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## Allometry of Metal Bioaccumulation and Toxicity

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### OVERVIEW

Many factors influence bioaccumulation and toxicity of inorganic contaminants. One such factor which varies within and between populations and species is animal size. Despite the prevalence and magnitude of scaling effects on accumulation and toxicity, relatively few studies have adequately quantified these effects or clearly elucidated underlying mechanisms. The purpose of this chapter is to synthesize the present literature on ecotoxicological allometry, to define potential techniques, to identify errors and their remedies, and to suggest future avenues for research. It is not the purpose of this chapter to provide an extensive review of such studies.

## INTRODUCTION

Advances in this area have been made in a variety of disciplines. Considerations of size in toxicokinetics stem from early research on effective dosages of drugs and poisons.<sup>1,2</sup> Allometric considerations for bioaccumulation have a more complex origin than those for toxicological allometry. Allometry studies became common in radiation epidemiology<sup>3,4</sup> and radioecology<sup>5-7</sup> after nuclear weapons appeared at the end of World War II. General results from such studies prompted assessment of radiotracers to measure metabolic processes in the field including the confounding effects of animal size.<sup>8-10</sup> The growing need for heavy metal biomonitoring and relative ease of heavy metal quantification (atomic absorption spectrophotometry) by the mid-1960s fostered the emergence of another large body of literature involving allometry and bioaccumulation.

By the 1970s, the emerging field of heavy metal ecotoxicology was generally characterized by an overabundance of data and a paucity of paradigms. Boyden<sup>11,12</sup> was one of the first individuals in this field to attempt to define a general quantitative model of size effects on bioaccumulation and to formulate falsifiable hypotheses of underlying mechanisms. Boyden's power model was used primarily to redescribe<sup>13</sup> or "fit" a data set to a simplifying model. This allowed a certain degree of description and limited extrapolation. Since the 1970s, many workers have attempted to move the power equation from the "redescription" to "generative representation" status (e.g., a model that describes the data and explains the phenomenon). For example, Boyden's suggestion that linkage to metabolic rate dictates the behavior of one class of power relations has been examined in attempts to increase the confidence in and generality of power models.<sup>14-17</sup> Such desirable model qualities are becoming increasingly important as the field becomes more intently focused on cause/effects models, especially bioenergetically based models.<sup>18-22</sup>

A similar process has been taking place relative to allometry and metal toxicity. In 1975, Anderson and Weber<sup>23</sup> formulated a relationship for the effects of body size on toxicity of poisons by modifying established size-effective dosage models.<sup>1,2</sup> The associated models remain in a state of transition between redescription and generative representation.<sup>24-26</sup>

Concepts and techniques applied in ecotoxicological allometry were borrowed exclusively from those of physiological and morphological allometry. This linkage to classic allometry provided a rapid infusion of techniques and concepts, and continuity among disciplines. Full advantage of this continuity was taken in the last decade with the emergence of bioenergetic models of metal accumulation and toxicity. However, several conceptual and procedural errors from

\* Taylor's classification of models as redescrptions or generative representations is used throughout this chapter. A redescriptive model summarizes observations and permits prediction "on the basis that past patterns might continue." Generative representations contain sufficient detail "to explain the phenomena observed [such that] we can make confident predictions for situations not yet observed."

physiological and morphological allometry were directly transplanted to ecotoxicology. Further, many concepts were overextended in attempts to link physiological or morphological relationships with ecotoxicological ones.

Despite the importance of scaling effects, a general review of ecotoxicological allometry has not been developed to date. The purpose of this chapter is to synthesize the present literature on ecotoxicological allometry, to define potential techniques, to identify significant errors and their remedies, and to suggest future avenues for research. It is not the purpose of this chapter to provide an extensive review of such studies.

## ALLOMETRY

“Although the curve fits well, it does not follow that the formula from which it is derived is the unique description of the relationships . . . and the theory from which it is based consequently ‘true’.”<sup>27</sup>

### Overview

Allometry is the study of size and its consequences.<sup>28</sup> Characters examined are most often morphological,<sup>28-32</sup> physiological,<sup>28,33,34</sup> or biochemical.<sup>35-38</sup> Huxley<sup>39</sup> is largely credited for firmly establishing the use of power equations to describe these relationships. Indeed, Huxley’s Law of Simple Allometry is a central paradigm of allometry. By 1987, more than 750 published allometric power relationships had been described.<sup>40</sup> Despite their clearly empirical nature, an enormous literature has been generated in an attempt to identify the “basic factor”<sup>29</sup> underlying allometric relationships. Numerous hypotheses now exist, but the underpinnings for this law remain ambiguous. For example, Rubner’s Law (metabolic rate is linked to size-dependent change in surface:volume ratio through its influence on heat loss in warm-blooded animals) failed to explain scaling of metabolism because protozoans and cold-blooded metazoans also conform to this relationship. A more recent example involves explanations derived from dimensional analysis<sup>41</sup> which are actively being debated at this time.<sup>42</sup>

### Quantification

The general power function can be written as follows:

$$Y = aX^b \quad (1)^*$$

where  $a$  and  $b$  = constants

$Y$  = size of body part

$X$  = some standard such as body weight

In Huxley’s work,<sup>39</sup> the constant  $b$  was the ratio of growth of  $Y$  to growth of

\* Throughout this chapter, the original constant and variable designations have been changed from those given in the source publications for the sake of uniformity.

X. It has been referred to as the constant specific growth ratio, coefficient of relative growth, or growth-partition coefficient. When physiological variables are scaled to weight using this relationship, the exponent is referred to as the mass exponent. When  $b = 1$ , there is a simple proportionality between Y and X (body size). When  $b < 1$ , Y increases more slowly than X; when  $b > 1$ , Y increases more rapidly than X. The constant a was attributed no biological or general significance by Huxley. It is the value of Y when  $X = 1$ . Consequently, it is often given such interpretations as "the rate of oxygen uptake for unit weight" or "mass independent metabolism" in studies of metabolic rate.<sup>28,40</sup> Schmidt-Nielsen<sup>43</sup> refers to it as the proportionality coefficient. In dimensional analysis of allometric relationships, this mass coefficient is also compared to Meeh's constants for solids expressed as mass and is interpreted in terms of geometric similitude.<sup>40</sup> Gould<sup>28</sup> suggests that vague assignment of biological meaning to this constant should be avoided as, depending on the units employed, it can lead to absurd units, e.g., brain weight of a 1-mm tall human. Biological interpretation of a is also complicated by its partial dependence on the value of b.<sup>28</sup> Gould<sup>28</sup> recommends that, until techniques are formulated that remove the influence of b on a, no biological meaning be attributed to this term.

Techniques for describing the allometric relationships between more than two variables have also been outlined. Adolph<sup>44</sup> suggested that several heterogonic equations (equations expressing extent of disproportionality) can be multiplied provided each contained a common variable. He outlined the following relationships. Given the two allometric relationships,

$$Y = a_1 X^{b_1} \quad (2)$$

$$Z = a_2 X^{b_2} \quad (3)$$

where X = body size

Y and Z = biological variables

Then

$$Y = a_1 (Z/a_2)^{(b_1/b_2)} \quad (4)$$

$$Z = a_2 (Y/a_1)^{(b_2/b_1)} \quad (5)$$

$$X = (Y/a_1)^{(1/b_1)} \quad (6)$$

He further explained that allometric equations [Equation (1)] can be regarded as the algebraic relationship between two separable, simultaneous exponential relationships:

$$Y = ce^{-\beta t} \quad (7)$$

$$X = de^{-\alpha t} \quad (8)$$

With

$$b = \beta/\alpha$$

$$a = c/(d^{\beta/\alpha})$$

Equation (2) can be rewritten in terms of these exponential equations [Equations (7) and (8)] as follows:

$$Y = [c/(d^{\beta/\alpha})]X^{\beta/\alpha} \quad (9)$$

This reexpression of the power relationship could be useful in metal ecotoxicology, a discipline which draws heavily upon exponential relationships from pharmacokinetics and toxicokinetics.

Frequently, biological rates are expressed on a per unit mass basis in allometric studies. The allometric relationship [Equation (1)] for such mass specific rates (e.g., specific metabolic rate) can be expressed with the equation,

$$Y = aX^{(b-1)} \quad (10)$$

where  $Y$  = independent variable expressed on a per unit mass basis  
 $X$ ,  $a$ , and  $b$  = same as defined for Equation (1)

Although the power equation [Equation (1)] dominates allometry, it is an empirical relationship without a clearly defined, underlying mechanism.<sup>28</sup> It is often used when simpler models would fit the data more accurately.<sup>27,28,45</sup> For example, Smith<sup>45</sup> reanalyzed 60 sets of allometric data by fitting them to both a simple linear relationship and a power relationship. Only in 12 cases did the power model provide a better fit (higher correlation coefficient) than the linear model. All 12 exceptions involved interspecific comparisons where the range of sizes was large (broad allometry<sup>45</sup>). He concluded that there was little statistical justification for the general application of a power relationship to allometric data. Heusner<sup>40</sup> suggested that the use of the power equation for intraspecies comparisons with narrow size ranges (narrow allometry<sup>45</sup>) may be particularly unwarranted. Uncritical use of this empirical relationship can compromise data description and subsequent interpretation.<sup>28,44-46</sup>

## Techniques

The same approach has been used to analyze data in an overwhelming majority

of allometric analyses. The power relationship is converted to a linear one by taking the logarithms of  $X$  and  $Y$ . The relationship [Equation (1)] is reexpressed as the following:

$$\text{Log } Y = b\text{Log } X + \text{Log } a \quad (11)$$

Least-squares regression techniques are performed on the  $\text{Log } X$  and  $\text{Log } Y$  variables. The intercept ( $\text{Log } a$ ) and slope ( $b$ ) are used to estimate the mass coefficient and mass exponent, respectively. The correlation coefficient ( $r$ ) and a bilogarithmic plot are used to support the goodness-of-fit for the resulting model.

There are several advantages and disadvantages of this approach. The transformation often enhances the statistical qualities of the model by improving the normality of the data, and it reduces the influence of outliers on the results. However, sole reliance on the correlation coefficient and bilogarithmic plot for assessing fit to the model can be unjustified.<sup>45</sup> The correlation coefficient is influenced by the ranges of  $X$  and  $Y$  as well as the fit of the data to the model.<sup>46</sup> Also, the visual appearance of the bilogarithmic plot is highly distorted.<sup>46</sup>

Several errors are frequently made during these statistical manipulations. The regression model associated with the transformed data includes an error term missing from Equation (11).

$$\text{Log } Y = b\text{Log } X + \text{Log } a + \epsilon \quad (12)$$

where  $\epsilon$  = random error of the model

After regression of the log-transformed variables, the results are usually back-transformed to Equation (1) without consideration of the error term. The model may then be used to make predictions. This can lead to a bias in predicted  $Y$  values (original units) as Equation (12) becomes

$$Y_p = aX^b 10^\epsilon \quad (13)$$

where  $Y_p$  = the predicted value of  $Y$

Unless the data fit the model perfectly ( $\epsilon = 0$ ), predicted values will be biased by [Equation (14)]<sup>47</sup>

$$10^{\sigma_e^2/2} \quad (14)$$

where  $\sigma_e^2$  = error variance of the Log-Log regression model

An estimate of

$$\sigma_e^2 = \sum_{i=1}^N r_i^2 / (N - 2) \quad (15)$$

where  $r_i$  = the  $i$ th regression residual  
 $N$  = the number of data pairs

The reader should refer to Beauchamp and Olson<sup>48</sup> for a more complete discussion of bias estimation.

The median response, not the mean response, is predicted from the model if this bias is ignored.<sup>47</sup> Assuming a normal distribution of residuals from the Log-Log regression, the unbiased, predicted  $Y$  can be estimated to be

$$Y_{\text{unbiased}} = \hat{Y}_p(10^{\sigma_e^2/2}) \quad (16)$$

where  $\hat{Y}$  = biased prediction

If the assumption of a normal distribution of residuals is rejected using statistics such as the Kolmogorov D Statistic ( $N > 50$ ) or Shapiro and Wilk W Statistic ( $N < 50$ ) the above bias correction is inappropriate. Koch and Smillie<sup>47</sup> suggest a "smearing estimate of bias" in such cases.

$$Y_{\text{unbiased}} = \hat{Y}_p(1/N \sum_{i=1}^N 10^{r_i}) \quad (17)$$

Bias correction procedures similar to Equation (16) have been outlined in other publications,<sup>48</sup> including those involving allometry.<sup>49</sup> Unfortunately, there has been a general failure to implement these corrections when necessary. Further, the residual distribution is not examined in most instances. Failure to present the complete regression model, including the model error [Equation (12)], in descriptive studies can compromise later use in predictive modeling. These shortcomings in allometric data analysis have been transferred to studies of scaling in ecotoxicology.

The regression technique described above assumes no measurement error or inherent variation in the independent variable,  $X$ . The technique minimizes the sum of the squares of deviations on the  $Y$ -axis only. In many allometric studies, this is an assumption of convenience, not a conclusion reached after careful examination of the data set.<sup>50</sup> When this assumption is not valid, functional regression techniques are more appropriate than the predictive regression techniques described above. In such techniques, the deviations in the  $Y$  and  $X$  directions are considered by minimizing "the sum of the products of the vertical and horizontal distance of each point from the line."<sup>50</sup> Ricker<sup>50</sup> outlines functional regression techniques relative to allometry with the following set of equations:

exponents for allometric relations should not be considered "anything more than multiple process statistics."

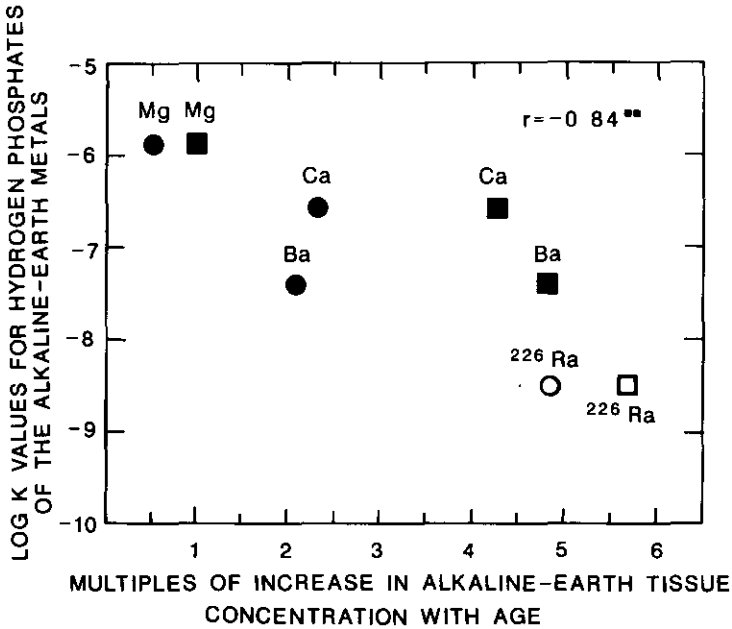
Temporal factors such as age, growth, and duration of exposure clearly influence body burden allometry. Often the relationship between size and age is so complex or difficult to quantify that it is left undefined. However, Williamson<sup>52</sup> was able to use multivariate techniques to identify the opposite effects of age and size on Cd concentrations in the snail, *Cepaea hortensis*. The effective retention of Cd in this snail resulted in a gradual accumulation of Cd with age. Such accumulation of Cd could be facilitated by incorporation into intracellular granules as described by Simkiss<sup>53</sup> (see also, Chapter 3). The biological half-life for this metal was long relative to the life-span of the snail; therefore, the body burden was not in equilibrium with environmental concentrations. The size of individuals had the opposite effect on Cd concentration. This effect was related by Williamson<sup>52</sup> to the higher specific ingestion rate for smaller snails relative to large snails. Hg, another group IIB metal with the potential for high lipid solubility, has shown a similar trend with fish age.<sup>54</sup> The influence of age was assessed indirectly for the last group IIB metal, Zn. Using shell dimension changes with age as a covariate with size, Lobel and Wright<sup>51</sup> demonstrated the importance of considering mussel age and size as covariates in biomonitoring efforts. Assuming different exposure duration for a range of mosquitofish sizes and size-dependent accumulation kinetics, b values were shown to increase slowly from 0.32 (10 days of exposure) to 0.53 (350 days of exposure).<sup>55</sup>

Jeffree's<sup>56</sup> examination of alkaline earth metals in freshwater mussels provides a clear example of one mechanism contributing to age effects on body burden. He examined body burdens of Ca, Ba, Mg, and <sup>226</sup>Ra. Ca and its two analogs (<sup>226</sup>Ra and Ba) increased with age and shell size. These strong relationships suggested that the concentrations in the animals were not in equilibrium with environmental concentrations. The relationship between Mg and age was not as clear as those for the other three elements. He gave the following explanation.

These metals were found associated with intracellular, calcium-magnesium pyrophosphate granules. The stability constants for the respective hydrogen phosphates of these metals were used to indicate their relative insolubilities when in association with granules (Figure 1) and suggest one potential mechanism for the age-dependent behavior of these metals. Mg, the most soluble of the four metals examined, had the poorest correlation with age. The least soluble metals had clearer trends with age, as they were less prone to dissolution from the granules and consequent clearance. As a result, the age-dependencies of Ca, Ba and <sup>226</sup>Ra concentrations were clearer than that of Mg.

Age of an individual is more than an indication of exposure duration. Physiological, cytological, and biochemical changes associated with reproduction or early development can have significant effects on size-dependent body burdens. Changes associated with sexual maturation can produce abrupt slope changes in the bilogarithmic plot of body burden versus size.<sup>57</sup> Seasonal changes associated





**FIGURE 1.** Multiples of increase in tissue concentration with mussel age versus log of stability constants for the hydrogen phosphates of Mg, Ca, Ba, and <sup>226</sup>Ra. The symbols (○ and □) refer to results from different locations. (Modified from Jeffree 1988.<sup>56</sup>)

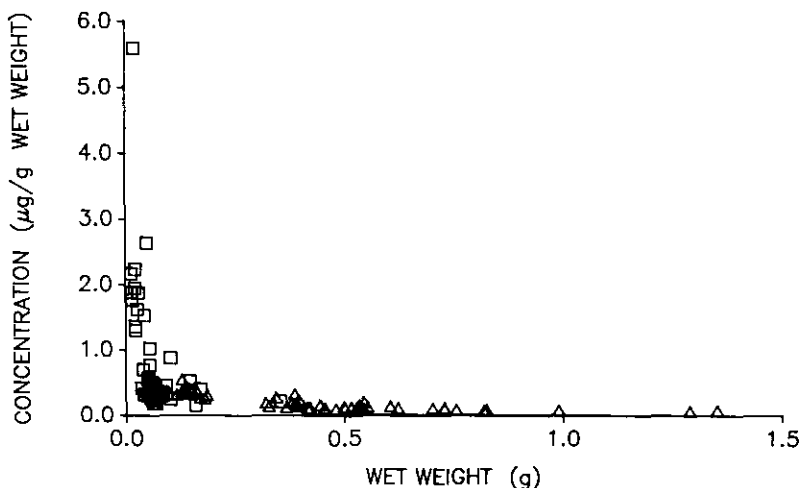
with gametogenesis can also influence size-body burden relationships.<sup>58-60</sup> More subtle effects associated with reproduction are also likely. For example, Cs excretion by women is modified significantly during pregnancy by a shift in aldosterone, a hormone involved in K regulation.<sup>61</sup>

Biochemical changes associated with ontogeny can also influence body burdens. For example, dusky shiners (Figure 2) displayed a decrease in Hg concentration with increasing size. This is contrary to many studies that have demonstrated an increase in Hg concentration with fish size.<sup>18,19,54,62-65</sup> Under the assumption that most of the accumulated Hg was present as methylmercury, this difference can be attributed to biochemical shifts associated to life history phenomena. The lipid content of this species during sampling decreased with fish size as described by a power function with a b value of  $0.62 \pm 0.04$ . The increase in Hg concentration with decreasing fish size was likely linked to the lipid content in fish cohorts as they developed and entered reproductive status. This apparently anomalous relationship for size-dependent Hg concentration could be attributed to lipid dynamics such as those described by Roberts et al.<sup>66</sup> for methylmercury and chlordane bioaccumulation.

Growth dynamics can also be important in the relationship between body burden and size. An apparent dilution will occur if growth is significant within the range of animal sizes examined.<sup>18,60,67</sup> Interactions between toxicant body burden and growth (inhibition<sup>26</sup> or hormesis<sup>68</sup>) have not been examined in studies of body burden allometry in contaminated environments. Feeding efficiency and ingestion rate also vary with size and could have a significant influence on these relationships.<sup>34,69</sup> Such effects of feeding can be confounded by many factors such as food quality.<sup>10,34</sup>

### Surveys and Redescription Models

Table 1 is a summary of regression models for elemental body burdens versus animal size. It is a retabulation of Boyden's<sup>11,12</sup> data (131 regressions from 13 marine molluskan species) which has been supplemented with 15 additional regressions from his papers<sup>11,12</sup> and 69 entries from other studies. As a result, the data remain biased toward marine mollusks. Boyden used *b* values from 131 of the regression models contained in Table 1 to identify different types of body burden relationships. When *b* values for suspect regression models\* were excluded from his consideration, three types of relationships were identified (Figure 13 of Boyden<sup>12</sup>). The two groupings containing most of the relationships had *b* values in the regions of 0.77 (generally between 0.70 and 0.90) and 1.03 (typically between 0.90 and 1.10). A third type contained a small number of the



**FIGURE 2.** Mercury concentration in various-sized dusky shiners (*Notropis cummingae*) from a southeastern U.S. stream.

\* Regression models generated from data sets with an inadequate range in animal size and those with associated significance of greater than  $P = 0.001$  were not included.

**Table 1**  
**Summary of Allometric Body Burden Relationships**

Element	Species	Type <sup>a</sup>	N	Size Range (g)	Conc. Range (µg/g)	Regression				Reference
						a(se)	b(se)	r	v	
As	<i>Helisoma trivolvis</i>	WB-D	50	0.0009-0.0413	48.0-138.0	27.2(0.1)	0.75(0.05)	0.91	0.83	70
	<i>H. trivolvis</i>	WB-D	27	0.0030-0.0199	3.0-6.1	7.2(0.1)	1.11(0.07)	0.96	1.16	70
Cd	<i>Buccinum undatum</i>	WB-D	20	0.06-21.4	8.3-12.7	6.5	1.18(0.14)	0.98	1.21	12
	<i>Cerastoderma edule</i>	WB-D					0.77(0.04)			11
	<i>Chlamys opercularis</i>	WB-D	20	0.2-3.7		7.3	0.96(0.11)	0.97	0.98	12
	<i>Cottus gobio</i>	WB-D	36			0.018	1.40(0.12)			71
	<i>C. gobio</i>	WB-D	20			0.030	1.38(0.08)			71
	<i>Crassostrea gigas</i>	WB-D	39	0.01-4.3		6.3	0.85(0.04)	0.99	0.86	12
	<i>C. gigas</i>	WB-D	22	0.02-4.0		25.9	0.86(0.09)	0.90	0.90	12
	<i>C. gigas</i>	WB-D	30	0.07-11.6		11.8	0.85(0.13)	0.92	0.92	12
	<i>Crepidula fornicata</i>	WB-D	21	0.05-0.78		11.5	1.12(0.17)	0.95	1.18	12
	<i>Donax trunculus</i>	WB-D	29		0.6(0.1) <sup>b</sup>	0.8	1.29(0.14)	0.88	1.47	72
	<i>Gambusia holbrooki</i>	WB-D	94	0.0039-0.298	0.24-1.34	0.52(0.05)	1.01(0.03)	0.96	1.05	76
	<i>H. trivolvis</i>	WB-D	50	0.0009-0.041	21.5-51.4	30.3(0.07)	0.99(0.04)	0.96	1.03	70
	<i>H. trivolvis</i>	WB-D	27	0.0030-0.0199	0.43-0.72	0.78(0.12)	1.09(0.06)	0.96	1.13	70
	<i>Littorina littorea</i>	WB-D	37	0.01-0.7		2.6	0.97(0.11)	0.96	1.00	12
	<i>Mercenaria mercenaria</i>	WB-D					0.77(0.04)			11
	<i>M. mercenaria</i>	WB-D	35	0.02-302		1.4	0.81(0.09)	0.97	0.83	12
	<i>M. edulis</i>	WB-D					1.03(0.02)			11
	<i>M. edulis</i>	WB-D	21	0.26-1.94		3.7	0.97(0.12)	0.97	1.00	12
	<i>M. edulis</i>	WB-D	17	0.18-1.3		5.8	1.05(0.28)	0.93	1.13	12
	<i>M. edulis</i>	WB-D	22	0.08-1.09		64.7	1.02(0.17)	0.94	1.09	12
<i>M. edulis</i>	WB-D	20	0.17-1.03		94.2	1.08(0.30)	0.87	1.24	12	
<i>M. edulis</i>	WB-D	40	0.04-3.5		1.6	0.95(0.06)	0.95	0.99	12	
<i>M. edulis</i>	WB-D	53			1.86	0.9	0.51	1.76	74	
<i>M. edulis</i>	WB-D	126	0.004-0.92		2.49(0.08)	0.65(0.06)			59	
<i>Ostrea edulis</i>	WB-D	38	0.02-2.5		5.2	0.94(0.07)	0.98	0.96	12	
<i>O. edulis</i>	WB-D	24	0.34-6.63		6.4	0.96(0.15)	0.94	1.02	12	
<i>Patella intermedia</i>	WB-D	14	0.021-1.71		4.7	1.35(0.38)	0.92	1.47	12	
<i>P. intermedia</i>	WB-D	16	0.021-1.71		6.3	1.49(0.21)	0.97	1.53	12	
<i>Patella vulgata</i>	WB-D	35	0.02-0.80		401.0	2.05(0.25)	0.96	2.13	12	

	<i>P. vulgata</i>	WB-D	29	0.01-0.80		686.4	1.98(0.28)	0.95	2.08	12
	<i>P. vulgata</i>	WB-D	30	0.01-0.85		716.9	1.96(0.11)	0.92	2.12	12
	<i>P. vulgata</i>	WB-D	34	0.02-1.10		704.2	1.70(0.11)	0.98	1.73	12
	<i>P. vulgata</i>	WB-D	32	0.01-1.10		190.7	1.37(0.09)	0.99	1.39	12
	<i>P. vulgata</i>	WB-D					2.00			11
	<i>Scaphander lignarius</i>	WB-D	20	0.09-3.8		6.8	0.94(0.04)	0.996	0.94	12
	<i>Venerupis decussata</i>	WB-D	30	0.17-2.77		8.9	0.77(0.22)	0.83	0.93	12
	<i>V. decussata</i>	WB-D					0.77(0.04)			11
Co	<i>B. undatum</i>	WB-D	20	0.06-21.4		7.3	0.67(0.05)	0.99	0.68	12
	<i>S. lignarius</i>	WB-D	20	0.09-3.8		26.4	1.07(0.06)	0.99	1.08	12
Cr	<i>H. trivolvis</i>	WB-D	50	0.009-0.041	1.26-7.15	0.80(0.13)	0.638(0.08)	0.77	0.83	70
	<i>H. trivolvis</i>	WB-D	27	0.003-0.0199	0.42-1.11	0.41(0.21)	0.888(0.10)	0.86	1.03	70
<sup>137</sup> Cs	<i>G. holbrooki</i>	WB-W	28	0.12-1.20	(0.80-3.37) <sup>c</sup>	0.39(0.15)	0.96(0.12)	0.85	1.13	67
	<i>G. holbrooki</i>	WB-W	55	0.15-0.96	(0.90-2.98) <sup>c</sup>	0.35(0.09)	0.88(0.08)	0.85	1.04	67
Cu	<i>Acanthopagrus butcheri</i>	WM-W	88	4.3-799.0		1.750	0.92			75
	<i>Aldrichetta forsteri</i>	WM-W	79	7.8-385.0		2.377	0.88			75
	<i>Amniataba caudavittatus</i>	WM-W	96	4.0-319.9		2.506	0.89			75
	<i>B. undatum</i>	WB-D	20	0.06-21.4	118-187	122.6	1.10(0.22)	0.94	1.17	11
	<i>C. edule</i>						0.77(0.04)			12
	<i>C. opercularis</i>	WB-D	20	0.02-3.7		35.0	0.96(0.10)	0.99	0.97	12
	<i>C. gigas</i>	WB-D	39	0.01-4.3	447.4-809.6	446.4	0.82(0.04)	0.99	0.83	12
	<i>C. gigas</i>	WB-D	22	0.02-4.0		260.6	0.80(0.13)	0.94	0.85	12
	<i>C. fornicata</i>	WB-D	21	0.05-0.73		198.5	1.13(0.23)	0.93	1.22	12
	<i>D. trunculus</i>	WB-D	33		11.8(1.5) <sup>b</sup>	8.8	0.83(0.09)	0.86	0.95	72
	<i>G. holbrooki</i>	WB-D	94	0.0039-0.298	4.3-21.6	11.26(0.04)	1.04(0.03)	0.97	1.07	76
	<i>H. trivolvis</i>	WB-D	50	0.0009-0.041	45-98	55.11(0.07)	0.95(0.04)	0.93	1.02	70
	<i>H. trivolvis</i>	WB-D	27	0.003-0.0199	7-16	7.02(0.18)	0.92(0.09)	0.90	1.02	70
	<i>L. littorea</i>	WB-D	37	0.01-0.7		642.2	1.07(0.20)	0.97	1.10	12
	<i>M. mercenaria</i>						0.77(0.04)			11
	<i>M. mercenaria</i>	WB-D	35	0.02-3.02		23.4	0.79(0.14)	0.94	0.89	12
	<i>Mugil cephalus</i>	WM-W	163	2.4-832.0		10.26	0.571			75
	<i>M. edulis</i>	WB-W	50		0.96-1.45		0.80			73
	<i>M. edulis</i>	WB-D	21	0.26-1.94		7.3	0.80(0.21)	0.90	0.89	12
	<i>M. edulis</i>	WB-D	17	0.18-1.3		6.9	0.77(0.19)	0.93	0.82	12
	<i>M. edulis</i>	WB-D	22	0.08-1.09		11.2	0.81(0.05)	0.99	0.82	12
	<i>M. edulis</i>	WB-D	20	0.17-1.03		12.7	0.83(0.22)	0.88	0.94	12

**Table 1 (continued)**  
**Summary of Allometric Body Burden Relationships**

Element	Species	Type*	N	Size Range (g)	Conc. Range ( $\mu\text{g/g}$ )	Regression				Reference
						a(se)	b(se)	r	v	
Fe	<i>M. edulis</i>		96				0.77(0.04)			11
	<i>M. edulis</i>	WB-D				14.95	0.89	0.65	1.37	74
	<i>M. edulis</i>	WB-W	119	0.004-0.92		3.69(0.04)	0.86(0.03)			59
	<i>Nematalosa vlaminghi</i>	WM-W	160	4.3-449.1		3.66	0.812			75
	<i>O. edulis</i>	WB-D	38	0.02-2.5	405.5-423.0	391.9	1.05(0.09)	0.97	1.08	12
	<i>P. intermedia</i>						0.77(0.04)			11
	<i>P. intermedia</i>	WB-D	14	0.02-1.71		19.2	0.81(0.11)	0.99	0.82	12
	<i>P. intermedia</i>	WB-D	16	0.02-1.71		19.9	0.73(0.10)	0.97	0.75	12
	<i>P. vulgata</i>	WB-D	35	0.02-0.80		26.6	0.81(0.10)	0.94	0.96	12
	<i>P. vulgata</i>	WB-D	29	0.01-0.80		31.2	0.79(0.06)	0.98	0.81	12
	<i>P. vulgata</i>	WB-D	30	0.01-0.85		36.9	0.80(0.12)	0.99	0.81	12
	<i>P. vulgata</i>	WB-D	34	0.02-1.10		24.0	0.70(0.12)	0.89	0.78	12
	<i>P. vulgata</i>	WB-D	32	0.01-1.10		25.4	0.76(0.07)	0.97	0.79	12
	<i>P. vulgata</i>						0.77(0.04)			11
	<i>Pecten maximus</i>	WB-D	37	0.16-8.30		22.3	0.65(0.10)	0.99	0.66	12
	<i>S. lignarius</i>	WB-D	20	0.09-3.80		44.5	0.98(0.15)	0.99	0.99	12
	<i>V. decussata</i>	WB-D	30	0.17-2.77		11.7	0.76(0.13)	0.89	0.85	12
	<i>A. butcheri</i>	WM-W	88	4.30-799.0		23.3	0.82			75
	<i>A. forsteri</i>	WM-W	79	7.80-385.0		29.1	0.84			75
	<i>A. caudavittatus</i>	WM-W	96	4.00-319.9		20.4	0.99			75
	<i>B. undatum</i>	WB-D	20	0.06-21.4		65.2	1.09(0.11)	0.98	1.00	12
	<i>C. edule</i>	WB-D					1.03(0.02)			11
	<i>C. gigas</i>	WB-D	39	0.01-4.3		236.5	0.70(0.12)	0.91	0.77	12
	<i>C. gigas</i>	WB-D	22	0.02-4.0		313.0	0.80(0.04)	0.99	0.81	12
	<i>C. gigas</i>	WB-D	30	0.70-11.6		365.3	0.80(0.05)	0.98	0.82	12
	<i>D. trunculus</i>	WB-D	33		663(146) <sup>e</sup>	377.0	0.64(0.14)	0.63	1.02	72
	<i>G. holbrooki</i>	WB-D	94	0.0039-0.298	10.8-155.6	40.2(0.06)	0.90(0.04)	0.93	0.97	76
	<i>H. trivolvris</i>	WB-D	50	0.0009-0.041	1956-3875	2035.2(0.06)	0.92(0.03)	0.97	0.95	70
<i>H. trivolvris</i>	WB-D	27	0.0030-0.019	756-2103	3031.4(0.17)	1.22(0.09)	0.94	1.29	70	
<i>L. littorea</i>	WB-D	37	0.01-0.7		364.3	0.74(0.20)	0.85	0.87	12	
<i>M. mercenaria</i>	WB-D	35	0.02-3.02		108.7	0.77(0.18)	0.95	0.81	12	

	<i>M. mercenaria</i>	WB-D				0.77(0.04)				11
	<i>M. cephalus</i>	WM-W	163	2.4-832.0		83.4	0.68			75
	<i>M. edulis</i>	WB-D	122	0.004-0.92		5.57(0.07)	0.65(0.06)			59
	<i>M. edulis</i>	WB-D					0.77(0.04)			11
	<i>M. edulis</i>	WB-D	21	0.26-1.94		91.1	0.69(0.09)	0.96	0.72	12
	<i>M. edulis</i>	WB-D	22	0.08-1.09		152.0	0.73(0.16)	0.90	0.81	12
	<i>M. edulis</i>	WB-D	20	0.17-1.03		228.1	0.80(0.35)	0.80	1.00	12
	<i>M. edulis</i>	WB-D	40	0.04-3.5		201.7	0.77(0.06)	0.96	0.80	12
	<i>N. viaminghi</i>	WM-W	160	4.3-449.1		67.5	0.75			75
	<i>O. edulis</i>	WB-D	38	0.02-2.5		223.3	0.85(0.07)	0.97	0.87	12
	<i>O. edulis</i>	WB-D	24	0.34-6.63		216.0	0.81(0.12)	0.95	0.85	12
	<i>P. intermedia</i>	WB-D	14	0.02-1.71		1195.9	0.76(0.04)	0.99	0.76	12
	<i>P. intermedia</i>	WB-D	16	0.02-1.71		1504.2	0.70(0.11)	0.97	0.72	12
	<i>P. vulgata</i>	WB-D	30	0.01-0.85		2594.2	0.68(0.19)	0.93	0.73	12
	<i>P. vulgata</i>	WB-D	34	0.02-1.10		1259.5	0.83(0.17)	0.90	0.92	12
	<i>P. vulgata</i>	WB-D	32	0.01-1.10		1368.0	0.74(0.07)	0.97	0.76	12
	<i>V. decussata</i>	WB-D					1.03(0.02)			11
	<i>V. decussata</i>	WB-D	30	0.17-2.77		367.9	1.03(0.31)	0.85	1.21	12
Mn	<i>A. butcheri</i>	WM-W	88		4.3-799	6.84	0.67			75
	<i>A. forsteri</i>	WM-W	79		7.8-385	2.60	0.71			75
	<i>A. caudavittatus</i>	WM-W	96		4.0-319.9	8.70	0.58			75
	<i>Arenicola marina</i>	WB-D			2.5-10		0.61			77
	<i>B. undatum</i>	WB-D	20	0.06-21.4		6.0	0.78(0.12)	0.93	0.84	12
	<i>C. gigas</i>	WB-D	39	0.01-4.3		33.0	1.00(0.11)	0.95	1.05	12
	<i>C. gigas</i>	WB-D	22	0.02-4.0		22.2	1.06(0.13)	0.97	1.10	12
	<i>C. gigas</i>	WB-D	30	0.07-11.6		16.9	1.05(0.20)	0.91	1.15	12
	<i>C. fornicata</i>	WB-D	21	0.05-0.78		22.6	0.79(0.29)	0.79	1.00	12
	<i>D. trunculus</i>	WB-D	18		12.4(2.0) <sup>p</sup>	6.2	0.56(0.14)	0.70	0.80	72
	<i>G. holbrooki</i>	WB-D	94	0.0039-0.2980	8.8-43.9	34.31	1.12(0.02)	0.99	1.13	76
	<i>H. trivolvis</i>	WB-D	50	0.0009-0.0413	65-276	60.85(0.11)	0.75(0.06)	0.86	0.87	70
	<i>H. trivolvis</i>	WB-D	27	0.0030-0.0199	131-501	202.89(0.31)	0.94(0.15)	0.77	1.21	70
	<i>L. littorea</i>	WB-D	37	0.01-0.7		34.1	0.61(0.18)	0.83	0.73	12
	<i>M. cephalus</i>	WM-W	163	2.4-832.0		17.42	0.45			75
	<i>M. edulis</i>	WB-D	119	0.004-0.92		3.77(0.06)	0.70(0.05)			59
	<i>M. edulis</i>	WB-D	22	0.08-1.09		4.5	0.80(0.26)	0.82	0.82	12
	<i>M. edulis</i>	WB-D	17	0.18-1.3		6.9	0.77(0.35)	0.81	0.95	12

**Table 1 (continued)**  
**Summary of Allometric Body Burden Relationships**

Element	Species	Type*	N	Size Range (g)	Conc. Range ( $\mu\text{g/g}$ )	Regression				Reference
						a(se)	b(se)	r	v	
Ni	<i>M. edulis</i>	WB-D	40	0.04-3.5		5.4	0.73(0.17)	0.91	0.80	12
	<i>N. vlaminghi</i>	WM-W	160	4.3-449.1		11.54	0.74			75
	<i>O. edulis</i>	WB-D	24	0.34-6.63		10.5	0.95(0.13)	0.95	1.00	12
	<i>O. edulis</i>	WB-D	38	0.02-2.5		17.9	1.04(0.14)	0.93	1.12	12
	<i>P. maximus</i>	WB-D	37	0.16-8.3		24.1	0.87(0.11)	0.93	0.93	12
	<i>S. lignarius</i>	WB-D	20	0.09-3.8		7.9	1.19(0.11)	0.98	1.21	12
	<i>B. undatum</i>	WB-D	20	0.06-21.4		5.6	0.68(0.07)	0.98	0.69	12
	<i>C. edule</i>	WB-D					1.03(0.02)			11
	<i>C. opercularis</i>	WB-D	20	0.2-3.7		5.5	0.78(0.11)	0.97	0.80	12
	<i>C. gigas</i>	WB-D	30	0.07-11.6		5.4	0.72(0.07)	0.97	0.75	12
	<i>C. fornicata</i>	WB-D	21	0.05-0.73		11.5	1.04(0.22)	0.92	1.13	12
	<i>M. mercenaria</i>	WB-D	35	0.02-3.02		9.4	1.05(0.20)	0.93	1.13	12
	<i>M. mercenaria</i>	WB-D					1.03(0.02)			11
	<i>M. edulis</i>	WB-D					1.03(0.02)			11
	<i>M. edulis</i>	WB-D	21	0.26-1.94		5.3	0.67(0.12)	0.83	0.81	12
	<i>M. edulis</i>	WB-D	17	0.18-1.3		7.6	0.75(0.26)	0.88	0.85	12
	<i>M. edulis</i>	WB-D	22	0.08-1.09		11.3	0.76(0.15)	0.92	0.82	12
	<i>M. edulis</i>	WB-D	40	0.04-3.5		3.5	0.75(0.25)	0.73	1.02	12
	<i>M. edulis</i>	WB-D	118	0.04-0.92		3.12(0.05)	0.73(0.04)			59
	<i>O. edulis</i>	WB-D	38	0.02-2.5		6.0	0.63(0.10)	0.90	0.70	12
<i>O. edulis</i>	WB-D	24	0.34-6.63		6.1	0.67(0.11)	0.94	0.71	12	
<i>S. lignarius</i>	WB-D	20	0.09-3.8		54.0	1.00(0.11)	0.99	1.00	12	
<i>V. decussata</i>	WB-D	30	0.02-3.02		22.5	1.05(0.20)	0.94	1.12	12	
<i>V. decussata</i>						1.03(0.02)			11	
Pb	<i>A. marina</i>	WB-D			10-40		0.74			77
	<i>B. undatum</i>	WB-D	20	0.06-21.4		9.1	0.71(0.09)	0.93	0.76	12
	<i>Campeloma decisum</i>	WB-D	57	0.0046-0.278		2.21	0.75	0.90	0.83	78
	<i>C. edule</i>	WB-D					0.77(0.04)			11
	<i>C. opercularis</i>	WB-D	20	0.2-3.7		32.1	0.98(0.10)	0.99	0.99	12
	<i>C. gobio</i>		36			0.00008	1.43(0.13)			71
	<i>C. gigas</i>	WB-D	22	0.02-4.0		20.7	0.75(0.10)	0.93	0.80	12

	<i>C. gigas</i>	WB-D	30	0.07-11.6		9.1	0.78(0.08)	0.97	0.81	12
	<i>C. fornicata</i>	WB-D	21	0.05-0.73		11.4	1.00(0.17)	0.94	1.06	12
	<i>L. littorea</i>	WB-D	37	0.01-0.79		6.5	0.73(0.18)	0.84	0.87	12
	<i>M. mercenaria</i>	WB-D					1.03(0.02)			11
	<i>M. mercenaria</i>	WB-D	35	0.02-3.02		7.8	1.01(0.18)	0.93	1.09	12
	<i>M. edulis</i>	WB-D					0.77(0.04)			11
	<i>M. edulis</i>	WB-D	22	0.08-1.09		19.0	0.83(0.15)	0.93	0.89	12
	<i>M. edulis</i>	WB-D	40	0.04-3.5		14.4	0.72(0.13)	0.88	0.81	12
	<i>M. edulis</i>	WB-D	88			25.14	0.73	0.57	1.28	74
	<i>P. intermedia</i>	WB-D	16	0.02-1.71		9.6	0.73(0.21)	0.93	0.80	12
	<i>P. intermedia</i>	WB-D					0.77(0.04)			11
	<i>P. vulgata</i>	WB-D					0.77(0.04)			11
	<i>P. vulgata</i>	WB-D	35	0.02-0.80		20.4	0.79(0.15)	0.90	0.88	12
	<i>P. vulgata</i>	WB-D	29	0.01-0.80		15.9	0.74(0.17)	0.83	0.89	12
	<i>P. vulgata</i>	WB-D	30	0.01-0.85		14.4	0.67(0.16)	0.87	0.77	12
	<i>P. maximus</i>	WB-D	37	0.15-8.3		13.2	0.68(0.06)	0.99	0.69	12
	<i>Physa integra</i>	WB-D	16	0.0007-0.0070		46.7	0.97	0.92	1.05	78
	<i>O. edulis</i>	WB-D	38	0.02-2.5		6.2	0.65(0.11)	0.90	0.72	12
	<i>O. edulis</i>	WB-D	24	0.34-6.63		7.8	0.76(0.12)	0.94	0.81	12
	<i>S. lignarius</i>	WB-D	20	0.09-3.8		44.5	0.97(0.03)	0.99	0.97	12
	<i>V. decussata</i>	WB-D	30	0.17-2.77		7.8	0.81(0.14)	0.93	0.87	12
	<i>V. decussata</i>						0.77(0.04)			11
Zn	<i>A. butcheri</i>	WM-W	88	4.3-799.05		46.45	0.86			75
	<i>A. forsteri</i>	WM-W	79	7.8-385.0		27.93	0.89			75
	<i>A. caudavittatus</i>	WM-W	96	4.0-319.9		61.80	0.79			75
	<i>A. marina</i>	WB-D			40-320		0.72			77
	<i>B. undatum</i>	WB-D	20	0.66-21.4	450-1040	508.4	1.20(0.10)	0.97	1.23	12
	<i>C. edule</i>	WB-D					0.77(0.04)			11
	<i>C. opercularis</i>	WB-D	20	0.2-3.7		980.4	0.97(0.17)	0.96	1.01	12
	<i>C. gigas</i>	WB-D	39	0.01-4.3		4293.4	0.95(0.03)	0.99	0.95	12
	<i>C. gigas</i>	WB-D	22	0.02-4.0		2570.4	1.0(0.10)	0.98	1.03	12
	<i>C. fornicata</i>	WB-D	21	0.05-0.78		81.9	0.94(0.18)	0.94	1.00	12
	<i>D. trunculus</i>	WB-D	33			68.0	0.74(0.09)	0.82	0.90	72
	<i>G. holbrooki</i>	WB-D	94	0.0039-0.2980	165-594	203.9(0.03)	0.899(0.02)	0.97	0.93	76
	<i>H. trivolvis</i>	WB-D	50	0.0009-0.0413	137-223	154.1(0.04)	0.97(0.02)	0.98	0.98	70
	<i>H. trivolvis</i>	WB-D	27	0.0030-0.0199	57-105	77.7(0.14)	1.008(0.07)	0.95	1.06	70



**Table 1 (continued)**  
**Summary of Allometric Body Burden Relationships**

Element	Species	Type <sup>a</sup>	N	Size Range (g)	Conc. Range ( $\mu\text{g/g}$ )	Regression				Reference
						a(se)	b(se)	r	v	
	<i>L. littorea</i>	WB-D	37	0.01-0.7		185.0	0.75(0.08)	0.97	0.77	12
	<i>M. mercenaria</i>	WB-D	35	0.02-3.02		177.3	1.04(0.16)	0.99	1.05	12
	<i>M. mercenaria</i>	WB-D					1.03(0.02)			11
	<i>M. cephalus</i>	WM-W	163	2.4-832.0		53.95	0.749			75
	<i>M. edulis</i>	WB-D	50	0.1-10	21.0-25.9		0.85			73
	<i>M. edulis</i>						0.77(0.04)			11
	<i>M. edulis</i>	WB-D	21	0.26-1.94		96.8	0.86(0.10)	0.97	0.87	12
	<i>M. edulis</i>	WB-D	17	0.18-1.3		147.0	0.84(0.31)	0.87	0.97	12
	<i>M. edulis</i>	WB-D	22	0.08-1.09		148.5	0.86(0.20)	0.89	0.97	12
	<i>M. edulis</i>	WB-D	20	0.17-1.03		227.3	0.86(0.25)	0.86	1.00	12
	<i>M. edulis</i>	WB-D	40	0.04-3.5		264.5	0.81(0.06)	0.97	0.83	12
	<i>M. edulis</i>	WB-D	48			189.67	0.41(0.28)	0.35	1.17	51
	<i>M. edulis</i>	WB-D	43			20.99	0.67(0.12)	0.41	1.62	51
	<i>M. edulis</i>	WB-D	20			706.32	0.13(0.26)	0.62	0.20	51
	<i>M. edulis</i>	WB-D	98	36.8-348.1	249-393	1.85	1.19(0.04)	0.43		51
	<i>M. edulis</i>	WB-D	98	238.4-4660		1.55	1.15(0.03)	0.46	2.50	51
	<i>M. edulis</i>	WB-D	96			218.0	0.187	0.69	1.26	74
	<i>M. edulis</i>	WB-D	119	0.004-0.92		4.95(0.04)	0.86(0.04)			59
	<i>N. viaminghi</i>	WM-W	160	4.3-449.1		48.87	0.81			75
	<i>O. edulis</i>	WB-D	38	0.02-2.5	1846.5-5823.6	3437.2	1.03(0.07)	0.98	1.05	12
	<i>O. edulis</i>	WB-D	24	0.34-6.63	1816.0-11185.5	4358.1	0.98(0.16)	0.93	1.05	12
	<i>P. intermedia</i>	WB-D					0.77(0.04)			11
	<i>P. intermedia</i>	WB-D	14	0.02-1.71		237.8	0.71(0.08)	0.99	0.72	12
	<i>P. intermedia</i>	WB-D	16	0.02-1.71		193.9	0.76(0.07)	0.99	0.77	12
	<i>P. vulgata</i>	WB-D	35	0.02-0.80		358.3	0.84(0.06)	0.98	0.86	12
	<i>P. vulgata</i>	WB-D	29	0.01-0.80		354.9	0.91(0.05)	0.99	0.92	12
	<i>P. vulgata</i>	WB-D	30	0.01-0.85		433.6	0.93(0.06)	0.98	0.95	12
	<i>P. vulgata</i>	WB-D	34	0.02-1.10	52	388.2	0.84(0.07)	0.97	0.86	12
	<i>P. vulgata</i>	WB-D	32	0.02-1.10	27	302.5	0.89(0.05)	0.99	0.90	12
	<i>P. vulgata</i>	WB-D					0.77(0.04)			11
	<i>P. maximus</i>	WB-D	37	0.15-8.3		672.5	0.72(0.10)	0.96	0.75	12

<i>S. lignarius</i>	WB-D	20	0.09-3.8	984.0	1.06(0.11)	0.98	1.00	12
<i>V. decussata</i>	WB-D	30	0.17-2.77	92.2	0.97(0.14)	0.96	1.01	12
<i>V. decussata</i>	WB-D				1.03(0.02)			11

Note: Boyden (1974) reports the same b value for several species for the metals Cd, Cu, Fe, Pb, Ni, and Zn. The b values are reported for the individual species in Table 1 but were used once in Figures 3 and 4.

- <sup>a</sup> WB, whole body; WM, white muscle tissue; D, dry weight; W, wet wt. WB in mollusks does not include shell.
- <sup>b</sup> Range indicated by standard deviation.
- <sup>c</sup> Bq/g.

relationships and was characterized by  $b$  values of greater than 1.30 [in the range of 2 (Reference 11)]. Although he was later found to be incorrect,<sup>60</sup> Boyden hypothesized that  $b$  values were generally constant for some species-metal combinations. This simplifying assumption is often made in bioaccumulation models (see Bergner<sup>79</sup>).

Boyden hypothesized that some process linked to metabolic rate fostered a relationship with a  $b$  value in the range of 0.77. This suggestion was based on the similarity to  $b$  values for size-dependent metabolic rate. Although this may seem a reasonable suggestion, it is inappropriate to assume a common mechanism based on similarity between  $b$  values alone.<sup>40</sup> Boyden himself suggests that alternative allometric relationships could produce similar  $b$  values. For example, the amount of gill or general body surface for influx per unit mass of tissue to bind the element decreases with increasing size<sup>30-32</sup> and the clearance rate could decrease with increasing size.<sup>7,8,55</sup> The combined effects of these two relationships could generate a power relationship with a  $b$  value less than unity. However, Boyden rejected the surface-to-volume ratio hypothesis based on the false assumption of an isometric relationship ( $b = 0.67$ ) between surface area and mass for most organisms.<sup>12</sup> He suggested that more research was needed to effectively assess these potential explanations. Boyden's hypothesized linkage to metabolism has received considerable criticism but, to date, it has not been rigorously tested.

The second set of relationships was characterized by  $b$  values in the range of unity. Boyden suggested that these relationships were determined by the number of tissue sites available to bind the element. This also seems to be a reasonable hypothesis. However, Fagerström<sup>15</sup> developed the following counterargument that a  $b$  value of unity would imply linkage to metabolism. If steady state is assumed for a biologically indeterminate element,\* the rate of its turnover will be directly proportional to the animal's energy metabolism. Under such conditions, the following relationships can be defined:

$$T_{1/2} \propto X^{1-b} \quad (22)$$

$$C \propto X^0 \quad (23)$$

$$\Theta \propto X^{1-b} \quad (24)$$

$$Y \propto X^1 \quad (25)$$

where  $T_{1/2}$  = biological half-life

\* An element is indeterminate if, at steady state, its concentration in the organism is directly proportional to the concentration in the environment.<sup>6</sup> Uptake and elimination of an indeterminate element are dominated by simple mass equilibria relations. An element is defined as biologically determinant if its concentration in the organism is relatively constant over a wide range of environmental concentrations.<sup>6</sup> Many essential elements or their analogs seem to be determinant.

C = whole body concentration  
 $\Theta$  = metabolic turnover rate  
 Y = whole body burden  
 X and b as defined previously

Equation (25) suggests that linkage to metabolic processes will produce a b value of approximately unity for a biologically indeterminate element. It should be kept in mind that the conclusions of this argument may not be applicable for systems under nonequilibrium conditions or for biologically determinant elements. Indeed, studies of elimination kinetics for essential elements (Zn and K)<sup>4,8-10</sup> or their analogs (<sup>134</sup>Cs and <sup>137</sup>Cs)<sup>3-5,7,61</sup> suggest that this [Equation (22)] may not be accurate for biologically determinant elements. It [Equation (23)] is certainly not true for concentrations of major elements such as Ca, P, N, and S which vary with size-dependent, relative proportions of bone to protein in fish.<sup>80</sup>

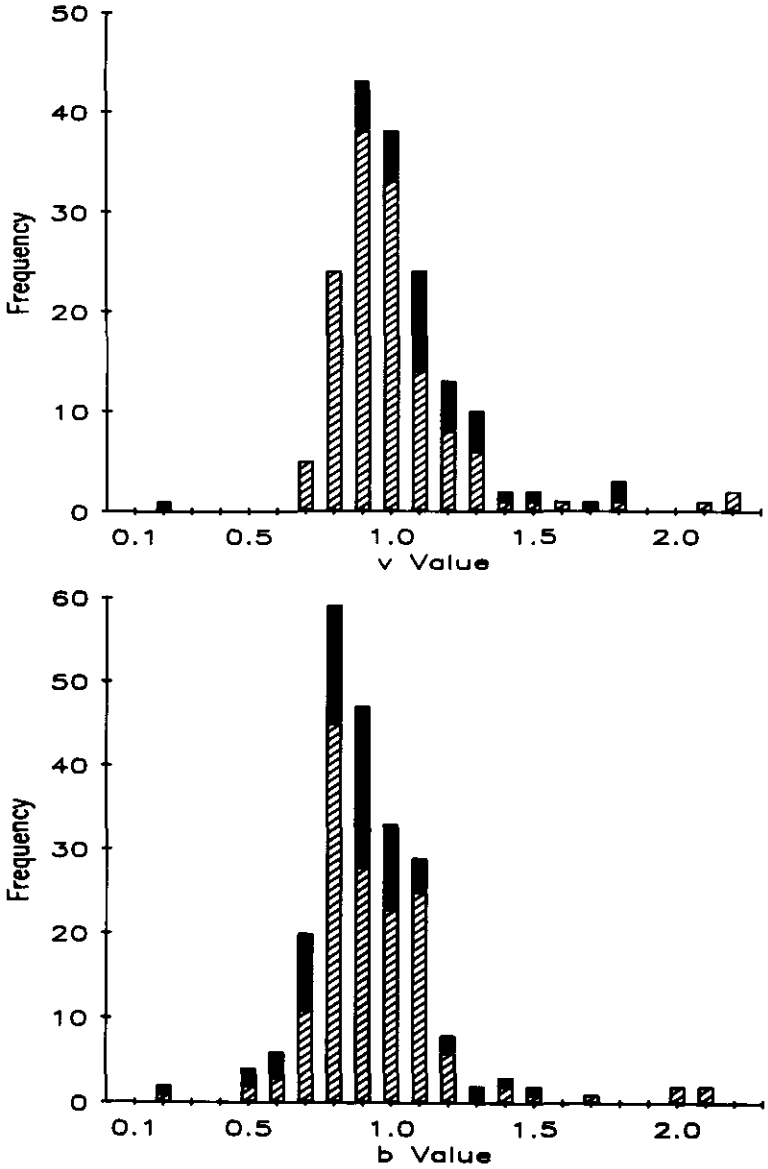
Finally, a small number of regressions were characterized by b values greater than 1 and approximating 2. Such relationships were thought to be due to a high affinity of the metal to some binding component and to consequent, rapid removal from circulation. Cd accumulation in several species had such high b values.

Although many of Boyden's suggestions have been found to be false or remain unsubstantiated, his work is cited and used to interpret most subsequent studies of metal body burdens and size. Further, his hypothesis are clearly stated and are amenable to the process of falsification. The central importance of this work warrants reexamination of associated data and conclusions.

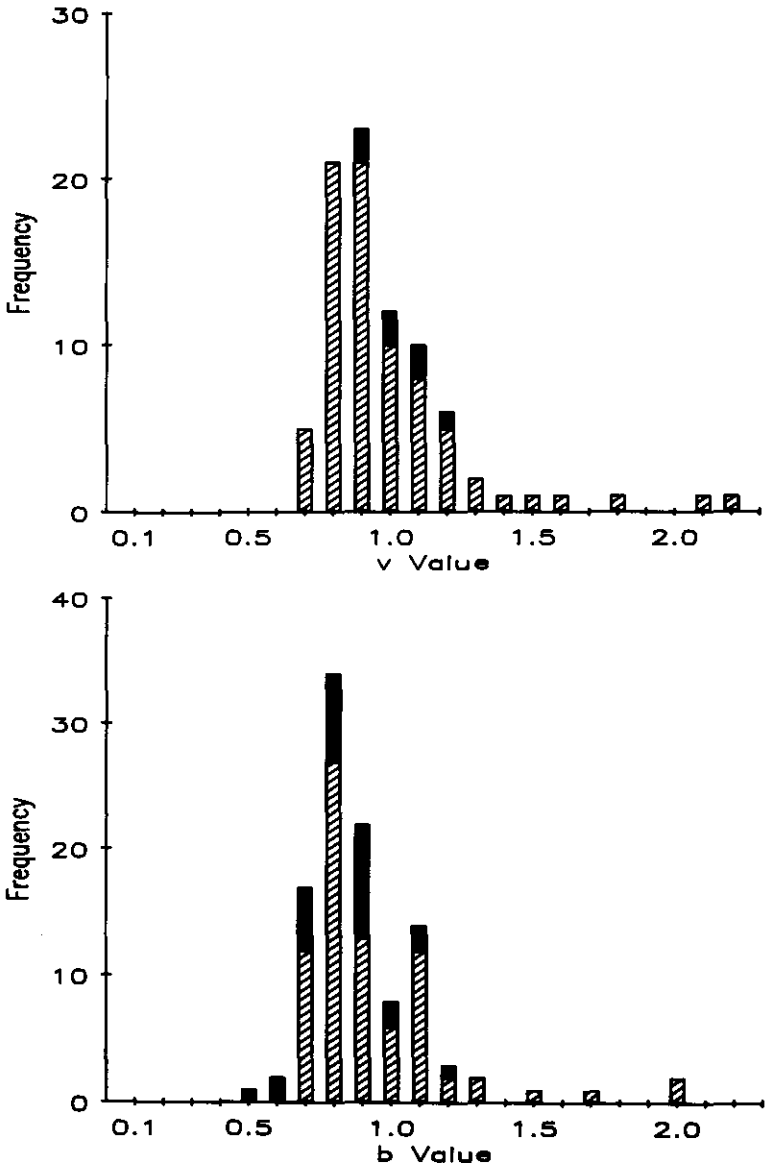
Boyden<sup>12</sup> estimated slopes for both predictive (b) and functional regression (v) models. He used a histogram of b values to define the three different relationships which he clearly stated were somewhat arbitrary. When all of Boyden's data and the supplemental data were reexamined (Figure 3), the present authors found no discrete distributions of b values. Rather, a skewed distribution with a median of 0.83 was suggested. When, as suggested by Boyden, only samples with sufficiently broad size ranges\* were used (Figure 4), the same skewed distribution was noted. There is only a slight indication of bimodality in these data. The median b value from this distribution was 0.80. One must conclude that clear evidence for three types of discrete relationships is still lacking more than a decade after Boyden's preliminary attempts to clarify the allometry of metal accumulation. An additional aspect of the regression results confounds interpretation of the b values. As discussed previously, there is a covariance between the r (correlation coefficient) and b such that, as the r becomes smaller, the b value will tend to be biased increasingly downward. When the b values are plotted against r (Figure 5), this bias is clear even for the data with a wide size range (Figure 5 inset).

Further, the b value will be strongly influenced by the range in concentrations.

\* In this chapter, this requirement was formalized to a size range of no less than 50-fold.



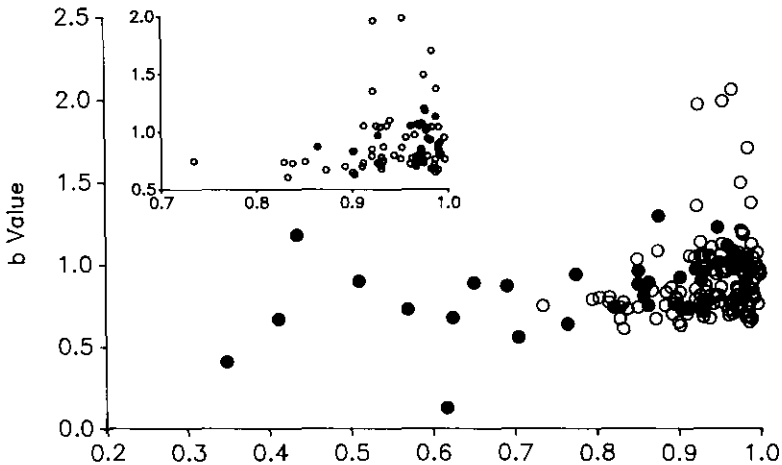
**FIGURE 3.** The frequency of b and v values from Boyden<sup>11,12</sup> (cross-hatching) and other studies (solid) regardless of weight range. B values: N = 214; median = 0.83; range = 0.13 to 2.05. V values: N = 170, median = 0.95, range = 0.20 to 2.13



**FIGURE 4.** The frequency of  $b$  and  $v$  values from Boyden<sup>11,12</sup> (cross-hatching) and other studies (solid) when the weight range was 50-fold or more.  $B$  values:  $N = 107$ ; median = 0.80; range = 0.45 to 1.98.  $V$  values:  $N = 85$ ; median = 0.85; range = 0.66 to 2.12.

Figure 2 shows Hg concentrations for dusky shiners (*Notropis cummingsae*) sampled from a southeastern U.S. stream.<sup>81</sup> Table 2 is a tabulation of a, b, and v estimates when the concentration range is progressively truncated. As the individuals with the highest concentrations of Hg (smaller fish) are discarded, the estimates of b increase. If a power model is to be used, it is essential to clearly define the ranges of body burdens or concentrations as well as the animal size range. The widest possible ranges for X and Y should be obtained.

Regardless, it was questionable if b values were the most appropriate statistics to tabulate for such discussion. The assumptions of no measurement error or no inherent variability in the surrogate measure of "size" (wet or dry wt) are not warranted in many studies. For example, Boyden and others, including the senior author, have estimated weights for smaller individuals by pooling similarly sized animals and taking an average weight. There is an inherent error associated with this technique. Even in the absence of such procedures, there can be significant error associated with estimating wet or dry wt. The confounding effects of age, growth, reproduction, mass of food in the gut, and a variety of factors make the measurement of "size" susceptible to variation. Consequently, the slope of the functional regression (v) would seem more appropriate than b as the basis for such discussion. Subsequent comparison to the allometric literature becomes confused as this body of information also contains many estimates of b but few estimates of v. Fortunately, Equation (19) can be used to estimate v when r is given.



**FIGURE 5.** The covariance of b value and correlation coefficient ( $r$ ) for all relationships, e.g., Figure 3, or those from relationships with 50-fold or wider range in size, e.g., Figure 4 (inset). Open circles are those used in Boyden's original Figure 13.

**Table 2**  
**Concentration Range Effects on Regression Results**

Concentration ( $\mu\text{g/g}$ )	N	$\hat{b}$	$\hat{a}$	r	v
$\leq 5.56$	96	0.321	0.082	0.86	0.37
<5.00	95	0.347	0.085	0.86	0.40
<2.00	92	0.381	0.092	0.86	0.44
<1.00	83	0.505	0.101	0.81	0.62
<0.80	82	0.512	0.101	0.82	0.62
<0.70	81	0.521	0.102	0.82	0.64
<0.60	80	0.528	0.103	0.81	0.65
<0.50	75	0.550	0.103	0.81	0.68
<0.40	64	0.601	0.105	0.77	0.78

When v values for body burden power equations are used (Figures 3 and 4), the suspected bimodality becomes even less apparent (Figure 4). Further, the medians of the associated slopes are closer to 0.90 than 0.77.

Although there was wide variation in values for each element and there was no clear bimodality (Figures 3 and 4), b or v values for some elements (As, Cd, and  $^{137}\text{Cs}$ ) did tend toward 1 and those for other elements (Co, Cu, Fe, Ni, Pb, and Zn) tended to be slightly less than 1 (Table 3). Median slopes for the essential elements (Co, Cr, Cu, Fe, Mn, Ni, and Zn) were only slightly lower than those for nonessential elements (As, Cd, and Pb). There are no further discernible patterns in median values for the tabulated elements. There is an obvious need for carefully designed experiments to clarify the ambiguity arising from interpretation of redescription models of field data. Further, when conclusions are drawn from this survey, the bias toward mollusks should be kept in mind. These invertebrates have mechanisms for uptake, sequestration, detoxification, and elimination that are common to all animals; however, the major role of such mechanisms as metal incorporation into intracellular granules<sup>53</sup> may not be applicable to certain phyla. Such characteristics which strongly influence body burden can restrict the generalization of findings from one species to another.

Despite attempts to define the mechanism(s) underlying physiological or morphological allometric equations, they remain empirical relationships. Certainly, the same may be said for body burden allometry. Consequently, there is no reason why alternate models should not be explored in redescription of body burden data. Such models would be most useful if they were amenable to interpretation using allometric or pharmacokinetic theory.

If warranted, a simple linear model may be as good or better than a power model for normalization of biomonitoring data. The argument associated with this statement is identical to that given above during discussion of narrow allometry. This approach was taken by Ashraf and Jaffar<sup>82</sup> relative to As concentrations in various sized tuna. Strong and Luoma<sup>60</sup> also found no advantage to transforming the body concentration and size data in their examination of body size effects on metal concentrations in a marine bivalve. Kumagai and Saeki<sup>83</sup> used an exponential model to relate Cu concentration in a marine mollusk to



shell height. Williamson<sup>52</sup> used a multivariate approach which incorporated estimated age into the power model. Although an overextension of the model, Williamson<sup>84</sup> expanded the allometric relation for body burden to include external factors such as day length, vapor pressure deficit, and rainfall.

## ACCUMULATION MODELS

### Overview

The simplest accumulation model describes the net effects of uptake and

**Table 3**  
Summary of *b* and *v* Values by Element and Essentiality

Element	All Regressions				Regression with Weight Range >50-fold			
	N	Median	Range	W	N	Median	Range	W
As								
<i>b</i>	2	0.93	0.74-1.11					
<i>v</i>	2	0.99	0.82-1.15					
Cd								
<i>b</i>	38	0.98	0.65-2.05	0.81 <sup>a</sup>	17	0.97	0.65-1.98	0.87 <sup>a</sup>
<i>v</i>	33	1.03	0.83-2.13	0.80 <sup>a</sup>	16	1.02	0.83-2.12	0.85
Co								
<i>b</i>	2	0.87	0.67-1.07		1	0.67		
<i>v</i>	2	0.88	0.68-1.08		1	0.68		
Cr								
<i>b</i>	2	0.77	0.64-0.89					
<i>v</i>	2	0.93	0.83-1.03					
<sup>137</sup> Cs								
<i>b</i>	2	0.92	0.88-0.96					
<i>v</i>	2	1.09	1.04-1.13					
Cu								
<i>b</i>	35	0.81	0.57-1.13	0.94	19	0.81	0.57-1.10	0.94
<i>v</i>	27	0.89	0.66-1.37	0.94	14	0.83	0.66-1.17	0.88
Fe								
<i>b</i>	30	0.79	0.65-1.22	0.88 <sup>a</sup>	18	0.77	0.65-1.04	0.91
<i>v</i>	22	0.83	0.72-1.29	0.87 <sup>a</sup>	13	0.81	0.72-1.00	0.92
Mn								
<i>b</i>	23	0.77	0.45-1.19	0.96	14	0.75	0.45-1.12	0.94
<i>v</i>	16	1.00	0.73-1.80	0.84 <sup>a</sup>	9	0.93	0.73-1.15	0.88
Ni								
<i>b</i>	15	0.75	0.63-1.05	0.81 <sup>a</sup>	7	0.73	0.63-1.05	0.78 <sup>a</sup>
<i>v</i>	13	0.82	0.69-1.13	0.87	6	0.89	0.69-1.13	0.81
Pb								
<i>b</i>	24	0.75	0.65-1.43	0.75 <sup>a</sup>	11	0.73	0.65-0.78	0.95
<i>v</i>	20	0.87	0.69-1.28	0.92	11	0.80	0.69-1.09	0.86
Zn								
<i>b</i>	41	0.86	0.13-1.20	0.88 <sup>a</sup>	20	0.86	0.71-1.20	0.94
<i>v</i>	31	0.95	0.20-1.62	0.88 <sup>a</sup>	15	0.92	0.72-1.23	0.95
Essential (Co, Cr, Cu, Fe, Mn, Ni, Zn)								
<i>b</i>	147	0.81	0.13-1.22	0.96 <sup>a</sup>	79	0.80	0.45-1.23	0.96 <sup>a</sup>
<i>v</i>	111	0.93	0.20-1.80	0.94 <sup>a</sup>	58	0.86	0.66-1.23	0.93 <sup>a</sup>
Nonessential (As, Cd, Pb)								
<i>b</i>	64	0.96	0.65-2.05	0.78 <sup>a</sup>	28	0.83	0.65-1.98	0.77 <sup>a</sup>
<i>v</i>	55	0.99	0.69-2.13	0.79 <sup>a</sup>	27	0.90	0.69-2.12	0.78 <sup>a</sup>

<sup>a</sup> The  $H_0$  of normality is rejected at an  $\alpha = 0.05$ .

elimination on the amount of metal within the organism. It is often expressed in the following form:

$$C_t = C_e(1 - e^{-k_e t}) \quad (26)$$

where  $k_e$  = elimination rate constant (1/time)

$C_t$  and  $C_e$  = concentrations at time,  $t$ , and equilibrium,  $e$ , respectively

Concentration units are  $\mu\text{g/ml}$  of tissue or  $\mu\text{g/g}$  if uniform densities are assumed as in the following discussion. An uptake rate constant ( $k_u$ ) can be incorporated into this model using the following relationship.

$$C_e = C_s(k_u/k_e) \quad (27)$$

where  $k_u$  = uptake rate constant (1/time)

$C_s$  = concentration in the source ( $\mu\text{g/ml}$  or  $\mu\text{g/g}$  assuming equivalent densities)

Combining Equations (26) and (27), the simple model becomes

$$C_t = C_s(k_u/k_e)(1 - e^{-k_e t}) \quad (28)$$

Within the context of its application, this simple model assumes the following conditions: one constant source of metal, instantaneous and homogeneous distribution of metal atoms within the organism, one compartment for elimination, a constant  $K_e$ , and a constant  $K_u$ .\*

If the process of uptake is simplified to involve only diffusion, the flux across the exchange surface ( $\mu\text{g/cm}^2/\text{sec}$ ) will be a function of the diffusion coefficient ( $\text{cm}^2/\text{sec}$ ) and the concentration gradient of the solute ( $\mu\text{g/ml}$  or  $\mu\text{g/g}$ )<sup>85</sup> across the exchange surface ( $\text{cm}^2$ ). The model described by Equation (28) assumes a constant area of exchange surface. As discussed previously, this assumption can be invalid in considerations of body burden scaling because the amount of gill or general body surface can change disproportionately with animal mass.<sup>30-32</sup> The incorporation of transport sites on surfaces of exchange lends an additional complication to the model as there are no compelling reasons to assume that the number of sites per unit surface for exchange will not change with animal size. The concentration gradient across gills will be influenced by respiratory processes such as ventilation volume.<sup>21</sup> These processes are related to size according to the allometric equation [Equation (1)]. If the route of uptake is associated with feeding, then scaling of related processes such as growth efficiency,<sup>86</sup> ingestion

\* The model described here is the most parsimonious model available. As such, it is often inadequate for description of accumulation data. The reader is referred to this volume, Chapter 7 for a richer discussion of compartmental models of bioaccumulation and associated assumptions.

rate,<sup>10</sup> and particle size-conversion efficiency<sup>87</sup> can influence the size dependence of body burden.

The elimination rate may also be linked to size. Elimination associated with the alimentary tract is influenced by factors such as size-dependent ingestion rate.<sup>10</sup> Size-dependent changes in processes (e.g., renal clearance) or structures (e.g., kidney weight to body weight) will also influence elimination rate.<sup>4</sup>

In the form presented above, this model [Equation (28)] and related models assume a constant volume (or mass) for the compartment. As discussed previously, this may not be a valid assumption depending on the relative rates of accumulation and growth. Growth can significantly contribute to body burden allometry.<sup>60</sup>

It can be concluded from the above discussion that  $k_e$  and  $k_a$  are not constants in the context of modeling size-dependent body burdens. Equations such as Equation (28) are inadequate for describing body burden allometry unless they are modified to incorporate size-dependent changes in processes and structures. Selected attempts to do so are discussed below to highlight the advantages and disadvantages of such approaches. They will also be used to identify problems associated with using redescription models uncritically in predictive modeling.

### Models Incorporating Allometry

Bioaccumulation of radionuclides has received attention primarily in the context of contaminated foodstuffs, health sciences, and radiotracers in ecological studies. Morgan<sup>5</sup> examined the accumulation of <sup>134</sup>Cs in finfish and shellfish near the Windscale nuclear facility in the United Kingdom and found that the biological half-life [ $T_{1/2} = -(\ln 0.5/k_e)$ ] increased slowly as weight increased (b values of 0.25 to 0.29 for plaice, eel, and lobster). He did not attribute this relationship to any single underlying mechanism; rather, he viewed the b values as multiple process statistics.

In an effort to extrapolate to humans, Fujita et al.<sup>4</sup> examined the interspecific, allometric relationship for equilibrium levels of Cs and K in mammals. Power relationships for both Cs and K had exponents of 0.45; however, the a values were 0.45 and 0.85 for Cs and K, respectively. The scatter in the K data was large;<sup>4</sup> therefore, a large model error term [Equation (12)] can be assumed. They used four relationships (with undefined model errors) to explain these findings: relationships between urinary excretion and total excretion, renal clearance and body size, kidney weight and body size, and total body concentration and plasma concentration. As judged by these four relationships, they predicted b values of 0.44 for both Cs and K, and a values of 0.39 and 0.67 for these same elements, respectively. This is an excellent fit of their observed data to a model involving four physiological and morphological relationships. However, it is suspected from the large model error term that this fit could be fortuitous. Similar interspecies studies with a primary focus on estimating radionuclide behavior in humans have demonstrated a size-dependent shift in pharmacokinetics. The basis for these shifts is most often linked to structural or physiological allometry.<sup>88,89</sup>

Anderson and Spear<sup>16</sup> examined Cu accumulation kinetics in gills of the pumpkinseed sunfish (*Lepomis gibbosus*) and fit the clearance of this metal to Equation (10) [see also Equation (22)]. The elimination rate constant relationship was  $k_e = 0.29X^{-1.8}$ . Total accumulation after 32 h of exposure was described by the relationship  $\mu\text{g Cu/g} = 0.0077X^{-0.35}$ . They suggested that physiological and morphological differences with size and perhaps changes in the number of binding sites on the gill with change in total gill surface likely accounted for these power relationships.

Newman and Mitz<sup>55</sup> used <sup>65</sup>Zn to measure the size-dependent accumulation kinetics of Zn in the mosquitofish, *Gambusia holbrooki* (formerly, *Gambusia affinis*). Although the model for elimination had significant error associated with it, the  $k_e$  and  $k_u$  for Zn were linked to size using the following relationships:

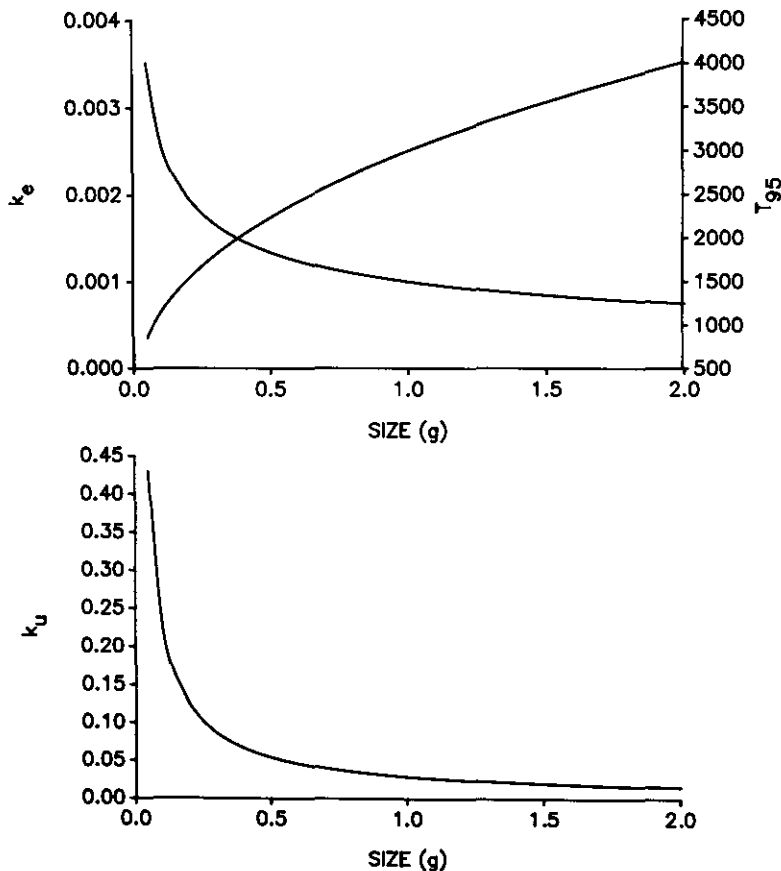
$$k_e = 0.001W^{-0.42} \quad (29)$$

$$k_u^* = 0.029W^{-0.90} \quad (30)^*$$

As previously stated, no direct linkage of  $k_e$  or  $k_u$  can be made with mosquito-fish metabolic rate<sup>90</sup> or surface:volume based on similarity of exponents alone; however, the similarity between several of these relationships encourages further work. For example, the metabolic rate has a b value of 0.64 ( $b - 1 = -0.36$ )<sup>90</sup> and the elimination rate constant for Zn had an mass exponent of  $-0.42$ . As suggested by Equation (24), the "b value" for  $k_e$  ( $= \Theta$ ) would be 0.58. This suggests, but certainly does not prove, that size-specific metabolic rate may play a significant role in determining the elimination rate for this element. Newman and Mitz<sup>55</sup> suggested that there was no direct connection between size-specific uptake (exponent =  $b - 1 = -0.90$ ) and gill surface:body mass allometry based on interpretation of b values for the gill surface:mass relationship. However, Murphy and Murphy<sup>14</sup> defined the b values for mosquitofish surfaces of exchange to mass as the following: whole body b value = 0.66; gill b value = 0.89. The amount of gill surface available for uptake per g of fish decreases disproportionately with fish mass ( $b - 1 = 0.11$ ). The uptake rate expressed in terms of  $\mu\text{g Zn/fish/day}$  decreases disproportionately with fish weight ( $b = 0.10$  assuming size-dependent elimination). This suggests a potentially significant role of surface:volume relationships in determining uptake rates for this fish.

The size-dependent relationships for  $k_e$  and  $k_u$  are shown in Figure 6 as is that estimated for time to reach 95% of equilibrium concentration ( $T_{95}$ ). Clearly, Equation (28) must be modified to accommodate size-dependent accumulation kinetics. An allometric model of accumulation kinetics can be generated by substituting Equations (29) and (30) into Equation (28). By doing so and solving

\* Note that the uptake rate ( $k_u^*$ ) used here has the units of  $\mu\text{g/g/day}$ . It is identical to  $C_u k_u$  in Equation (28) under the assumptions given for that equation.



**FIGURE 6.** Size dependence of the elimination rate constant ( $k_e$ ), time to 95% equilibrium concentration ( $T_{95}$ ), and uptake rate constant ( $k_u$ ) for zinc accumulation in mosquitofish (*Gambusia holbrooki*).

this model at different times of exposure, the  $b$  values estimated from a range of simulated fish sizes were shown to increase with duration of exposure. It should also be noted that, considering the values for  $T_{95}$  (days) and the relatively short life-span of this species, any argument regarding these  $b$  values based on the assumption of equilibrium conditions is inappropriate. This was not the case, however, when Newman and Doubet<sup>69</sup> repeated this exercise with ionic Hg accumulation by mosquitofish. With this metal, concentrations rapidly approached equilibrium. Although uptake rates were higher for smaller than those for larger fish, there were no statistically significant effects of size on Hg elimination. These data are discussed more extensively in this volume, Chapter 7.

The model generated by combining Equations (29) and (30) with Equation

(28) remains unrealistic because no consideration is given to growth during the period of exposure. Growth will produce an apparent dilution of metal concentration and potentially shift the  $k_c$  and  $k_u$  as a fish becomes larger with time. A variety of growth models may be linked to these equations during simulation. In selecting the appropriate growth model, the availability of the necessary constants for the species, the model's ability to accurately describe growth of the particular species, and the potential for linkage to bioenergetics should be considered. Fagerström et al.<sup>18</sup> used the von Bertalanffy growth model [Equation (31)] combined with the relationship between fish length and fish size<sup>50</sup> [Equation (32)] to simulate fish growth in models of Hg accumulation.

$$l = l_{\infty}[1 - e^{-k_g(u-u_0)}] \quad (31)$$

$$W = \tau l^{\Phi} \quad (32)$$

where  $l$  = fish length  
 $l_{\infty}$  = theoretical maximum fish length  
 $k_g$  = growth rate constant  
 $u$  = age  
 $u_0$  = initial age of fish  
 $W$  = fish weight  
 $\tau, \Phi$  = constants

The flexibility of the Richards model for description of growth<sup>91</sup> also makes it an attractive candidate during simulations. Depending on the value of the shape parameter ( $m$ ), this relationship becomes the logistic ( $m = 2$ ), von Bertalanffy ( $m = 0.67$ ), Gompertz ( $m \rightarrow 1.0$ ), or single exponential ( $m = 0$ ) models. Brisbin and co-workers recently reparameterized this model as discussed in Brisbin et al.<sup>92</sup> These reparameterized equations should be considered prior to use of the Richards model for growth.

Bioenergetics models that incorporate allometric relationships such as those discussed above have been developed for bioaccumulation of organic<sup>84,86,93</sup> and inorganic<sup>18,20,22,94</sup> contaminants. Fagerström et al.<sup>18,63</sup> incorporated growth, size-dependent uptake from food and water, and size-dependent clearance into a model describing methylmercury accumulation in northern pike (*Esox lucius*). Boddington et al.<sup>20</sup> attempted to link oxygen uptake efficiency and pollutant (methylmercury) uptake efficiency of fish. Braune<sup>94</sup> included growth dilution, temperature, gill transfer efficiency, and size-dependent processes such as food conversion efficiency, metabolic rate, ventilation rate, and clearance to simulate Hg accumulation in herring (*Clupea harengus harengus*). Recently, Rose et al.<sup>22</sup> examined radionuclide accumulation in shellfish using a similar bioenergetics approach. Bias in predicted values [Equations (16) and (17)] associated with the use of these redescription models for predictive purposes were not generally

considered in development of these predictive models. The information necessary to perform the necessary bias corrections was usually not available.

## ALLOMETRY AND TOXICITY

### Overview

Allometric aspects of metal toxicity are often eliminated by use of a narrow range of size and/or age classes. This is done to enhance the precision of the toxicity test; however, most field populations are composed of individuals with a wide range of sizes. To describe or predict the toxic response of field populations to metals, an understanding of scaling is necessary. Table 3 in Anderson and Weber<sup>23</sup> attests to the frequent use of power equations [Equation (1) with  $Y = LD_{50}$  or  $LC_{50}$ ] to describe size effects on toxic end points. However, relationships between toxic response and size are often more complex than indicated by the allometric equation. Shepard<sup>95</sup> found that tolerance levels of small brook trout (*Salvelinus fontinalis*) to low concentrations of oxygen were similar to those of larger trout, but the small trout died more quickly when exposed to lethal concentrations. Threshold  $LC_{50}$  increased with fish size, but there were no size effects on the 96-h  $LC_{50}$  for goldfish (*Carassius auratus*).<sup>96</sup> Developmental stage may further confound scaling effects.<sup>1,97</sup>

### Models Incorporating Allometry

Dosage (amount given to an individual based on weight) can have different intensities of effect for different size, age, and sex classes.<sup>98-100</sup> In 1909, Moore, as cited in Bliss,<sup>2</sup> argued that dosage should be modified to be proportional to surface of absorptive tissue, e.g.,  $^{2/3}$  power of mass. Early studies that modified dosage according to such power relationships incorrectly referred to this approach as "dose to body surface."<sup>100</sup> Bliss<sup>2</sup> formulated the following relationship for size effects on toxic response.

$$\text{Log(rate of toxic action)} = a + b\text{Log}(m/W^h) \quad (33)$$

where rate of toxic action =  $1/T$  (or 1000/min survival),

$h$  = size coefficient

$W$  = weight (cg)

$m$  = mg As per individual  $\times 1000$

$a, b$  = regression constants

This relationship was derived for silkworm larvae fed As. The  $h$  value was 1.5 under these test conditions. It took more As to get a toxic response from the larger than from the small larvae. Although he expressed caution regarding excessive speculation, Bliss suggested that some biochemical constituent to which As binds (such as glutathione) increases in concentration as animal size increases. This sequesters the As that otherwise would combine with and inactivate cell constituents present at relatively low concentrations.

When the Log (rate of toxic action) was plotted against Log of dose [10 (mg As/g body wt<sup>1.50</sup>)], a straight line was generated. Bliss provided a time to response-concentration expression of the data set using the slope of this plot:

$$C^n t = \text{constant} \quad (34)$$

where C = amount of As/unit mass  
 n = slope of Log-Log curve  
 t = time

Anderson and Weber<sup>23</sup> took the relationship developed by Bliss for dose [Equations (33) and (34)] and extended it to incorporate size-dependent responses of aquatic biota (% mortality as probit) to ambient concentrations of toxicants. Guppies (*Poecilia reticulata*) were exposed to a series of toxicants including Cu, Ni, and Zn. The mean daily toxicant concentration was used as m in Equation (33). This provided good fit to the data sets. Anderson and Weber<sup>23</sup> then linked these relationships to the following regression of weight effects on LC<sub>50</sub>:

$$\text{LogLC}_{50} = \text{Log}a + b\text{Log}W \quad (35)$$

or

$$\text{LC}_{50} = aW^b \quad (36)$$

or

$$\text{Log}(\text{LC}_{50}/W^b) = \text{Log}a \quad (37)$$

To show the similarity between Equation (37) and Bliss' linear time to response-concentration model, they substituted the 50% probit score into Bliss' relationship,

$$\text{Log}(m/W^h) = \text{Log}X \quad (38)$$

where m is now the LC<sub>50</sub> and X is the probit score at 50%.

Equation (36) was recommended by Anderson and Weber<sup>23</sup> "as a standard format for reporting LD<sub>50</sub> and LC<sub>50</sub> values for drugs, toxicants, and toxins for varying sizes of animals." Hedtke et al.<sup>24</sup> also began with Bliss' work<sup>2</sup> and developed a similar approach. As long as conditions regarding bias corrections are kept in mind and confounding biological factors<sup>17</sup> are clearly acknowledged, these relationships provide effective tools for simulation of size-dependent toxic response.



Other related approaches to modeling size-dependent mortality have been developed.<sup>25,26</sup> For example, proportional hazard model techniques were used by the authors and co-workers<sup>101,102</sup> to link time-to-death to a variety of factors, including size. No description of these techniques will be given here as a detailed description is presented in this volume, Chapter 8.

## CONCLUSION

1. Allometry is the study of size and its consequences. Huxley established the power equation [Equation (1)] as the primary redescription model for the allometric relation. This model remains empirical, with no clear, underlying mechanism(s).
2. Concepts and techniques applied to ecotoxicological allometry were borrowed exclusively from those of physiological and morphological allometry. This linkage provided a rapid infusion of ideas and techniques. It also allowed linkage to bioenergetics during modeling efforts. However, many conceptual and technical errors were also transferred to ecotoxicological allometry.
3. The mass exponent (b) indicates the extent of disproportional change between some quality or structure and size. The mass coefficient (a) has no clear biological meaning.
4. Log-Log transformation, regression on transformed data, and backtransformation are the standard approaches for determining the constants, a and b. A variety of errors associated with this process are present. Methods for coping with these errors and correcting bias for predictive purposes are outlined in this chapter.
5. Significant measurement error in X and inherent variability in X are often ignored in allometric analyses. Often functional regression techniques should be used instead of predictive regression techniques.
6. Constants from allometric relationships of accumulation or toxicity should be considered multiple process statistics unless clearly shown to be otherwise. A complex array of factors, not simply metabolic rate or surface-to-volume ratio, can influence ecotoxicological allometry.
7. Boyden clearly defined testable hypotheses regarding allometry of body burden. Some have been rejected, whereas the validities of others are still unknown.
8. Contrary to the suggestions of Boyden, there is no clear evidence for the existence of three discrete types of allometric relationships for elemental body burden. Regardless, it is doubtful that such a classification scheme should have been based on b rather than v values.
9. Allometric models linked to bioenergetics provide excellent tools for modeling bioaccumulation. However, biases in predicted values from descriptive models can compromise the utility of predictive models which incorporate them.
10. Allometric aspects of metal toxicity are often eliminated by the use of a narrow range of animal sizes. This is done to enhance assay precision. However, this practice limits our ability to predict toxic impacts on field populations.

11. Allometric relationships for toxic effects are influenced by a variety of factors. The power relationship was used to describe the relationship between toxic end points and animal size.
12. Equations developed by Bliss were successfully modified to describe the relations among rate of toxic action, ambient toxicant concentrations, and animal size.
13. Despite the magnitude and prevalence of size-dependent effects, a variety of hypotheses remain untested or poorly tested in the area of ecotoxicological allometry. Necessary decisions are made and models are built despite this ambiguity. For example, many weak inferences about the body burdens of elements remain untested more than a decade after the original hypothesis was formulated. In our opinion, the field is progressing slowly because it lacks a tradition of strong inference.<sup>103</sup>

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