Modeling the influence of body size on trace element accumulation in the mussel *Mytilus edulis*

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ABSTRACT: We measured assimilation efficiencies (AEs) from ingested algal food, uptake rates from the dissolved phase, and efflux rate constants of 4 trace elements (Cd, Co, Se and Zn) in 3 size classes (1.5, 2.5, and 5.0 cm) of the mussel *Mytilus edulis*. AEs of Se and Zn remained constant among the 3 body sizes. AEs of Cd decreased with increasing body size, whereas AEs of Co increased with body size. The rate constant of metal uptake from the dissolved phase decreased with increasing body size, but the calculated metal absorption efficiencies remained relatively constant or increased slightly in larger mussels. Efflux rate constants were comparable among the 3 body sizes, except for Cd which was lost about 2 times faster in the smaller mussels than in the largest mussels. A bioenergetic-based kinetic model was used to calculate the allometric coefficient (b) of metal accumulation with mussel body size; predicted b values were comparable to field measurements. However, b increased exponentially with the growth rate constant, indicating that no single b value is likely to be observed in nature for a specific metal. The growth rate constant is needed for the model to predict metal concentration and allometry of metal accumulation in mussels, especially for smaller mussels. The relative importance of trace element uptake from the dissolved phase versus particulate ingestion in the overall metal uptake in mussels was relatively independent of mussel body size, primarily because the influx rates from the dissolved phase and from food were comparably related to body size.

KEY WORDS: Allometry · Mussels · Bioaccumulation · Modeling · Cadmium · Cobalt · Selenium · Zinc

INTRODUCTION

Marine mussels, especially *Mytilus edulis*, have been extensively employed as biomonitors of coastal contamination in many parts of the world. Since 1986, the US National Status and Trends (NS&T) Program has annually monitored trace element concentrations in mussels and oysters from coastal waters of the US. Unambiguous interpretation of these monitoring data requires an understanding of the factors underlying the variability in trace element concentration in mussels. Biological factors, such as growth or body size/age, can contribute to variability of metal accumulation (Langston & Spence 1995, Wang & Fisher 1997). Consequently monitoring programs sample mussels of uniform size (typically 5 to 6 cm shell length) in winter to avoid variability due to body size and spawning (Phillips 1980, O'Connor et al. 1994).

Boyden (1974) reviewed the size-dependence of metal concentration in marine bivalves and found that it covers the full range of possibilities, that is, metal concentrations can increase, decrease, or remain constant with body size. Although Boyden (1974, 1977) proposed that the allometric relationships remain rather constant for a given combination of organism and metal, it has been frequently observed that these relationships can in fact vary greatly among locations or seasons. For example, for Cd and Zn in mussels positive (Harris et al. 1979, Lobel & Wright 1982), negative (Phillips 1976, Boyden 1977, Cossa et al. 1980, Borchardt et al. 1988), or no (Phillips 1976, Boyden 1977, Fischer 1983, Popham & d'Auria 1983) correlations of metal concentration in mussels with body size have been reported. Most recently, Riget et al. (1996) measured trace element concentrations in mussels collected from pristine Arctic environments. Both positive

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(Cd) and negative (Se) relationships between element concentration and body size were observed. For other metals (Zn, Cr and Hg), concentrations were relatively independent of body size. The allometric relationship is likely related to the growth rate of mussels, ambient metal concentrations and other environmental conditions, but mechanistic explanations for these patterns have not emerged (Langston & Spence 1995).

Recently, a bioenergetic-based kinetic model has been employed to quantify metal bioavailability and accumulation in marine mussels (Wang et al. 1996, 1997, Wang & Fisher 1997). The model-predicted metal concentrations in mussel tissue were very close (within 2 to 3×) to tissue concentrations independently measured in national monitoring programs, suggesting that the biological and geochemical processes identified in the model can account for metal accumulation in mussels. In addition, with this model, which incorporates first-order physiological processes, it is possible to (1) diagnose processes critical to metal accumulation by performing sensitivity analyses and (2) separate the sources of metal accumulation in aquatic invertebrates (e.g. dissolved uptake vs particulate ingestion) (Wang & Fisher 1997). Central to this model is the measurement of key physiological and geochemical parameters such as metal assimilation efficiency from ingested food particles (AE), metal uptake rate constant from the dissolved phase (k_u) and metal efflux rate constant (k_e) from mussel tissues. While the influences of several abiotic and biotic factors on these physiological processes have been investigated (Wang & Fisher 1997), there is little information concerning the effect of body size on each metal-specific physiological parameter described in the model.

The main objectives of this study were to measure the size-dependence of each metal-specific physiological parameter described in the bioenergetic-based bioaccumulation model, including AE, k_u and k_e. These physiological measurements were then incorporated into the kinetic model to predict the allometric relationship of metal concentration in mussels with body size. Sensitivity analysis was performed to determine the importance of factors influencing the allometry of metal accumulation. The significance of the growth rate constant in the kinetic model was emphasized. Finally, this model was used to separate the relative importance of uptake routes in different size classes of mussels, as such information is critical for setting appropriate water quality criteria.

MATERIALS AND METHODS

Mussels (*Mytilus edulis*) of 3 size classes (1.5, 2.5, and 5.0 cm shell length, SL, or 0.05, 0.15 and 1.0 g tis-

sue dry wt) were collected from Old Field, Long Island Sound, New York, USA, during September and October, 1996 and were acclimated in the laboratory in 10 l at 15°C and 28‰ filtered seawater for about 1 wk prior to experiments. All experiments were conducted at this temperature and salinity. During the acclimation period mussels were continuously fed with the diatom *Thalassiosira pseudonana*.

Assimilation efficiencies of trace elements in mussels. The diatom *Thalassiosira pseudonana* (clone 3H) was radiolabeled with the gamma-emitting radioisotopes ^{109}Cd, ^{57}Co, ^{75}Se and ^{65}Zn, as described in Wang & Fisher (1996a). Radioactivity additions were 148 kBq l^{-1} (corresponding to 10 nM) for ^{109}Cd (in 0.5 N HCl), 111 kBq l^{-1} (corresponding to 6.4 nM) for ^{57}Co (in 0.1 N HCl), 74 kBq l^{-1} (corresponding to 0.9 nM) for ^{75}Se (in distilled water, $Na_2^{75}SeO_3$), and 185 kBq l^{-1} (corresponding to 30 nM) for ^{65}Zn (in 0.1 N HCl). After 4 d growth, the diatom cells had undergone 6 divisions and were considered to be uniformly labeled. These cells were then collected onto 3 μm polycarbonate membranes and resuspended into 50 ml filtered seawater before adding to the feeding beakers.

Five individual mussels of 2.5 and 5.0 cm SL and 10 individual mussels of 1.5 cm SL were each placed into 800 ml of 28‰ filtered seawater. Five batches of radiolabeled diatom cells were then added into each beaker at 5 min intervals, each giving a cell density of 4 to 5 × 10^4 cells ml^{-1}. The amount ingested by each individual mussel corresponded to an ingestion rate of 0.3 to 0.5 mg h^{-1}; at these ingestion rates, assimilation efficiencies are not affected by mussel ingestion activity (Wang et al. 1995). After 25 to 30 min of radioactive feeding, the mussels were rinsed with seawater and analyzed for their radioactivity. Fecal pellets were also collected and found to contain negligible radioactivity, suggesting that the radioactivity measured for whole individual mussels after the 20 min feeding represented the total amount of radioactivity ingested by the mussels. Individual mussels were then placed into separate polypropylene beakers (150 ml seawater) held within a 20 l enclosed recirculating flow-through seawater aquarium, as described in Wang et al. (1995). *Thalassiosira pseudonana* was continuously dosed via a peristaltic pump into the aquarium. There were 5 replicate individuals for 2.5 and 5.0 cm mussels. For 1.5 cm mussels, 2 individual mussels were placed in each beaker and the radioactivity was measured as the composite of the 2 individuals (5 replicate composites). Radioactivity retained in the mussels was measured over a 4 d depuration period. Fecal pellets were collected frequently to minimize desorption of radiotracers from fecal material into the surrounding water. Assimilation efficiencies were determined as the percentage

of initial radioactivity retained in the mussels after 72 h of depuration (mussels complete digestion and assimilation of trace elements within 72 h; Wang et al. 1995).

Influx rates of trace elements from the dissolved phase. Detailed experimental procedures are described in Wang et al. (1996). Briefly, mussels which had been fed continuously with diatom cells were exposed to 0.5, 2, 5, and 20 µg l^{-1} of Cd (in CdCl$_2$), Co (in CoCl$_2$), and Se (in Na$_2$SeO$_3$), and 2, 8, 20, and 100 µg l^{-1} of Zn (in ZnCl$_2$), respectively, for 1 h in 28‰ 0.2 µm-filtered seawater. Radioisotopes of ^{109}Cd, ^{57}Co, ^{75}Se and ^{65}Zn were added into seawater as radiotracers; radioactivity additions were 4.6 kBq l^{-1} (corresponding to 0.3 nM) for ^{109}Cd, 9.2 kBq l^{-1} (corresponding to 0.5 pM) for ^{57}Co, 13.8 kBq l^{-1} (corresponding to 0.2 nM) for ^{75}Se, and 9.2 kBq l^{-1} (corresponding to 1.5 nM) for ^{65}Zn. There were 8 replicate individuals for 2.5 and 5.0 cm SL mussels (4 pairs of 2 individuals, each pair in 500 ml seawater) and 10 replicate individuals for 1.5 cm SL mussels (2 sets of 5 individuals, each set in 1 l seawater). After 1 h exposure, mussels were dissected and radioactivities of soft tissues were measured. The loss of radioactivity in the dissolved phase due to uptake by mussels accounted for <3% for Cd, <1% for Co and Se, and <7% for Zn of the initial radioactivity in the water. In addition, the short-term (1 h) exposure minimized the decline in mussel pumping activity due to the absence of food particles (Wang et al. 1996). The tissues were then dried at 70°C overnight and the dry weights were determined.

Efflux rates of trace elements from mussels. Two groups of mussels (8 individuals of 5.0 cm SL and 8 individuals of 2.5 cm SL plus 13 individuals of 1.5 cm SL) were each placed in 1.5 l filtered seawater and fed with radiolabeled *Thalassiosira pseudonana* cells for 7 d (the diatoms were radiolabeled as described above). Each day, log-phase cells were collected onto polycarbonate membranes and resuspended twice into unlabeled filtered seawater to remove metals (via desorption) bound weakly to cell surfaces, after which they were fed to the mussels for 4 to 6 h. Radiolabeled diatoms were added at 0.5 to 1.0 h intervals into the feeding beakers. The mussels were then returned to the unlabeled seawater and fed with unlabeled diatom cells for another 18 to 20 h. The water for both radiolabeling and non-radiolabeling feeding was replaced each day. After 7 d feeding, mussels were rinsed with filtered seawater and then measured for radioactivity. Three individuals from each size class were dissected to determine the distribution of radiotracers in the shell and soft tissues. The remaining 5 individuals (for 2.5 and 5.0 cm) or 10 individuals (for 1.5 cm, 5 replicate composites of 2 individuals each) were then placed into individual chambers within an enclosed recirculating aquarium, as described above and unlabeled diatom food (*T. pseudonana*) was pumped continuously into the aquarium to provide a daily ration of about 2% of the mussel tissue dry wt (Wang et al. 1997). The dissected empty shells were depurated in the same recirculating system. Each day, the radioactivity remaining in the whole mussel was determined. Water was replaced every week to minimize the build-up of radioisotopes and metabolites in the water. After 28 d of depuration, mussels were dissected and the distribution of radiotracers in the shell and soft tissues was determined.

Clearance rates of mussels. To measure the clearance rates of mussels, 10 individuals of 1.5, 2.5, and 5.0 cm SL were each placed into 2 l (for 5.0 cm) or 1.5 l (for 1.5 and 2.5 cm) filtered seawater within a polypropylene beaker. Five to 10 min after the mussels opened their shell valves and pumped normally, *Thalassiosira pseudonana* was added into each beaker at a concentration of 1.2×10^4 cells ml^{-1}. These cells were collected from a log-phase culture and resuspended into 30 ml filtered seawater (to remove algal metabolites and nutrients which may have affected the feeding activity of mussels; Ward & Targett 1989). The algal suspension in each beaker was homogenized by a magnetic stirrer or by gentle aeration. Immediately after adding the algae and homogenization, an aliquot of 15 ml water sample was taken and the cell density was counted using a Coulter Multisizer. Every 20 min (for 5.0 cm) or 30 min (for 1.5 and 2.5 cm), a 15 ml sample was taken and the cell density was determined. The clearance rate was measured over a 1 to 1.5 h period and then calculated using the following equation (Widdows et al. 1997):

$$CR = Vol \times [\ln(C_1) - \ln(C_2)]/t \qquad (1)$$

where, CR is the clearance rate of mussels (l h^{-1}), C_1 is the cell density (cells ml^{-1}) at time 1, C_2 is the cell density (cells ml^{-1}) at time 2, t is the time interval of measurement ($t_2 - t_1$, in h), and Vol is the volume of water (l). The clearance rate of each individual was finally calculated from the mean of 3 consecutive measurements at 20 or 30 min intervals.

Radioactivity measurements. Radioactivity of the whole mussel was measured non-invasively with a large-well NaI(Tl) gamma detector; radioactivity of water, labeled phytoplankton, the mussel's fecal pellets, and the mussel's soft tissues was determined with a Pharmacia-Wallac LKB NaI(Tl) gamma detector. All measurements were related to appropriate standards and calibrated with both spillover and radioactive decay. The gamma emission of ^{109}Cd was determined at 88 keV, of ^{57}Co at 122 keV, of ^{75}Se at 264 keV, and of ^{65}Zn at 1115 keV. Counting times in all samples were adjusted to yield propagated counting errors <5%.

Kinetic modeling of allometry of trace element accumulation in mussels. According to the bioenergetic-based kinetic model, the metal concentration in mussels under steady-state conditions (C_{ss}, in µg g^{-1}) can be described by the following equation (Wang et al. 1996):

$$C_{ss} = \frac{k_u C_w + AE \times IR \times C_f}{k_e + g} \quad (2)$$

where k_u is the metal uptake rate constant from the dissolved phase (l g^{-1} d^{-1}), C_w is the dissolved metal concentration (µg l^{-1}), AE is the assimilation efficiency from ingested food particles, IR is the ingestion rate of the mussel (g g^{-1} d^{-1}), C_f is the metal concentration in ingested food particles (µg g^{-1}), k_e is the metal efflux rate constant (d^{-1}), and g is the growth rate constant of the mussel (d^{-1}).

If C_f is not known, it can be calculated from:

$$C_f = Kd \times C_w \quad (3)$$

where Kd is the partition coefficient (l g^{-1}) of the metal for suspended particles. Thus Eq. (3) can be rewritten as:

$$C_{ss} = \frac{(k_u + AE \times IR \times C_t) \times C_w}{k_e + g} \quad (4)$$

or

$$BCF = \frac{C_{ss}}{C_w} = \frac{(k_u + AE \times IR \times Kd)}{k_e + g} \quad (5)$$

where C_{ss}/C_w is defined here as the bioconcentration factor (BCF), and is directly related to the metal concentration in the mussel. The coefficient of metal allometry (b) can then be calculated assuming that BCF is a power function of mussel tissue dry weight (W):

$$BCF = aW^b \quad (6)$$

or

$$\log(BCF) = \log(a) + b\log(W) \quad (7)$$

from which b can be calculated as the slope of the log-log relationship between BCF and W. This equation is comparable to the power equation relating metal concentration with body size (Boyden 1974, 1977). A b value >0 indicates that metal accumulation (or metal concentration in mussels) increases with growth and a b value <0 indicates that metal accumulation decreases with a mussel's growth. When the b value is close to 0, metal accumulation is relatively independent of a mussel's growth.
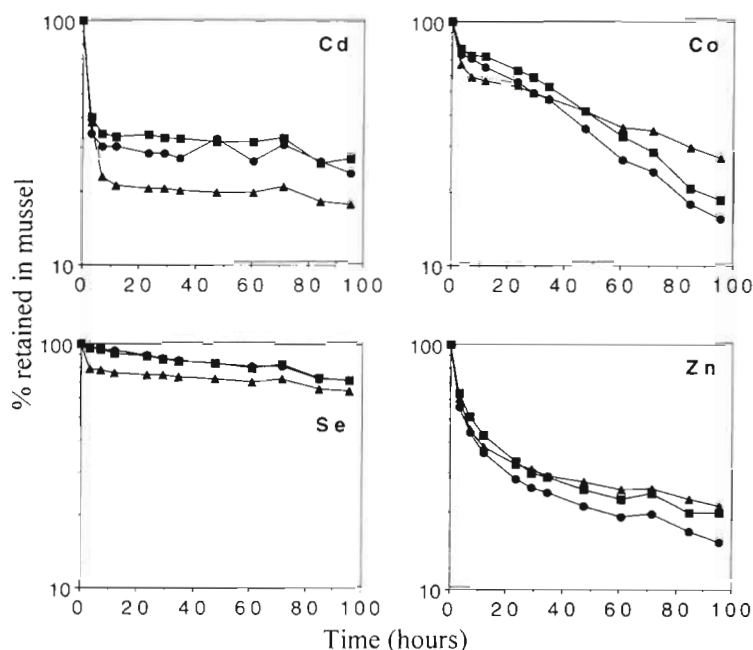

Fig. 1. *Mytilus edulis*. Depuration of radiotracers in marine mussels following pulse-chase feeding of radiolabeled diatoms (*Thalassiosira pseudonana*). Only means are presented. Standard deviations of calculated assimilation efficiencies are shown in Table 1. (●) 1.5 cm mussels, (■) 2.5 cm mussels, (▲) 5.0 cm mussels

RESULTS

Assimilation efficiencies of trace elements in mussels from ingested diatoms

Depuration patterns of radiotracers in mussels during the 96 h depuration period are shown in Fig. 1. Generally, depuration was characterized by a rapid loss within the first day, and then a slower loss between 24 and 96 h. There was very little loss of Cd during the second phase of digestion (24 to 72 h), whereas notable loss was observed for Co. Se and Zn were intermediate between Cd and Co in their depuration during the second phase of digestion (Table 1).

AEs for Se and Zn did not differ significantly among the 3 body sizes (Table 1). AEs for Cd were significantly lower in 5.0 cm mussels than in smaller mussels but for Co AEs increased with body size. Differences in Cd assimilation among the 3 body sizes were mainly attributable to variations in the first phase of digestion (within the first day), whereas differences in Co assimilation were attributable to variations in the second phase of digestion (1 to 3 d). The calculated depuration rate constant during the second phase was 2× lower in 5.0 cm mussels than in smaller mussels. A similar trend of metal assimilation was also observed in mussels feeding on the diatom *Phaeodactylum tricornutum* in which Cd assim-

Table 1. *Mytilus edulis*. Assimilation efficiencies (AE) of trace elements in different size classes of mussels feeding on the diatom *Thalassiosira pseudonana*. The depuration rate constant (k_2) during the second phase of digestion (24 to 72 h) is also presented. k_2 is calculated from the regression: $A = a \times \exp(-k_2 \times t)$, where A is the percentage of radioactivity retained in mussels at time t. Values are means ± 1 SD (n = 5). [A] and [B] indicate that there is a statistically significant difference (p < 0.05) in AE or k_2 between 2 corresponding mussel size treatments

| | AE (%) | | | k_2 (d^{-1}) | | |
	1.5 cm	2.5 cm	5.0 cm	1.5 cm	2.5 cm	5.0 cm
Cd	31 ± 4[A]	33 ± 8	21 ± 6[A]	0.055 ± 0.047	0.076 ± 0.048	0.038 ± 0.023
Co	24 ± 6[A]	29 ± 6	36 ± 4[A]	0.446 ± 0.041[A]	0.441 ± 0.085[B]	0.220 ± 0.088[A,B]
Se	81 ± 5	82 ± 6	72 ± 11	0.075 ± 0.014[A]	0.070 ± 0.007[B]	0.048 ± 0.009[A,B]
Zn	20 ± 7	24 ± 3	26 ± 2	0.189 ± 0.065	0.136 ± 0.030	0.118 ± 0.008

ilation decreased and Co assimilation increased with increasing mussel body size (data not shown).

Influx rates of trace elements from the dissolved phase

The influx rates of metals from the dissolved phase in mussels at different ambient dissolved concentrations are shown in Fig. 2. There was a log-log linear relationship between the influx rate and the dissolved metal concentration (Table 2). The coefficient of this relationship was close to 1, suggesting that dissolved uptake of metals in mussels was dominated by passive
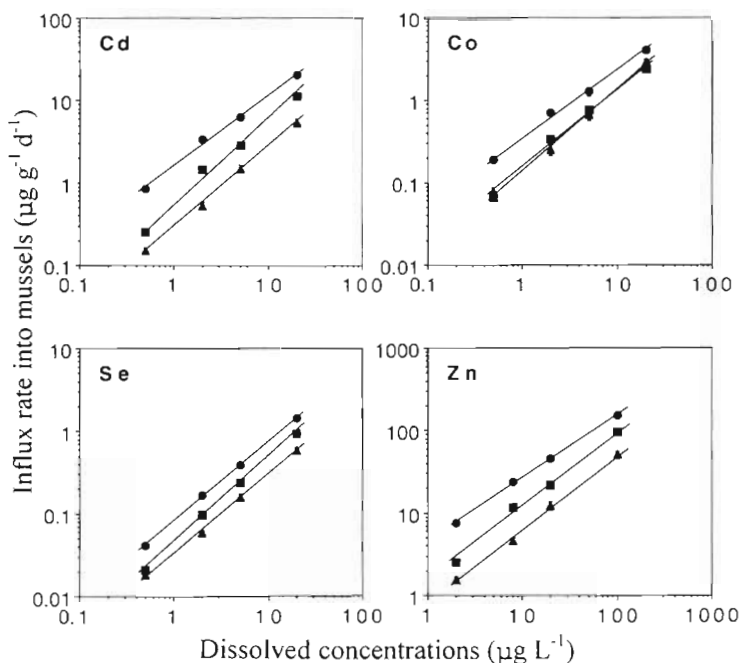

Fig. 2. *Mytilus edulis*. Influx rates of trace elements from the dissolved phase into mussels at different ambient metal concentrations. Values are means ± 1 SD (n = 8); in most cases SD was smaller than the symbols. (●) 1.5 cm mussels, (■) 2.5 cm mussels, (▲) 5.0 cm mussels

and/or facilitated diffusion. For 1.5 cm mussels, the coefficient was <1, being smallest for Zn, indicating that these juvenile mussels might be able to slightly regulate their metal uptake from the dissolved phase. The dissolved uptake rate constants (k_u), calculated from the intercept of the log-log relationship between metal influx rate and dissolved metal concentration (assuming that the coefficient of this relationship was 1), are shown in Table 2. Values of k_u were highest for Zn, followed by Cd > Co > Se. k_u increased with decreasing body size (Fig. 3). The coefficient describing the power function between metal k_u and tissue dry weight was –0.56 for Cd, –0.30 for Co, –0.29 for Se, and –0.57 for Zn. Thus, the uptake of dissolved Cd and Zn was most affected by body size. The absorption efficiency (α_w) was also calculated from the k_u divided by the clearance rate (CR) of mussels (see below) (Table 2). Although notable differences in k_u were measured among the 3 body sizes, α_w generally did not vary greatly with size, the greatest variation being 2- to 3-fold for Co and Se. Given the high variation of CR measured for 2.5 and 5.0 cm mussels, it could be concluded that the α_w for these metals were relatively independent of body size or slightly higher in larger mussels. α_w was highest for Zn, followed by Cd > Co > Se.

Efflux rates of trace elements from mussels

Depuration of metals following 7 d feeding on radiolabeled diatoms generally did not follow a single exponential decay (Fig. 4). Efflux rate constants were calculated (Table 3) from metal depuration curves between 7 and 28 d to minimize possible interference from metal lost due to digestive processes. The calculated efflux rate constants for all metals ranged between 0.01

Table 2. *Mytilus edulis*. Relationships between metal influx rate from the dissolved phase (I_u) and dissolved metal concentration (C_w). Also shown are the estimated dissolved uptake rate constant (k_u) and absorption efficiency from the dissolved phase (α_w) in different size mussels

	Size	Equation	r^2	k_u (l g^{-1} d^{-1})	k_u range (l g^{-1} d^{-1})	α_w (%)
Cd	1.5 cm	$I_u = 1.648[C_w]^{0.850 \pm 0.041}$	0.995	1.648	1.475–1.842	0.287
	2.5 cm	$I_u = 0.578[C_w]^{1.013 \pm 0.071}$	0.990	0.578	0.477–0.700	0.184
	5.0 cm	$I_u = 0.289[C_w]^{0.981 \pm 0.024}$	0.999	0.289	0.271–0.308	0.352
Co	1.5 cm	$I_u = 0.355[C_w]^{0.823 \pm 0.037}$	0.996	0.355	0.321–0.392	0.062
	2.5 cm	$I_u = 0.148[C_w]^{0.972 \pm 0.066}$	0.991	0.148	0.124–0.176	0.047
	5.0 cm	$I_u = 0.142[C_w]^{0.989 \pm 0.042}$	0.996	0.142	0.126–0.159	0.172
Se	1.5 cm	$I_u = 0.082[C_w]^{0.963 \pm 0.013}$	0.999	0.082	0.080–0.085	0.014
	2.5 cm	$I_u = 0.044[C_w]^{1.027 \pm 0.020}$	0.999	0.044	0.042–0.047	0.014
	5.0 cm	$I_u = 0.033[C_w]^{0.960 \pm 0.027}$	0.996	0.033	0.030–0.035	0.040
Zn	1.5 cm	$I_u = 4.639[C_w]^{0.765 \pm 0.015}$	0.999	4.639	4.449–4.639	0.808
	2.5 cm	$I_u = 1.464[C_w]^{0.916 \pm 0.048}$	0.994	1.464	1.276–1.681	0.467
	5.0 cm	$I_u = 0.788[C_w]^{0.904 \pm 0.031}$	0.998	0.788	0.722–0.860	0.960

and 0.03 d^{-1}. No statistically significant difference was detected for Co, Se, and Zn among the 3 body sizes (p > 0.05). Cd was lost at a significantly slower rate (2× less) from 5.0 cm mussels than from 1.5 cm or 2.5 cm mussels (p < 0.01). The percentage of metals in the slowest exchanging compartment for Cd, Se and Zn was comparable among 3 size classes, but was higher for Co in

Table 3. *Mytilus edulis*. Efflux rate constants of trace elements (k_e) in different size classes of mussels. Efflux rate constants were calculated from the slowest exchanging compartments (7 to 28 d), using the equation: $A = a \times \exp(-k_e \times t)$, where A is the percentage of radioactivity retained in mussels at time t. The retention half-times ($tb_{1/2}$) of metals and the percentage of metals in the slowest exchanging compartment are also shown (values are means ± 1 SD, n = 5). [A] and [B] indicate that there was a statistically significant difference (p < 0.05) between 2 treatments (mussel size). Depuration rate constants and retention half-times of metals in dissected shells are also shown (values are means ± 1 SD, n = 2 for 2.5 cm shell, n = 1 for 5.0 cm shell). nd: not determined

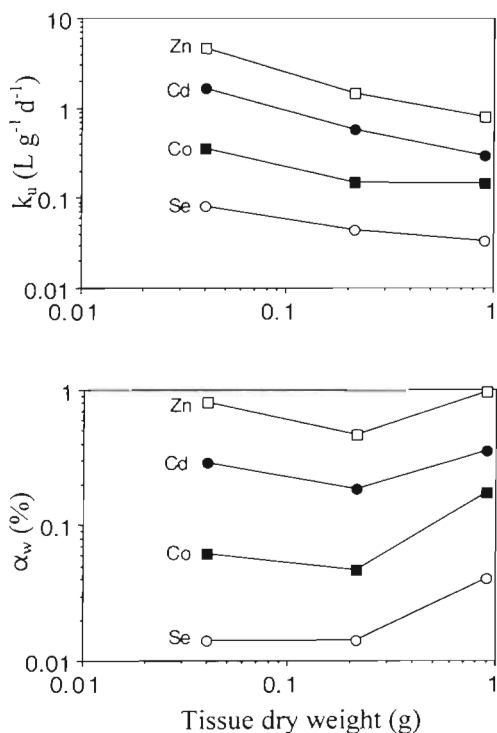|	1.5 cm	2.5 cm	5.0 cm
Efflux from whole mussels			
k_e (d^{-1})			
Cd	0.0345 ± 0.0076[A]	0.0324 ± 0.0046[B]	0.0167 ± 0.0022[A,B]
Co	0.0331 ± 0.0071	0.0326 ± 0.0029	0.0271 ± 0.0081
Se	0.0216 ± 0.0009	0.0200 ± 0.0028	0.0180 ± 0.0020
Zn	0.0123 ± 0.0023	0.0141 ± 0.0031	0.0141 ± 0.0030
$tb_{1/2}$ (d)			
Cd	21.4 ± 6.0[A]	21.8 ± 2.9[B]	42.2 ± 5.2[A,B]
Co	22.1 ± 5.7	21.4 ± 1.9	27.3 ± 5.9
Se	32.1 ± 1.3	35.3 ± 5.3	38.8 ± 4.2
Zn	58.5 ± 12.3	51.3 ± 10.6	52.0 ± 13.0
% in slowest exchanging compartment			
Cd	83.3 ± 10.6	90.1 ± 9.3	84.4 ± 6.8
Co	17.4 ± 5.3[A]	19.1 ± 2.6[B]	41.9 ± 11.8[A,B]
Se	74.3 ± 1.5	74.2 ± 4.4	83.4 ± 3.7
Zn	51.1 ± 2.5	55.9 ± 4.8	58.9 ± 6.4
Depuration from dissected shells			
k_e (d^{-1})			
Co	nd	0.0070 ± 0.0003	0.0049
Se	nd	0.0094 ± 0.0005	0
Zn	nd	0.0171 ± 0.0033	0.0158
$tb_{1/2}$ (d)			
Co	nd	99.4 ± 4.7	142.0
Se	nd	73.6 ± 3.6	∞
Zn	nd	42.2 ± 8.3	43.9

Fig. 3. *Mytilus edulis*. Relationships of estimated uptake rate constants (k_u) and absorption efficiencies (α_w) of trace elements from the dissolved phase with the tissue dry weight of mussels
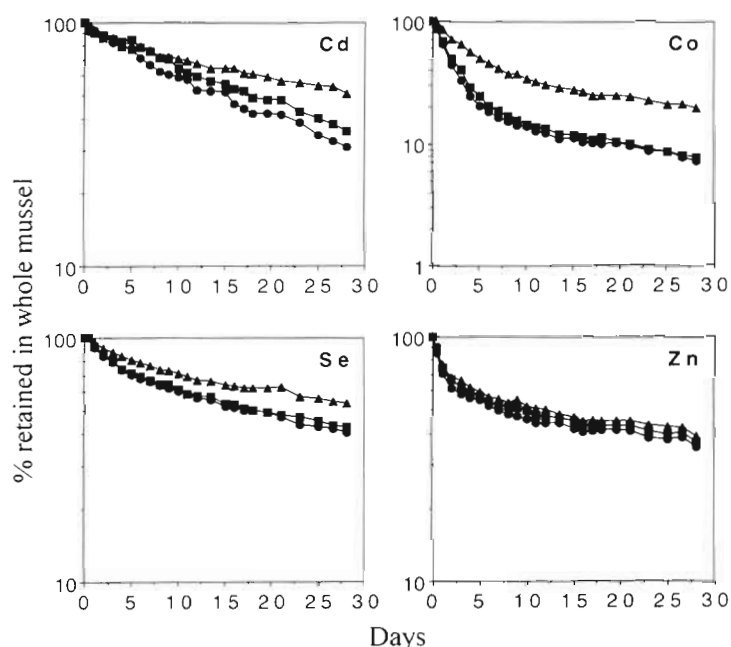
Fig. 4. *Mytilus edulis.* Depuration of radiotracers in whole mussels (soft tissues plus shell) over 28 d following 7 d ingestion of the radiolabeled diatom *Thalassiosira pseudonana.* Values are means (n = 5). (●) 1.5 cm mussels, (■) 2.5 cm mussels, (▲) 5.0 cm mussels
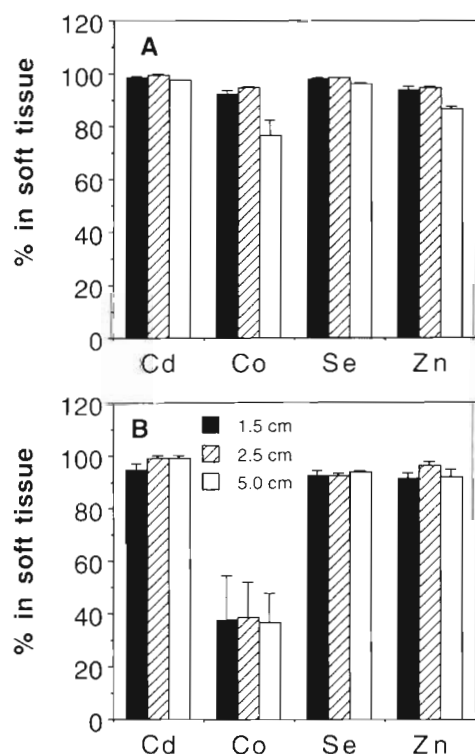

Fig. 5. *Mytilus edulis.* Distribution of radiotracers in the soft tissues of mussels (A) after 7 d ingestion of the radiolabeled diatom *Thalassiosira pseudonana,* means + 1 SD (n = 3), and (B) after 28 d depuration, means + 1 SD (n = 5)

5.0 cm mussels than in smaller mussels (p < 0.01), consistent with the AE measurements described above. During the 4 wk depuration period, shell length of the 1.5 and 2.5 cm groups of mussels increased by 0.28 ± 0.07 cm (n = 10) and 0.26 ± 0.07 cm (n = 5), respectively. Because there was very little difference in the efflux rate constants between these 2 body sizes for all of the trace elements, the variation in metal efflux rate as a result of mussel growth should have little effect on our calculations (see below).

Following 7 d ingestion of radiolabeled diatoms, most metals were distributed in the mussels' soft tissues, while the shells only contained a small fraction [<7%, except for Co (23%) and Zn (13%) in the largest mussels] of total radioactivity ingested by the mussels (Fig. 5). Consequently, efflux rate constants of metals measured for whole mussels (shell plus soft tissues) probably represented the efflux of metals from soft tissues. By the end of 28 d of depuration, most of the Cd, Se and Zn (>92%) was still in the soft tissues, whereas only 40% of Co was in the soft tissues in all 3 body sizes. The loss of metals from dissected shells was characterized by a 1-compartmental (Co, Se) or 2-compartmental (Zn) depuration (data not shown). Depuration of Cd from dissected shells was not determined due to very little Cd associated with the shells. Depuration rate constants calculated between 7 and 28 d were much lower (except for Zn) than the efflux rate constant determined for whole mussels, especially for 5.0 cm mussels (Table 3).

Clearance rates of mussels

The clearance rates of mussels ($l\ h^{-1}$) increased with body size, from $1.28\ l\ h^{-1}$ in 1.5 cm mussels to $4.18\ l\ h^{-1}$ in 5.0 cm mussels (Fig. 6). However, the weight-specific clearance rate decreased with body size, from $23.93\ l\ g^{-1}\ h^{-1}$ in 1.5 cm mussels to $3.42\ l\ g^{-1}\ h^{-1}$ in 5.0 cm mussels. The power relationship between weight-specific clearance rate and tissue dry weight (g) can be described as:

$$CR\,(l\,g^{-1}\,h^{-1}) = 3.65\,W^{-0.622\,\pm\,0.058\,(SE)}\ (n=3;\,r^2=0.991)\ (8)$$

Kinetic modeling of allometry of trace element accumulation in mussels

Three size classes of mussels (1.5, 2.5, and 5.0 cm SL, or 0.05, 0.15, and 1.0 g tissue dry wt) were included in
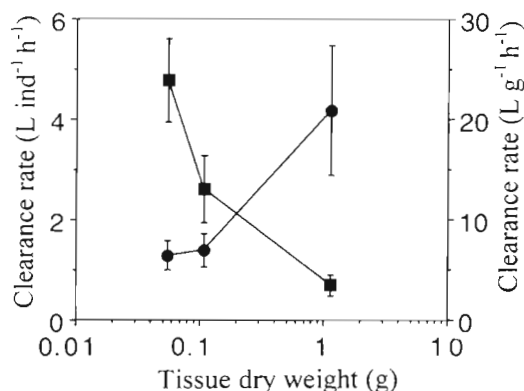
Fig. 6. *Mytilus edulis*. Individual (●) and weight-specific (■) clearance rates of different sizes of mussels. Values are means ± 1 SD (n = 10)

our modeling analysis. Values of k_u, AE, and k_e for each size class were taken from this study (Tables 1–3). The mussel's IR was calculated by:

$$IR = CR \times TSS \tag{9}$$

where TSS is the total suspended solid load (mg l^{-1}). This calculation assumed that mussels had a 100% retention efficiency of particles >3 μm (Bayne & Newell 1983) and that mussel ingestion rate has a linear relationship with food concentration. However, at higher TSS loads, mussels can produce pseudofeces and maintain a maximum ingestion rate. The TSS loads at which mussels produce pseudofeces can vary with body size. The threshold concentration increases from about 2.5 mg l^{-1} in juvenile mussels (1.7 cm SL) to 4.5 mg l^{-1} in large mussels (5 cm SL) (Widdows et al. 1979). Assuming that TSS loads in estuarine waters are >5 to 6 mg l^{-1}, the maximum ingestion activity can be calculated from Eq. (9) as 1.44 g g^{-1} d^{-1} for 1.5 cm mussels, 0.94 g g^{-1} d^{-1} for 2.5 cm mussels (with a threshold concentration of TSS for pseudofeces production of 3 mg l^{-1}), and 0.37 g g^{-1} d^{-1} for 5.0 cm mussels. To make our modeling applicable to natural waters which contain diverse particle assemblages, we have used mean Kd (l kg^{-1}) values for each trace element for suspended marine particles (5000 for Cd, 5000 for Co, 10000 for Se and 20000 for Zn; see discussion in Wang et al. 1996).

There are great uncertainties of the growth rate constant (g) in marine mussels, which can vary greatly with environmental conditions (location, food composition, food quantity, temperature, season; Seed & Richardson 1990). Recently, Clausen & Riisgård (1996) determined a maximum g of 8.0% d^{-1} in mussels transferred in net bags to a fjord system. Generally g is within 1 to 10% d^{-1} in various ecosystems (Jørgensen 1996). In our calculations, we set g for the 1.5 cm mussels and then calculated g for the 2 larger sizes
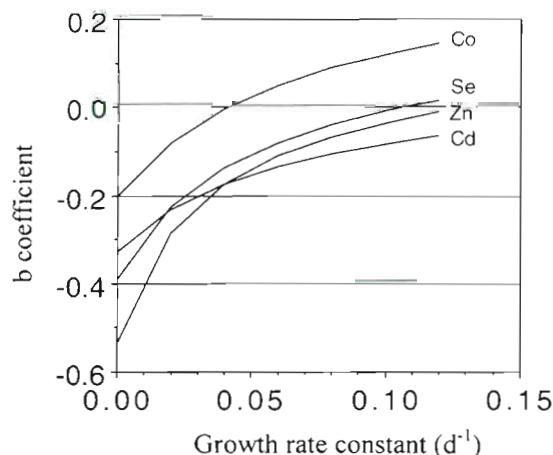

Fig. 7. *Mytilus edulis*. Predicted b values (power function of metal accumulation with body size) of trace elements as a function of the growth rate constant (g) of a juvenile mussel of 50 mg dry wt. See text for mathematical treatment of the calculation

of mussels assuming that it scaled with body size (following a power function) with a coefficient of 0.67 (Bayne & Worrall 1980), thus g values for 2.5 cm and 5.0 cm mussels can be calculated accordingly. This is probably the simplest approach in modeling g in mussels. A range of g values for 1.5 cm mussels (0 to 0.12 d^{-1}) was therefore used to initialize our modeling analysis. The BCF for each body size of mussel was calculated using Eq. (5) (using different g values for each body size) and the allometric coefficient (b) was calculated using Eq. (7).

Fig. 7 shows the calculated b values as a function of g in 1.5 cm mussels. Clearly, allometry of metal accumulation in mussels is sharply influenced by g. Such allometry ranges from positive (e.g. Co at higher g) to negative relationships (e.g. Cd, Se, and Zn). Under most circumstances the model predicts that metal concentrations in mussels decrease with increasing body size or are relatively constant throughout the size range investigated in this study (0.05 to 1.0 g dry wt). An increase in g in juvenile mussels results in an exponential increase in the b value. With a decrease in g (such as brought on by limited food conditions or winter), b values become more conspicuously negative, indicating that metal concentrations in mussels are more dependent on body size. When g is not incorporated into the model ($g = 0$), the b values decrease sharply and become −0.33 for Cd, −0.20 for Co, −0.40 for Se, and −0.54 for Zn, respectively. These values are much lower than the empirical measurements in mussels collected from the field (e.g. −0.1 for Cd, −0.1 to −0.2 for Zn; Boyden 1977), indicating that g must be included in the kinetic model to predict the allometry of metal accumulation.
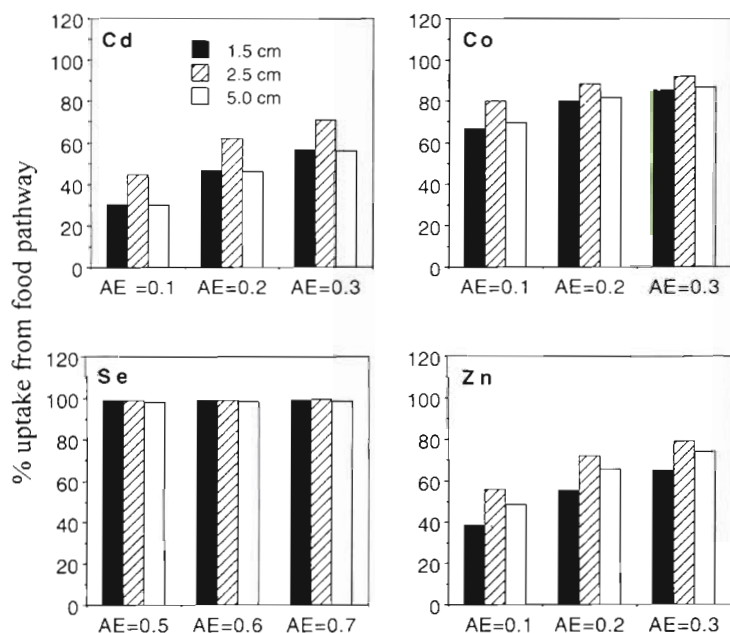
Fig. 8. *Mytilus edulis*. Predicted percentage uptake of trace elements from the food source into different size mussels over a range of metal assimilation efficiencies (AE)

Kinetic separation of the uptake routes of trace elements in mussels

The percentage of trace element uptake from food (R) can be calculated from Eq. (5):

$$R = (AE \times IR \times Kd)/[(k_u) + (AE \times IR \times Kd)] \quad (10)$$

Estimations of the ratio R at different AEs for each trace element are shown in Fig. 8. Clearly, the relative importance of dissolved versus food ingestion in metal uptake is relatively unaffected by mussel body size; for Zn there is a slight increase in the percentage of uptake from food in 5.0 cm mussels. Under the conditions employed in this study, most Se (98%) is predicted to accumulate from the food ingestion pathway. Uptake from food accounts for 30 to 75% of Cd, 67 to 92% of Co, and 40 to 84% of Zn in mussels. The relative importance of a metal's uptake from the dissolved phase is inversely related to its AE.

DISCUSSION

Kinetic modeling of allometry of metal accumulation in mussels

Our model suggests that the growth rate constant should be incorporated into kinetic models to evaluate the effects of body size on metal accumulation in mussels. When g is not considered, the predicted allometric coefficients are significantly lower than b values determined with field samples of varying sizes (Table 4). Previously (Wang et al. 1996), g was ignored in a kinetic model describing metal accumulation in adult *Mytilus edulis*, and the predicted metal concentrations in the mussels were within 2 to 3 times the actual metal concentra-

Table 4. *Mytilus edulis*. Empirical measurements of b values of the power relationship between metal concentration and tissue dry weight in marine mussels from different locations

Metal	Location	Tissue dry wt (g)	b	Source
Cd	Poole Harbour, UK	0.26–1.94	−0.03	Boyden (1977)
	Cornwall, UK	0.04–3.5	−0.05	Boyden (1977)
	Gulf of St. Lawrence, Canada	0.004–0.92	−0.35	Cossa et al. (1980)
	Baie de Bourgneuf, France	0.05–0.2	−0.10	Amiard et al. (1986)
	Eckernförde Bight, Germany	0.04–1.0	−0.07	Fischer (1983)
	Arctic Fjord, Greenland	0.02–4.8	0.16[a]	Riget et al. (1996)
Co	Arctic Fjord, Greenland	0.02–4.8	−0.04[a]	Riget et al. (1996)
Se	Arctic Fjord, Greenland	0.02–4.8	−0.13[a]	Riget et al. (1996)
Zn	Poole Harbour, UK	0.26–1.94	−0.14	Boyden (1977)
	Cornwall, UK	0.04–3.5	−0.19	Boyden (1977)
	Tyre Estuary, UK	0.02–0.7	0.19	Lobel & Wright (1982)
	Gulf of St. Lawrence, Canada	0.004–0.92	−0.14	Cossa et al. (1980)
	British Columbia, Canada	0.02–0.5	0.06	Popham & d'Auria (1983)
	Baie de Bourgneuf, France	0.05–0.24	−0.13	Amiard et al. (1986)
	Arctic Fjord, Greenland	0.02–4.8	0.01[a]	Riget et al. (1996)

[a]b values were calculated from coefficients of metal concentration with mussel shell length (Riget et al. 1996) based on relationships of mussel tissue dry wt and shell length (F. Riget pers. comm.)

tions measured in the NS&T Program. In juvenile mussels which may have higher g values relative to metal efflux rate constants, g should be considered in predicting metal concentrations in mussels. In the NS&T Program, mussels (5 to 6 cm) are sampled during winter (November to March) to avoid the possible effect of spawning on contaminant concentration in mussel tissues. During these periods mussels may also exhibit slow growth (tissue weight) due to low temperature and limited food supply (Bayne & Worrall 1980). Under such circumstances metal concentration in tissues is less likely to be affected by mussel growth.

Different allometric patterns have been found for mussels in the field, depending on season, location, reproductive condition of mussels and other environmental conditions (Table 4). Boyden (1977) distinguished 3 patterns of metal allometry (metal concentration vs tissue weight) in marine molluscs. In some cases b values were not significantly different from 0 (typically ranging from −0.1 to 0.1) and metal concentration in tissues was therefore independent of size. A second pattern showed b values averaging −0.23 (ranging from −0.1 to −0.3), where metal concentration decreased with size. In a few samples b was >0.3, and metal concentration increased with size. All 3 patterns were observed for Cd and Zn. For any allometric pattern, b values for individual metals can vary appreciably between locations and seasons (Langston & Spence 1995). Riget et al. (1996) recorded a very high b value (0.16) for Cd in mussels collected from a Greenland fjord, but found mean b values not different from zero for Zn and possibly Co, indicating that Zn and Co concentrations in mussels were independent of body size.

The mechanisms underlying the allometry of metal concentration in bivalve tissues are not clearly addressed in these field studies. The kinetic model is invaluable in diagnosing processes controlling metal allometry in aquatic organisms. Our study suggests that many biological factors, such as the AE, k_u, k_e, and IR, are responsible for the allometry observed in nature. Specifically, the higher k_u and IR in smaller individuals result in greater metal influx from both the dissolved and food ingestion pathways, and therefore increased influx rates should be accompanied by an increase in growth in smaller mussels. Any changes in these physiological parameters will result in a different outcome of metal allometry.

For Co, positive values of b are predicted when mussels have high growth rates (e.g. g >0.04 d^{-1} for juvenile mussels), primarily as a result of a 1.5- to 2-fold increase in Co AE in larger mussels. Riget et al. (1996) indicated that b values for Co were either negative or close to zero in Arctic mussels. These values are predicted by our model when mussels have a low g, which often may be the case for mussels in Arctic waters. For

Cd, Se, and Zn, the predicted b values range between −0.3 and 0 when g values are between 0.02 and 0.12 d^{-1} for juvenile mussels; these predictions are consistent with most field measurements. Several field studies also measured a positive allometry for Cd and Zn in mussels (Table 4; Lobel & Wright 1982, Riget et al. 1996), which is not predicted by our model. The kinetic model indicates that a positive allometry would occur for Se and Zn only when g is much higher in juvenile mussels (e.g. >0.15 d^{-1}). Our model cannot account for the positive allometry of Cd in slowly growing Arctic mussels (Riget et al. 1996). It is possible that the low temperature in these waters may affect the allometry of AE, k_u, k_e and IR, leading to a positive allometry for Cd. For example, g can probably be ignored in these regions due to the very slow growth of mussels, thus significantly higher efflux in smaller individuals may result in a lower Cd concentration compared to larger individuals.

Given the experimentally determined allometry of metal AE, k_u, k_e, and IR, our model predicts that b values are significantly influenced by g. No single value of b is likely for a specific metal, as indicated by Boyden (1977). The numerous environmental and biological factors (e.g. temperature, salinity, season, light, food supply, water depth, intraspecific competition; Seed & Richardson 1990) affecting mussel growth will also influence metal allometry. For example, sampling mussels at different seasons may cause a change in b values due to variation in g. Seasonal differences in growth rate appear to interact with size-dependent differences in metal uptake, as shown for Cu and Ag in the clam *Macoma balthica* by Strong & Luoma (1981). They found a negative correlation in the summer when the growth of the clams was slowest and a positive correlation during the growing season, observations that are consistent with our model prediction that b increases with g. Similarly, Goede et al. (1993) demonstrated that the decrease of Se concentration in mussels with length was less obvious or absent when the mussels were collected in late spring and summer in the Dutch Wadden Sea when growth rate was highest.

It should be emphasized that all the parameters identified in the kinetic model are not constant under field conditions. Metal AE is a function of food concentrations and food composition (Wang et al. 1995, Wang & Fisher 1996a). Metal k_u can be affected by the biological conditions (e.g. metallothionein induction), the physico-chemical behavior of the metal (e.g. metal speciation), and other environmental conditions (salinity, dissolved organic carbon concentration). Mussel IR values are dependent on food concentration, feeding selectivity and season (Bayne & Newell 1983). Metal Kds in seston can fluctuate by up to an order of magnitude, although the Kds based on weak acid (e.g. 0.5 N

HCl) extraction appear to be rather constant (S. Sañudo-Wilhelmy pers. comm). Variations of these parameters may have a considerable bearing on metal allometry. Furthermore, application of the kinetic model can be complicated by spawning, during which there is negative growth in somatic tissue.

Wang et al. (1996) quantified the relative importance of metal uptake from the dissolved phase and particulate ingestion pathway in mussels. Uptake from each source depended greatly on metal AE and Kd on food particles. The kinetic model is probably the most realistic approach in separating uptake pathways in aquatic organisms because it can incorporate variations in each physiological and geochemical factor affecting metal uptake (Wang & Fisher 1997). Model calculations in this study are comparable to those in Wang et al. (1996), where only AE, Kd, k_u, and IR were shown to influence the proportion of uptake from the dissolved phase and from food. Thus, when the k_u scales in a similar allometry as IR, the relative importance of dissolved uptake remains constant among different-sized animals.

Allometry of metal specific physiological parameters

AEs for each trace element measured in this study were within the range reported previously for mussels feeding on diverse food particles, with highest values for Se followed by Cd > Co > Zn (Wang & Fisher 1996a). The effects of mussel body size on Se and Zn AEs are consistent with observations for C assimilation in mussels (Widdows 1978, Winter 1978). In addition, similar allometric responses to these metals were observed in mussels feeding on the 2 diatom diets (*Thalassiosira pseudonana* and *Phaeodactylum tricornutum*). Because all 4 trace elements were fed simultaneously to the mussels, any differences in the fate of the trace elements cannot be attributed to experimental variability in food or mussels.

The variation in Co AEs with mussel size may have reflected the redox behavior of Co (Lee & Fisher 1993) within the mussel's gut. Specifically, we speculate that the shorter diffusion distance in smaller individuals may result in a more oxygenated gut than in larger individuals. Thus, in smaller mussels more Co would be present as Co^{3+} which can scavenge onto unassimilated particles that are egested as feces. In larger mussels, with a presumably more anoxic gut, Co^{3+} may be reduced to the more soluble Co^{2+} which can then be assimilated by mussels after crossing the gut epithelium. Differences in Co assimilation among the 3 body sizes were mainly associated with the second phase of digestion (intracellular digestion), suggesting that digestion in larger individuals might be oxygen limited.

Differences in Cd assimilation among the 3 body sizes were largely evident during the first few hours of digestion, during which Cd desorption from ingested food particles within the gut probably occurred. The assimilation efficiency of Cd in *Mytilus edulis* is highly dependent on its desorption from ingested diatoms or sediment particles at pH 5.5 (Wang & Fisher 1996b, Gagnon & Fisher 1997), a gut pH typical of marine bivalves (Owen 1974).

Metal uptake in mussels from the dissolved phase was probably dominated by a passive and/or facilitated diffusion (Wang et al. 1996). Because only 3 body sizes were considered in this study, it is difficult to conclude whether allometry of metal uptake from the dissolved phase is controlled by a change in gill surface area. The small sample size also increased the confidence interval of the b coefficients. However, the 2-fold variation of the coefficient describing the power function of k_u and tissue dry weight among the 4 trace elements (-0.3 to -0.57) indicates that gill surface area is not solely responsible for the observed allometry. For Cd and Zn, it is likely that metabolic processes (e.g. clearance rate, protein ligand) control the allometry. Metal transport across the membranes may be dominated by an initial binding with protein ligands within the membrane before being released intracellularly (Wang et al. 1996, Wang & Fisher unpubl.). Newman & Mitz (1988) also found a size-dependence of k_u for Zn in mosquitofish *Gambusia holbrooki* with a simple power function (b increased from -0.32 after 10 d exposure to -0.53 after 350 d exposure), but a clear relationship was not found for Hg uptake (Newman & Doubet 1989). Newman & Heagler (1991) speculated that both metabolic rate and gill surface area:volume ratio in fish may determine these relationships for Zn accumulation. In a study of PCB (polychlorinated biphenyl) accumulation in different-sized mussels, Gilek et al. (1996) similarly showed that uptake rate decreased significantly with body weight with a power function of -0.32. They also showed that the weight-specific gill surface area decreased with body weight with a power function of -0.32, suggesting that variations in the gill surface area were responsible for the different uptake rates displayed by different-sized mussels. If this weight-specific gill surface area to body weight relationship is also applicable to our study, it can be concluded that change in gill surface area can account for the allometry of uptake of dissolved Se and Co (which had a comparable power function of -0.3).

Metal efflux rate constants in mussels measured in this study are comparable to previous measurements (0.01 to 0.03 d^{-1}; Wang et al. 1996). Our study indicates that k_e remained constant or decreased slightly with body size (except for Cd). In a previous study, efflux rate was unaffected by the route (food vs dissolved

uptake) or duration of exposure (Wang et al. 1996). Comparable depuration rates of PCB among different body sizes were also demonstrated in mussels after 24 h feeding (Gilek et al. 1996). However, several other studies have shown that efflux rate constants of both inorganic and organic contaminants were inversely correlated with body size in aquatic animals (Landrum 1988, Newman & Mitz 1988). In mussels, only Cd exhibited a decline in efflux rate with increasing body size. The biochemical mechanisms underlying the variation in Cd release from different-sized mussels remains unknown. Our study also suggests that physiological efflux is not related to the assimilation of metal from food. For example, there was no size-dependence on Co efflux rate, but the larger individuals generally had a higher AE. Smaller mussels generally had a higher AE for Cd but had a higher efflux rate for this metal. In the long-term efflux experiments, most (>83%) of the Cd was partitioned in the slowest exchanging pool, thus the assimilability of Cd is difficult to determine from these 7 d food uptake experiments.

In conclusion, this study demonstrated that major physiological parameters such as AE, k_u, IR, and k_e in mussels are directly dependent on body size. Any changes in these parameters will affect the allometry of metal accumulation in marine mussels. The bioenergetic-based kinetic model can be used to predict the allometry of metal accumulation by incorporating major physiological processes involved in metal bioaccumulation. The growth rate constant is critical for determining metal allometry in mussels. With an increase in mussel growth rate, metal allometry is less dependent on body size.

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