

The assimilation of detritus-bound metals by the marine copepod *Acartia spinicauda*

Abstract—The bioavailability of Cd, Se, and Zn associated with detritus of different biological origins to the marine copepod *Acartia spinicauda* was examined under laboratory conditions using the radiotracer approach. Three types of detritus, from the macroalga *Ulva lactuca*, cell debris of the diatoms *Thalassiosira weissflogii* and *Thalassiosira rotula* derived after natural decomposition or extraction, and copepod fecal pellets, were examined. The assimilation of metals from the ingested natural phytoplankton assemblage was also experimentally quantified. The assimilation efficiencies (AEs) of metals in copepods fed with different types of detritus were 47–83% for Cd, 30–59% for Se, and 41–75% for Zn. These values were comparable to the AEs measured previously for copepods fed on living algal cells, indicating that metals associated with biogenic particles were directly available to marine copepods. Labeling time had no effect on the metal AEs in copepods fed on detritus derived from *U. lactuca*. The metal AEs were higher in copepods fed on the freshly prepared diatom debris than on naturally decomposing debris. Zn associated with fecal pellets was assimilated at comparable efficiencies to those associated with macroalgal and microalgal debris, but Cd and Se were assimilated at a lower efficiency when associated with fecal pellets. The AEs of Cd (84–94%) in copepods fed on the natural phytoplankton assemblage were the highest among all the experiments. There was no obvious effect of the metal distribution in the cytosol of the natural phytoplankton assemblage on the metal AE. The calculated elimination rates of the metals were independent of detritus type and were similar to previous studies. Our study indicated that detritus is a potential food source for marine copepods and the metals associated with the detritus can be efficiently used with a relatively high AE. Detritus may thus play an important role in the overall biogeochemical cycling of metals in the ocean.

Sources of detritus in the marine environment are diverse and include nonliving phytoplankton debris, decaying macrophytes, fecal materials, carcasses and molts of zooplankton, marine snow, and resuspended sediments in coastal waters (Roman 1984; Melack 1985; Nelson 1993). The concentration of detritus in the ocean is generally greater than living phytoplankton biomass (Parsons and Strickland 1962; Poulet 1976, 1983; Bouillon et al. 2000). Many studies have demonstrated the importance of detritus as a food source for zooplankton (Gerber and Marshall 1974; Heinle and Flemer 1975; Suh et al. 1991). Poulet (1983) has pointed out that the crucial factors controlling the use of detritus are the type and chemical composition of aging detritus and the physiological conditions of the animals.

Detritus contributes significantly to carbon and metal biogeochemical cycling in the ocean through zooplankton grazing and bacterial remineralization (Angel 1984; Poulet 1983). Detritus can also transport carbon and metals to deeper waters through their rapid sinking (Fowler and Knauer 1986; Reinfelder and Fisher 1991). However, the residence time of elements associated with the detritus in the upper

water column depends on the extent to which zooplankton ingest, assimilate, and regenerate them during grazing. Because detritus can effectively scavenge metals from the ambient seawater and introduce metals into the trophic transfer process (Fisher and Fowler 1987), the physiological parameters controlling metal use by copepods from detritus need to be quantitatively assessed.

While there have been extensive measurements of metal assimilation efficiency by marine copepods fed on living algal diets (e.g., Reinfelder and Fisher 1991; Fisher et al. 1991; Wang et al. 1996; Hutchins et al. 1995; Wang and Fisher 1998), no study thus far has measured the metal uptake and assimilation from detrital particles. Reinfelder and Fisher (1991) first proposed that metal assimilation in marine copepods was proportional to metal distribution in algal cytoplasm. Accordingly, metals associated with the cytoplasm of phytoplankton were assumed available to marine copepods with a 100% absorption efficiency, whereas metals associated with the cell walls were assumed to be unavailable. However, there is no direct experimental evidence to demonstrate that metals bound to the cell walls/frustules of phytoplankton, which may be a significant source of detritus, are not assimilated by copepods. In this study, we experimentally determined the assimilation efficiency of Cd, Se, and Zn by the marine copepod *Acartia spinicauda* after feeding on detritus from diatoms, macrophytes, and fecal pellets. Among the three metals, Se and Zn are essential to the animals, whereas Cd has no known function.

Copepods and metals—Adult copepods, *Acartia spinicauda*, were collected by plankton tow (250- μ m mesh size) from the Port Shelter, Clear Water Bay, Hong Kong. The copepods were sorted in the laboratory and maintained under laboratory conditions for 1 d and fed with the algal food *Thalassiosira weissflogii* at a food concentration of about 1–2 mg C L⁻¹. Preliminary experiments demonstrated that metal assimilation efficiency from ingested detritus was independent of whether the animals were previously acclimated to the detritus before the radioactive feeding. All experiments described below were carried out at 23°C in glass fiber filtered (GF/F) seawater with a salinity of 30 psu. Three metals were considered in this study: Cd, Se(IV), and Zn. The assimilation of these metals by copepods was studied using radiotracer techniques. ¹⁰⁹Cd ($t_{1/2}$ = 462 d, in 0.1 N HCl) and ⁶⁵Zn ($t_{1/2}$ = 244 d, in 0.1 N HCl) were purchased from New England Nuclear, and ⁷⁵Se ($t_{1/2}$ = 120 d, as selenite, in distilled water) was purchased from Livermore National Laboratory.

Radiolabeling of detritus—The green macroalga *Ulva lactuca* was collected from a fish farm in Sai Kung, Kowloon, Hong Kong. The alga was cut into pieces (70 to 120 mg dry weight), and their tissue surfaces were carefully cleaned to remove any epibiotics. The macroalgae were then main-

tained at 18°C in 150 ml 0.22- μm filtered seawater with an addition of N (882 μM nitrate) and P (16.6 μM) and exposed to light illumination of 100 $\mu\text{E m}^{-2} \text{ s}^{-1}$. The amounts of radioisotope additions were 74 kBq ^{109}Cd and 74 kBq ^{65}Zn . We did not consider Se in this experiment because the green macroalgae had a low ability to accumulate selenite from the dissolved phase (Wang and Dei 1999). The pH of the seawater was adjusted to 8.0 by adding 0.5 N Suprapur NaOH. The medium was changed every 2 d. After 2 or 4 d radiolabeling, *U. lactuca* pieces were rinsed with filtered seawater and dried at 60°C for 24 h. The plant materials were then grounded with a mortar and a pestle and passed through a 40- μm nylon mesh. The detritus was finally collected by filtration onto 3- μm polycarbonate membranes before being resuspended in 0.22- μm filtered seawater and fed to the copepods.

Two species of unialgal diatoms, *Thalassiosira weissflogii* (CCMP 1048) and *Thalassiosira rotula* (CCMP 1647), were maintained in axenic cultures in an f/2 medium at 18°C with a light illumination of 100 $\mu\text{E m}^{-2} \text{ s}^{-1}$ on a 14:10 h light:dark cycle. Cells in the late log phase were collected onto 3- μm polycarbonate membranes and resuspended in 0.22- μm filtered seawater, enriched with f/2 levels of N, P, Si, vitamins, and f/20 trace metals without addition of Cu, Zn, and EDTA. The initial cell concentration in the media was generally 3×10^4 cells ml^{-1} . The amounts of radioisotope additions were 111 kBq ^{109}Cd , 148 kBq $^{75}\text{Se(IV)}$, and 111 kBq ^{65}Zn . The pH of the seawater was adjusted to 8.0. After 4–5 d growth, the cell density reached $1\text{--}2 \times 10^5$ cells ml^{-1} for *T. weissflogii* and $8\text{--}9 \times 10^4$ cells ml^{-1} for *T. rotula*. The distribution of radioisotopes in the phytoplankton cell walls was determined by the methods described in Reinfeldler and Fisher (1991). Cells were then collected by filtration onto polycarbonate membranes, and half of the cells was resuspended in distilled water and immediately frozen (freshly prepared debris). Microscopic examination showed that the diatom cells were broken following these physical treatments. Another half of the cells was resuspended in 0.22- μm filtered seawater and killed by heating at 60°C for 5 min. The cells were then maintained in 0.22- μm filtered unlabeled seawater at 18°C for 4–5 d (decomposing debris). Microscopic examination indicated that the cells lysed after 4–5 d of decomposition. The debris (freshly prepared and decomposing debris) were finally collected by filtration onto 3- μm polycarbonate membranes before being resuspended in a small volume of filtered seawater and fed to the copepods.

Two species of phytoplankton, *Thalassiosira weissflogii* and *Prorocentrum minimum* (CCMP 696), were radiolabeled with radiotracers in 0.22- μm filtered seawater with f/2 levels of N, P, Si, vitamins, and f/20 levels of trace metals without addition of Cu, Zn, and EDTA. Radioisotopes were spiked at 111 kBq ^{109}Cd , 111 kBq $^{75}\text{Se(IV)}$, and 111 kBq ^{65}Zn . After 7 d growth for *P. minimum* or 5 d growth for *T. weissflogii*, the cells were collected and fed to 800 individuals of *Acartia spinicauda* held in 1 liter GF/F seawater for 24 h. Every 6 h, the fecal pellets produced during feeding were collected onto a 40- μm nylon mesh and rinsed with seawater. The fecal pellets were pooled together and ground with a mortar and pestle until they passed through the 40- μm nylon mesh.

The pellet debris were finally collected by filtration onto 3- μm polycarbonate membrane before being resuspended in 0.22- μm filtered seawater and fed to the copepods.

Natural phytoplankton (3–40 μm) was collected from Tolo Harbor, Hong Kong in the summer of 2000. The water was first passed through a 40- μm nylon mesh to remove zooplankton and large phytoplankton, and 250 ml of this seawater was enriched with f/2 levels of N, P, Si, and vitamins and f/20 levels of trace metals without addition of Cu, Zn, and EDTA. Another 2 liters of seawater were filtered onto a 3- μm polycarbonate membrane, and any seston retained on the membrane was resuspended in 400-ml filtered seawater. Microscopic examination indicated that the dominant phytoplankton was the diatom *Skeletonema* sp. Radioisotope additions were 55.5–88.8 kBq for ^{109}Cd , $^{75}\text{Se(IV)}$, and ^{65}Zn each. The pH of the seawater was adjusted to 8.0. After 2 d labeling, the assemblage was collected by filtration onto a 3- μm polycarbonate membrane and resuspended in 0.22- μm filtered seawater before being fed to the copepods.

Metal assimilation and elimination by copepods—The radiolabeled particles were added into 150 ml of GF/F seawater at a biomass about 2 mg L^{-1} . Copepods (75–105 individuals) were added into the feeding beakers at densities of 0.5–0.7 ind ml^{-1} and were allowed to feed on the radiolabeled particles for 15–20 min in the dark. There were three replicated beakers for each treatment. After the radioactive feeding, the copepods were collected with a 250- μm nylon mesh, rinsed with filtered seawater, and placed in 5 ml of filtered seawater. The radioactivity of the copepods was counted nondestructively for 2 min. The fractions of metals associated with the radiolabeled particles were also quantified by filtering a 10-ml water sample onto 1- μm polycarbonate membrane. The copepods were returned to 100 ml of filtered seawater to depurate their ingested radiolabeled food materials for 1 d with the presence of unradiolabeled diatom *T. weissflogii* as food. The cell concentration in the depurating water was maintained at about 1×10^4 cells ml^{-1} . Any fecal pellets egested during the radioactive feeding period were also collected onto a 40- μm nylon mesh, rinsed with filtered seawater, and assayed for radioactivity. The total amount of radioactivity ingested by the copepods during the radioactive feeding period was calculated as the sum of radioactivity in the copepods and in the feces produced during the radioactive feeding period (Wang and Fisher 1998). The radioactivity of the copepods was measured every 1–4 h over the 1-d depuration period. The seawater and food were replaced each time the radioactivity of the copepods was counted.

Radioactivity was measured with a Wallac 1480 NaI(Tl) gamma detector. All measurements were related to appropriate standards and calibrated with spillover. The gamma emission of ^{109}Cd was determined at 88 keV, of ^{75}Se at 264 keV, and of ^{65}Zn at 1115 keV. Counting times were adjusted to yield a propagated counting error <5%.

Results—Table 1 shows the metal distribution and partitioning in the particles across different experiments. By the end of radiolabeling (before fed to the copepods), >70% of Cd and Se was bound to the cell walls of the diatom *Thal-*

Table 1. The percentage of metals associated with the cell wall of phytoplankton after radiolabeling, and the distribution of metals in the particles after 15–20 min radioactive feeding by the copepods. Mean \pm semirange ($n = 2$).

Experiments	% associated with the cell walls after radiolabeling			% on particles after radioactive feeding		
	Cd	Se	Zn	Cd	Se	Zn
<i>U. lactuca</i> detritus						
4-d labeling				56.2		47.1
2-d labeling				31.5		40.3
Diatom detritus						
<i>T. weissflogii</i> (decomposing)	42.9 \pm 2.7	45.2 \pm 2.2	76.1 \pm 3.6	70.4	81.0	76.4
<i>T. weissflogii</i> (freshly prepared)	42.9 \pm 2.7	45.2 \pm 2.2	76.1 \pm 3.6	78.4	69.2	67.5
<i>T. rotula</i> (decomposing)	73.1 \pm 0.7	76.5 \pm 0.6	66.5 \pm 1.9	76.9	81.4	71.6
<i>T. rotula</i> (freshly prepared)	73.1 \pm 0.7	76.5 \pm 0.6	66.5 \pm 1.9	71.1	87.9	76.0
Fecal pellets by copepods feeding on						
<i>T. weissflogii</i>				86.2	73.5	72.2
<i>P. minimum</i>				68.0	74.0	54.9
Natural assemblage						
Nutrient enriched	66.0 \pm 2.9	48.3 \pm 1.3	82.2 \pm 2.4	83.4	67.3	72.3
Nutrient depleted	81.5 \pm 2.7	52.1 \pm 0.5	88.6 \pm 1.4	94.3	77.8	82.6

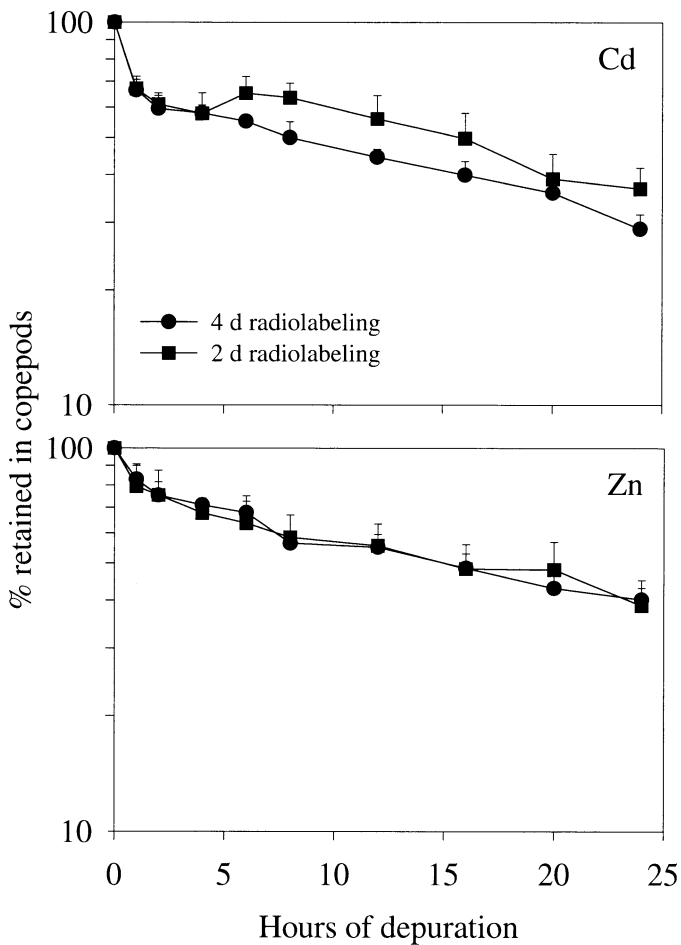


Fig. 1. The retention of Cd and Zn in copepod *Acartia spinicauda* following a pulse ingestion of radiolabeled (2 d and 4 d) detritus derived from macroalgae *Ulva lactuca*. Data are mean \pm SD ($n = 3$).

Thalassiosira rotula compared with 43–45% of metals bound to the cell walls of *Thalassiosira weissflogii*. About 66–76% of Zn was associated with the cell walls of the two diatoms. For natural phytoplankton assemblage, more metals were bound with the surfaces of nutrient-depleted particles than of nutrient-enriched particles, especially for Cd. After the radiolabeled particles were fed to the copepods for 15 to 20 min, >70% of the metals were generally retained on the particles. However, for detritus derived from macroalgae *Ulva lactuca*, only 31–56% of Cd and Zn remained in the particles after the radioactive feeding. The amount of uptake from the dissolved phase due to radioisotope desorption from the radiolabeled particles was negligible compared with the total ingestion of metals by copepods during the short-term radioactive feeding period (15–20 min).

Generally, the patterns of metal depuration were similar among the different experiments and among different metals and were characterized by a rapid loss within the first 2 h, followed by a more gradual loss (Figs. 1–4). No major difference in the depuration pattern was observed among different types of detritus. The AEs were calculated as the y-intercept of the regression between the natural log of the percentage of metals retained in the copepods and the time of depuration during the second phase of depuration (6 to 24 h). For each metal, the AEs were comparable across different experiments, with a few exceptions noted (Table 2). For example, the AEs of Cd ranged from 61 to 83% in experiments with macroalgal and diatom detritus, but were lower for fecal pellet detritus (47–54%) and higher for the natural assemblage (84–94%). The AEs of Se ranged between 44 and 59%, but again were lower from fecal pellet derived detritus (30–43%). The AEs of Zn were rather comparable among the different experiments (41 to 48%), except from the *Ulva* detritus (73–75%). Among the different metals, the AEs of Cd were generally the highest, and the AEs of Se and Zn were somewhat comparable.

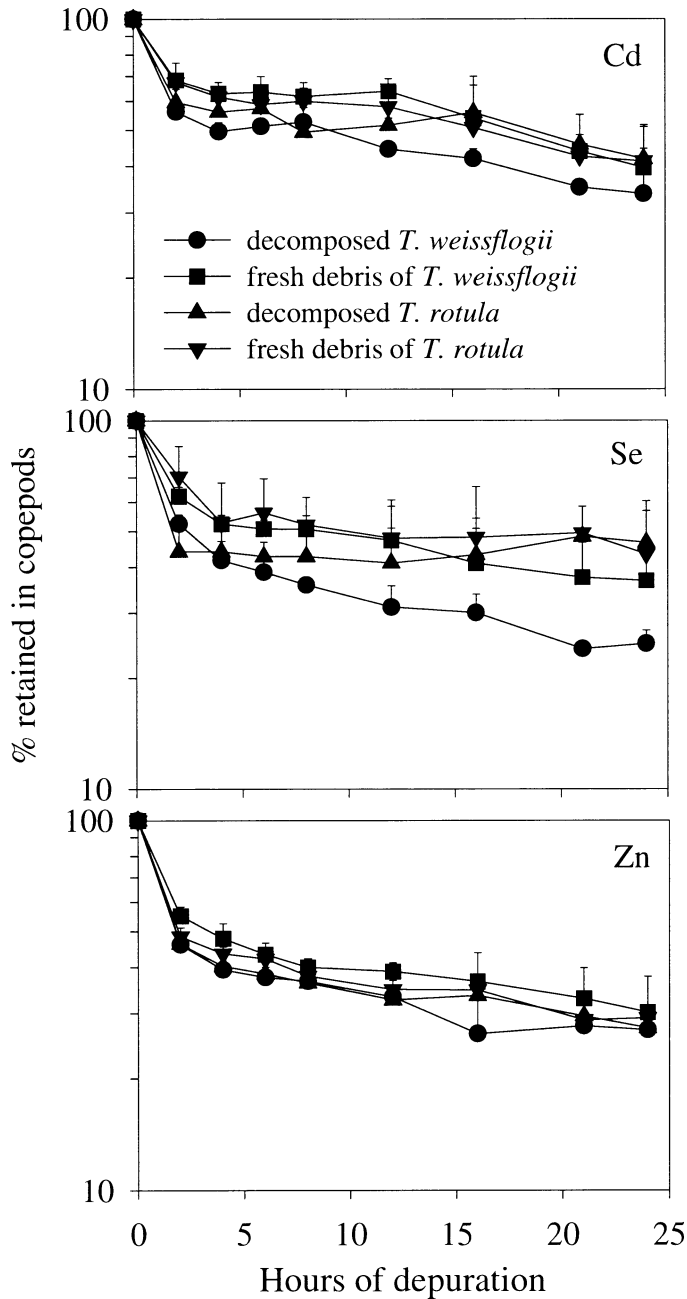


Fig. 2. The retention of Cd, Se, and Zn in copepod *Acartia spinicauda* following a pulse ingestion of radiolabeled detritus derived from diatoms *Thalassiosira weissflogii* and *Thalassiosira rotula*. Data are mean + SD ($n = 3$).

When comparing the AEs within each experiment, different radiolabeling times (2 d vs. 4 d radiolabeling) did not affect the assimilation of Cd and Zn from the macroalgal detritus. Metals associated with the freshly prepared detritus (by direct cell extraction) were generally assimilated at a higher efficiency than metals bound with the aging detritus (by cell decomposition), and in some cases the differences were statistically significant (e.g., Cd bound with the detritus of *Thalassiosira weissflogii*). Significantly higher Se AE was

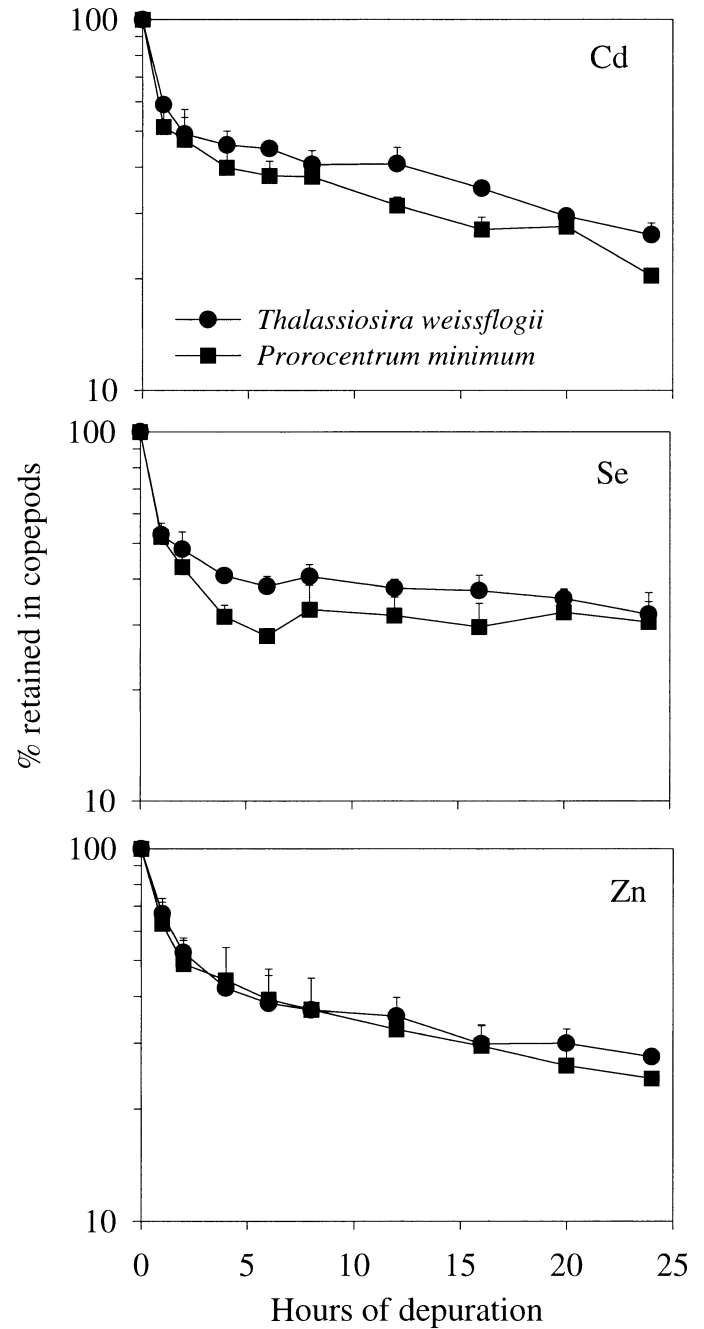


Fig. 3. The retention of Cd, Se, and Zn in copepod *Acartia spinicauda* following a pulse ingestion of radiolabeled fecal pellets produced by *A. spinicauda* fed with diatoms and dinoflagellates. Data are mean + SD ($n = 3$).

found when the element was associated with the fecal pellets produced by copepods feeding on *T. weissflogii* than on *Prorocentrum minimum*. Cd was assimilated at a higher efficiency from natural assemblage incubated in a nutrient-enriched medium. In this experiment, we also quantified the cytosolic distribution of metals in the natural assemblage (Table 1). There was no significant relationship between the metal AEs and the distribution of metals in the cytoplasm

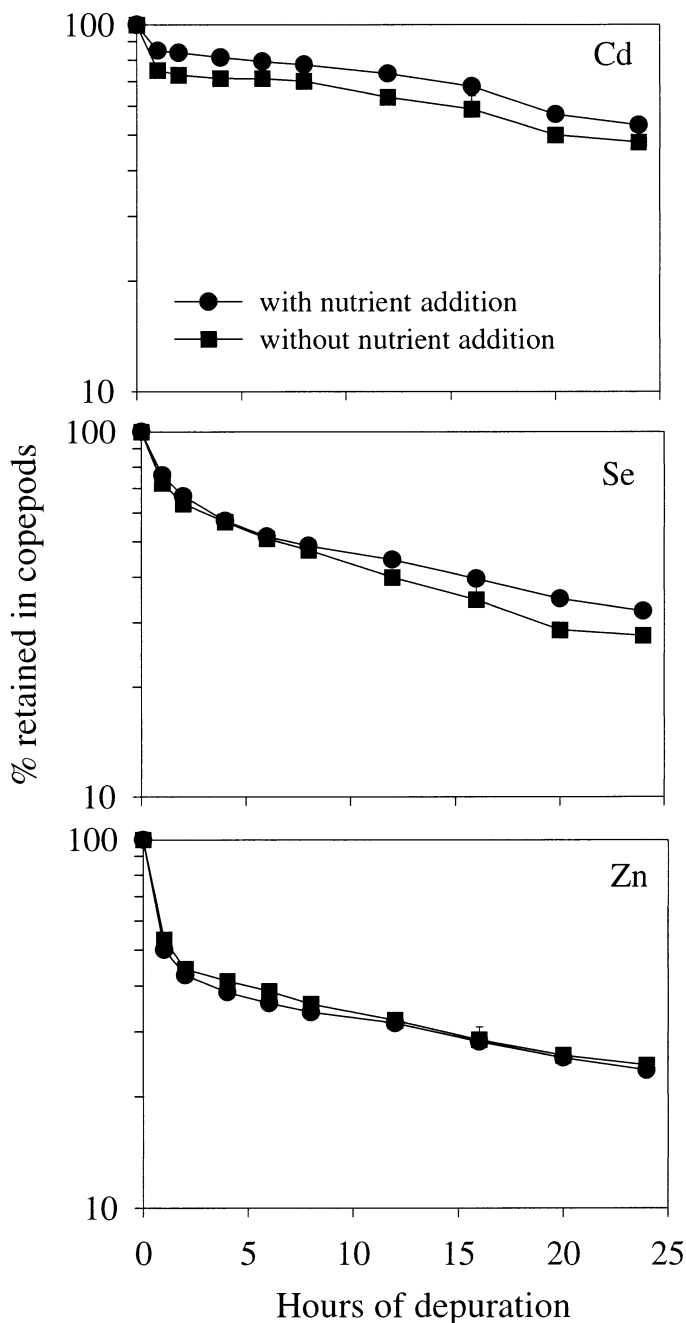


Fig. 4. The retention of Cd, Se, and Zn in copepod *Acartia spinicauda* following a pulse ingestion of radiolabeled natural assemblage maintained with nutrient (N and P) addition and without nutrient addition. Data are mean + SD ($n = 3$).

of the natural assemblage when all three metals were considered.

The elimination rate constants, calculated as the slope of the linear regression between the natural log of the percentage of metals retained in copepods and the time of depuration (between 6 and 24 h), were similar for each metal (Table 2). The metals were therefore eliminated at a similar rate. However, Se was eliminated at a conspicuously slower rate

when the copepods were fed with fecal pellets. In one experiment (decomposing debris of *Thalassiosira rotula*), the elimination of Se was undetectable. In general, the elimination rate constants were 0.52–0.83 d^{-1} , 0.42–0.87 d^{-1} , and 0.41–0.65 d^{-1} for Cd, Se, and Zn, respectively. Extrapolation of the elimination rate constant quantified within a short depuration period (e.g., <24 h) to metal efflux rate in natural copepod population may have been overestimated.

Discussion—Our study suggests that metal AEs in the copepod *Acartia spinicauda* fed on different types of detritus are comparable to those fed on phytoplankton. Xu et al. (2001), working with the same copepod species (*Acartia spinicauda*), found that the metal AEs were 43 to 67% for Cd and 35 to 38% for Se at different metal concentrations in the algal cells (*Prorocentrum minimum*). The AEs of Zn (4 to 9%), however, were much lower than our present measurements from biogenic particles. In the copepod *Calanus sinicus*, the AEs of Cd, Se, and Zn ranged from 30 to 81% for the diatom *Thalassiosira weissflogii* and the dinoflagellate *Prorocentrum minimum* at different food concentrations (Xu and Wang 2001). Very high metal AEs (>88% for Cd, >73% for Se, >76% for Zn) were documented in *Acartia tonsa* and *Temora longicornis* fed on different algal species (Wang et al. 1996).

Given the relatively high metal AEs from detritus, detritus may be at least as important as phytoplankton in contributing to the dietary exposure of metals to marine copepods. Trace metal influx into copepods is a function of metal AE, metal concentration in the particles, and the ingestion activity of the copepods on a specific diet (Wang and Fisher 1998). The ingestion rate of copepods is a function of the particle concentration as well as the clearance rate of copepods. The dominance of nonliving particulate organic matter (e.g., >85% in the northeastern Pacific, and >70% in the Canadian Bedford Basis, Parsons and Strickland 1962; Poulet 1976), as well as the high ingestion rate (e.g., comparable to the ingestion rate on phytoplankton, Paffenhöfer and Knowles 1979; Roman 1977, 1984), suggest that detritus can be a significant source of diets for marine copepods. For example, *Acartia tonsa* ingested aged *Fucus vesiculosus* detritus at rates of 6–292% of their body weight per day (Roman 1984). Gerber and Marshall (1974) found that detritus comprised 34–95% of the gut materials in the copepod *Undinula vulgaris*. Thus, the influx rate of metals from the detritus may be comparable or even higher than that from the phytoplankton.

The green macroalga *U. lactuca* concentrated a great amount of Cd and Zn from the dissolved phase (Wang and Dei 1999). Metals accumulated in macroalgae may either be further transported to higher trophic levels or may be associated with the detritus as a result of macrophyte decomposition, and then enter the classical food chains by acting as food source for zooplankton or detritivores. In our experiments, the nutritional value of the detritus and the ingestion rate of the copepods on detritus were not quantified. Roman (1984) showed that the detritus derived from *Thalassia testudinum* contained approximately 10× less protein and 15× less carbohydrate than that derived from the diatom *Thalassiosira weissflogii*. However, detritus could support

Table 2. The assimilation efficiencies (AEs) and the elimination rate constant (K) of Cd, Se, and Zn in copepods *Acartia spinicauda* feeding on detritus prepared from different sources. See text for calculation of AE and K . Values are means \pm SD ($n = 3$). Statistically significant effect of different treatments was indicated by * ($p < 0.05$), ** ($p < 0.01$), *** ($p < 0.001$). Nd, not determined.

Experiments	AE (%)			K (d^{-1})		
	Cd	Se	Zn	Cd	Se	Zn
<i>U. lactuca</i> detritus						
4-d labeling	66.8 \pm 2.8	Nd	75.0 \pm 4.3	0.80 \pm 0.06	Nd	0.65 \pm 0.01
2-d labeling	82.8 \pm 8.5	Nd	73.4 \pm 12.7	0.83 \pm 0.07	Nd	0.59 \pm 0.12
Diatom detritus						
<i>T. weissflogii</i> (decomposing)	62.0 \pm 1.5***	44.2 \pm 3.7*	41.7 \pm 5.6	0.63 \pm 0.07	0.63 \pm 0.01	0.50 \pm 0.09
<i>T. weissflogii</i> (freshly prepared)	80.8 \pm 2.3***	59.2 \pm 5.3*	48.5 \pm 2.3	0.72 \pm 0.37	0.69 \pm 0.27	0.48 \pm 0.29
<i>T. rotula</i> (decomposing)	61.0 \pm 6.0	46.9 \pm 16.0	41.9 \pm 1.4*	0.52 \pm 0.16	0	0.41 \pm 0.04
<i>T. rotula</i> (freshly prepared)	71.2 \pm 8.6	56.9 \pm 2.9	45.7 \pm 0.8*	0.54 \pm 0.05	0.42 \pm 0.35	0.48 \pm 0.06
Fecal pellets by copepods feeding on						
<i>T. weissflogii</i>	54.0 \pm 2.8	42.6 \pm 3.2**	42.8 \pm 6.9	0.70 \pm 0.07	0.25 \pm 0.07	0.44 \pm 0.15
<i>P. minimum</i>	47.2 \pm 3.8	30.1 \pm 1.5**	46.1 \pm 12.0	0.78 \pm 0.02	0.16 \pm 0.0	0.64 \pm 0.18
Natural assemblage						
Nutrient-enriched	94.1 \pm 1.0**	60.7 \pm 0.62*	41.3 \pm 2.0	0.56 \pm 0.03	0.64 \pm 0.04	0.57 \pm 0.02
Nutrient-depleted	83.8 \pm 2.2**	62.4 \pm 0.41*	44.2 \pm 0.44	0.57 \pm 0.01	0.87 \pm 0.02	0.62 \pm 0.04

the survival of *Acartia tonsa* despite its low nutritional values, indicating that it may supplement the energy demands of zooplankton. Our results showed that the AEs of Cd and Zn from macroalgal detritus were surprisingly high (67–83%). Thus, metals associated with the macrophyte detritus may potentially contribute to metal accumulation in marine copepods.

A few studies have proposed that marine copepods only assimilated metals from the cytoplasm of prey cells (i.e., liquid digestion strategy), and metals associated with cell walls may pass through the guts and be egested rapidly with fecal pellets (Reinfelder and Fisher 1991; Hutchins et al. 1995). However, our result showed that metal AEs from the diatom detritus with the cytosol pool removed were similar to (40–80%) those measured in copepods fed on living algal cells (Xu et al. 2001). When compared with the naturally decomposing diatom detritus, the AEs of Cd, Se, and Zn from the freshly prepared diatom detritus were even higher. Our data thus provide direct experimental evidence that the metals associated with cell walls were directly bioavailable to marine copepods. Previous microscopic observations and incubation experiments on freshly produced fecal pellets showed that several algal species can pass through the copepod gut with their viability intact, especially at a relatively high food concentration when copepods exhibit superfluous feeding (Silver and Alldredge 1981; Fowler and Fisher 1983). In our study, no intact cells were found in the fecal materials produced by the copepods during the radioactive feeding period. Because the fecal pellets may be largely composed of cell wall/membrane materials or diatom frustules, our data further indicated that metals associated with these materials are also bioavailable to copepods.

One potential factor affecting our measurements on metal assimilation from detrital particles was the bacteria-detritus interaction. In our study, it was unlikely that metals were associated with the bacteria before being assimilated by the copepods. The macroalgae were carefully cleaned of their

surface epibionts before the radiolabeling, and the plant tissues were dried at 60°C for 1 d before grounding. The diatoms were maintained in axenic culture before and during the radiolabeling, and the fresh debris was prepared by resuspending the cells in freshwater before freezing and filtration. We do not know the extent to which bacteria colonized the decomposing diatom debris or the fecal pellets produced by the copepods. Heinle et al. (1977) suggested that the presence of microbiota could be important in the transfer of detrital energy to copepods.

As a direct trophic link between phytoplankton and secondary consumers, copepods play a fundamental role in particle transport in marine ecosystems as a result of their grazing activity and production of fecal pellets. Biological processes such as ingestion, assimilation and elimination by marine copepods may be essential in the overall biogeochemical cycling of metals in the ocean (Fisher and Reinfelder 1995). Edwards (2001) recently suggested that the dynamics of planktonic ecosystem can be significantly affected by zooplankton grazing on the detritus. In previous studies, the AEs of Cd, Se, and Zn in copepods fed on living phytoplankton varied from 10 to 80% under diverse feeding conditions (Wang and Fisher 1998; Xu and Wang 2001). Thus, about 20 to 90% of ingested metals may be egested as fecal pellets. These metals in the fecal pellets were rapidly released into the dissolved phase and may be recycled many times in surface waters (Lee and Fisher 1992; Wang et al. 1996), thus increasing their residence times in the upper water column. Small copepods or copepodites may have a greater contribution than the large copepods because their pellets have a lower sinking rate and a high potential of being ingested by large zooplankton. Alternatively, metals in fecal pellets may further enter into the food chains due to the ingestion of fecal materials by zooplankton. Consequently, detritus grazing adds further complexity to the biogeochemical fates of metals in planktonic food chains.

Yan Xu and Wen-Xiong Wang¹

Department of Biology
The Hong Kong University of Science and Technology
(HKUST)
Clear Water Bay
Kowloon, Hong Kong, China

References

- ANGEL, M. V. 1984. Detrital organic fluxes through pelagic ecosystems, p. 475–516. In M. J. Fasham [ed.], *Flows of energy and materials in marine ecosystems: Theory and practice*. Plenum.
- BOUILLON, S., P. C. MOHAN, N. SCREENIVAS, AND F. DEHAIRS. 2000. Sources of suspended organic matter and selective feeding by zooplankton in an estuarine mangrove ecosystem as traced by stable isotopes. *Mar. Ecol. Prog. Ser.* **208**: 79–92.
- EDWARDS, A. M. 2001. Adding detritus to a nutrient-phytoplankton-zooplankton model: A dynamical-systems approach. *J. Plankton Res.* **23**: 389–413.
- FISHER, N. S., AND S. W. FOWLER. 1987. The role of biogenic debris in the vertical transport of transuranic wastes in the sea, p. 197–207. In T. P. O'Connor, W. V. Burt, and I. W. Duedall [eds.], *Physicochemical processes and wastes in the ocean*. Krieger.
- , C. V. NOLAN, AND S. W. FOWLER. 1991. Assimilation of metals in marine copepods and its biogeochemical implications. *Mar. Ecol. Prog. Ser.* **71**: 37–43.
- , AND J. R. REINFELDER. 1995. The trophic transfer of metals in marine systems, p. 363–406. In D. R. Turner and A. Tessier [eds.], *Metal speciation and bioavailability*. Wiley.
- FOWLER, S. W., AND N. S. FISHER. 1983. Viability of marine phytoplankton in zooplankton fecal pellets. *Deep-Sea Res.* **30(A)**: 963–969.
- , AND G. A. KNAUER. 1986. Role of large particles in the transport of elements and organic compounds through the oceanic water column. *Prog. Oceanogr.* **16**: 147–194.
- GERBER, R. P., AND N. MARSHALL. 1974. Ingestion of detritus by the lagoon pelagic community at Eniwetok Atoll. *Limnol. Oceanogr.* **19**: 815–824.
- HEINLE, D. R., AND D. A. FLEMER. 1975. Carbon requirements of a population of the estuarine copepod *Eurytemora affinis*. *Mar. Biol.* **31**: 235–247.
- , R. P. HARRIS, J. F. USTACH, AND D. A. FLEMER. 1977. Detritus as food for estuarine copepods. *Mar. Biol.* **40**: 341–353.
- HUTCHINS, D. A., W.-X. WANG, AND N. S. FISHER. 1995. Copepods grazing and the biogeochemical fate of diatom iron. *Limnol. Oceanogr.* **40**: 989–994.
- LEE, B.-G., AND N. S. FISHER. 1992. Decomposition and release of elements from zooplankton debris. *Mar. Ecol. Prog. Ser.* **88**: 117–128.
- MELACK, J. M. 1985. Interactions of detrital particulates and plankton. *Hydrobiol.* **125**: 209–220.
- NELSON, J. R. 1993. Rates and possible mechanism of pigments in detritus derived from phytoplankton. *J. Mar. Res.* **51**: 155–179.
- PAFFENHÖFER, G.-A., AND S. C. KNOWLES. 1979. Ecological implications of fecal pellet size, production and consumption by copepods. *J. Mar. Res.* **37**: 35–49.
- PARSONS, T. R., AND J. D. H. STRICKLAND. 1962. Oceanic detritus. *Science* **136**: 313–314.
- POULET, S. A. 1976. Feeding of *Pseudocalanus minutes* on living and non-living particles. *Mar. Biol.* **34**: 117–125.
- . 1983. Factors controlling utilization of non-algal diets by particle-grazing copepods. A review. *Oceanol. Acta* **6**: 221–234.
- REINFELDER, J. R., AND N. S. FISHER. 1991. The assimilation of elements ingested by marine copepods. *Science* **251**: 794–796.
- ROMAN, M. R. 1977. Feeding of the copepod *Acartia tonsa* on the diatom *Nitzschia closterium* and brown algae (*Fucus vesiculosus*) detritus. *Mar. Biol.* **42**: 149–155.
- . 1984. Utilization of detritus by the copepod, *Acartia tonsa*. *Limnol. Oceanogr.* **29**: 949–959.
- SILVER, M. W., AND A. L. ALLDREDGE. 1981. Bathypelagic marine snow: Deep-sea algal and detrital community. *J. Mar. Res.* **39**: 501–530.
- SUH, H. L., T. TODA, AND M. TERAZAKI. 1991. Diet of calyptopes of the euphausiid *Euphausia pacifica* in the Yellow Sea. *Mar. Biol.* **111**: 45–48.
- WANG, W.-X., AND R. C. H. DEI. 1999. Kinetic measurements of metal accumulation in two marine macroalgae. *Mar. Biol.* **135**: 11–23.
- , AND N. S. FISHER. 1998. Accumulation of trace elements in a marine copepod. *Limnol. Oceanogr.* **43**: 273–283.
- , J. R. REINFELDER, B.-G. LEE, AND N. S. FISHER. 1996. Assimilation and regeneration of trace elements by marine copepods. *Limnol. Oceanogr.* **41**: 70–81.
- XU, Y., AND W.-X. WANG. 2001. Individual responses of trace element assimilation and physiological turnover by marine copepod *Calanus sinicus* to changes in food quantity. *Mar. Ecol. Prog. Ser.* **218**: 227–238.
- , ———, AND D. P. H. HSIEH. 2001. Influences of metal concentration in phytoplankton and seawater on metal assimilation and elimination in marine copepods. *Environ. Toxicol. Chem.* **20**: 1067–1077.

¹ Corresponding author (wwang@ust.hk).

Acknowledgment

We are grateful to Dr. Michael Landry and the two anonymous reviewers for their constructive comment on this work. This study was supported by a Competitive Earmarked Research Grant from the Hong Kong Research Grant Council (HKUST6113/00M) to W.-X.W.

Received: 9 June 2001
Amended: 13 November 2001
Accepted: 4 December 2001