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Trace element trophic transfer in aquatic organisms: A critique of the kinetic model approach

J.R. Reinfelder[a,*], N.S. Fisher[b], S.N. Luoma[c], J.W. Nichols[d], W.-X. Wang[e]

[a]*Department of Environmental Sciences, Rutgers University, 14 College Farm Rd, New Brunswick, NJ 08901-8551, USA*
[b]*Marine Sciences Research Center, State University of New York, Stony Brook, NY 11794-5000, USA*
[c]*Mail Stop 465 U.S.G.S. 345 Middlefield Rd, Menlo Park, CA 94025, USA*
[d]*US EPA, National Health and Environmental Effects Laboratory, Mid-Continent Ecology Division, 6201 Congdon Blvd, Duluth, MN 55804, USA*
[e]*Department of Biology, The Hong Kong University of Science and Technology, Clear Water Bay, Kowloon, Hong Kong*

Abstract

The bioaccumulation of trace elements in aquatic organisms can be described with a kinetic model that includes linear expressions for uptake and elimination from dissolved and dietary sources. Within this model, trace element trophic transfer is described by four parameters: the weight-specific ingestion rate (IR); the assimilation efficiency (AE); the physiological loss rate constant (k_e); and the weight-specific growth rate (g). These four parameters define the trace element trophic transfer potential (TTP = IR·AE/[$k_e + g$]) which is equal to the ratio of the steady-state trace element concentration in a consumer due to trophic accumulation to that in its prey. Recent work devoted to the quantification of AE and k_e for a variety of trace elements in aquatic invertebrates has provided the data needed for comparative studies of trace element trophic transfer among different species and trophic levels and, in at least one group of aquatic consumers (marine bivalves), sensitivity analyses and field tests of kinetic bioaccumulation models. Analysis of the trophic transfer potentials of trace elements for which data are available in zooplankton, bivalves, and fish, suggests that slight variations in assimilation efficiency or elimination rate constant may determine whether or not some trace elements (Cd, Se, and Zn) are biomagnified. A linear, single-compartment model may not be appropriate for fish which, unlike many aquatic invertebrates, have a large mass of tissue in which the concentrations of most trace elements are subject to feedback regulation.

Keywords: Bioaccumulation; Model; Trace element; Metal; Aquatic; Biomagnification

* Corresponding author. Tel.: +1 732 9328013; fax: + 1 732 9328644; e-mail: reinfelder@aesop.rutgers.edu

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1. Introduction

Trace element accumulation in aquatic consumers is of interest to environmental scientists concerned with the fate and effects of contaminants as well as ecologists interested in food web dynamics and trace element biogeochemical cycles. Whether their goal is to assess the toxic impact of Hg in fish or to explain the distribution of Cd in the ocean, both environmental scientists and ecologists need to predict how elements move through aquatic food webs. Such predictions depend in part on an understanding of how organisms accumulate trace elements from their environment which for aquatic consumers is complicated by the presence of both soluble and dietary sources. For many aquatic invertebrates, trophic transfer accounts for a major portion of total trace element accumulation (Luoma et al., 1992; Fisher and Reinfelder, 1995; Wang et al., 1996a; Munger and Hare, 1997). Predictive trace element bioaccumulation models therefore need to account for accumulation from both water and food.

The traditional concentration factor approach predicts trace element concentrations in animals based on those in the water (typically total dissolved concentatrations) using the ratio of the trace element concentration in the animal to that in the water at a presumed steady-state (sometimes referred to as the equilibrium partitioning model). This approach may provide general information about how enriched in particular elements organisms are with respect to their environment, but is insensitive to changes in the pathway of accumulation and environmental and physiological conditions. As alternatives to the concentration factor model, models that include parameters for each of the constituent processes of trace element bioaccumulation have been developed (Landrum et al., 1992; Thomann et al., 1995; Wang and Fisher, 1997). These kinetic models account separately for bioaccumulation from the dissolved phase and from food thus permitting a quantitative evaluation of the two sources. In addition, trophic transfer is broken down into the separately quantifiable parameters of ingestion, assimilation, elimination and growth, each of which can be subjected to sensitivity analysis (e.g. Wang et al., 1996a; Wang and Fisher, 1998a) to discern which processes are most important to overall bioaccumulation in a given trophic step. By quantifying the parameters controlling trace element trophic transfer in various consumers it may be possible to explain why a trace element is accumulated by one organism, but not by another, and when and why biomagnification occurs.

A number of abiotic criteria including the dissolved concentration, partitioning between dissolved and particulate phases, and the ways in which such factors as salinity, water hardness, and dissolved organic carbon concentrations influence these values, affect trace element accumulation in aquatic animals. The concentrations and geochemical partitioning of metals in aquatic systems have been relatively well characterized elsewhere (e.g. Bruland, 1983; Hart and Hines, 1995), thus our focus is a discussion of the physiological processes involved in trace element trophic transfer, the quantification of these processes, and their application to the study of trace element bioaccumulation.

2. Kinetic models of trace element trophic transfer in aquatic organisms

Kinetic models of trace element bioaccumulation are based on a simple conceptual model in which the concentration of an element in a single compartment organism is controlled by the balance between uptake, elimination, and growth. Although trace elements likely accumulate in multiple compartments in aquatic organisms, the single compartment model can be used to predict trace element accumulation when different compartments have similar turnover times or when the exchangeable pool is large relative to the total, conditions that apply reasonably well to invertebrates, perhaps less well to fish. Trace element uptake includes contributions from food ($AE \cdot IR \cdot C_f$) and water ($\alpha_w \cdot FR \cdot C_w$), where AE is the assimilation efficiency of ingested element (%), IR is the weight-specific ingestion rate (day^{-1}), α_w is the dissolved uptake efficiency (%), FR is the filtration rate ($l\ g^{-1}\ day^{-1}$), and C_f and C_w are the element concentrations in the

prey (μg g^{-1}) and the water (μg l^{-1}), respectively. Uptake from water can be quantified with a dissolved uptake rate constant, k_u (l g^{-1} day^{-1}), which is the product of α_w and FR. Overall trace element dilution in a consumer occurs through growth (g, day^{-1}) and elimination which includes physiological loss (k_e, day^{-1}) and chemical transformation (k_R, day^{-1}). Chemical transformation may be important in the elimination of organometallic compounds such as methylmercury and tributyltin or elements subject to redox chemistry such as iron and cobalt, but will not be considered explicitly in the model below. The time-dependent concentration of a trace element in a consumer is described by the following equation:

$$C_t = \frac{(k_u \cdot C_w) + (\mathrm{AE} \cdot \mathrm{IR} \cdot C_f)}{(k_e + g)}(1 - e^{-(k_e+g)t}) \quad (1)$$

At steady-state, uptake is balanced by elimination and growth to give a constant concentration in the consumer (C_{ss}, μg g^{-1}):

$$C_{ss} = \left[(k_u \cdot C_w) + (\mathrm{AE} \cdot \mathrm{IR} \cdot C_f)\right]/(k_e + g) \quad (2)$$

[It should be noted that this model assumes that the physiological loss rates of a trace element accumulated from food and the dissolved phase are similar and can be characterized by a single rate constant, k_e, which has been shown to be valid in marine mussels (Wang et al., 1996a).] The concentration of a trace element in a consumer due to the ingestion of food alone ($C_{ss,f}$) is therefore given by:

$$C_{ss,f} = (\mathrm{AE} \cdot \mathrm{IR} \cdot C_f)]/(k_e + g) \quad (3)$$

Trace element trophic transfer therefore depends on four physiological parameters, AE, k_e, IR, and g. The trophic transfer potential (TTP) of a given element which is equal to the ratio of its concentration in the consumer to that in the prey ($C_{ss,f}/C_f$) is given by:

$$\mathrm{TTP} = (\mathrm{AE} \cdot \mathrm{IR})/(k_e + g) \quad (4)$$

Reasonably good estimates of these four parameters are needed in order to make even first-order predictions of trace element accumulation in aquatic consumers from food using the kinetic model. We therefore discuss the means by which these parameters are measured, how well they are constrained for different elements and organisms, and their current and future application to trace element bioaccumulation problems.

3. Physiological parameters: how are they measured and how well are they known?

3.1. Assimilation efficiency

As discussed at length elsewhere (Wang and Fisher, 1997a), assimilation is a physiological process which can be quantitatively compared among trace elements and animal species under diverse environmental conditions. The assimilation of trace elements from food can be thought to result from the passage of the trace element across the gut lining during digestion. Thus, assimilation efficiency effectively represents that fraction of ingested element that remains in the tissues of an animal after it has emptied its gut of undigested material. Once generated, assimilation efficiencies can be used in kinetic models to predict metal concentrations in animals on a site-specific basis (Wang et al., 1996a) and can as well be used to quantitatively compare the importance of different uptake pathways (that is, uptake from food or water) to the overall bioaccumulation of trace elements in an animal, as shown for bivalves (Luoma et al., 1992; Wang et al., 1996a) and copepods (Wang and Fisher, 1998a).

The relative paucity of data on assimilation efficiencies of ingested trace elements in aquatic animals reflects, in part, the difficulty in quantifying this process. Recent developments in experimental protocols, primarily using gamma-emitting radioisotopes, have resulted in a more standardized and rigorous data set on assimilation efficiencies. The basic approach involves the uniform radiolabeling of a food supply, allowing the animal in question to feed on the food for a short time period (typically less than the gut transit time of the animal to minimize recycling of the radiolabel during the feeding period), followed by a sustained period of feeding on unlabeled food

to purge the guts of undigested radioactive material. This 'pulse-chase' approach is readily conducted with gamma-emitting radioisotopes which enable working with low, environmentally realistic atom concentrations of trace elements, and which afford rapid and non-destructive analyses to assess the kinetics of uptake and release of a trace element in the same individual animals over time. Details of experimental approaches and methods of calculating assimilation efficiencies are given elsewhere (e.g. Reinfelder and Fisher, 1991; Wang et al., 1995, 1996b). Most previous studies have focused on marine herbivores such as copepods and bivalve molluscs, although a few recent studies have examined the assimilation of ingested metals and metalloids by carnivorous marine animals (Reinfelder and Fisher, 1994b; Hutchins et al., 1996; Anastasia et al., 1998).

A variety of biological and abiotic factors have been identified which can affect the efficiency with which marine animals assimilate ingested metals and metalloids. Consequently, it is more appropriate to consider a range of assimilation efficiency values than one single 'correct' value for each trace element/species combination. [For compilations of trace element AEs in marine invertebrates, see Fisher and Reinfelder (1995) and Reinfelder et al. (1997).] The effects of environmental variables on trace element assimilation have been best studied in marine bivalve molluscs, particularly the mussel *Mytilus edulis* which is widely used as a bioindicator of coastal contamination. Factors such as food quantity, the trace element content of the food, and especially the composition of the food can significantly affect trace element assimilation in bivalves (Wang et al., 1995; Wang and Fisher, 1996a,b, 1997a). Other factors, such as temperature and the protein content of the food have been shown to have relatively minor effects on trace element assimilation efficiencies in marine bivalves (Wang and Fisher, 1996b, 1997a; Hutchins et al., 1998). Generally, the variation in assimilation efficiencies of trace elements in marine bivalves, which is greater between trace elements than within a given trace element, is caused by environmental variability. Of the elements which have been best studied in mussels, Se displays the highest assimilation efficiencies, with values usually $>50\%$ (however, the AE of elemental Se, a common form in sediments, is 20%; Johns et al., 1988); Cr and Am display the lowest values, with efficiencies typically $<5\%$ (Reinfelder et al., 1997; Wang and Fisher, 1997a).

Marine bivalves can also assimilate trace elements from ingested sediment particles, as shown for Cr (Decho and Luoma, 1996), Hg (Gagnon and Fisher, 1997a), and Cd, Co, and Ag (Gagnon and Fisher, 1997b), but trace element assimilation efficiencies depend on the inorganic and organic chemical composition of the sediments (Luoma and Fisher, 1997). When sediment particles are enriched in iron oxides, the assimilation of sediment-bound metals is generally found to decrease (Luoma and Jenne, 1977; Luoma and Bryan, 1978; Langston, 1980; Tessier et al., 1994). Conversely, organic coatings such as bacterial extracellular polymers or fulvic acids tend to significantly enhance the assimilation of ingested metals in bivalves (Harvey and Luoma, 1985; Gagnon and Fisher, 1997b) as does the addition of a living component (e.g. benthic microalgae) to a sediment or particle assemblage (Lee and Luoma, 1998).

It is presumed that for trace elements to be assimilated in animals, they must first desorb from ingested particles in the digestive tract of the animal. A variety of factors would be expected to influence the rate and extent of this desorption, but probably most important are the pH of the gut (Fisher and Teyssié, 1986; Wang et al., 1995) and the concentration of trace element binding ligands (Mayer et al., 1996). For example, digestive fluids rich in amino acids from two marine deposit-feeding invertebrates were able to extract significant amounts of sediment-bound Cu, significantly increasing the potential for Cu assimilation (Mayer et al., 1996).

A striking relationship has been observed between the assimilation efficiencies of ingested elements (including metals) and the cytological distribution of the elements in food. Specifically, assimilation efficiencies in herbivores have been shown to be directly proportional to the cytoplasmic content of the element in the algal cells which serve as food for copepods (Reinfelder and

Fisher, 1991; Hutchins et al., 1995) and bivalve larvae (Reinfelder and Fisher, 1994a). Generally, it appears that trace elements bound to algal cell walls and membranes are not assimilated and are packaged into fecal pellets. This is particularly evident for herbivores with short gut transit times. Consequently, those trace elements bound to cell surfaces may be expected to display relatively short residence times in surface waters because the fecal pellets sink at rates >50 m day^{-1}, whereas trace elements which are in the cytoplasm of the algal cells display longer oceanic residence times because they get recycled biologically in surface waters (Fisher et al., 1991; Fisher and Reinfelder, 1995).

With adult bivalves, which have much longer gut transit times and more complicated gut morphologies than macrozooplankton, the correlation between assimilation efficiencies of ingested metals and distribution in algal cytoplasm is weaker. As was found for animals with shorter gut residence times, the cytoplasmic fraction of trace elements is assimilated in adult bivalves, but additional fractions of some elements are also absorbed (Wang and Fisher, 1996b; Reinfelder et al., 1997). For example, adult oysters and clams can assimilate approx. 40% of the non-cytoplasmic fractions of ingested Ag and Cd in addition to the cytoplasmic fraction (Reinfelder et al., 1997).

It should be recognized that the composition of food particles can greatly affect trace element trophic transfer. Aquatic invertebrates can selectively ingest food particles of higher nutritional values, especially at high food concentrations. In marine mussels, the assimilation of essential trace elements (e.g. Se and Zn) is directly coupled to the assimilation of carbon. Thus the trophic transfer of these trace elements may increase disproportionately when mussels preferentially ingest nutritionally rich food particles (Wang and Fisher, 1996b). Lee and Luoma (1998) showed that enriching the algal content of a natural assemblage of sedimentary or suspended particles (as during a phytoplankton bloom) can nearly double the AE of Cd and Zn for the deposit feeding clam *Macoma balthica* and especially for the suspension feeding clam *Potamocorbula amurensis*. Thus phytoplankton blooms, which transform Cd and Zn from dissolved to particulate forms in the water column of San Francisco Bay (Luoma et al., 1998), can result in increased bioaccumulation of these metals. It is important to realize, however, that the increase in trophic transfer due to higher trace element AEs may be diminished if animals consuming food of higher nutritional value lower their ingestion rates. For many non-essential trace elements, assimilation is not directly coupled to carbon assimilation, and the overall effect of food quality on trophic transfer may be rather complicated. Trace element assimilation in marine copepods is relatively independent of food composition, thus the effect of food composition on tropic transfer may be less straightforward (Wang et al., 1996b).

Trace element assimilation efficiencies in aquatic carnivores may be affected by the transformation of trace elements by prey organisms for the purposes of detoxification. Some invertebrates sequester trace metals in calcium or phosphate precipitates (George, 1982; Nott and Nicolaidou, 1990). Unlike soluble species, granular forms of trace elements in invertebrate tissues are not assimilated by predators (Nott and Nicolaidou, 1990; Wallace and Lopez, 1996). Ag and Pb occur in very low concentrations in cell solution in microalgae (Fisher et al., 1983; Reinfelder and Fisher, 1994) and in invertebrates (Reinfelder and Fisher, 1994b; Cain et al., 1995). Clearly, there is a need for further investigations of trace element assimilation in carnivorous animals (see *Applications to fish* below), as only a few such studies have been conducted to date. Studies of trace element assimilation in animals with different gut morphologies (e.g. annelids) and the influence of surfactants on assimilation in these animals should also be performed.

3.2. Trace element efflux rate in aquatic invertebrates

In many aquatic systems, animals are subject to chronic trace element exposure (although episodic exposure also occurs). Thus the rate of trace element loss is presumably limited by loss from each animal's slowest exchanging compartment. Assimilated trace elements may be stored in granular forms and then lost across the alimen-

tary tract in the form of feces, or stored in the kidneys and then lost through excretion (George, 1982). Marine mussels tend to eliminate trace elements by egestion (Wang et al., 1996a; Wang and Fisher, 1997a) while marine copepods release assimilated trace elements by excretion (Wang and Fisher, 1998b). The biochemical mechanisms underlying trace element turnover in aquatic invertebrates need further investigation. For example, binding sites and pathways of physiological turnover may differ among various organisms and trace elements.

Rate constants describing trace element efflux in aquatic invertebrates can be determined using radiotracers. With this approach, the retention of radiotracers in labeled animals is followed after transfer to depuration aquaria set up with radiotracer-free water and food. Sufficient dilution of lost radioisotope in the depuration water ensures that the measured flux is the gross loss rate. Gamma-emitting radiotracers have the added advantage that the measurement is non-destructive thereby permitting loss rates to be determined in individual live organisms for extended depuration periods. Rate constants for rapidly and slowly exchanging compartments can be determined, but more study is needed to compare radiolabel partitioning between these compartments in the laboratory and the true trace element partitioning between them in nature. In most model applications to date, efflux from the slowest exchanging compartment has been used to determine k_e. The duration of radiolabeling may affect the determination of trace element efflux rates such that short-term radiolabeling (hours) may result in a greater proportion of radiotracer concentrated in rapidly exchanging compartments making it difficult to follow the depuration pattern of trace elements from the slowest exchanging pool (Cutshall, 1974).

In marine bivalves, efflux rates appear to be relatively constant both among different trace elements and among different species. Efflux rate constants for a variety of trace elements in four marine bivalves (oysters, clams, and mussels) range from 0.01 to 0.03 day^{-1} (Wang et al., 1996a; Reinfelder et al., 1997). Similarly, B.-G. Lee (personal communication) recently measured the efflux rate constants of Cd, Cr, and Zn in two marine clams (*Macoma balthica* and *Potamocorbula amurensis*) and found these values were within 0.01–0.04 day^{-1}. Wang et al. (1996a) also found that the duration of exposure (12 h vs. 6 days) and the pathway (food vs. water) of accumulation do not significantly affect efflux rate constants in marine mussels. In addition, trace element efflux rates in mussels maintained in the laboratory are directly comparable to mussels transplanted into the field (Fisher et al., 1996), suggesting that efflux rates determined in the laboratory can be used to predict trace element bioaccumulation in natural populations.

Small differences in efflux rates, however, may have substantial affects on trace element trophic transfer and accumulation. For example, ignoring growth dilution, an increase in trace element efflux rate from 0.01 to 0.02 day^{-1} can result in a twofold decrease in trophic transfer. It is, however, difficult to distinguish such subtle differences in radiotracer experiments if the depuration period is too short or analyses are not sufficiently frequent to obtain statistically meaningful measurements. Long-term depuration studies are practically challenging, but probably necessary to accurately quantify trace element efflux in aquatic animals.

Crustacean zooplankton, which primarily excrete assimilated trace elements in soluble forms, have markedly different trace element efflux kinetics than bivalves. Recent studies have shown that trace element efflux rate constants in marine copepods (*Temora longicornis*; 0.07–0.3 day^{-1}) are an order of magnitude higher than in marine bivalves and are comparable to N and P excretion rates (Wang and Fisher, 1998b). Such high efflux rates in copepods may affect the biogeochemical cycling of trace elements in aquatic systems by increasing their residence times in surface waters (Wang and Fisher, 1998b). Non-essential elements (Ag, Cd) appear to be excreted at a faster rate than the essential elements and the efflux rates of the non-essential trace elements are significantly affected by the quantity of food the copepods are given during depuration and the pathway of trace element accumulation. For these metals, higher efflux rates were documented at

higher food concentrations or when the metals were obtained from food. In contrast, efflux rates of essential elements (Se and Zn) are relatively independent of food concentration and pathway of accumulation (Wang and Fisher, 1998a,b). Duration of exposure (2 days vs. 6 days food ingestion) does not affect trace element efflux rates in *T. longicornis*.

We do not have a complete mechanistic explanation for the higher trace element efflux rates in copepods than in marine bivalves. The smaller body size and higher weight-specific metabolic rate of the zooplankters could play a role, but differences in animal body size probably do not account for all differences in trace element efflux rates. Wang and Fisher (1997b) found that the efflux rate constants for Co, Se, and Zn in marine mussels are relatively independent of body size, but for Cd, the efflux rate in juvenile mussels is twice that in adults. More studies are needed of the effects of differences in biochemical trace element partitioning and detoxification capabilities on the rates of trace element elimination in organisms of different size and developmental stage.

3.3. Ingestion rates in aquatic invertebrates

Until recently, feeding activity has been largely ignored in studying trace element accumulation and bioavailability in aquatic invertebrates, presumably because food ingestion was not considered to be an important source of trace element uptake in many previous studies. Most physiological studies were concerned with the feeding responses of suspension feeders and deposit feeders to different environmental and food conditions in the laboratory. There are very few measurements of the feeding rates of aquatic invertebrates in the field.

Although ingestion rates in many aquatic animals are likely related to growth rates by fairly complicated relationships that vary with species and age, much evidence shows that for suspension feeders, ingestion rates depend on suspended particle loads and growth and ingestion are relatively independent (as implied by Eqs. 1–3). The feeding physiology of mussels has been studied extensively over the last few decades (Bayne and Newell, 1983; Jørgensen, 1990; Bayne, 1993) and illustrates key aspects common to all invertebrate suspension feeders. Mussels live in environments where seston composition and concentration exhibit diurnal to seasonal variations. At low season concentrations mussels essentially ingest any particles that can be retained in the gills by filtration activity. In this situation, mussel ingestion rates (IR, day^{-1}) can be estimated to a first approximation as a simple function of the total suspended solids (TSS, mg dry wt. l^{-1}) concentration ($IR = 0.137[TSS]^{0.421}$, Bayne, 1993). Retention efficiencies are $< 50\%$ for particles < 2 μm, but close to 100% for particles > 4 μm. Above the threshold concentration for pseudofeces production ($TSS \cong 5$ mg dry wt. l^{-1}, Widdows et al., 1979), however, mussels are able to sort particles such that nutritionally desirable food particles are preferentially ingested and a relatively constant rate of C absorption is maintained (Arifin and Bendell-Young, 1997). Sorting efficiencies of 40–65% have been reported (Kiørboe and Møhlenberg, 1981; Bayne et al., 1989). Because mussels typically live in environments where seston concentrations are higher than the threshold concentration for pseudofeces production, it is expected that some sorting of particles during the preingestive period is common for mussels.

As with mussels, ingestion rates in planktonic invertebrates increase with increasing concentrations of food (Conover, 1978). Recent studies of copepods in coastal and estuarine waters (Dam and Peterson, 1991, 1993; Lonsdale et al., 1996) report maximum ingestion rates of 42% of their body dry wt. day^{-1}. Feeding rates in copepods may depend on food quality, since copepods selectively ingest particles based on size and chemical composition (Houde and Roman, 1987; Cowles et al., 1988), but this is not always observed in the field (Turner and Tester, 1989).

In deposit feeding invertebrates, ingestion rate (IR, mg sediment day^{-1}) can be related to animal body weight (W, mg dry wt.) through a power function ($IR = 1.97\ W^{1.12}$) as shown by Cammen (1980) who studied the ingestion rates of 19 species of deposit feeders and detritivores from three phyla. Such models tend to over-estimate

the ingestion rates of deposit feeders eating organic-rich material and underestimate ingestion rates of animals feeding on organic-poor sediment. Some deposit feeding animals ingest at least twice their body weight of total sediment per day in order to obtain sufficient nutrition (Lopez and Levinton, 1987). Such high sediment ingestion rates can result in significant trace element accumulation in deposit-feeding animals. Trace element bioaccumulation estimated with a kinetic model suggests that nearly all (> 98%) of the Cd, Co, Se and Zn in a marine facultative surface deposit feeding polychaete (*Nereis succinea*) are accumulated from ingested sediments (Wang et al., in press), largely due to high ingestion rates of sedimentary particles. Much remains to be learned about ingestion rates in aquatic animals; this basic biological information is crucial to developing an accurate understanding of trace element bioaccumulation.

3.4. Growth rates in aquatic invertebrates

Growth rate is incorporated into the kinetic model to calibrate for growth dilution of trace elements in the tissues. When the growth rate constant is much smaller than the efflux rate constant, growth dilution can be ignored in the model calculation, but when the growth rate constant exceeds or is comparable to the efflux rate constant, it should be incorporated. For example, growth dilution is important in cases where $g \gg k_e$ such may occur for methylmercury in fish ($k_e \cong 0.002$ day^{-1}, Trudel and Rasmussen, 1997), and is less important when $k_e \gg g$, as is the case for a number of trace elements in mussels ($g = 0.002$ day^{-1}, Connolly, 1991; $k_e \cong 0.02$ day^{-1}, Wang et al., 1996a). Steady-state trace element concentrations in the soft tissues of adult mussels predicted using a kinetic model in which growth dilution is neglected are within a factor of two to three of the actual trace element concentrations measured in field-collected mussels (Wang et al., 1996a). In general, growth rates are related by a power law to body size. Thus growth dilution can become a significant factor in trace element trophic transfer and bioaccumulation in smaller organisms and in adult organisms (such as bivalves) that experience seasonal changes in tissue mass related to their reproductive cycles. Growth rate constants in juvenile mussels (0.01–0.1 day^{-1}, Jørgensen, 1996) are equal to or higher than trace element efflux rate constants and thus need to be included in kinetic model predictions (Wang and Fisher, 1997b). More concerted effort is needed to link growth and bioaccumulation studies in different species and on different time scales. Kinetic models offer one context to study such linkages.

4. Applications of the kinetic model approach

4.1. Biomagnification

Trace element biomagnification occurs when concentrations in the tissues of one organism exceed those in its food or in an adjacent trophic level ($C_{ss}/C_f > 1$). Thus trace elements that are biomagnified as a result of trophic transfer have trophic transfer potentials ($\mathrm{TTP} = \mathrm{AE} \cdot \mathrm{IR}/k_e + g$) that are > 1 (see Eq. 4). Biomagnification of methylmercury in aquatic food webs is well known and is evident in repeated observations of the highest concentrations in large, long-lived, upper trophic level organisms (Lindqvist et al., 1991; Watras and Bloom, 1992; Cabana et al., 1994; Hill et al., 1996). The enrichment of methylmercury over inorganic mercury in aquatic consumers is partly due to greater trophic transfer of methylmercury (Boudou and Ribeyre, 1985; Riisgard and Hansen, 1990; Saouter et al., 1993; Mason et al., 1996). It is less widely reported, but Se is also usually biomagnified when concentrations are compared between adjacent trophic levels (Luoma et al., 1992) or when the highest trophic levels are compared to the lowest (Brown and Luoma, 1995a).

Mercury and selenium aside, conventional wisdom holds that biomagnification is of limited occurrence for most trace elements (Young et al., 1980; Amiard-Triquet et al., 1980; Timmermans et al., 1989), but supporting observations can be ambiguous. Biomagnification is often evaluated by comparing element concentrations in generalized feeding guilds at high trophic levels with concentrations in feeding guilds at lower levels. For example, Timmermans et al. (1989) compared

Cd, Pb, Cu and Zn concentrations in whole bodies of 15 species of macroinvertebrates from three feeding categories in Marrseeveen Lake, The Netherlands. Although biomagnification did not always occur among feeding categories, when specific predator–prey pairs were compared, cadmium and zinc concentrations were magnified between trophic levels. Knowledge of trophic links is admittedly difficult to obtain with certainty in many aquatic communities (Mihuc and Minshall, 1995), but it may be an important requirement for a careful analysis of biomagnification.

The evaluation of biomagnification is also ambiguous when it involves comparisons of element concentrations in whole bodies of predators with concentrations in whole bodies of primary producers or consumer species or among fish or between fish and invertebrates. Comparisons between fish and invertebrates can be biased by important biological differences among species (e.g. Young et al., 1980). Trace elements are accumulated as a function of environmental exposure in certain organs such as the liver in fish (Bollingberg and Johnasen, 1979; Bendell-Young and Harvey, 1986), but concentrations of many trace elements (e.g. Ag, Cd, Cu, Cr Pb, Zn; Hg and Se are notable exceptions) are regulated to very low levels in fish muscle (Wiener and Giesy, 1979; Bohn and Fallis, 1978). Muscle contributes the most mass to the whole body of a fish so whole body trace element concentrations in fish constitute a large mass in which trace element concentrations are regulated and a small mass of organs like the liver and kidneys in which trace element concentrations reflect exposure. For most trace elements, whole tissues of invertebrates are much more responsive to exposure than whole tissues of fish.

A hypothetical calculation of this effect is possible from existing data. Moore et al. (1991) analyzed metal concentrations in predatory trout and detritus feeding aquatic insects (often the prey of trout) along a river gradient affected by upstream mine waste inputs. At the most contaminated station, concentrations of Cu in the livers of brook trout were 311 ± 51 $\mu g\ g^{-1}$ and concentrations in whole bodies of the mayfly *Limnophilus* were 27 $\mu g\ g^{-1}$. A liver vs. whole body comparison would suggest Cu is biomagnified in this river. However, if a typical trout from these waters had 2 $\mu g\ g^{-1}$ Cu in muscle tissue (S.N. Luoma, personal communication; this number is at the high end of Cu concentrations in fish muscle from all the studies cited above) and approx. 3% of the body weight is liver, then the whole body trout concentration would be $(0.97)(2) + (0.03)(311) = 1.9\ \mu g\ g^{-1} + 9.3\ \mu g\ g^{-1} = 11.2\ \mu g\ g^{-1}$. A whole body comparison indicates that Cu is not biomagnified.

It may be difficult to use field data to unambiguously determine if a trace element is being transported into a predator from its food at a high enough rate to be biomagnified. Kinetic models might aid such analyses. For example, if we assume a food concentration of one unit and a constant feeding rate, then what combination of assimilation efficiency and loss rate (or loss plus growth) would yield a steady-state concentration in the feeding organism of greater than one unit (i.e. what combination of AE and k_e results in a trophic transfer potential $[AE \cdot IR/k_e + g]$ that is > 1)? Fig. 1 shows the areas of the relationship between AE and k_e where biomagnification would be expected and where it would not for zooplankton (copepods), bivalves, and fish. The boundary between the regions of biomagnification and non-biomagnification shift as feeding rates change or if growth adds to the loss constant. The figure is informative with regard to specific metals and species, and it illustrates important needs for greater knowledge. In general, rate constants of loss for methylmercury are low for most species (0.001 day^{-1} or less, Cunningham and Tripp, 1975; Fowler et al., 1978; Riisgaard et al., 1985; Trudel and Rasmussen, 1997). Even if assimilation efficiencies from food sources were moderately low (10–30%) some biomagnification would be expected. However, because AEs of methylmercury are in fact often high, biomagnification of methylmercury is commonly observed. The low rate constant of loss also means that bioaccumulation will extend for long periods of time before steady-state is attained, thus the phenomena is accentuated in the longest lived organisms.

Selenium is lost at a more rapid rate than Hg (the k_e for Se in bivalves ranges from 0.01 to 0.03 day^{-1}, Reinfelder et al., 1997), but assimilation

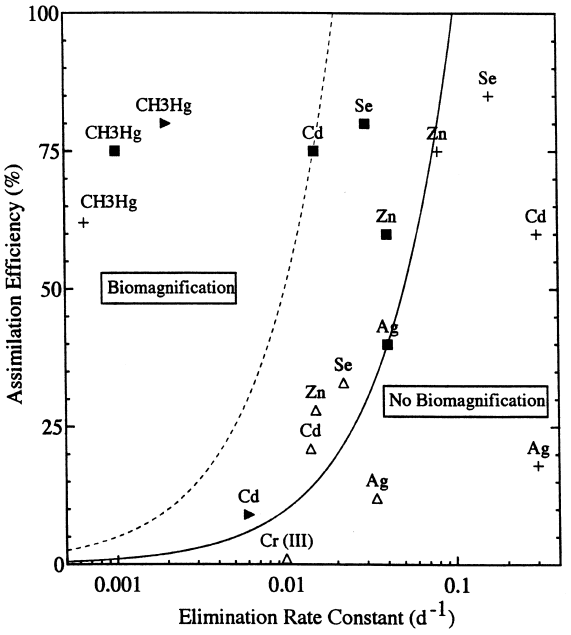

Fig. 1. Regions of trace element biomagnification and non-biomagnification in zooplankton (marine copepods, +), bivalves (*Crassostrea virginica*, *Mercenaria mercenaria*, *Macoma balthica*, ■; *Mytilus edulis*, Δ), and fish (►) as predicted by measured assimilation efficiencies (AE) and elimination rate constants (k_e) for each trace element–organism pair assuming a constant ingestion rate (IR) and a negligible growth rate ($g \ll k_e$). Lines represent steady-state trophic transfer potentials ($AE \cdot IR/k_e$) of 1 ($C_{consumer}/C_{prey} = 1$) for fish (dashed line, IR = 0.02 day^{-1}) and invertebrates (solid line, IR = 0.1 day^{-1}) and divide the graph into areas where biomagnification is expected ($AE \cdot IR/k_e > 1$) and where it is not ($AE \cdot IR/k_e < 1$). Copepod AEs are from Reinfelder and Fisher (1991) and Wang et al. (1996b) except for CH_3Hg (Mason et al., 1996). Copepod k_es are from Wang and Fisher (1998a) except that for CH_3Hg which was based on data for euphausiids (Fowler et al., 1978) and crayfish (Headon et al., 1996). Bivalve AEs and k_es are from Reinfelder et al. (1997) except for CH_3Hg: AE, Riisgard and Hansen (1990); k_e, Okazaki and Panietz (1981). Mussel AEs and k_es are from Wang et al. (1996a) except for Cr(III) (Wang et al., 1997). For Cd in fish, the AE is from Reinfelder and Fisher (1994b) and the k_e is from Schultz et al. (1996). For CH_3Hg in fish, the AE is from Norstrom et al. (1976) and the k_e is from Trudel and Rasmussen (1997).

efficiencies of Se from most living food sources are very high (often > 70%) (Luoma et al., 1992; Reinfelder and Fisher, 1994b; Wang et al., 1996a). Selenium biomagnification would be expected, and is observed, in these cases because of the high AE. We might, however, expect exceptions to this generalization when organisms ingest forms of Se such as elemental Se in sediments for which AEs are reduced (Luoma et al., 1992). Similar logic applies to Cd. Rate constants of loss are more often approx. 0.01 day^{-1} for Cd, but AE varies widely among food types. Biomagnification of Cd is rarely recognized, but might in fact be expected for organisms like filter feeders, that assimilate Cd from phytoplankton with AEs in excess of 20% (Reinfelder et al., 1997), or predators that assimilate Cd with greater than 20% efficiency from their prey. High Cd AEs may be likely if a relatively high proportion of Cd occurs in the cytoplasmic fraction (the most transferable form of the element — Reinfelder and Fisher, 1991; Wallace and Lopez, 1996; Munger and Hare, 1997) of ingested food. Biomagnification of Cd might not be expected in organisms with a large component of detritus or sulfide-rich sediment in their diet such as deposit feeders. Cr is an example of an element that is probably never biomagnified because of its overall low AE and relatively high rate constants of loss (Decho and Luoma, 1991; Wang et al., 1997). High rate constants of loss for many trace elements in copepods suggest that biomagnification may be generally rare in zooplankton.

Biomagnification is most important when applied to upper trophic levels. If an element is biomagnified at each trophic step, then organisms several steps from the base of the food web could be affected to a greater extent by contamination at lower environmental concentrations than the rest of the food web (e.g. Se). One of the important functions of a model is to generate hypotheses. The above analysis raises the possibility that biomagnification of elements like Cd and Zn is possible. If Cd in particular has the potential to be biomagnified, then investigation of trophic transfer in upper trophic level species and trace element effects on these organisms (a largely under-studied area) takes on more significance in polluted environments.

4.2. Comparisons among species

Kinetic models can provide a framework for

understanding why concentrations of trace elements in tissues differ among species, and whether such differences reflect different exposures (and thus different potentials for adverse effects) in the same environment. Only a few such comparitive analyses have been made, but intriguing explanations of bioaccumulation differences are beginning to emerge. For example, it is possible to make first-order predictions of trace element trophic transfer potentials among related organisms such as marine bivalves by comparing their AE:k_e ratios since bivalve growth rates are an order of magnitude lower than efflux rates and IR values vary more with environmental conditions (particle concentration) than between species. This kind of analysis showed that mussels (*Mytilus* spp.) have significantly lower trophic transfer potentials for the important contaminant metals Ag, Cd, and Zn than oysters (*Crassostrea virginica*) or clams (*Macoma balthica* and *Mercenaria mercenaria*) (Reinfelder et al., 1997), but that all four bivalves have relatively low Co trophic transfer potentials and high Se trophic transfer potentials. The relative importance of assimilation and elimination to differences in the trophic transfer potential among species can also be evaluated. For example, the elimination rate constant (k_e) accounted for 67, 72 and 92% of the difference in AE:k_e ratios between oysters (*C. virginica)* and mussels (*Mytilus edulis*) for Ag, Cd, and Zn, respectively (Reinfelder et al., 1997).

The analysis of AEs and k_es has also been used to compare trace element trophic transfer in two bivalves (*Potamocorbula amurensis* and *Macoma balthica*) that live in the same environment (San Francisco Bay), but employ different feeding and digestion strategies (Decho and Luoma, 1991, 1994, 1996; Lee and Luoma, 1998). Both of these species pass a substantially greater proportion of ingested food through the digestive gland than do mussels or oysters, but the filter feeder, *P. amurensis* is more flexible in the proportion of food shunted through the digestive gland than the deposit feeder *M. balthica* (Decho and Luoma, 1994). As a result, *P. amurensis* absorbs more Cr from bacterial food than *M. balthica* because of the larger proportion of bacteria shunted through the digestive gland and a more efficient assimilation of Cr in the digestive gland than in the intestine (Decho and Luoma, 1991). Unlike most bivalves, *P. amurensis* can have high Cr concentrations in North San Francisco Bay (Brown and Luoma, 1995b), perhaps as a result of Cr assimilation from available food (see also Wang et al., 1997). Because of its long gut retention time and high proportion of glandular digestion, *M. balthica* assimilates some elements (Am) normally considered recalcitrant to bioaccumulation (Reinfelder et al., 1997).

4.3. Comparison of model predictions with trace element bioaccumulation in nature

The kinetic model can not only be used to quantify the relative importance of trace element bioaccumulation from food and from water, it can also be used to provide site-specific predictions of metal concentrations in marine animals. For example, Luoma et al. (1992) found that model-predicted Se concentrations (1.1–8.6 $\mu g\ g^{-1}$) in clams (*Macoma balthica*) in a variable San Francisco Bay habitat compared well with independently measured values (2.95–6.7 $\mu g\ g^{-1}$). This approach has been applied to a number of trace elements in the mussel *Mytilus edulis* in which good agreement between model-predictions and field measurements was found for Ag in San Francisco Bay (0.35–0.77 $\mu g\ g^{-1}$ measured, 0.3–2.09 $\mu g\ g^{-1}$ predicted) and Long Island Sound (0.04–0.44 $\mu g\ g^{-1}$ measured, 0.43–0.93 $\mu g\ g^{-1}$ predicted), Cd in San Francisco Bay (4.4–9.4 $\mu g\ g^{-1}$ measured, 2.7–10.1 $\mu g\ g^{-1}$ predicted) and Long Island Sound (1.5–6.2 $\mu g\ g^{-1}$ measured, 2.9–7.0 $\mu g\ g^{-1}$ predicted), Cr in San Francisco Bay (3.0–5.1 $\mu g\ g^{-1}$ measured, 2.6–7.5 $\mu g\ g^{-1}$ predicted), Se in San Francisco Bay (2.5–6.7 $\mu g\ g^{-1}$ measured, 1.0–5.6 $\mu g\ g^{-1}$ predicted), and Zn in San Francisco Bay (54–130 $\mu g\ g^{-1}$ measured, 54–265 $\mu g\ g^{-1}$ predicted) and Long Island Sound (52–142 $\mu g\ g^{-1}$ measured, 34–157 $\mu g\ g^{-1}$ predicted) (Wang et al., 1996a, 1997). In this study, there were no instances in which model predictions were appreciably different from measurements of field collected mussels, although more detailed comparisons of field and monitoring results are certainly in order. Recent work by Fisher

and colleagues (in preparation) indicates that model predictions of trace element concentrations in marine calanoid copepods are also similar to field measurements. These comparisons suggest that the kinetic bioaccumulation model may account for the most important factors governing trace element accumulation in these animals and that the experimentally generated numerical values of the parameters used in the model are applicable to natural waters. The model is sufficiently flexible for use in complicated natural settings; further applications to such settings, including comparisons of model predictions with field data, will be an important area of new research.

4.4. Application of kinetic trophic transfer models to fish

The importance of trophic transfer to the accumulation of the biomagnified trace elements (Hg as CH_3Hg, Se, Cs) in fish is widely accepted (Lemly, 1996; Wiener and Spry, 1996; Rowan, 1998). For most other trace elements (including Ag, Al, Cd, Co, Cu, Pb, Mn, Ni, and Zn), however, there is a lack of consensus about the importance of dietary uptake by fish. These trace elements typically are not considered to biomagnify in fish (but see *Biomagnification* above), but because of their occurrence in impacted environments and demonstrated toxicity to aquatic life, may present an environmental hazard.

Laboratory studies have suggested that food may contribute substantially to total uptake of some trace metals, even in the absence of biomagnification, but the environmental relevance of these results has been questioned due to methodological shortcomings. In laboratory studies with these metals, dietary assimilation efficiencies estimated from tissue residues are generally $< 5\%$. Nevertheless, trace element uptake by fish has been demonstrated in feeding studies with Cd (Williams and Giesy, 1978; Hatakeyama and Yasuno, 1987; Harrison and Klaverkamp, 1989; Douben, 1989a; Wicklund-Glynn et al., 1992; Kraal et al., 1995), Cu (Julshamn et al., 1988; Miller et al., 1993), Zn (Spry et al., 1988), and Co (Baudin and Fritsch, 1989). A limited number of studies suggest that little or no Pb is taken up by fish from the diet (Hodson et al., 1978) and feeding studies with Al have not been conducted, but the absence of Al accumulation in any tissue except the gills in fish collected from the field argues against dietary uptake (Spry and Wiener, 1991). Trophic accumulation of 'non-biomagnified' metals has also been reported in field studies (Dallinger and Kautzky, 1985; Bendell-Young et al., 1986; Douben, 1989b), but unambiguous evidence of trophic transfer has been elusive (Miller et al., 1992).

The relative importance of food and water to trace element accumulation in fish can be evaluated quantitatively using the kinetic model approach (Thomann et al., 1997). Linear one-compartment kinetic models of metal bioaccumulation in fish have been developed by assuming that k_u, AE, and k_e are fixed values; that is, the system is first-order with respect to chemical concentrations in water, food, and the organism (Douben, 1989a; Harrison and Klaverkamp, 1989). Linear models of greater complexity have also been developed to describe the multiexponential kinetics that are frequently observed during depuration studies (Baudin and Fritsch, 1989; Wicklund-Glynn et al., 1992).

Increasingly, however, it appears that while trace element uptake from water tends to be proportional to the concentration in water (k_u not regulated), uptake of some trace elements from the diet tends to be 'regulated' resulting in a less than proportional increase in tissue concentration for a given increase in the trace element concentration in food. This phenomena has been observed for both essential (Zn) and non-essential (Cd) trace metals (Spry et al., 1988; Douben, 1989a). The net effect of this route-specific difference in uptake kinetics is that, assuming equilibrium between the food and the water, as the dissolved metal concentration increases, the relative importance of water as a route of uptake increases. The mechanism by which fish regulate the accumulation of dietary trace element is poorly known and could conceivably involve concentration-dependent changes in absorption across the gut (AE) or adaptive changes in elimination pathways (k_e). The extent of regulation

may also vary among different tissues. When rainbow trout were exposed to Zn in food and water, Zn residues in plasma were regulated within a narrow range of concentrations except under conditions of Zn deprivation. Zn concentrations in muscle also appeared to be regulated, but less tightly than in other tissues (Spry et al., 1988).

The disposition of trace elements once they are absorbed by fish is poorly known. In general, metals accumulate in tissues that comprise the site of uptake (gill and/or intestine), while metal concentrations above average whole-body levels are usually found in the liver and kidney regardless of the route of uptake. These patterns have been attributed to high levels of metal-binding proteins in all four tissues (Roesijadi, 1992). The role of metal binding proteins in the movement of metals across biological membranes and from the site of uptake to various tissues and organs is less well known. In depuration experiments with rainbow trout, Cd concentrations in the liver and kidney increased for a period of weeks while levels in the gut tissues and white muscle steadily declined (Harrison and Klaverkamp, 1989; Wicklund-Glynn et al., 1992). A similar finding was reported by Schultz et al. (1996) for catfish administered a single intravascular dose of Cd. Cu taken up from the diet by rainbow trout also redistributed to liver and kidney during depuration, but less strongly so than Cd (Handy, 1992). These tissue-specific observations provide an explanation for the biexponential kinetic behavior seen when depuration data are collected on a whole-animal basis. Moreover, the value of k_e estimated from the terminal phase of depuration time-course data may vary with the route of exposure. In depuration studies with carp, Co taken up from food was eliminated faster than that taken up from water (Baudin and Fritsch, 1989). A similar finding was reported by Harrison and Klaverkamp (1989) for rainbow trout exposed to Cd. In the same study, however, the value of k_e did not differ for lake whitefish exposed via food or water.

Whether or not diet is an important route of trace element uptake in fish is more than just a matter of academic interest. Metals taken up across the gills and gut accumulate in different tissues and therefore pose different toxicological threats to receptor fish. Evidence of this was provided by Miller et al. (1993), who found that waterborne preexposure to Cu conferred a significant increase in Cu tolerance to rainbow trout, while dietary preexposure resulted in only a marginal increase in Cu tolerance. As waterborne Zn had been shown to induce metallothionein (MT) in fish (Bradley et al., 1985) while dietary exposure did not (Overnell et al., 1988), Miller et al. (1993) speculated that a possible cause for the observed difference in Cu tolerance was a route-specific difference in MT induction. These observations have important implications for toxicity testing and the interpretation of field residues.

Based upon laboratory studies, the strongest evidence for the trophic transfer of 'non-biomagnified' trace elements in fish exists for Cd. However, much of the research conducted to date presents problems of interpretation. Future studies should be performed using realistic prey organisms that have been uniformly radiolabeled over several weeks of continuous exposure, since bioavailability likely varies for trace elements in different prey tissues. For example, trace elements associated with chitin in the exoskeleton of invertebrates are not assimilated by fish (Reinfelder and Fisher, 1994b). Because animals transport, sequester and detoxify trace elements via specific biochemical pathways, it is important to test trace element concentrations and chemical species in food and water that are likely to be encountered in the environment and to evaluate the concentration dependence of all relevant measurements.

A need exists to obtain independent estimates of k_u, AE, and k_e. Numerous studies have suggested that branchial uptake of metals (k_u) occurs in fish and tends to be proportional to the total metal concentration in the water. The absolute rate, however, is likely to be highly dependent upon factors such as ionic strength and organic ligand concentration that control the concentrations of bioavailable species. Major differences in soluble trace element uptake are expected between freshwater and saltwater fish. Because of osmoregulatory constraints, saltwater fish drink substantial quantities of water and produce

small amounts of very concentrated urine. They are also adapted to deal with potentially toxic levels of ions in the external medium. In contrast, freshwater fish drink very little if at all, produce large quantities of dilute urine and are adapted to recover needed ions from an extremely dilute pool.

Direct measurements of gill uptake rate are not available for most metals and may be very difficult to obtain. Whole-body trace element concentrations measured after a period of waterborne exposure provide a lower bound estimate of branchial uptake, but will underestimate true uptake if there is any extrabranchial elimination. Using fish respirometer–metabolism chambers, Choi et al. (1998) measured methylmercury uptake across the gills of Sacramento blackfish (*Orthodon microlepidotus*) and evaluated the effect of changing DOC concentrations. These measurements depended, however, on there being a measurable difference between chemical concentrations in inspired and expired water. Low rates of metal uptake may not be sufficient to provide this difference.

Accurate measurements of AE may also be difficult to obtain. In most instances, AE has been estimated from metal residues in fish after feeding them for a period of time ranging from days to weeks. For some organic contaminants that are very poorly eliminated, AE estimates obtained in this manner are a good surrogate for true AE. With metals, however, substantial elimination may occur during the course of an experiment. Thus, AE determined from tissue residues represents the net result of true AE and k_e. Alternatively, researchers have used simple kinetic models and independent estimates of k_e (from depuration studies) to calculate AE (Harrison and Klaverkamp, 1989). This approach is preferred to the residue-based method but is dependent upon the validity of the model.

An alternative way to estimate AE is to employ the method used by pharmacologists to measure the oral bioavailability of drugs. In this procedure, the element or compound of interest is administered in food. Later, after the first dose has been cleared, the animal is administered an equivalent amount of the element or compound as an intravascular dose. The AE is then calculated as the ratio of the area under the plasma concentration–time curve (AUC) for oral dosing to the AUC for intravascular dosing. Recently, this technique was employed to estimate the AE for methylmercury in channel catfish (McCloskey et al., 1998). To date, it has not been used for any other metals in fish. This method has the advantage that it is model independent and is only minimally impacted by elimination. A disadvantage is that subsequent to oral dosing, pathways for metal uptake and/or clearance may be induced impacting the disposition of the intravascular dose. This technique also requires the collection of repeated blood samples and is therefore best suited to fish that are large enough to cannulate.

As a compliment to these investigations, there is a need to understand AE in terms of the form of metal that is taken up. In the GI tract it is likely that nearly all metal is bound to biological material and that mechanisms exist to facilitate the absorption of this material. Thus bioavailability in the gut may not depend on the free ion or total inorganic metal concentration as is observed in biota that are in direct contact with water (e.g. bacterioplankton, phytoplankton, and zooplankton; see Campbell, 1995). As indicated previously, the accumulation of several metals from dietary sources appears to be regulated. One possibile mechanism for regulation is the induction of elimination pathways, in which case k_e would change (increasing with the concentration of metal), but not true AE. However, the possibility also exists that metal uptake from the gut is itself regulated. One possible mechanism for this is saturation of the uptake pathway at high metal concentrations. If a specific transport system is involved in metal uptake, animals could also respond to high dietary levels by regulating the numbers and/or properties of the transporter. Finally, studies with mammals have shown that high metal concentrations in the diet can induce increased MT levels in the gut tissues themselves, effectively sequestering metal at the site of uptake (Ohta and Cherian, 1991). Elimination would then occur due to the high rates of epithelial cell sloughing that are typical of the GI tract. Limited

data indicate that, contrary to what might be expected, regulation of dietary metal does not bear any obvious relationship to whether the metal is essential or non-essential. Additional work is needed, however, to confirm this suggestion.

Improved estimates of k_e are also required. As indicated previously, biexponential kinetics have been observed in depuration studies with several metals. The 'fast' phase of elimination has been conceptualized as metal that is adsorbed to external surfaces or complexed to low-affinity ligands, while the 'slow' phase corresponds to metal that is sequestered by calcified structures or tightly bound by high-affinity ligands (Roesijadi and Robinson, 1994). The elimination half-lives ($t_{1/2}$, equal to $0.693/k_e$) of Cd and inorganic Hg for the fast compartment is on the order of hours to days, while that for the slow compartment is on the order of weeks to months (Schultz et al., 1996). Mechanisms by which metals are eliminated by fish remain largely unknown (Roesijadi and Robinson, 1994). In mammals, metals are eliminated in urine and bile, the predominant route depending upon both the metal and the species. Urinary elimination depends upon glomerular filtration of metal-binding proteins (e.g. albumin) present in plasma. Limited estimates of glomerular filtration rate are available for freshwater fish (the saltwater-adapted kidney is essentially aglomerular). However, the activity of metal-binding proteins in fish plasma is essentially unknown.

There is a need to develop improved kinetic models of trace element accumulation in fish. In general, modeling efforts for trace elements lag behind those for organic compounds. Advanced compartmental models such as that of Thomann et al. (1997) for Cd in trout represent a significant improvement in the state of the science. Eventually, however, there is a need to develop more physiological models that explicitly incorporate mechanistic observations. Future models for dietary uptake of trace elements in fish will require the adoption of 'saturable' (i.e. non-linear) kinetics. Many examples of such models that treat regulatory processes (e.g. protein binding in blood, metabolic biotransformation) explicitly exist in the mammalian literature, but nothing of this kind has been used to model trace element uptake by fish.

5. Conclusions

Kinetic bioaccumulation models are increasingly being used for basic research of trace element uptake in aquatic organisms and the establishment and assessment of regulatory guidelines. In addition to these applications, kinetic bioaccumulation models may find use in other areas of aquatic ecology and environmental science. For example, model predicted trace element bioaccumulation in specific organs of target species could be used to link uptake with expected toxicity. Kinetic bioaccumulation models could also be used to compare the fate of trace elements in different ecosystems and may provide a new tool for the study of trophic linkages in aquatic food webs.

The predictive power of kinetic bioaccumulation models (at least with respect to aquatic invertebrates) has improved recently as a result of the development and use of methods for the quantification of trace element assimilation efficiencies and elimination rate constants, but further refinement of these and other model parameters is needed. Furthermore, in only a few cases have these models been field tested. This review suggests a number of specific informational needs for model improvement:

- thorough assessment of the independence of model parameters; e.g. How do ingestion rates and trace element assimilation efficiencies vary with growth rate?
- trace element assimilation efficiencies in deposit feeders and carnivores using realistic prey;
- comparison of real trace element partitioning between rapidly and slowly exchanging pools with that of radiotracers in laboratory experiments to assess reliability of experimental elimination rate constants;
- assessment of how trace element elimination rate constants vary with organism size and developmental stage;

- development of non-linear (saturable uptake) bioaccumulation models for fish and target tissues in other aquatic organisms in which trace element accumulation is largely regulated.

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