish between these fractions.

The magnification ratios for warm-blooded animals (panel 8 of Fig. 6) were calculated without taking absorption from drinking water into account because data on birds and mammals were not present in the calibration data set. In addition, the validation data apply to laboratory experiments and field surveys where contamination via drinking is absent and uncertain, respectively. As described in the Methods section, liver and kidney residues were often one and occasionally two orders of magnitude higher. The organ residues calculated by the model were therefore plotted as whole body ratios multiplied by 10.

For various metals and species, (near-)equilibrium accumulation ratios decreased with increasing exposure concentrations, as expected from the model (Table 2 and Fig. 6). The slope of the regressions for exposure to water, suspended solids, sediment, soil, and food in laboratory and field studies was remarkably similar. On average, the exponent equaled −0.47, almost equal to the opposite of the uptake exponent κ_ρ of 0.41. Concentration ratios of Hg decreased with exposure concentrations at an average slope of about −1, twice as steep as noted for other metals (panel 6 vs panels 1–5 and 7 of Fig. 6). The intercepts of the correlations were usually within about 2 orders of magnitude. To compare regressions with different slopes and intercepts, differences will be discussed focusing on the middle part value of each correlation.

Differences between species. Accumulation of most metals by aquatic microphytes and macrophytes varied around the level estimated by the model (Table 2 and panels1–7 of Fig. 6). The highest values were noted for algae, up to 10 times higher than the predicted average for high exposure levels. Concentration ratios for terrestrial plants were usually about

Table 2. Organism–solids concentration ratios $C_i/C_{0.5}$ ($\mu g \cdot kg^{-1}$ dry wt/$\mu g \cdot kg^{-1}$ dry wt) for plants and cold-blooded animals (1–7) and organ–food concentration ratios C_i/C_{i-1} ($\mu g \cdot kg^{-1}$ dry wt/$\mu g \cdot kg^{-1}$ dry wt) for warm-blooded organisms (8). Regressions (ratio = a·exposure concentration[a]) or geometric averages (if only one exposure concentration) on laboratory or field measurements

X	Taxon[b]	Species (group)	Exposure			a	b	*n*	r^2	Source
1 a Cr	Tr	Angiospermae	a	se	f	5.9×10^{-1}	−0.09	7	0.08	[88]
b Cr		[c]	t	so	f	2.0×10^{2}	−0.92	1,600	0.07	[6]
c Cr	An	Tubificidae	a	su	r	6.5×10^{2}	−0.80	9	0.35	[89,90,91,92]
d Cr		*Eisenia fetida, Lumbricus rubellus*	t	so	r	1.8×10^{-1}	—	3	—	[8,92]
2 a Ni	Ph	Coccochloris, Oscillatoria . . .	a	wa	l	3.5×10^{-2}	—	16	—	[93]
b Ni	Tr	Angiospermae	a	se	f	5.8×10^{3}	−0.87	16	0.73	[88]
c Ni		*Potamogeton pectinatus*	a	su	r	2.0×10^{-8}	1.53	17	0.01	[94,95]
d Ni		Angiospermae[c]	t	so	f	6.6×10^{2}	−0.88	2,109	0.13	[6]
e Ni		Graminae	t	so	r	3.1×10^{-2}	—	4	—	[96,97]
f Ni	An	Tubificidae	a	su	r	7.9×10^{0}	−0.28	9	0.15	[89,90,91,92]
g Ni		*E. fetida, L. rubellus*	t	so	r	2.2×10^{-1}	−0.05	15	0.01	[8,92]
3 a Cu	Ph	*Anacystis nidulans, Spirulina platensis*	a	wa	l	6.5×10^{1}	−0.58	10	0.96	[93]
b Cu		Anabaena	a	wa	r	4.1×10^{-1}	−0.09	4	1.00	[98]
c Cu		Phycophyta	a	se	r	3.0×10^{-1}	—	>	—	[99]
d Cu	Tr	Angiospermae	a	se	f	1.7×10^{1}	−0.39	32	0.31	[88]
e Cu		*P. pectinatus*	a	su	r	7.4×10^{3}	−0.90	17	0.45	[94,95]
f Cu		Angiospermae[c]	t	so	f	2.4×10^{3}	−0.84	2,231	0.33	[6]
g Cu		Monocotyledones	t	so	r	3.6×10^{0}	−0.28	14	0.08	[96,97]
h Cu	Mo	*Dreissena polymorpha*	a	se	r	9.2×10^{2}	−0.72	6	0.63	[5,99,100]
i Cu	An	Tubificidae	a	su	r	7.7×10^{4}	−1.00	21	0.84	[89,90,91,92]
j Cu		Lumbricidae	t	so	f	1.7×10^{2}	−0.54	22	0.75	[101]
k Cu		*E. fetida, L. rubellus*	t	so	r	4.2×10^{2}	−0.63	16	0.95	[8,92]
l Cu	Cr, In[+]	Crustacea, Insecta[+]	a	se	f	2.1×10^{0}	−0.34	197	e	[7]
m Cu		Cladocera, Chironomidae	a	se	r	4.4×10^{-9}	1.58	6	0.23	[5,99,102]
n Cu	Ar	Araneida, Opiliones[+]	t	so	f	1.1×10^{3}	−0.65	49	0.45	[101]
o Cu	Di	Diplopoda	t	so	f	1.3×10^{4}	−0.74	9	0.76	[101]
p Cu	In	Coleoptera	t	so	f	7.4×10^{2}	−0.69	40	0.36	[101]
q Cu	Pi	*Rutilus rutilus, Anguilla anguilla*[+]	a	se	r	2.3×10^{-2}	—	3	—	[5,99]
4 a Zn	Ph	*Fucus serratus,* Skeletonema[+]	a	wa	l	1.4×10^{3}	−0.56	7	0.93	[93]
b Zn		Phycophyta	a	se	r	2.2×10^{-1}	—	>	—	[99]
c Zn	Tr	Angiospermae	a	se	f	1.5×10^{2}	−0.48	43	0.19	[88]
d Zn		*P. pectinatus*	a	su	r	3.9×10^{4}	−0.88	17	0.96	[94,95]
e Zn		Angiospermae[c]	t	so	f	2.0×10^{3}	−0.67	2,233	0.28	[6]
f Zn		Monocotyledones	t	so	r	2.3×10^{2}	−0.56	14	0.41	[96,97]
g Zn	Mo	Bivalvia, Gastropoda	a	wa	l	9.8×10^{1}	−0.24	15	0.15	[93]
h Zn		*D. polymorpha*	a	se	r	2.0×10^{4}	−0.82	6	0.83	[5,99,100]
i Zn	An	Tubificidae	a	su	r	2.7×10^{7}	−1.29	21	0.84	[89,90,91,92]
j Zn		Lumbricidae	t	so	f	1.9×10^{4}	−0.83	19	0.70	[101]
k Zn		*E. fetida, L. rubellus*	t	so	r	3.9×10^{3}	−0.62	16	0.39	[8,92]
l Zn	Cr, In[+]	Crustacea, Insecta . . .	a	se	f	2.5×10^{0}	−0.23	295	e	[7]
m Zn		Cladocera, Chironomidae	a	se	r	1.1×10^{19}	−3.28	6	0.83	[5,99,102]
n Zn	Cr	Decapoda, Amphipoda	a	wa	l	1.4×10^{0}	−0.30	13	0.28	[6]
o Zn	Ar	Araneida, Opiliones	t	so	f	6.0×10^{3}	−0.66	43	0.49	[101]
p Zn	Di	Diplopoda	t	so	f	2.1×10^{4}	−0.71	6	0.35	[101]
q Zn	In	Coleoptera	t	so	f	6.0×10^{3}	−0.76	34	0.13	[101]
r Zn	Pi	*P. platessa, R. clavata*	a	wa	l	5.4×10^{-2}	—	24	—	[6]
s Zn	Pi	*R. rutilus, A. anguilla* . . .	a	se	r	5.0×10^{-2}	—	3	—	[5,99]
5 a Cd	Ph	*Chlorella vulgaris,* Scenedesmus[+]	a	wa	l	2.0×10^{4}	−0.76	37	0.30	[6]
b Cd		Anabaena	a	wa	r	9.7×10^{-1}	−0.17	7	0.99	[98]
c Cd		Phycophyta	a	se	r	2.2×10^{-1}	—	>	—	[99]
d Cd	Tr	*Lemna minor, L. trisulca*	a	wa	l	5.8×10^{0}	−0.28	8	0.31	[6]
e Cd		Angiospermae	a	se	f	2.2×10^{1}	−0.47	36	0.28	[88]
f Cd		*P. pectinatus*	a	su	r	3.0×10^{6}	−1.93	17	0.27	[94,95]
g Cd		Angiospermae[c]	t	so	f	1.0×10^{1}	−0.42	2,223	0.11	[6]
h Cd		Monocotyledones	t	so	r	2.2×10^{1}	−0.70	14	0.69	[96,97]
i Cd	Mo	Bivalvia, Gastropoda	a	wa	l	6.7×10^{0}	−0.31	13	010	[93]
j Cd		*D. polymorpha*	a	se	r	2.3×10^{0}	−0.23	6	0.08	[5,99,100]
k Cd	An	Tubificidae	a	su	r	4.4×10^{2}	−0.78	21	0.62	[89,90,91,92]
l Cd		Lumbricidae	t	so	f	8.5×10^{2}	−0.61	17	0.54	[101]
m Cd		*E. fetida, L. rubellus*	t	so	r	3.3×10^{3}	−0.77	16	0.64	[8,92]
n Cd	Cr, In[+]	Cladocera, Chironomidae	a	se	r	7.5×10^{-4}	0.59	6	0.27	[5,99,102]
o Cd	Cr	Decapoda, Amphipoda	a	wa	l	5.7×10^{2}	−0.73	28	0.64	[93]
p Cd	Ar	Araneida, Opiliones	t	so	f	3.1×10^{2}	−0.53	61	0.37	[101]
q Cd	Di	Diplopoda	t	so	f	6.3×10^{1}	−0.40	9	0.73	[101]
r Cd	In	Coleoptera	t	so	f	1.3×10^{1}	−0.40	50	0.45	[101]
s Cd	Pi	*Gasterosteus aculeatus,* Carassius[+]	a	wa	l	1.7×10^{1}	−0.57	27	0.57	[93]
t Cd		*R. rutilus, A. anguilla*[+]	a	se	r	2.8×10^{-5}	0.54	11	0.03	[5,99]
6 a Hg	Ph	Chaetoceros	a	wa	l	1.0×10^{7}	−1.45	7	0.80	[93]
b Hg	Tr	*P. pectinatus*	a	su	r	6.0×10^{0}	−0.47	17	0.01	[94,95]
c Hg		Graminae	t	so	r	1.8×10^{1}	−0.89	4	0.99	[96,97]
d Hg	Mo	*D. polymorpha*	a	se	r	2.2×10^{2}	−1.07	12	0.97	[5,99,100]

Table 2. Continued

X	Taxon[b]	Species (group)	Exposure			a	b	*n*	r^2	Source
e Hg	An	Tubificidae	a	su	r	3.2×10^{1}	−0.66	9	0.86	[89,90,91,92]
f Hg	Cr, In+	Cladocera, Chironomidae	a	se	r	3.0×10^{2}	−0.99	14	.072	[5,99,102]
g Hg	Pi	*Carassius auratus*, Salvelinus+	a	wa	l	9.5×10^{-13}	2.70	17	0.35	[93]
h Hg		*R. rutilus, A. anguilla*+	a	se	r	6.1×10^{1}	−0.82	32	0.46	[5,99]
7 a Pb	Ph	*C. vulgaris*	a	wa	l	3.2×10^{-5}	0.26	6	0.68	[93]
b Pb		Anabaena	a	wa	r	1.1×10^{-1}	—	7	0.94	[98]
c Pb	Tr	Angiospermae	a	se	f	6.8×10^{4}	−1.13	44	0.42	[88]
d Pb		[c]	t	so	f	7.4×10^{1}	−0.71	1,992	0.16	[6]
e Pb		Monocotyledones	t	so	r	1.7×10^{3}	−0.89	4	0.98	[96,97]
f Pb	Mo	*M. edulis*	a	wa	l	3.9×10^{-3}	−0.06	8	—	[93]
g Pb		*D. polymorpha*	a	se	r	9.5×10^{-1}	−0.31	3	0.28	[5,99,100]
h Pb	An	Tubificidae	a	su	r	1.4×10^{3}	−0.74	20	0.69	[89,90,91,92]
i Pb		Lumbricidae	t	so	f	6.9×10^{0}	−0.38	14	0.09	[101]
j Pb		*E. fetida, L. rubellus*	t	so	r	6.2×10^{2}	−0.73	15	0.77	[8,92]
k Pb	Cr, In+	Crustacea, Insecta . . .	a	se	f	3.2×10^{-3}	0.17	293	e	[7]
l Pb	Ar	Araneida, Opiliones+	t	so	f	5.4×10^{1}	−0.51	41	0.52	[101]
m Pb	Di	Diplopoda	t	so	f	1.2×10^{1}	−0.53	6	0.78	[101]
n Pb	In	Coleoptera	t	so	f	1.4×10^{-2}	−0.02	34	0.78	[101]
Geometric (a, n) or arithmic (b,r^2) mean for 1–7:						2.5×10^{1}	−0.47	19	0.31	
8 a Cu		*B. taurus*	t	fo	r	1.1×10^{-1}	0.51	3	0.20	[96]
b Cu	Av, Ma	Aythya, Phalacrocorax, Soricidae+	at	fo	r	7.2×10^{4}	−1.07	16	0.46	[5,8,99]
c Zn	Ma	*B. taurus*	t	fo	r	9.9×10^{5}	−1.11	3	0.67	[96]
d Zn	Av, Ma	Aythya, Phalacrocorax, Soricidae+	at	fo	r	2.0×10^{5}	−1.05	16	0.93	[5,8,99]
e Cd		*Anas platyrhynchos*, Rattus+	t	fo	l	8.9×10^{0}	−0.16	22	0.05	[13,14]
f Cd	Ma	*B. taurus*	t	fo	r	9.8×10^{0}	−0.22	3	0.71	[96]
g Cd	Av, Ma	Aythya, Phalacrocorax, Soricida+	at	fo	r	7.6×10^{0}	−0.28	17	0.24	[5,8,99]
h Hg	Av, Ma	*A. rubripes, B. taurus*	at	fo	l	2.9×10^{1}	−0.79	3	1.00	[13]
i Hg	Ma	*Bos taurus*	t	fo	r	2.9×10^{1}	−1.02	10	0.71	[96,103]
j Hg	Av	*Aythya fuligula, Phalacrocorax carbo*+	a	fo	r	5.5×10^{3}	−0.98	5	0.67	[5,99]
k Pb	Ma	*B. taurus*	t	fo	l	1.0×10^{3}	−0.82	5	0.15	[13]
l Pb		Soricidae	at	fo	r	1.0×10^{12}	−3.19	6	0.33	[8]

[a] Abbreviations: a = aquatic, e = fit by eye, f = field, fo = food, l = lab, r = Rhine–Meuse field, t = terrestrial, se = sediment, so = soil, su = suspended solids, wa = water (converted with Table 1). Regressions 6a + g: $Hg(CH_3)$, 7f: $Pb(CH_n)$, 9: liver or kidney.

[b] Taxon: An(nelida) = worms, Ar(archnida) = spiders, Av(es) = birds, Cr(ustacea) = crustaceans, Di(plopods) = millipeds, In(secta) = insects, Ma(mmalia) = mammals, Mo(llusca) = mollusks, Ph(ycophyta) = algae, Pi(sces) = fish, Tr(acheophyta) = vascular plants, + dominant species.

[c] Crops (converted from exponential regression, original r^2 given).

10 times below that in aquatic species and within the wide terrestrial plant range estimated by the model for different soil–water partition ratios. Accumulation in aquatic mollusks and arthropods generally followed the trend predicted by the model well. Organism–solids concentration ratios for benthic annelids were somewhat higher than expected from the model and equal to or above those for terrestrial annelids, with exception of Cd. Accumulation by terrestrial invertebrates was also within the wide range allowed by the soil–water partition ratios. Concentration ratios for terrestrial beetles tended to be similar to those predicted for aquatic herbivores and below those measured for diplopods and spiders. Regressions for fish were occasionally substantially below those for aquatic mollusks and crustaceans on which they fed.

Differences between substances. Organism–water concentration ratios at comparable exposure levels increased in the sequence Pb ≤ Cd ≤ Zn ≤ Hg for all laboratory species tested (Table 2 and panels 1–7 of Fig. 6). An exception was noted for Zn preceding Cd in mollusks. Accumulation in living matter versus sorption to dead solids fitted into the series Cr ≤ Hg ≤ Ni ≤ Pb ≤ Cd ≤ Cu ≤ Zn for most species. If one of the metals was allowed to change one position, the sequence applied to the other species too. In addition, Cd preceded both Ni and Pb in aquatic macrophytes and benthic annelids of the Rhine–Meuse delta. Occasional observations on other elements (data not shown) suggested that organism–solids concentration ratios of Ag, As, Fe, and Mn may have an intermediate position, whereas accumulation of Se may be higher.

The level of Cu, Zn, and Cd magnification in avian and mammalian livers or kidneys were at least 10 times higher than that of Hg and Pb (8a–g vs 8h–l of Table 2 and panel 8 of Fig. 6). The values measured for small metals (M ≤ 112 g/mol) in herbivores (8a, c, e, and f) were just below (nonessential metal Cd) and at or just above (essential metals Cu, Zn) the average expected from the model. Magnification of Cu, Zn, and Cd by herbivores was higher than that by carnivores (8a > b and c > d and e ≈ f > g), as predicted by the model. Magnification of mercury followed the pattern suggested by the model (8h–j), but levels for Pb were lower than expected for both herbivores and carnivores (8k–l).

Differences between conditions. Accumulation of a metal by a species group as measured in the Rhine–Meuse delta (r in Table 2) was similar to values collected from laboratory or field studies elsewhere (l + f in Table 2) in 19 cases. Accumulation was about a factor of 10 higher in the Rhine–Meuse delta than reported in literature for Cu and Pb in algae, Cu in crustaceans, and Zn in mollusks. The reverse was noted for Cd in terrestrial plants and fish.

One may conclude that metal accumulation in plants and animals was a function of the exposure concentration with an exponent of about −0.5, as expected from the model. The highest and lowest levels were noted for detritivorous annelids

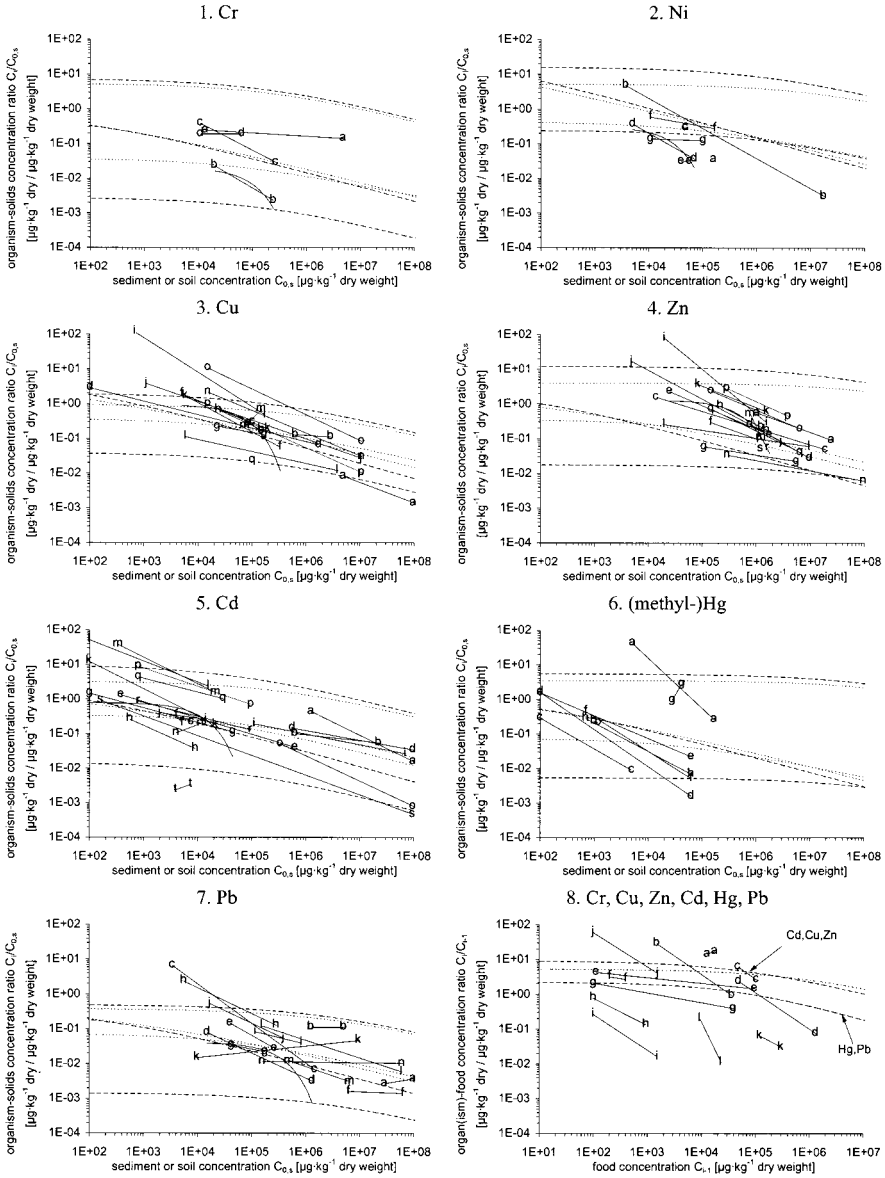


Fig. 6. Organism–solids concentration ratios $C_i/C_{0,s}$ (μg·kg^{-1} dry wt/μg·kg^{-1} dry wt) for plants and cold-blooded animals (panels 1–7) and organ–food concentration ratios C_i/C_{i-1} (μg·kg^{-1} dry wt/μg·kg^{-1} dry wt) for warm-blooded organisms (panel 8) versus exposure concentration $C_{0,s}$ and C_{i-1}. Regressions or geometric averages (solid lines with letters) of laboratory or field measurements (Table 2). Model estimations for producers and herbivores (dashed curves in 1–8), detritivores (dotted curves in 1–7), and carnivores (dotted curves in 8) after aquatic (middle) or terrestrial exposure for low (upper) and high (lower curves) K_{sw}.

and carnivorous fish, respectively. In general, levels in aquatic plants and annelids were higher than in their terrestrial equivalent, as anticipated by the model for high solid–water partition ratios. The accumulation of essential metals, such Cu and Zn, in organisms relative to their sorption at dead solids was almost always higher than those of nonessential metals.

DISCUSSION

Model specification, lab calibration, and field validation

Rate constants for exchange $k_{j,x,in}$ and $k_{j,x,out}$ have been measured for many species and elements (Figs. 2 to 5). Yet most data have been collected for aquatic species. For plants, no studies were found. Organism–solids $C_i/C_{0,s}$ and organism–food C_i/C_{i-1} concentration ratios were found for major taxonomic and ecological groups, especially for the transition metals Cu, Zn, Cd, Hg, and Pb.

The major phenomena specified by the equations were confirmed by the laboratory rate constants used for calibration and the independent lab or field concentration ratios used for validation. Both absorption and elimination rate constants decreased with species weight w, often with an exponent $-\kappa$ in the range of -0.25 to -0.33, well known from ecological allometry [4]. Since both data and model suggested that influx $k_{j,x,in}$ and as well as efflux $k_{j,x,out}$ have about the same weight exponent $-\kappa$, equilibrium concentration ratios were expected to be largely independent of the organism size w. Dividing absorption by elimination regressions for each metal present in both Figure 2 and Figure 4 gave concentration ratios $C_i/C_{0,w}$ of $100/w^{0.04}$, $180/w^{0.03}$, $410/w^{0.05}$, and $6{,}300/w^{0.03}$ (μg·kg^{-1} dry wt/μg·kg^{-1} dry wt) for Co, Zn, Cd, and Hg, respectively. However, intraspecific body residues within one species scaled to size with an exponent of -0.25 to 0, depending on the species and element concerned [3,77]. It indicates that a constant growth dilution as assumed in our model may be to simple

to predict differences between young and old individuals of the same species.

Assimilation efficiencies $p_{1,x}$ of elements depended mainly on food type, as known for food digestibility p_1 itself [4]. The distribution of elements among egested and digested food fractions $K_{e:d}$ as measured or estimated from efficiencies of assimilation $p_{1,x}$ by cold-blooded animals was largely confirmed by magnification ratios C_i/C_{i-1} for warm-blooded species. Rate constants for uptake from water and food were a reciprocal function of the exposure level ($k_{j,x,in} \sim 1/C^{\kappa\rho}$), as partly confirmed by rate constants and strongly supported by accumulation ratios. According to the model, the accumulation ratios for metals decreased at approximately 10^3 $\mu g \cdot kg^{-1}$ dry wt, equivalent to about 10^{-2} $\mu g \cdot L^{-1}$ (Fig. 6). The current parameter setting (Table 1) thus suggests that partial saturation for transition metals will occur at 10^{-2} $\mu g \cdot L^{-1}$, whereas their specific carriers became saturated only at about 100 $\mu g \cdot L^{-1}$ [24].

(In)complete saturation may partly explain why plant–solids ratios were remarkably similar, even among very different soils and sediments. At the same total soil or sediment concentration, levels in pore-water $C_{0,w}$ are a linear function of the solids–water partition ratio K_{sw}. The accumulation in the organism, however, is only approximately a square root function of the pore-water concentration. The same applied to animals in cases where water exchange is dominant. In addition, accumulation in detritivores of various soils and sediments may be similar because they take in elements from both pore water and particles. They take in more elements from water and food at low and high solids–water partition ratio, respectively, possibly arriving at similar body burdens.

Total elimination rate constants ${}^3\Sigma_0 k_{j,x,out}$ have been derived to be $0.002/w^{\kappa}$ (d^{-1}) for plants and cold-blooded animals and $0.01/w^{\kappa}$ (d^{-1}) for warm-blooded animals. On average, production by plants and cold-blooded animals k_2 equaled $0.0006/w^{\kappa}$ (d^{-1}), whereas that of warm-blooded animals was about $0.006/w^{\kappa}$ (d^{-1}) [4,78]. It suggests that, on average, 30 to 60% of the elimination can be attributed to growth dilution. In some cases, efflux may be solely driven by biomass increase, such as for irreversibly bound metals and some species. Macrophytes are considered to loose metals by growth dilution only, whereas depuration in metal-adapted *Chironomus riparius* was close to growth dilution [79]. In fact, a somewhat higher than average growth rate constant may also be responsible for the remarkably similar intercepts observed for different inorganic substances (Figs. 4 and 5). In reality, the origin of the substances in depurations studies will be difficult to determine because the concentration in the test medium may be determined by metals egested by feces, shedded from the skin or adsorbed to particulate material after excretion via gills or urinary organs.

The model can be improved by taking into account variables, such as temperature, assimilation, and ingestion rates, that are known to govern water and biomass fluxes. Unfortunately, empirical studies so far have seldom reported these factors in sufficient detail to allow incorporation into the model.

Differences between metals

With the exception of Hg, laboratory organism–water and field organism–solids concentration ratios followed the same sequence of Pb ≤ Cd ≤ Zn ≤ Hg and Cr ≤ Hg ≤ Ni ≤ Pb ≤ Cd ≤ Cu ≤ Zn, respectively. Differences between metals were only accounted for by the model by different values for solids–water partition ratios and for the distribution over egested and digested fractions $K_{e:d}$. Additional differentiation was not possible because the calibration data set was too small to allow additional subdivision. However, consistent differences noted between accumulation ratios of the data collected for validation may be understood from substantial deviations observed during calibration.

The overestimation of Cr accumulation (see the Validation section; Fig. 6) can be understood from the overestimation of Cr absorption (see the Calibration section; Fig. 2). Elimination data were equally distributed around the expected values. Analogously, the underestimation of Zn concentration ratios can be explained from the overestimation of elimination. In addition, Zn organism–solids concentrations ratios measured for mollusks and crustaceans but not algae were higher than those converted from organism–water concentration ratios (4a > b, g > h, l+m > n in Table 2 and Fig. 6). This indicates that underestimation of Zn accumulation may also be attributed to the use of a high average solids–water partition ratio.

Differences between species

The lowest organism–solids concentration ratios for Cu, Zn, and Cd were noted for fish (see the Validation section; Fig. 6). All rate constants for absorption of these metals by fish were lower than calculated by the model (see the Calibration section; Fig. 2). Elimination of Cu, Zn, and Cd by fish was faster than the average level in 3 of 3, 1 of 12, and 5 of 8 cases. Accumulation of metals was generally highest in annelids, diplopods, and spiders. Of the few rate constants collected for spiders, elimination tended to be slower than on average, whereas absorption did not consistently deviate from the model. For annelids, nearly all influx and efflux measurements were higher than expected.

Concentration ratios for terrestrial species were lower than those for their aquatic equivalents of the same species group (Fig. 6). Since elimination rate constants for land and water species did not differ consistently (Fig. 4), accumulation differences appear to be caused by variability in uptake (conditions).

Whole body concentrations in birds and mammals were lower than those in their food. Both rate constants and equilibrium concentration ratios suggested that metals, with the exception of Hg, do not magnify in food chains. Similar conclusions have been drawn in reviews on radionuclides and metals [22,80].

Differences between species and metals can be only partly explained by differences between trophic levels (producers, herbivores, detritivores, and carnivores) and habitat (aquatic, benthic, and terrestrial). The exceptions noted suggest that physiological differences may be at least equally important. In general, lower concentration ratios coincided with a lower absorption or higher elimination. The reverse held for increased accumulation. The patterns described so far may be attributed to taxonomic differences as well. It will be far more difficult to relate accumulation to taxonomic factors than to ecological factors because the mechanisms are even less well known quantitatively.

SUMMARY

We have specified a model for concentration kinetics of inorganic substances, in particular metals. The model considered influx and efflux to depend on several variables, primarily the exposure concentration and the weight and trophic level

of the species. The ecological parameters for the delay imposed by water, food, and biomass flows have been taken from a previous review on allometric regressions. The water layer resistances have been obtained from a study on organic substances, whereas lipid layer resistances have been calibrated on influx and efflux rate constants in the present study. Calibration data have been collected for many species and substances, but most applied to aquatic organisms, in particular mollusks and fish, and to transition metals, in particular group IIB (Zn, Cd, Hg). Keeping in mind this heterogeneity of data, the following conclusions were drawn.

Rate constants for absorption from water and for elimination decreased with species weight at an exponent of about −0.25, known from ecological allometry. In addition, uptake rate constants probably decreased approximately with the reciprocal square root of the exposure concentration.

About 71 and 30% of the variation in absorption and elimination was explained by the model, respectively. Though elimination of each metal in different species was variable, average efflux levels for metals were similar. Measured and estimated rate constants were repeatedly noted to differ by more than a factor of 5. Most deviations cannot consistently be attributed to specific factors, species, or metal groups. Assimilation efficiencies were highly variable but appeared to depend mainly on the food type. The general differences observed between detritivores, herbivores, and carnivores were attributed to the food digestibility and the distribution of elements between egested and digested fractions. Uptake of nonionic metals and nonmetals from water was much faster than that of ionic metals, but elimination was similar.

Equilibrium accumulation and magnification for metals decreased approximately with the reciprocal square root of the exposure concentration. The level of the organism–solids concentration ratios roughly varied between one and two orders of magnitude, depending on the number of elements and species groups investigated. Despite taxonomic variability, metal concentrations did not increase with increasing trophic levels. Organism–solids concentration ratios for terrestrial species tended to be somewhat lower than those for their aquatic equivalents.

Most patterns described here are unlikely to be artifacts because they were noted for most metals, species, exposure types (water, sediment, suspended solids, soil, food) and conditions (laboratory, field), and parameters (concentration ratios, rate constants).

Note—The kinetic constants in Figures 1 to 4 were obtained from references 104 to 155 and others previously cited.

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Erratum:
p 1427-... Reference 58 has to be deleted, reference 59 in text refers to reference 58 in reference list and so on. Reference i in text refers to i-1 in list.