Trace metals in marine copepods: a field test of a bioaccumulation model coupled to laboratory uptake kinetics data

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ABSTRACT· A first order bioenergetic-based kinetic model has been developed to describe metal accumulation in marine copepods. To field-test predictions of the kinetic model regarding metal concentrations in marine zooplankton, we analyzed Cd, Zn, Ag, Co, and Se in water, phytoplankton, and zooplankton samples collected off the coast of Monaco. Mean concentrations in copepods were 1.3 nmol g^{-1} for Ag, 22.2 nmol g^{-1} for Cd, 9.5 nmol g^{-1} for Co, 16.0 nmol g^{-1} for Se, and 2570 nmol g^{-1} for Zn; mean dissolved metal concentrations were 10.5 pM Ag, 72.3 pM Cd, 260 pM Co, and 4270 pM Zn. For each metal, model-predicted concentrations in zooplankton using kinetic parameters for influx rates from the dissolved phase, assimilation from ingested phytoplankton, and efflux rates measured in laboratory experiments generally matched field measurements, although discrepancies were noted, especially for Cd where a 4-fold difference between predicted and measured concentrations was observed. Overall, it appears that it is possible to account for the major processes governing metal accumulation from food and water in marine copepod populations.

KEY WORDS: Modeling · Zooplankton · Copepods · Silver · Cadmium · Cobalt · Selenium · Zinc

INTRODUCTION

Zooplankton are key links in the transfer of carbon and trace elements through marine food webs. Metals can accumulate in marine zooplankton from both the dissolved phase and from ingested food. Losses of metals from zooplankton include metal excretion or metal egestion by feces production. Understanding the rates and routes of metal bioaccumulation in marine zooplankton is important for predicting their biogeochemical fates in marine surface waters. Experimental stud-

ies have described the bioaccumulation of trace metals in marine copepods from diverse algal foods and from the dissolved phase (Fisher et al. 1991, Reinfelder & Fisher 1991, Wang et al. 1996, Wang & Fisher 1998a). Key first-order parameters of bioaccumulation, particularly metal assimilation efficiency from ingested food, uptake rate constants from the dissolved phase, and efflux rate constants following uptake from either food or water, were measured in these studies. By combining this information with known ingestion and growth rates of these animals, it has been possible to model the bioaccumulation of these metals in copepods using a first order bioenergetic-based kinetic model (Wang & Fisher 1998a). This model is similar to a kinetic model developed for copepods by Ritterhoff & Zauke (1997a,b), although the latter did not distinguish between uptake from food and from water. Assuming

that marine animals accumulate metals from the dissolved phase and from food, the concentration of a metal in an animal (C_{ss}, nmol g^{-1}) under steady-state conditions can be described as:

$$C_{ss} = \frac{(k_u \times C_w)}{(K_{ew} + g)} + \frac{(IR \times AE \times C_f)}{(k_{ef} + g)} \qquad (1)$$

where, k_u is the uptake rate constant of the metal from the dissolved phase (l g^{-1} d^{-1}), C_w is the metal concentration in the dissolved phase (nM), IR is the ingestion rate of the animal (g g^{-1} d^{-1}), AE is the assimilation efficiency (%) of the metal from ingested food particles, C_f is the metal concentration in the food (nmol g^{-1}), k_{ew} is the efflux rate constant from animals following uptake from the dissolved phase (d^{-1}), k_{ef} is the metal efflux rate constant from animals following uptake from food (d^{-1}), and g is the growth rate constant of the animals (d^{-1}).

This model provides a quantitative separation of the routes of metal uptake in these animals on a metal-specific basis. The model also enables predictions to be made, on site-specific bases, about metal concentrations in zooplankton if the dissolved and phytoplankton metal concentrations are known. Note that the model considers metal accumulation that is related to physiological processes (e.g., ingestion rates, assimilation of ingested metals, excretion rates) as well as chemical factors (e.g., dissolved and particulate metal concentrations). If the model's predicted metal concentrations match closely with measured concentrations in field-collected zooplankton, it could be concluded that all the principal biological and chemical factors which govern metal uptake in these animals are taken into account and that the laboratory measurements of kinetic parameters are applicable to field situations. To test the field applicability of our laboratory work and the validity of the model's assumptions, we conducted a study to make field measurements of zooplankton metal concentrations using trace-metal clean techniques and simultaneously measured metal concentrations in water and in suspended particulate assemblages which serve as food for the copepods. The metal concentrations measured in copepods from the field were then compared with metal concentrations predicted by the kinetic model.

MATERIALS AND METHODS

Field sampling took place from 7 to 11 July 1997 (surface water temperature of 21°C) during a copepod bloom in the Ligurian Sea off the coast of Monaco; the sampling stations in Monaco Bay are marked on 2 transects in Fig. 1. Because zooplankton are comprised of species from several different taxonomic groups, con-

centrations of trace elements in undifferentiated samples are difficult to inter-compare because species composition changes over time. Therefore, it is important to separate microzooplankton down to organism type in order to get realistic estimates of trace metal content. This task becomes much easier when zooplankton blooms occur which normally involve 1 or 2 dominant species (as in the present study). Alternatively, individuals of a single species must be hand-picked using a dissecting microscope, which often introduces the possibility of significant trace metal contamination.

Zooplankton were collected with surface plankton tows using an all-plastic 102 µm mesh plankton net (Sea Gear Corp.). The net was placed about 2 m away from the boat with the help of a mechanical arm connected to a winch. Plastic sieves of 1500 and 800 µm mesh size separated copepods from larger zooplankton. Copepods were allowed to defecate for 12 h prior to metal analysis so that measured metal concentrations primarily reflected tissue concentrations without pronounced influence of undigested food within the gut. From microscopic examination we estimate that >90% of the gut contents were lost from the copepods. To separate fecal material from the copepods, the animals were placed into a large 40 l modified funnel system (La Rosa 1976) where fecal pellets released by the copepods fell to the bottom of the funnel through a 100 µm mesh.

Seawater samples were collected 1 m below the surface using a peristaltic pump equipped with acid-washed C-flex tubing in the pump head and in-line filtration (acid-washed 0.2 µm polypropylene cartridge filter, MSI Inc.). Water was drawn through acid-
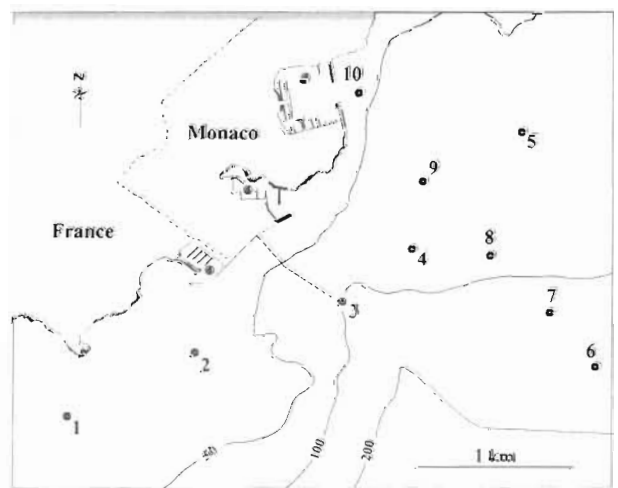

Fig. 1. Map depicting location of sample stations in the Mediterranean

washed Teflon tubing attached to a stainless steel pole which was oriented 5 m upstream of the ship's drift. The tubing was allowed to purge at least 5 volumes before the sampling began. The water column protocols and acid-washed cleaning techniques have been detailed elsewhere (Flegal et al. 1991). Samples for the particulate metals were collected independently. Suspended particulate matter out of 8 l of seawater at each station was collected on acid-washed Nuclepore filters (0.2 μm) mounted on an in-line filtration system (Savillex). Microscopic examination of the filtered particulate matter indicated that phytoplankton made up a small fraction of the suspended particles, confirmed by the measured chlorophyll values. For chlorophyll determinations, water samples were collected with a plastic bucket and stored in the dark in 2 l polypropylene bottles. Samples were filtered within 24 h through a GF/C glass fiber filter and stored at −20°C. Chlorophyll was extracted and analyzed according to Parsons et al. (1984a) with a Turner Designs Fluorometer. The dry weights of total suspended particles caught on tared 0.2 μm Nuclepore filters were measured after drying at 80°C.

Dissolved trace metals were preconcentrated using ammonium 1-pyrrolidinedothiocarbamate-/dimethyl-ammonium diethyldithiocarbamate (APDC/DDDC) organic extraction (Bruland et al. 1985). Particulate matter and zooplankton samples were digested for 2 h in Teflon bombs immersed in boiling water with 1 ml each of concentrated Q-HNO$_3$ and 6 N Q- HCl. After this initial digestion, the samples were digested again for another 2 h with 100 μl of Q-HF added (Landing & Bruland 1987). Metal concentrations were determined by graphite furnace atomic absorption spectroscopy (AAS) (Hitachi 8100) with a Zeeman background correction, using standard addition protocols. As an independent check on metal concentrations in the copepods, aliquots of copepod tissue were also measured by ICP-MS, following standard protocols. Briefly, freeze-dried copepod tissues were mineralized with small quantities of high purity HNO$_3$ in a microwave oven, taken to dryness by evaporation, redissolved in 1 ml HNO$_3$ and made up to volume. Cadmium, Ag, Co and Zn were measured by ICP-MS using direct calibration with internal standard normalization (Ge, In, Re). Multiple isotopes were used wherever possible to screen for possible interferences. Results are given as an average of acceptable values. The quality of the copepod measurements was controlled by analyzing 3 different certified reference materials: DORM-1 dogfish muscle from NRCC, TORT-2 lobster hepatopancreas from NRCC, and MA-A-2/TM fish muscle from the IAEA. Our results were in good agreement (within the 95% confidence limits of expected values) with the certified values.

RESULTS AND DISCUSSION

Total suspended particle loads ranged from 0.48 to 1.44 mg dry wt l^{-1} and chlorophyll a (chl a) concentrations ranged from 2.7 to 162 ng l^{-1} at all stations. The selective sieving of the zooplankton net hauls was effective in isolating adult copepods and eliminating larger or smaller zooplankton. The copepods sampled were dominated by adult calanoids, particularly *Acartia clausi*; other abundant species included *Centropages typicus*, *Paracalanus parvus*, and *Clausocalanus* sp. Previous distribution studies have demonstrated that copepod abundance among the zooplankton off Monaco averages 60 to 70% (max. 95%), with calanoids often being the dominant group (Corletti & Boisson 1988).

Metal concentrations in water, suspended particles (including phytoplankton), and mixed copepods are presented in Table 1. Dissolved Ag ranged from 7 to 17 pM, Cd from 50 to 97 pM, Co from 200 to 322 pM, and Zn from 3140 to 8680 pM. Metal concentrations in suspended particles were enriched relative to ambient seawater; enrichment factors (k_d values) of the metals for suspended particles are plotted in Fig. 2 as a function of total suspended load and fraction of total suspended dry wt as phytoplankton (chl a × 200 [Parsons et al. 1984b] divided by total particle dry wt). k_d values for suspended particles were highest for Co (10.8 ± 4.6 × 10^4), followed by Ag (3.1 ± 2.0 × 10^4), Zn (1.8 ± 2.6 × 10^4) and Cd (7.2 ± 3.3 × 10^3). Overall, these values are comparable to concentration factors for these metals in marine phytoplankton, expressed on a dry wt basis (Fisher & Reinfelder 1995). There was no significant relationship between k_d values for any metal and relative phytoplankton abundance, but k_d values were negatively correlated with total suspended particle load for Co and Ag (Fig. 2), suggesting the possibility of colloidal association of these metals (Benoit et al. 1994). Zooplankton were enriched, on average, about 3 times greater than suspended particles for Ag and Cd, and 50 times greater for Zn, whereas suspended particles were 4 times more enriched than zooplankton in Co and Se (Table 1). Mean metal concentrations in copepod samples measured by ICP-MS did not differ significantly (p > 0.05) from concentrations measured by AAS (Table 1).

Table 2 shows levels of selected trace elements in what are reported to be pure, or near-pure, samples of marine copepods. More information is available for Cd and Zn than for Co, Ag, or Se, and reported concentrations vary spatially. For each element, the concentrations we measured in copepods are in the range of those which have been reported previously.

Table 3 presents the mean values used in the kinetic modeling calculations. These values, based on

Table 1. Metal concentrations in the dissolved phase, suspended particles (>0.2 μm), and copepods collected at 10 stations off the Monaco coast. Dissolved Se was not measured. Mean metal concentrations in mixed copepods (nmol g^{-1} dry wt) measured by ICP-MS were 2.39 ± 0.84 (Ag), 12.8 ± 8.2 (Cd), 13.3 ± 5.0 (Co), and 2320 ± 1068 (Zn); Se was not measured by ICP-MS. Model-predicted metal concentrations in copepods are given in parentheses for each station. Concentration factors for Ag, Cd, Co, and Zn in copepods (mol metal g^{-1} dry wt animal/mol metal ml^{-1} water) are given in brackets. nd: not determined

Stn	Dissolved (pM)				Particles (nmol g^{-1} dry wt)[a]					Copepods (nmol g^{-1} dry wt)[a]				
	Ag	Cd	Co	Zn	Ag	Cd	Co	Se	Zn	Ag	Cd	Co	Se	Zn
1	7.6	81.1	322	3140	0.30	0.46	14.6	8.7	27.3	1.57 (0.52)	17.3 (6.2)	8.16 (4.88)	12.9 (8.10)	2150 (3894)
2	11.6	85.8	300	4660	0.59	0.97	65.6	50.5	72.0	0.66 (0.82)	14.6 (5.15)	6.97 (13.0)	17.7 (47.3)	1770 (4020)
3	9.8	59.6	213	4500	0.25	0.50	28.6	28.8	53.5	0.67 (0.64)	21.3 (4.73)	13.4 (6.40)	14.7 (26.7)	2070 (4016)
4	8.6	49.8	202	8680	0.38	0.62	23.3	41.2	31.5	1.64 (0.60)	23.8 (4.56)	6.78 (5.46)	21.8 (38.6)	3320 (4116)
5	8.6	58.8	298	4230	0.20	0.46	30.2	30.0	30.1	1.79 (0.56)	22.7 (4.72)	6.71 (7.26)	8.68 (28.1)	4040 (4009)
6	9.2	76.9	246	3230	0.20	0.32	24.1	39.6	16.2	1.49 (0.60)	35.1 (5.01)	14.3 (5.90)	16.0 (37.1)	2900 (3983)
7	10.6	57.6	200	3480	0.15	0.29	19.7	11.7	23.0	1.37 (0.67)	18.5 (4.69)	7.82 (4.86)	15.6 (11.0)	2870 (3990)
8	11.4	95.8	289	3420	0.27	0.42	23.8	8.2	19.0	1.02 (0.74)	26.5 (5.30)	7.31 (6.15)	13.2 (7.63)	1340 (3988)
9	10.7	60.7	289	3440	0.34	0.49	22.6	11.4	52.8	1.36 (0.71)	20.2 (4.75)	13.3 (5.96)	22.0 (10.7)	1770 (3989)
10	16.6	96.9	238	3930	1 36	0.42	20.3	50.3	138	1.78 (1.29)	21.4 (5.32)	10.4 (5.23)	17.5 (47.0)	3470 (4002)
Mean	10.5	72.3	260	4270	0.41	0.49	27.3	28.0	46.4	1.34 (0.72) [1.3e5]	22.1 (5.04) [3.1e5]	9.52 (6.51) [3.7e4]	16.0 (26.2) [nd]	2570 (4001) [6.0e5]
SD	2.4	16.2	43	1550	0.34	0.18	13.4	16.2	35.0	0.40 (0.22)	5.7 (0.49)	2.9 (2.41)	3.8 (16.0)	830 (54)

[a]To convert to ppb dry wt, multiply Ag values by 108, Cd by 112, Co by 59, Se by 79, and Zn by 65

laboratory radiotracer experiments, were applied to each station with its dissolved (C_w) and particulate (C_f) metal concentrations. Although dissolved Se concentrations were not measured, this element has been consistently shown to accumulate in aquatic invertebrates, including copepods, predominantly (>98%) from food (Luoma et al. 1992, Wang et al. 1996, Wang & Fisher 1998a). Therefore we only modeled Se uptake from ingested food and ignored Se uptake from the dissolved phase. For the model calculations, the weight-specific ingestion rate of *Acartia clausi* was assumed to be at the low end of the measured range—0.33 g g^{-1} d^{-1}—because of the low algal biomass in the water (Roman 1977, Mauchline 1998). Growth rate (g) in adult copepods was considered negligible compared to the high efflux rate constants in copepods (8 to 30% d^{-1}, Table 3). Metal concentrations in marine organisms are often assumed to be a function of the free metal ion activity in ambient seawater but exceptions have been noted (Campbell 1995, Hudson 1998). Given the uncertainties of metal complexation by dissolved organic matter at each location and the bioavailability of these complexes,

we use total dissolved metal concentration (<0.2 μm) rather than calculated free metal ion activity as the C_w term. The values of k_u were based on experimental work in coastal surface seawater using total dissolved metal (Wang & Fisher 1998a) and it is assumed that the metal complexation by the dissolved organic matter in the experimental water resulted in metal bioavailability not greatly different from that in the Mediterranean.

In our modeling, we applied physiological parameters measured at 15°C for adults of another calanoid copepod, *Temora longicornis*, to the copepods off Monaco. Although some physiological parameters (e.g., IR) may vary with different food conditions and among different copepod species, metal assimilation does not vary appreciably among different calanoid copepod species and is determined principally by metal distribution in algal cytoplasm (Reinfelder & Fisher 1991, Hutchins et al. 1995), not by the feeding physiology of the animals or food quantity/quality (Wang et al. 1996, Wang & Fisher 1998a). Furthermore, sensitivity analysis to evaluate the relative importance of each parameter's variability on metal concentration
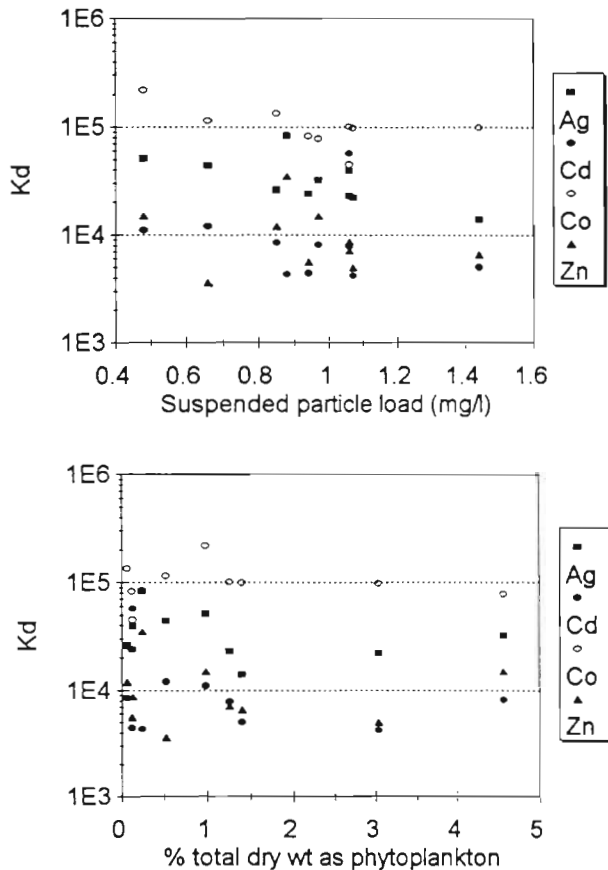
Fig. 2. Relationship between particle-water distribution coefficients (K_d values, l kg^{-1}) of metals and suspended particulate loads. Ag: $y = 75\,236 - 42\,015x$, $r^2 = 0.30$; Cd: $y = 9847 + 2522x$, $r^2 = 0$; Co: $y = 214\,212 - 115\,422x$, $r^2 = 0.413$; Zn: $y = 19\,076 - 8199x$, $r^2 = 0.05$. Also shown are relationships of metal K_d values with the proportion of total particle load attributable to phytoplankton biomass. Ag: $r^2 = 0.08$; Cd: $r^2 = 0.07$; Co: $r^2 = 0.01$; Zn: $r^2 = 0.01$

in *T. longicornis* indicated that >50% of Ag, Cd and Co accumulates in these animals from the dissolved phase (Wang & Fisher 1998a); thus for these metals changes in feeding activity due to change in food conditions would be expected to have only a modest effect on the overall metal accumulation in copepods. Excretion rate constants (= efflux rate constants) are generally comparable for different algal diets (Wang & Fisher 1998a,b). Food quantity can significantly affect the excretion rate of Ag, Cd, and Co but it has little effect on Se and Zn (Wang & Fisher 1998b). Because the total suspended particle load in the Mediterranean waters we studied was low (typically about 1 mg l^{-1}) and the phytoplankton abundance was also very low, we used the efflux rates measured at the lowest food concentrations in our model (Wang & Fisher 1998b). Assimilation efficiencies of ingested metals in marine copepods do not vary greatly among different food types, including abiotic particles found in seston (Wang & Fisher 1998a), so it was assumed that the metal assimilation efficiencies given in Table 3, based primarily on work performed with unialgal cultures, would be applicable to the particle assemblage in the Mediterranean.

The metal concentrations predicted for copepods for each metal by the kinetic model are compared with the measured values for each station (Table 1). Because metal concentrations in the dissolved phase, suspended particulate matter, and copepods were all determined with AAS, we used the copepod AAS metal measurements (rather than the ICP-MS copepod data) to compare with the model-predicted values. Our modeling results indicate that metal concentrations in copepods predicted by the model were generally comparable to the metal concentrations measured in the field-collected samples. For example, the field mea-

Table 2. Comparison of trace metal concentrations in marine copepods (nmol g^{-1} dry wt) in this study with previous reports. nr: not reported. Values in parentheses represent the range of measured values

Dominant species	Location	Ag	Cd	Co	Se	Zn	Source
Acartia clausi	Medit. Sea	1.3 ± 0.4	22 ± 6	10 ± 3	16 ± 4	2570 ± 830	This study
Acartia sp.	German Bight	nr	7.1 ± 0.6	nr	nr	5000 ± 231	Zauke et al. (1996)
Temora longicornis	German Bight	nr	8.8 ± 3.2	nr	nr	5846–7662	Zauke et al. (1996)
Anomalocera patersoni	Medit. Sea	nr	13	nr	nr	nr	Polikarpov et al. (1979)
Acartia clausi	Greek coast	nr	5	5	nr	19418	Zafiropoulos & Grimanis (1977)
			(4–7)	(3–9)		(12232–38226)	
Calanus helgolandicus	Black Sea	(1.2–2.6)	nr	(9–14)	nr	(1269–12614)	Vinogradova & Koval'skiy (1962)
Calanus plumchrus	N. Pacific	nr	59 ± 39	nr	nr	1774 ± 505	Hamanaka & Tsujita (1981)
Mixed copepods	N. Pacific	nr	68 ± 58	nr	nr	2156 ± 688	Hamanaka & Mishima (1981)
Mixed copepods	Monterey Bay	nr	38 ± 16	nr	nr	1772 ± 520	Martin & Knauer (1973)
Mixed copepods	Arctic	nr	(25–44)	nr	nr	(917–1147)	Bohn & McElroy (1976)
Mixed copepods	Medit. Sea	nr	22 ± 6	nr	nr	4037 ± 452	Hardstedt-Romeo & Laumond (1980)
Mixed copepods	Medit. Sea	nr	17 ± 4	nr	nr	2803 ± 124	Hardstedt-Romeo (1982)
Mixed copepods	Medit. Sea	nr	nr	nr	8	nr	Boisson & Romeo (1996)
Mixed copepods	Medit. Sea	nr	nr	nr	39 ± 3	nr	Cutter (1985)

Table 3. Mean values (±1 SD) for kinetic parameters used in modeling metal concentrations in marine copepods (AE, k_u, k_{ew} from Wang & Fisher 1998a; k_{ef} from Wang & Fisher 1998b). C_w: dissolved metal concentration, IR: ingestion rate

Metal	AE (%)	k_u (l g^{-1} d^{-1})	k_{ef} (d^{-1})	k_{ew} (d^{-1})	IR (g g^{-1} d^{-1})
Ag	0.10	$10.42 C_w^{1.042 \pm 0.076}$	0.158 ± 0.051	0.173 ± 0.007	0.33
Cd	0.40	$0.666 C_w^{0.738 \pm 0.023}$	0.157 ± 0.065	0.108 ± 0.001	0.33
Co	0.15	$0.573 C_w^{0.873 \pm 0.040}$	0.304 ± 0.040	0.122 ± 0.014	0.33
Se	0.55	–	0.194 ± 0.041	–	0.33
Zn	0.60	$2.678 C_w^{0.83 \pm 0.040}$	0.078 ± 0.018	0.108 ± 0.007	0.33

sured concentrations were 0.8 to 3.2 times the predicted values for Ag, 2.8 to 7.0 times predicted values for Cd, 0.5 to 2.4 times predicted values for Co, 0.3 to 2.1 times predicted values for Se, and 0.4 to 1.4 times predicted values for Zn. Because the 10 stations were separated from each other by small distances (typically <1 km) in a well-mixed area and because the animals could swim or be transported across such distances over their lifespans, it is more appropriate to evaluate mean concentrations of metals in zooplankton samples with mean predicted values (Table 1). In so doing, the mean field measured concentrations were 1.9 times the mean predicted value for Ag, 4.4 times the mean predicted value for Cd, 1.5 times the mean predicted value for Co, and 0.6 times the mean predicted values for Se and Zn. Thus, the greatest discrepancy between predicted and measured metal concentrations in copepods was for Cd. Given the errors around these means (Table 1), significant differences ($p < 0.05$) were noted for Cd and Ag, for which the model under-predicted the concentrations, and for Zn, for which the model over-predicted the concentration. It is noteworthy that the greatest discrepancies between predicted and measured concentrations were only 4-fold different from each other; given that the predictions were based on laboratory studies with a different species and that the field measurements were conducted entirely independently from the laboratory experiments, these discrepancies are not considered very great, and reasons for them are not clear. One possibility is that the copepods fed selectively on the phytoplankton and avoided abiotic particles, or fed selectively on particular species of phytoplankton, and that the ingested phytoplankton had significantly different metal concentrations from the rest of the seston; that is, the C_f term used in the model calculations was not accurate.

The relationship within and among metals for the predicted and measured metal concentrations in copepods is shown in Fig. 3. For each metal, there is some discrepancy between the model's predictions and measured values, as noted above; however among metals the model's predictions correspond with measured values quite well. This cannot be attributed sim-

ply to differences in the concentrations of each metal in seawater since the elements considered here are accumulated very differently from the dissolved phase (from negligibly for Se to very high uptake rate constants for Ag; Wang & Fisher 1998a) and display up to 16-fold differences in overall bioconcentration factors (Table 1). The model predictions field-tested here used the mean values for the kinetic parameters given in Table 3. Sensitivity analyses (Wang & Fisher 1998a) have shown that variations in these parameters attributable to environmental conditions and to such biological factors as copepod species, food type, and physiological state of the animals can all influence C_{ss} values. However, given the relatively small variations in the kinetic parameters (Table 3), the predicted C_{ss} values would not be expected to vary greatly from those presented here. The relatively close match between field measurements and model-predicted C_{ss} values suggests, among other things, that the mean values assumed by the model were applicable to the coastal
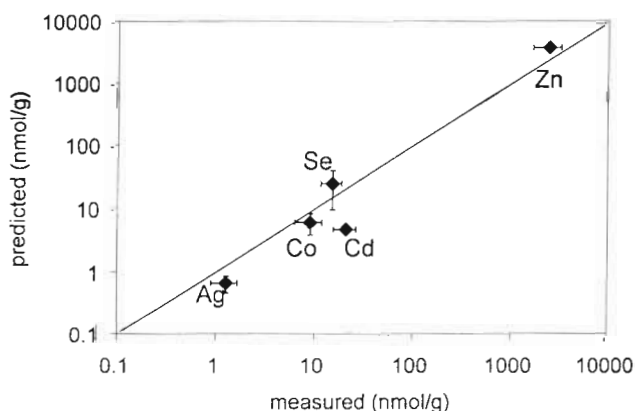

Fig. 3. Relationship between mean predicted and measured metal concentrations in copepods. The line drawn shows a hypothetical 1:1 fit. Calculations used recently published phytoplankton concentrations (C_f) of 1328 nmol g^{-1} for Zn and 4.0 nmol g^{-1} for Cd (Luoma et al. 1998) because some filters used for collecting phytoplankton were found to be contaminated with these metals and suspended particle measurements of these metals were considered questionable

Mediterranean sampled in this study. Further, as noted above, the relative importance of metal uptake in copepods from food varies with each metal. Our model indicates that, for most environmental conditions likely to be encountered by zooplankton, including those prevailing in the waters sampled in this study, typically about 60 to 80% of Ag and Co, about 50 to 60% of Cd, about 20% of Zn, and <2% of Se are taken up by copepods directly from the dissolved phase (Wang & Fisher 1998a). Metals accumulated from the dissolved phase concentrate primarily in the exoskeleton of crustacean zooplankton (Fowler et al. 1970, Fisher et al. 1983, Reinfelder & Fisher 1994), and this is reflected in field-collected zooplankton exoskeletons cast off during molting that are highly enriched in metals (Fowler 1977). Further, our study only considered adult copepods, both in the laboratory experiments which provided values for the kinetic parameters and the field samples which were dominated by adults. The extent to which metal uptake can be similarly modeled in juvenile copepod stages remains to be determined; certainly factors such as growth rate and rates of ecdysis could exert very different effects on C_{ss} values in juveniles and adults.

With the many factors which can influence metal uptake and retention in copepods, it would seem unlikely that an identical match between C_{ss} values predicted from a particular set of laboratory conditions and C_{ss} values observed in the ocean would occur for any metal. However, among the metals, given the generally close match of predicted and field measurements (which were independent of each other), it appears that it is possible to account for the major processes governing metal accumulation from food and water in marine zooplankton and that the kinetic parameters generated in laboratory experiments for monospecific copepod assemblages are applicable to at least some zooplankton communities.

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