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Toxicity and toxicokinetics of cadmium in *Capitella* sp. I: relative importance of water and sediment as routes of cadmium uptake

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ABSTRACT: The importance of dissolved versus sediment-bound cadmium as uptake routes for the deposit-feeding polychaete *Capitella* species I and the toxicity and toxicokinetics of cadmium from these exposure routes were investigated. Effects were reported as changes in worm growth rate, egestion rate and allometry. Radioactive cadmium (^{109}Cd) was used as a tracer to examine the uptake (5 d) and subsequent depuration (6 d) of cadmium. Both effects and kinetics were investigated in systems with and without sediment. Individual *Capitella* sp. I were exposed to (1) dissolved (i.e. <0.45 µm) cadmium (water-only treatment), (2) sediment-bound cadmium (sediment-bound only treatment), or (3) both dissolved and sediment-bound cadmium (porewater & sediment treatment). The porewater concentration of dissolved cadmium in porewater & sediment treatments was set approximately equal to the dissolved concentration in water-only treatments (0, 25, 50 µg Cd l^{-1}). Worms in water-only treatments showed negative growth rates, which decreased linearly from −5 to −10% d^{-1} with increasing cadmium concentration. Cadmium had no detectable effect on egestion rate or growth in the presence of sediment in either sediment-bound only (ca 36% d^{-1}) or porewater & sediment (ca 30% d^{-1}) treatments. Cadmium exposure had no detectable effect on the allometric exponent (i.e. area-length relation) in any of the treatments; however, worms in water-only treatments were relatively thinner than in the 2 treatments with sediment. Worms in porewater & sediment treatments took up ca 50-fold more cadmium (ca 195 ng Cd $worm^{-1}$) than worms in water-only treatments (3.9 ng Cd $worm^{-1}$) during 5 d of exposure. Sediment-bound cadmium was calculated to contribute 95% of the total amount taken up by feeding worms. Starving worms retained all of the cadmium during the subsequent depuration period (6 d), and exhibited an increased weight-specific body burden (µg Cd g^{-1} dry wt worm) due to shrinkage. In feeding worms, the decrease in weight-specific body burden was faster ($T_{1/2}$ = 3 d) than the decrease in total body burden (µg Cd $worm^{-1}$; $T_{1/2}$ = 11 d), indicating that both active excretion and dilution of cadmium body burden as a result of growth contributed to the change in cadmium tissue concentration during the depuration period. Thus, our results indicate that in *Capitella* sp. I sediment-bound cadmium is the major route of uptake. We found that cadmium affects starving but not fed worms, despite the fact that fed worms took up considerably more cadmium than starving worms. Our results suggest that stress associated with food limitation increases the susceptibility of worms to cadmium stress.

KEY WORDS: Bioavailability · Sediment quality criteria · Deposit feeder · Infauna

INTRODUCTION

Deriving biologically relevant exposure concentrations for sediment-associated contaminants remains a key challenge in the development of sediment quality criteria. Sediments can serve as both a sink and a source of anthropogenically derived contaminants, partly as a result of the influence of benthic fauna on sediment biogeochemistry and contaminant fate (e.g. Reynoldson 1987, Baudo & Muntau 1990, Power & Chapmann 1992, Campbell & Tessier 1996). Since benthic fauna both influence and are influenced by contaminant fate in sediments, there is likely to be rather

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tight coupling between the geochemical fate and biological effects of sediment-associated contaminants (Rhoads 1974, Reynoldson 1987, Forbes & Forbes 1994).

Like many anthropogenically derived metals, cadmium accumulates in aquatic sediments and reaches its highest concentrations mainly in coastal and estuarine areas (Theede 1980, Ankley et al. 1994, Campbell & Tessier 1996). Benthic organisms are able to accumulate cadmium via overlying water, porewater and ingested particles, and the determination of the relative importance of these different routes of uptake and subsequent toxicity to bottom-dwelling organisms is critical for assessing the risks associated with contaminated sediments. Results to date on the relative importance of the different routes of uptake remain inconclusive. Experiments with the facultative deposit feeder *Macoma balthica* showed that dissolved cadmium was most important when the bivalve was suspension feeding (Harvey & Luoma 1985a) and much less important when the bivalve deposit-fed on cadmium-contaminated sediment (Harvey & Luoma 1985b). Much of the uptake of cadmium by the deposit-feeding bivalve *Scrobicularia plana* was attributed to ingestion of sediment (Bryan & Uysal 1978). However, survival and reburial of the amphipod *Rhepoxynius abronius* was related to the amount of cadmium dissolved in the porewater rather than to the total cadmium concentration in bulk sediment (Kemp & Swartz 1988). Bryan & Hummerstone (1973) found that the polychaete *Nereis diversicolor* mainly absorbed cadmium from solution in the porewater, but uptake from food could not be neglected. In *Nereis virens*, accumulation rates of cadmium from the bulk sediment (i.e. sediment plus porewater) were equal to the rates from seawater (water-only exposure), indicating that uptake in this species occurs primarily via the aqueous phase (Ray et al. 1980). The same was found for *Nereis japonica* (Ueda et al. 1976). Thus, the available results suggest that interspecific physiological and behavioral differences (e.g. feeding behavior, feeding rate and metal excretion) may be crucial in determining the relative importance of different routes of metal uptake.

The objectives of this study were to investigate the relative importance of dissolved (i.e. <0.45 µm) versus sediment-bound cadmium as uptake routes and the toxicity and toxicokinetics of cadmium from these exposure routes to the deposit-feeding polychaete *Capitella* sp. I. *Capitella* species typically occur in depositional environments containing organically enriched sediments (Tsutsumi 1987, 1990, Tsutsumi et al. 1990, 1991, Forbes et al. 1994). The genus *Capitella* consists of numerous sibling species of which *Capitella* sp. I is the most opportunistic (Grassle & Grassle 1974). *Capitella* species live in tubes in the top few centimeters of the sediment, where they ventilate and feed (Grassle & Grassle 1976). *Capitella* sp. I was chosen for the present study, because its feeding strategy includes processing large quantities of fine-grained sediment and because the environments containing organically enriched sediments, which are ideal habitats for this species, often are sites of high heavy metal contamination (Pearson & Rosenberg 1978). Cadmium was chosen because it is characterized as one of the most toxic heavy metals (Theede 1980, Baudo & Muntau 1990) and is known to have an important influence on the energetics of benthic invertebrates (e.g. Theede 1980, Forbes 1991, Forbes & Depledge 1992).

Cadmium toxicity and toxicokinetics were investigated both in systems with and without sediment. Individual worms were exposed to (1) dissolved, (2) sediment-bound or (3) both dissolved and sediment-bound cadmium. ^{109}Cd was used as a tracer to investigate worm uptake and depuration, and the effects of cadmium were reported as changes in worm growth rate, egestion rate and allometry.

MATERIALS AND METHODS

General. Sediment for all experiments was collected from the Isefjord (station 63; Rasmussen 1973), Denmark, by scraping off and removing the top few centimeters of the sediment surface with a spatula. This station is located far from any sources of metal contamination and is routinely used for culturing worms. The sediment was sieved (to <250 µm) and subsequently frozen (–20°C) until use. Percent particulate organic matter was 3.32% (±0.05%, n = 4) as determined by loss on ignition (6 h at 500°C). Sediment was blended before use to disrupt particle aggregates.

A laboratory culture of *Capitella* sp. I was reared in an aerated aquarium (10 l) at 13°C on sediment with regular additions of ground fish food (Tetra Min) as a supplementary food.

Preparation of contaminated sediments. Contaminated seawater was made by adding a known volume of cadmium stock solution ($CdCl_2$ dissolved in 0.5 M HCl) to a known volume of filtered (0.2 µm) seawater (31‰). Cadmium-contaminated sediments were made by pipetting a known volume of wet sediment (<250 µm) into a known volume of the previously contaminated seawater. Cadmium was allowed to equilibrate among overlying water, porewater and sediment for 24 h after addition of sediment. Preliminary studies showed that cadmium concentration in each compartment attained a constant concentration within this time scale. Sediments were prepared at 4 cadmium concentrations and controls (i.e. without Cd addition) (see below). All of the Cd treatments were within the range of concentrations occurring in polluted sediments (Bryan 1984). Radioactive cadmium was used to trace cadmium administered via different exposure routes and to determine the amount of cadmium taken up or depurated by *Capitella* sp. I. Radioactively labeled seawater and sediments were made by adding a small amount of radioactive cadmium ($^{109}CdCl_2$ in 0.5 M HCl) to the contaminated seawater prior to addition of wet sediment.

Experimental treatments. Three different groups of treatments were used, namely 'water-only' (WO), 'sediment-bound only' (SBO) and 'porewater & sediment' (PWS) (see Tables 1 & 2). WO worms were exposed to dissolved cadmium (i.e. free Cd ions and other Cd species in solution; <0.45 µm) whereas SBO worms were exposed to sediment-bound cadmium only. The total amount of cadmium added to WO and SBO treatments was equal. Based on results of the preliminary studies, in which the porewater concentration in similar treatments was below detection, the porewater concentration in SBO was estimated as zero. PWS worms were exposed to both dissolved and sediment-bound cadmium. The dissolved porewater concentration of cadmium in PWS was set approximately equal to the concentration to which worms in WO were exposed.

Each treatment was subdivided into a control and 2 cadmium concentrations. Details of exposure conditions within treatments are given in Table 1. Experiments were maintained in light, and initial worm body volumes (BV) were between 0.9 and 1.3 mm^3 in WO and PWS treatments and between 0.1 and 0.25 mm^3 in SBO treatments. Only male worms were used, so as to minimize potential effects of reproductive condition (e.g. presence of lipid-rich eggs) on worm physiology and/or cadmium kinetics.

The nominal dissolved cadmium concentrations involved in WO and SBO (before sediment was added) were 0, 25 and 50 µg Cd l^{-1}. The initial nominal dissolved cadmium concentrations in PWS were 0, 4.1 and 8.2 mg Cd l^{-1}, which resulted in porewater concentrations of approximately 0, 25 and 50 µg Cd l^{-1}, respectively (Table 1). Note that the consequence of setting the porewater concentration in PWS equal to the dissolved concentration in WO was that worms in PWS were exposed to a very large sediment-bound pool of cadmium. The relation between the total amount of cadmium added ($[Cd]_{total}$) to PWS treatments and the subsequent equilibrium concentration in the porewater ($[Cd]_{porewater}$) was described by:

$$[Cd]_{porewater} = 0.0055\,[Cd]_{total} + 3.99$$
$$(r = 0.849,\ p << 0.001)$$

and the concentration of cadmium in the sediment was estimated as:

$$[Cd]_{sediment} = \{Cd_{total} - (Cd_{porewater} + Cd_{ovl.\ water})\}/(\text{g dry wt sed.}_{added})$$

where Cd_{total} = the total amount of cadmium added (µg Cd), $Cd_{porewater}$ and $Cd_{ovl.\ water}$ = measured amounts of cadmium (µg Cd) in the porewater and overlying water, respectively, and g dry wt sed.$_{added}$ = dry weight of sediment.

Experimental set-up. Experiments were performed at 22°C (±2°C), and worms were acclimated in the laboratory for 1 d prior to the experiments. WO worms were starved individually in 20 ml vials (diam. = 2.5 cm) containing 10 ml of filtered (<0.2 µm) seawater (31‰, pH: ca 6.8). Worms in PWS and SBO were grown individually in either 20 ml vials (PWS, diam. = 2 cm) containing 10 ml of filtered seawater and 3 ml of wet sediment (i.e. 3.12 g dry wt sed.) or in 20 ml petri dishes (SBO, diam. = 5 cm) to which were added 5 ml filtered (GFC, 0.45 µm) seawater and 5 ml wet sediment (ca 5.2 g dry wt sed). The vials were covered with plastic lids (each with a small hole) and the petri dishes with parafilm to minimize water evaporation during the experiments. The overlying water (WO, PWS: ca 9 ml; SBO: ca 3.5 ml) was renewed with aerated seawater at the same cadmium concentration 2 h before the start of an experiment and thereafter daily during all experiments. A summary of experiments, treatments, number of worms and measurements is provided in Table 2.

Table 1. Relation between the initial dissolved (<0.45 µm) cadmium concentration, the subsequently measured concentrations (24 h after addition of sediment) of dissolved cadmium in the overlying water and porewater, and the estimated sediment concentration (see text for further explanation). $WO_{25,50}$ and $SBO_{25,50}$ refer to the nominal dissolved [Cd] in the water-only and sediment-bound-only treatments (before addition of sediment), respectively, and $PWS_{25,50}$ to the nominal porewater [Cd] in the porewater and sediment treatments. Results are given as means (±1 SD). nd: not determined

Treatment	[Cd] added[a] (µg Cd l^{-1})	Porewater [Cd][b] (µg Cd l^{-1})	Overlying water [Cd][b] (µg Cd l^{-1})	Sediment [Cd][c] (µg Cd g^{-1} dry wt sed.)
WO_{25}	25	–	24.92 ± 0.28	–
WO_{50}	50	–	49.85 ± 0.55	–
SBO_{25}	25	nd	<0.38 (0)	0.024
SBO_{50}	50	nd	<0.55 (0.07)	0.048
PWS_{25}	4100	26.7 (2.9)	132.4 (79.5)	12.8
PWS_{50}	8200	48.3 (11.2)	264.9 (159.1)	25.7

[a]Nominal concentrations
[b]Measured concentrations
[c]Estimated concentrations

Table 2. Relations among experiments, treatments and measurements taken. Cadmium concentrations (µg Cd l^{-1} seawater) refer to the nominal dissolved concentration in WO and SBO (before addition of sediment) and the porewater concentration in PWS (see text for further explanation). n: total number of worms. (+) indicates that the measurement was made

Experiment	WO 0	WO 25	WO 50	SBO 0	SBO 25	SBO 50	PWS 0	PWS 25	PWS 50	N
Growth experiment										
Growth rate	+	+	+	+	+	+	+	+	+	75[a]
Egestion rate							+	+	+	30
Uptake and depuration experiment			+						+	30
Additional measurements										
Overlying water [Cd]		+	+					+	+	
Porewater [Cd]								+	+	

[a]30 of these worms were also used for egestion rate determination in PWS

Sampling and analysis of overlying water and porewater. Radioactive cadmium was used as a tracer to determine the concentration of cadmium in the overlying water and porewater. It was assumed that radioactive cadmium behaved identically to non-radioactive cadmium. Thus, the concentration of cadmium was calculated from the ratio of radioactive and non-radioactive cadmium.

The concentrations of dissolved cadmium in the overlying water ($WO_{25,50}$, $PWS_{25,50}$) and in the porewater ($PWS_{25,50}$) were measured to test whether the concentration changed during the experiments (5 d). Before the start of an experiment, overlying water was sampled (100 µl) from 4 different vials in WO and PWS prior to addition of sediment and gamma-counted. Hereafter, samples from the overlying water in WO and PWS were counted daily during the experiment. Porewater concentration of dissolved cadmium was measured in PWS treatments on Day 0 (n = 12) and Day 5 (n = 4) according to the following procedures. Overlying water (ca 10 ml) and wet sediment from each vial were transferred separately into 2 glass centrifuge tubes and centrifuged (16 min at 3180 × *g*). Subsequently, the supernatant from the sediment tube (i.e. the porewater) was transferred to a new tube and was recentrifuged to remove particles that were resuspended during the transfer. The supernatants from the centrifuged overlying water and the recentrifuged porewater were decanted to new tubes. The tubes were shaken and triplicate samples from each tube were gamma-counted.

Growth. The effects of dissolved ($WO_{0,25,50}$), sediment-bound ($SBO_{0,25,50}$), and both dissolved and sediment-bound ($PWS_{0,25,50}$) cadmium on worm growth were investigated. There were 5 replicate worms in each cadmium treatment in SBO and 10 each in WO and PWS. Worms (WO, PWS and SBO) and pellets produced during 5 d in PWS treatments were gently removed from each vial or petri dish at the conclusion of the growth experiment. Worms were used for measurements of growth rate and worm allometry, and pellets were used for determination of egestion rate.

Growth rate and allometry: Individual worm surface area (*A*) and length (*L*) were measured, and worm body volumes (BV, mm^3) were estimated regularly during an 8 d period in a preliminary study. The results showed that individual BV was exponentially related to time such that BV = $k_1e^{(Rt)}$, where k_1 = constant, *R* = individual growth rate (d^{-1}) and *t* = time in days. The relation between *A* (mm^2) and *L* (mm) was described by the power function: $\log(A) = \log(k_2) + a\log(L)$, where k_2 = constant and *a* = allometric exponent (the slope on a log-log scale). Growth rates and worm allometry were described by the same type of function for all cadmium exposures, in systems both with and without sediment. To avoid stressing the worms by frequently removing them from the sediment, individual worm BV was only estimated at the beginning ($t = 0$) and at the end ($t = 5$) of the experiment in PWS and WO. However, BV was measured 5 times in SBO during the experiment (9 d). Growth rates were determined as changes in individual BV with time. The relation between individual worm surface area and length was used to test the effect of cadmium on worm allometry in WO, SBO and PWS treatments.

A video camera mounted on a dissection microscope was used to record live worms. Individual BVs were estimated from measurements of projected *A* and *L* assuming that worms are cylindrical in shape (Self & Jumars 1978): BV = $[(\pi \times A^2)/(4 \times L)]$. Area and length were estimated using JAVA software (Jandel, Germany). Each worm-size estimate used in the analysis was the mean of 3 replicate volume determinations (SD < 10%).

Egestion rate: Individual egestion rates were determined for worms in PWS treatments (same 30 worms for which growth rates were measured). Pellets were sieved (125 µm) from each vial, cleaned in seawater and placed in a tube containing 75% EtOH until analysis. Pellets were cleaned in distilled water and transferred to a small tube prior to disaggregation by ultrasound (ca 1 h). Each tube was shaken (6 to 8 times) during this period to promote disaggregation of pellets. Disaggregated pellets were passed through a 63 µm filter to separate dissolved pellets from large mineral grains that had been trapped on the 125 µm sieve, dried (24 h at 105°C) and weighed. Body-size-specific egestion rates were calculated as dry weight of pellets produced over 5 d divided by BV on Day 5 (BV_{end}).

Uptake and depuration. This experiment was designed to investigate the kinetics of cadmium uptake and depuration in *Capitella* sp. I exposed to cadmium in the dissolved form (WO_{50}; n = 15) or from both sediment and porewater (PWS_{50}; n = 15) (Table 2). At the end of each exposure interval (i.e. at 1, 3 and 6 h, and thereafter daily), individual worms were removed from their vials, cleaned in seawater (<0.2 µm), gamma-counted and placed in fresh, clean seawater (WO_{50}) and natural sediment (PWS_{50}) for 1 h to purge their guts. Subsequently, the worms were recounted and transferred to new vials containing contaminated sediment and/or water. Worms measured after 1 and 3 h exposure were not used again. Thus, 5 worms in each treatment were used during the remaining period. Following an uptake period of 5 d, the worms were allowed to depurate in unlabeled filtered seawater (WO_{50}) and sediment (PWS_{50}) for 6 d. During the depuration period, worms were sieved from their containers, removed from their tubes, rinsed in seawater, gamma counted and subsequently placed in new uncontaminated vials on a daily basis.

Cadmium body burdens in individual *Capitella* sp. I were assessed as total body burdens (TBB, i.e. total [Cd] worm^{-1}) and as weight-specific body burdens (BB, i.e. total [Cd] g^{-1} dry wt worm) (see below). Individual growth rates were determined from BV measured at the beginning and end of the uptake and depuration period. For every day of the uptake and depuration period, BV was estimated by linear interpolation from the estimated overall growth rate. BV was converted to dry weight according to Forbes & Lopez (1987): DW = 150.9BV + 2.08, where DW = worm dry weight (µg) and BV = body volume (mm^3). Net uptake rate (k_u), depuration rate (k_d) and half-life ($T_{½}$, i.e. time to 50% reduction in TBB or BB) were calculated as described by Spacie & Hamelink (1985). The relation between $T_{½}$ and k_d is given by: $T_{½} = \ln 2/k_d$. The concentration factors (CF) were calculated as: $CF_{WO} = [BB_5/(\mu g\ Cd\ g^{-1})]$, and $CF_{PWS} = BB_5/Q$, where BB_5 = µg Cd g^{-1} dry wt worm on Day 5. BB was either related to the porewater concentration alone, in which case Q = µg Cd g^{-1}; to the sediment-bound pool of cadmium alone, in which case Q = µg Cd g^{-1} dry wt sed.; or to both porewater and sediment-bound cadmium, in which case Q = µg Cd g^{-1} + µg Cd g^{-1} dry wt sed.

Statistical analysis. Analysis of data included 1-way ANOVA to test the significance of cadmium effects (significance level: $p < 0.05$). Tukey's HSD test was used to test for significant differences in pairwise comparisons among concentrations within treatments. Bartlett's test was used to test the homogeneity of variances among cadmium concentrations within treatments. Student's *t*-tests were performed when only 2 groups were involved. ANCOVA was used to test for significant Cd effects on the relation between worm area and length.

RESULTS

Analysis of overlying water and porewater

The dissolved cadmium concentration in WO remained constant at 99.3% (± 1.7) of the initial (t = 0) cadmium concentration (ANOVA; p = 0.641) throughout the course of the experiment (WO_{25}: 24.7 ± 0.4, WO_{50}: 49.5 ± 0.8 µg Cd l^{-1}). The cadmium content in the overlying water in PWS declined significantly (Tukey; p << 0.001) from Day 0 (8.71 ± 1.2%) to Day 1 (3.23 ± 1.9%), and thereafter remained constant at 2.36 (± 1.3)% of the initial concentration (ANOVA; p = 0.355). This corresponds to overlying water concentrations of 96.8 (± 53.3) µg Cd l^{-1} in PWS_{25} and 193.5 (± 106.6) µg Cd l^{-1} in PWS_{50}.

The porewater concentration of dissolved cadmium did not differ significantly between the beginning (t = 0) and the end (t = 5) of the experiment in PWS treatments (Table 3). The porewater concentrations of cadmium in PWS were on average 3.6 times lower than in the overlying water.

Table 3. Comparisons (Student's *t*-test) of measured porewater cadmium concentrations [mean ± 1 SD (number of measurements)] on Day 0 and Day 5 of the experiment. PWS_{25} and PWS_{50} refer to the nominal porewater concentrations of cadmium in the porewater & sediment treatment

	PWS_{25} (µg Cd l^{-1})	PWS_{50} (µg Cd l^{-1})
$t = 0$	26.7 ± 2.9 (12)	48.3 ± 11.2 (12)
$t = 5$	26.6 ± 2.2 (4)	52.5 ± 5.0 (4)
Probability	0.918	0.489

Effect of cadmium on growth rate, egestion rate and worm allometry

Worms in WO treatments had negative growth rates (degrowth rates) due to the absence of food (Fig. 1A). Cadmium had a significant negative effect on the degrowth rate in *Capitella* sp. I (ANOVA; p = 0.009). The degrowth rates were −5 (± 2.3)% d^{-1} for controls (0 µg Cd l^{-1}), −7.3 (± 2.8)% d^{-1} at 25 µg Cd l^{-1} and −9.7% d^{-1} (± 3.1) at 50 µg Cd l^{-1} seawater. Degrowth rates did not differ significantly between controls (WO_0) and worms exposed to a dissolved cadmium concentration of 25 µg Cd l^{-1} (Tukey, p = 0.211) or between worms exposed to 25 and 50 µg Cd l^{-1} (Tukey, p = 0.181).

There was no significant effect of cadmium on growth rate in *Capitella* sp. I exposed to sediment-bound cadmium (SBO: ANOVA, p = 0.552) or exposed to cadmium from both porewater and sediment (PWS: ANOVA, p = 0.151) (Fig. 1B, C). Worms maintained

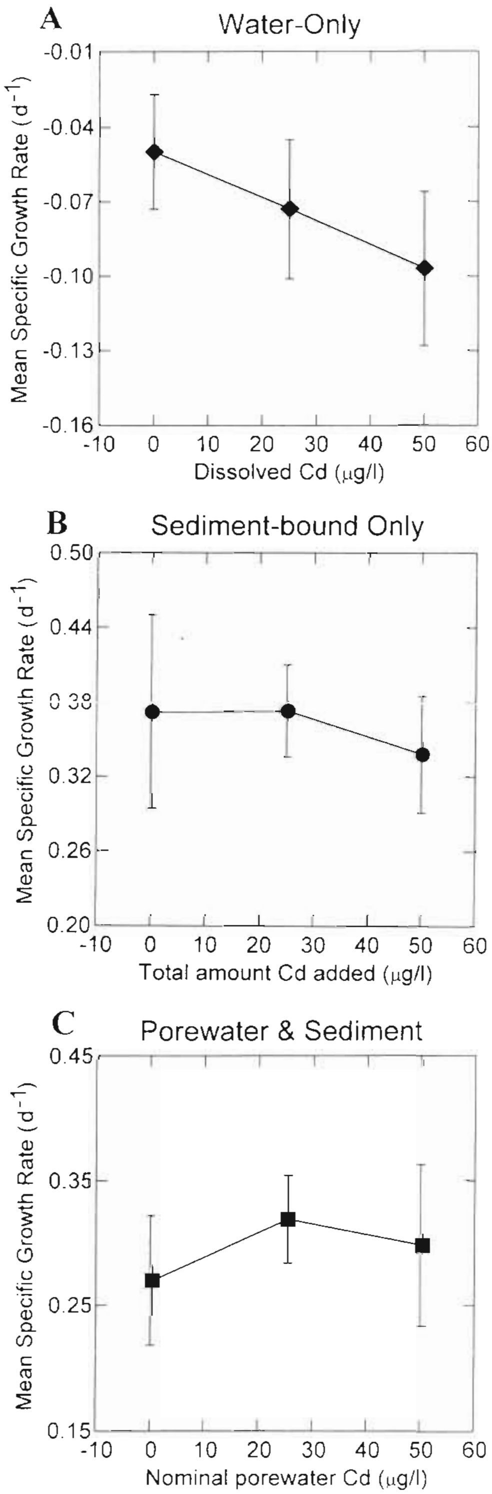

Fig. 1. *Capitella* sp. I. Individual volume-specific growth rates (mean ± SD) versus (A) dissolved nominal cadmium concentration in WO treatments (n = 10), (B) the initial nominal dissolved cadmium concentration in SBO treatments (n = 5) before addition of sediment and (C) nominal dissolved porewater concentration in PWS treatments (n = 10). Relation between growth rate (*R*) and dissolved cadmium ($[Cd]_{total}$) in WO treatments followed: $R = -0.001\,[Cd]_{total} - 0.05$ (r = 0.578, p = 0.002)

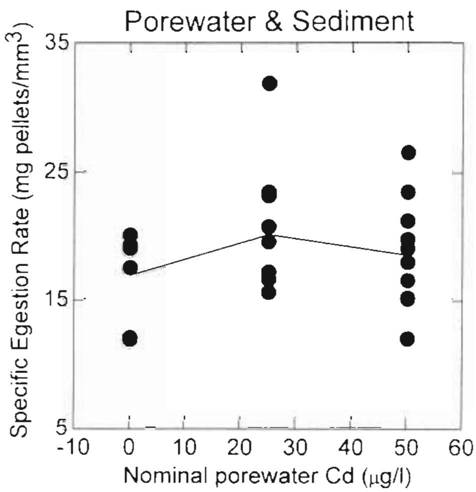

Fig. 2. *Capitella* sp. I. Relation between individual volume-specific egestion rate and the nominal porewater concentration of dissolved cadmium in PWS treatments

very high growth rates in both of these treatments regardless of cadmium exposure, with an average of 36.1 (± 5.5) and 29.5 (± 5.5)% d^{-1}, respectively.

The volume-specific egestion rate of *Capitella* sp. I was not affected by cadmium exposure (ANOVA; p = 0.198) in PWS treatments. *Capitella* produced an average of 18.8 (± 4.6) mg pellets BV_{end}^{-1} during 5 d (Fig. 2).

The allometric exponent (i.e. slope) was independent of cadmium exposure within all 3 treatments (ANCOVA: WO, p = 0.134; SBO, p = 0.099; PWS, p = 0.234) (Table 4). Intercepts did not differ significantly among cadmium groups within WO and PWS (ANCOVA: p = 0.465 and p = 0.177, respectively), but did within SBO (ANCOVA: p = 0.008). Comparison of the 95% confidence limits for the intercepts within SBO treatments showed that the intercept in SBO_{25} differed from SBO_0. SBO_{25} and SBO_{50} overlapped, as did SBO_0 and SBO_{50}. Data were pooled within treatments, and the effect of treatment on allometry was determined by ANCOVA (Table 5). The slopes were significantly different among the 3 treatments (ANCOVA: p < 0.001). The confidence limits for the allometric exponent (*a*) and the *y*-intercept ($\log k_2$) did not overlap among the 3 treatments (Table 5).

Analysis of cadmium uptake and depuration

Total radioactivity in purged (for 1 h) versus non-purged *Capitella* sp. I did not differ significantly (p >> 0.05), and the data presented below are for purged worms. Worms in WO_{50} decreased their BV by 12.5% d^{-1}, and worms in PWS_{50} increased their BV by 15.9% d^{-1} during the entire 11 d period (Fig. 3).

Table 4. Statistics for the relation between worm area (*A*) and length (*L*) in the different cadmium concentrations within treatments: $\log(A) = a\log(L) + \log(k_2)$, where $\log(k_2)$ is the *y*-intercept of the regression and *a* is the slope (i.e. allometric exponent). n: number of measurements (*A*, *L*); r: correlation coefficient

Treatment	Mean *a*	Confidence limits (95%)		Mean $\log(k_2)$	Confidence limits (95%)		r	n
		Lower	Upper		Lower	Upper		
WO_0	1.049	0.891	1.207	−0.332	−0.439	−0.225	0.996	57
WO_{25}	0.901	0.701	1.100	−0.238	−0.372	−0.103	0.993	57
WO_{50}	1.152	0.964	1.340	−0.411	−0.539	−0.284	0.994	45
SBO_0	1.785	1.738	1.832	−0.777	−0.803	−0.743	0.991	138
SBO_{25}	1.869	1.820	1.917	−0.847	−0.879	−0.816	0.992	134
SBO_{50}	1.828	1.758	1.897	−0.820	−0.864	−0.766	0.984	137
PWS_0	1.525	1.394	1.657	−0.637	−0.749	−0.526	0.995	61
PWS_{25}	1.607	1.516	1.697	−0.688	−0.764	−0.613	0.997	60
PWS_{50}	1.661	1.564	1.758	−0.733	−0.816	−0.650	0.997	57

Table 5. Statistics for the relation between worm area (*A*) and length (*L*) within treatments (i.e. data are pooled among Cd concentrations): $\log(A) = a\log(L) + \log(k_2)$, where $\log(k_2)$ is the *y*-intercept of the regression and *a* is the slope (i.e. allometric exponent). n: number of measurements (*A*, *L*); r: correlation coefficient

Treatment	Mean *a*	Confidence limits (95%)		Mean $\log(k_2)$	Confidence limits (95%)		r	n
		Lower	Upper		Lower	Upper		
WO	1.038	0.933	1.142	−0.330	−0.402	−0.259	0.994	154
SBO	1.822	1.790	1.854	−0.810	−0.831	−0.789	0.989	409
PWS	1.598	1.536	1.659	−0.686	−0.738	−0.635	0.996	176

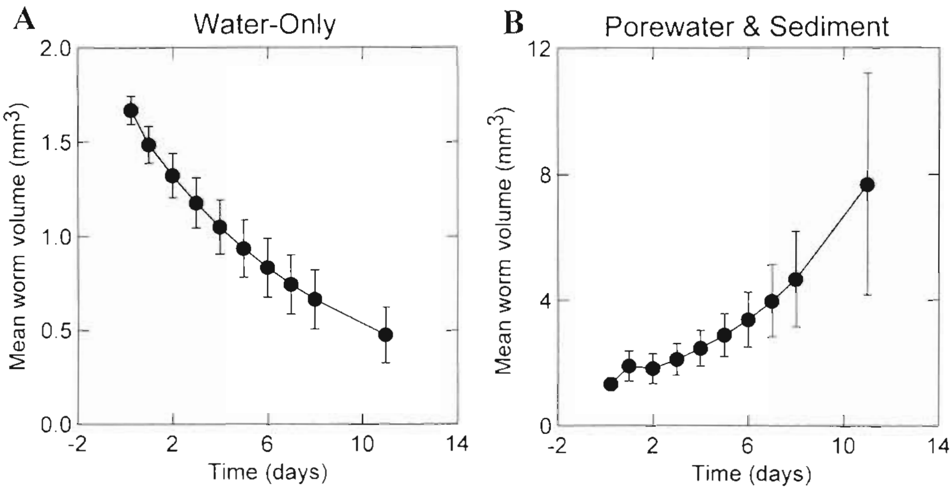

Fig. 3. *Capitella* sp. I. Relations between estimated worm body volume (mean ± SD, n = 4) and time. Exposure period: Days 0 to 5; depuration period: Days 5 to 11. (A) WO_{50}: mean growth rate = −12.5% d^{-1}; 95% confidence limits, lower = −15.8% and upper = −9.2%. (B) PWS_{50}: mean growth rate = 15.9% d^{-1}; 95% confidence limits, lower = 13.0% and upper = 18.9%

Cadmium uptake

The increases in TBB and BB of worms with exposure time were best described by power functions in both WO_{50} and PWS_{50} treatments (Fig. 4). Accumulation of cadmium was considerably higher in PWS_{50} than in WO_{50}. The total body burden of cadmium was ca 50 times higher in worms in PWS_{50} compared to worms in WO_{50} at the end of the uptake period, but only 17 times higher on a weight basis. These differences were reflected in k_u values that on average were ca 24 times higher in PWS_{50} (Table 6). The net k_u declined as the weight-specific concentration of cadmium increased, indicating a trend toward a steady-state level, whereas TBB continued to increase as worms grew in PWS (Fig. 4). Worms in WO_{50} increased TBB and BB continuously, and no trend toward a steady state level was observed.

Comparison of cadmium concentration factors (CF) between WO_{50} and PWS_{50} depended on the pool of cadmium in PWS to which BB was related. CF was highest when related to the porewater alone and low-

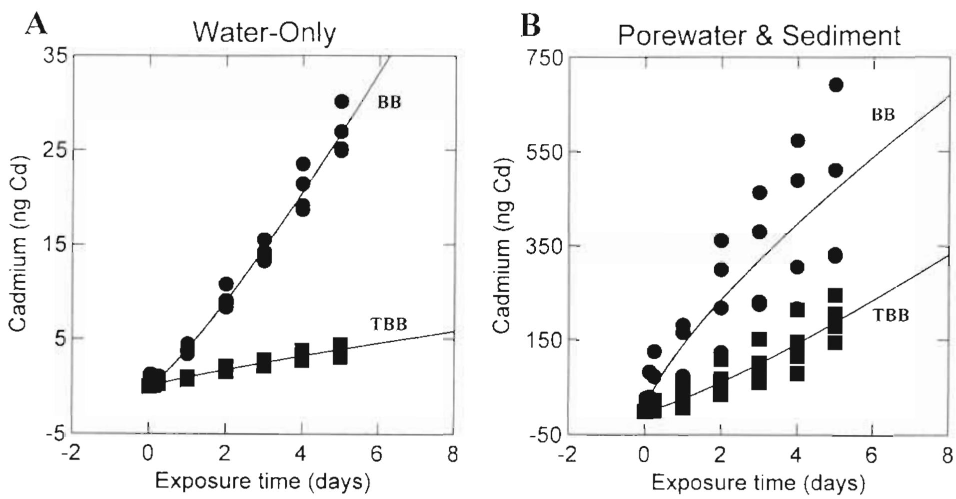

Fig. 4. *Capitella* sp. I. Relations between total body burden (TBB; ng Cd worm^{-1}), weight-specific body burden (BB; ng Cd mg^{-1} dry wt worm) and exposure time for individual worms in (A) WO treatments (n = 4) and (B) PWS treatments (n = 4). Power functions: WO_{50}, TBB = 0.99 day$^{0.854}$ (r = 0.991), BB = 3.97 day$^{1.187}$ (r = 0.996); PWS_{50}, TBB = 26.64 day$^{1.22}$ (r = 0.961), BB = 140.16 day$^{0.753}$ (r = 0.944)

est when related to porewater and sediment (Table 7). Hence, CF for *Capitella* sp. I in PWS_{50} is ca 17 times higher than in WO_{50} if the porewater is considered as the sole route of uptake, but approximately 30 times lower if the sediment-bound pool of cadmium is also included as a route of uptake.

Table 6. *Capitella* sp. I. Net uptake rates (k_u; µg Cd g^{-1} dry wt worm^{-1} d^{-1}) from the uptake period

Hour	WO	PWS
1	23.86	281.5
3	-4.43	292.5
6	3.26	165.7
24	3.80	76.8
48	5.35	137.2
72	4.94	74.4
96	6.59	71.4
120	6.08	69.9
Average k_u	6.18	146.11

Table 7. *Capitella* sp. I. Cadmium concentration factors (CF) for worms in WO_{50} and PWS_{50} treatments. CF = BB_5/Q, where BB_5 is the volume-specific body burden at the end of the exposure period, and Q is the [Cd] in (1) the dissolved pool (0.05 µg Cd g^{-1}), (2) the sediment bound pool (25.7 µg Cd g^{-1}), (3) in the dissolved plus sediment bound pool (0.05 + 25.7 µg Cd g^{-1}), and (4) the overlying water on Day 1 of the experiment (i.e. 0.194 µg Cd g^{-1})

Treatment	Pool of cadmium	Concentration factor
WO_{50}	Dissolved	536.8
PWS_{50}	Only dissolved porewater	9343.8
	Only sediment-bound	18.2
	Porewater and sediment	18.1
	Only overlying water	2420.7

Cadmium depuration

In general, an exponential function provided the best fit to the change in BB and TBB with depuration time (Fig. 5), indicating that depuration could adequately be described by a 1-compartment model. A possible exception was TBB in PWS_{50}, which appears to show a slower loss rate after 2 d (Fig. 5B).

Worms in WO_{50} treatments did not decrease TBB significantly (ANOVA; p = 0.127), and TBB remained constant at 99.4% (± 2.2) during the depuration period. In contrast, BB increased significantly (ANOVA; p << 0.05) from 100% (t = 0) to 195% (± 22.3; t = 6) in WO_{50} worms (Fig. 5A).

Worms in PWS_{50} treatments decreased both BB and TBB, though BB decreased at a faster rate (Fig. 5B). Hence, the weight-specific half-life ($T_{½}$: 3.0 d) was approximately 3.5 times shorter than the half-life of the total body burden ($T_{½}$: 10.7 d). Furthermore, growing worms (PWS_{50}) were able to halve the total body burden of cadmium ca 16 times faster than starving worms (WO_{50}; $T_{½}$ = 173.3 d).

DISCUSSION

Effect of cadmium on growth rate, egestion rate and worm allometry

Cadmium significantly increased the shrinkage rate of *Capitella* sp. I in water-only treatments (from -5 to -9.7% d^{-1}). However, there was no negative effect of cadmium on growth in sediment-bound only and porewater & sediment treatments, despite the fact that the dissolved cadmium concentration in WO was equal to the concentration in the porewater and lower than the concentration in the overlying water in PWS. This dif-

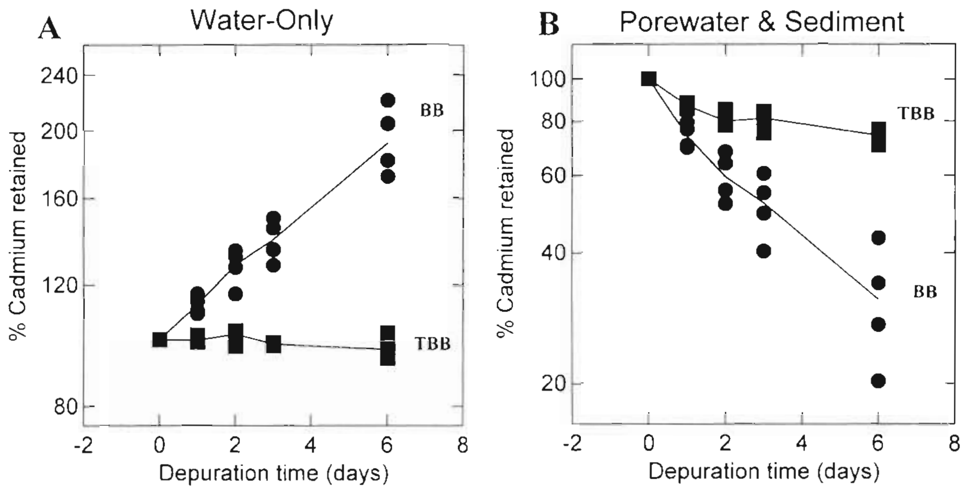

Fig. 5. *Capitella* sp. I. Relations between BB, TBB and depuration time for individual worms (n = 4) in the (A) WO treatment and (B) PWS treatment. Abbreviations as in Fig. 4. Lines are locally weighted scatterplot smooths. Exponential functions: WO_{50}, TBB = $100e^{-0.004 day}$ (r = 1.00), BB = $100e^{0.111 day}$ (r = 0.997); PWS_{50}, TBB = $100e^{-0.065 day}$ (r = 0.998), BB = $100e^{-0.228 day}$ (r = 0.994)

ference in effect may be related to differences in energy intake (as well as route of Cd uptake) between worms in WO (= starved) and SBO/PWS (= fed) treatments. Organisms allocate the energy absorbed from food to both maintenance requirements and growth (Calow & Sibly 1990). Dealing with chemical stress is likely to involve some degree of added energy expenditure, which can be obtained by increasing energy intake or by use of energy reserves otherwise used for growth and maintenance requirements (Calow & Sibly 1990, Langston & Spence 1995). There was no indication in the present experiments that worms responded to cadmium exposure by increasing energy intake, as egestion rates did not differ among cadmium concentrations in PWS treatments.

When food is limited, *Capitella* sp. I is able to use its own tissue as an energy source and can survive substantial reductions in its body volume (Eckelbarger et al. 1984, Forbes et al. 1994). Our results suggest that starving worms use their own tissue to maintain the metabolic process(es) required to deal with metal stress. Thus, we observed more rapid shrinkage rates of cadmium-exposed worms relative to unexposed worms in the absence of food.

The mean growth rates of worms in SBO and PWS were higher (30 and 36 % d^{-1}, respectively) than previously reported (up to 25 % d^{-1}; Tenore & Chesney 1985, Forbes & Lopez 1987, Forbes & Lopez 1990). The difference in average growth rate between SBO and PWS is not likely to be an effect of cadmium. Oxygen concentration may have been lower in PWS relative to SBO, because of a deeper water column and partitioning of the sediment into an oxic and anoxic phase in PWS. A decrease in oxygen level is known to reduce the growth of *Capitella* sp. I (Forbes & Lopez 1990).

Cadmium had no effect on worm allometry within the 3 treatments, and there were no differences among the *y*-intercepts within WO and PWS treatments. It is not likely that the difference in intercepts among cadmium concentrations in the SBO treatment was a response to exposure, since the intercepts only differed between SBO_0 and SBO_{25} and not between SBO_0 and SBO_{50}. Comparison of the allometric exponent and the intercepts among treatments (WO, SBO, PWS) for worms not exposed to cadmium indicated a significant difference (Table 5). Therefore, the data suggest that worm allometry is affected by feeding conditions. The relation between area and length was very close to being linearly proportional in starving worms (WO: a = 1.04), whereas growing worms were relatively wider (SBO: a = 1.82; PWS: a = 1.60). The allometry of the polychaete *Streblospio benedicti* is also dependent on feeding conditions; in contrast to *Capitella* sp. I they are relatively wider and shorter when starving, compared to thinner and longer during growth and regrowth (P. Huggins pers. comm.). The importance of changes in worm allometry is a subject that needs further consideration, and the growth dynamics of *Capitella* sp. I may be more complex than can be described by a single average allometric exponent (Forbes & Lopez 1989).

Cadmium uptake and depuration kinetics

The estimated growth rate in *Capitella* sp. I was lower (PWS_{50}: ca 15.9 % d^{-1}) and the shrinkage rate faster (WO_{50}: −12.5 % d^{-1}) in the uptake and depuration experiment compared to measured rates in the growth experiment (ca 30 and −10 % d^{-1}, respectively). Worms in the uptake and depuration experiment were shifted among vials and gamma tubes several times daily and such disturbance likely acted as an additional source of stress and/or reduced feeding rates in this experiment.

Capitella sp. I has 3 possible uptake routes for cadmium in systems with sediment (PWS_{50}): (1) from ingestion of sediment and subsequent accumulation over gut epithelium; (2) from porewater; and (3) from overlying water. The last 2 routes involve diffusion from water across the worm body surface, followed by accumulation over epidermal membranes. Epidermal membranes are possible uptake routes for worms in WO_{50} as well. The rate of cadmium uptake by *Capitella* sp. I depended on the presence of sediment, with starving worms (WO_{50}) having a much slower (ca 24 times) uptake rate than feeding worms (PWS_{50}). Also the total body burden and the weight-specific body burden were lower (ca 50 and 17 times, respectively) in WO_{50} compared to PWS_{50} at the end of the experiment. Worms in WO_{50} concentrated cadmium 537-fold in 5 d. The concentration factors in PWS_{50} depended on whether the amount of cadmium taken up was related to porewater cadmium alone (CF: ca 9344) or if the concentration of cadmium in the sediment was included (CF: ca 18).

Metal uptake is believed primarily to involve an initial interaction of the free metal ion with a transport system (i.e. channel or carrier) in the epithelium (external and/or internal), though uptake of other metal species, apart from free ions, can occur (e.g. Mason & Jenkins 1995, Simkiss & Taylor 1995, Simkiss 1996). The uptake of metal-ligand complexes is presumed to occur in response to a concentration gradient, such that cadmium goes from dissolved complexes to more stable sulfide groups in the cells (Mason & Jenkins 1995). Most literature suggests that the free cadmium ion is the most bioavailable cadmium species in the aquatic environment (e.g. Blust et al. 1995, Dai et al. 1995). Assuming that the free cadmium ion is the most bioavailable fraction for uptake in *Capitella* sp. I and that the concentrations of dissolved cadmium ions were equal between WO and the porewater in PWS, we expected that worms in WO_{50} would accumulate at least as much cadmium as worms in PWS_{50}. One possible explanation for the substantially higher body burdens in PWS_{50} compared to WO_{50} is that the cadmium dissolved in the porewater in PWS_{50} was in a more bioavailable form than the dissolved cadmium in WO_{50}. However, complexation of metals with organic ligands and colloids dissolved in porewater results in a decrease in the concentration of free cadmium ions and is thought to result in reduced bioavailability of the metal to aquatic organisms (e.g Blust et al. 1995, Dai et al. 1995, Landrum et al. 1996). Therefore, even though the total concentration of dissolved cadmium was equal between WO and PWS, it is likely that a greater fraction of dissolved cadmium was present as free ions (and hence was more bioavailable) in WO than in PWS treatments (because of a higher concentration of organic ligands and colloids in sediment-containing treatments). Therefore, a greater bioavailability of porewater cadmium is not a likely explanation for the higher uptake in PWS compared to WO treatments.

A second possible explanation for the substantially higher body burdens in PWS_{50} compared to WO_{50} is that worms in PWS accumulated cadmium from the overlying water, the concentration of which was 4 times greater than the porewater concentration (Table 1). Although infauna are often viewed as being in intimate contact with sediment porewater, worms living in tubes may actually be in closer contact with cadmium dissolved in overlying water than in porewater because (1) the tube creates a barrier for cadmium in the porewater, reducing direct contact between worms and porewater, and (2) worms exchange the water in their tubes with overlying water during irrigation (Aller 1982, Cammen 1987, Landrum et al. 1996). If we assume that worms mainly took up cadmium from the overlying water in PWS_{50}, this gives a concentration factor of 2421 (which is still 4.5 times higher than in WO_{50}). Likewise, if we include both porewater and overlying water as routes of cadmium uptake, the concentration factor in PWS_{50} is still 3.58 times higher than in WO_{50}.

A third possible explanation for the substantially higher body burdens in PWS_{50} compared to WO_{50} is that *Capitella* sp. I in PWS_{50} were able to absorb sediment-associated cadmium. Deposit feeders, such as *Capitella* sp. I, select and ingest large amounts of fine sediment particles that tend to be enriched in organic material, and hence metals. Thus worms can be exposed to a very high concentration of cadmium from ingested sediment (Campbell & Tessier 1996). Absorption of cadmium across the gut will involve alteration of the ingested particulates to a dissolved form, followed by a facilitated diffusion across the intestinal epithelium (Luoma 1983). Metal absorption is dependent on food type, gut retention time and pH (Luoma 1983). Uptake of cadmium by mice is pH dependent, as cadmium is taken up over the epithelium cells at pH values between 1 and 4, but hardly at all at higher pH (Sørensen et al. 1993). Cadmium is present as free cadmium ions at low pH, which are easily absorbed, whereas high pH promotes complexation of cadmium with various food components and subsequently decreases absorption (Sørensen et al. 1993). The digestive pH of most deposit-feeding organisms ranges between 6 and 7 (Luoma 1983, Frithsen 1984), suggesting that H^+ is not likely responsible for solubilization of sedimentary metals. Alternatively, gut amino acids appear to play a major role in the release of metals from ingested sediments (Chen & Mayer 1998).

Following Langston & Spence (1995) we can estimate the contribution of sediment-bound cadmium to the total cadmium body burden by comparing the weight-specific body burdens of cadmium in starved and fed animals. By relating the weight-specific body burden for worms in WO_{50} (BB_{WO}) with body burden for worms in PWS_{50} (BB_{PWS}), we estimate that 95% of the cadmium taken up by *Capitella* sp. I in PWS_{50} was from the sediment-bound pool. The concentration factor for uptake from the sediment-bound pool was ca 17 as calculated by relating the 'corrected' concentration of cadmium ($BB_{PWS} - BB_{WO}$) taken up during the exposure period (440.35 µg Cd g^{-1} dry wt worm) to the concentration of cadmium in the sediment (25.7 µg Cd g^{-1} dry wt sediment).

Starving worms did not reduce their total body burden of cadmium significantly ($T_{½}$: 173 d), but increased their weight-specific body burden during the depuration period. Since excretion of cadmium was essentially zero, the increase in the weight-specific body burden was a direct result of the shrinkage of starving worms. In contrast, feeding worms decreased both their total body burden and weight-specific body burden of cadmium during the depuration period. Because worms were actively growing, weight-specific body burdens decreased approximately 3.5 times faster than total body burdens. Thus, both active excretion of cadmium and dilution of cadmium body burden by incorporation of new tissue contributed to the cadmium content of feeding worms.

Differences in excretion between worms exposed to cadmium via water versus water and sediment suggest that cadmium taken up by epidermal cells is eliminated at a slower rate than cadmium taken up over the gut wall. In addition, worms exposed to Cd in water experienced a more pronounced reduction in body volume compared to worms exposed to Cd via ingested sediment, despite the much higher Cd body burdens attained by the latter group. Together, these results suggest that cadmium absorbed over the body wall enters the target sites more readily, is harder to depurate and is thereby more toxic than cadmium absorbed across the gut.

CONCLUSIONS

It is known that food limitation controls deposit-feeder populations in nature. Although the present design included an extreme food situation, the results indicate that heavy metals may be especially important for population growth during periods of food scarcity when organisms seem to be physiologically more sensitive to heavy metal stress.

Increasing concern that sediments may be important sources of contaminants in aquatic systems has led to efforts toward developing sediment-quality criteria, and in this regard the most common approaches for estimating sediment-quality criteria have involved the assumption that benthic organisms, like pelagic species, are exposed to primarily dissolved contaminants. Our results show that uptake from the sediment-bound fraction is the primary route of cadmium absorption for *Capitella* sp. I and therefore question the relevance of present approaches for assessing sediment-quality criteria for contaminants. Exclusive focus on the dissolved phase is likely to substantially underestimate the actual accumulation of contaminants by benthic deposit-feeding organisms. However, subsequent toxicity does not appear to be a simple function of contaminant body burden, and both the route(s) and rates of uptake need to be considered.

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LITERATURE CITED

Aller RC (1982) The effects of macrobenthos on chemical properties of marine sediment and overlying water. In: McCall PL, Tevesz MJS (eds) Animal-sediment relations. Plenum, New York, p 53–102

Ankley GT, Thomas NA, DiToro DM, Hansen DJ, Mahony JD, Berry WJ, Swartz RC, Hoke RA, Garrison AW, Allen HE, Zarba CS (1994) Assessing potential bioavailability of metals in sediments: a proposed approach. Environ Manag 18:331–337

Baudo R, Muntau H (1990) Lesser known in-place pollutants and diffuse source problems. In: Baudo R, Giesy JP, Muntau H (eds) Sediments: chemistry and toxicity of in-place pollutants. Lewis Publishers, Inc, Boca Raton, FL, p 1–14

Blust R, Baillieul M, Decleir W (1995) Effect of total cadmium and organic complexing on the uptake of cadmium by the brine shrimp, *Artemia franciscana*. Mar Biol 123:65–73

Bryan GW (1984) Pollution due to heavy metals and their compounds. In: Kinne O (ed) Marine ecology, Vol 5, Part 3. John Wiley & Sons Ltd, Chichester, p 1289–1431

Bryan GW, Hummerstone LG (1973) Adaptation of the polychaete *Nereis diversicolor* to estuarine sediments containing high concentrations of zinc and cadmium. J Mar Biol Assoc UK 53:839–857

Bryan GW, Uysal H (1978) Heavy metals in the burrowing bivalve *Scrobicularia plana* from the Tamar estuary in relation to environmental levels. J Mar Biol Assoc UK 58: 89–108

Calow P, Sibly RM (1990) Essay review. A physiological basis of population processes: ecotoxicological implications. Funct Ecol 4:283–288

Cammen LM (1987) Polychaeta. In: Pandian TJ, Vernberg FJ (eds) Animal energetics, Vol 1 Academic Press, Inc, San Diego, p 217–260

Campbell PGC, Tessier A (1996) Ecotoxicology of metals in the aquatic environment: geochemical aspects. In: Newman MC, Jagoe CH (eds) Ecotoxicology: a hierarchical treatment. Lewis Publishers, Inc, Boca Raton, FL, p 11–58

Chen Z, Mayer LM (1998) Digestive proteases of the lugworm (*Arenicola marina*) inhibited by Cu from contaminated sediments. Environ Toxicol Chem 17(3):433–438

Dai M, Martin JM, Cauwet G (1995) The significant role of

colloids in the transport and transformation of organic carbon and associated trace metals (Cd, Cu and Ni) in the Rhône delta (France). Mar Chem 54:159-175
Eckelbarger KJ, Linley PA, Grassle JP (1984) Role of ovarian follicle cells in vitellogenesis and oocyte resorption in *Capitella* sp. I. Mar Biol 79:133-144
Forbes TL, Forbes VE, Depledge MH (1994) Individual physiological responses to environmental hypoxia and organic enrichment: implications for early soft-bottom community succession. J Mar Res 52:1080-1100
Forbes TL, Lopez GR (1987) The allometry of deposit feeding in *Capitella* species I (Polychaeta: Capitellidae): the role of temperature and pellet weight in the control of egestion. Biol Bull (Woods Hole) 172:187-201
Forbes TL, Lopez GR (1989) Determination of critical periods in ontogenetic trajectories. Funct Ecol 3:625-632
Forbes TL, Lopez GR (1990) Ontogenetic changes in individual growth and egestion rates in the deposit-feeding polychaete *Capitella* sp. I. J Exp Mar Biol Ecol 143:209-220
Forbes VE (1991) Response of *Hydrobia ventrosa* (Montagu) to environmental stress: effects of salinity fluctuations and cadmium exposure on growth. Funct Ecol 5:642-648
Forbes VE, Depledge MH (1992) Cadmium effects on the carbon and energy balance of mudsnails. Mar Biol 113: 263-269
Forbes VE, Forbes TL (1994) Ecotoxicology in theory and practice. Chapman & Hall, London
Frithsen JB (1984) Metal incorporation by benthic fauna: relationships to sediment inventory. Estuar Coast Shelf Sci 19: 523-539
Grassle JF, Grassle JP (1974) Opportunistic life histories and genetic systems in marine benthic polychaetes. J Mar Res 80:3032-3043
Grassle JF, Grassle JP (1976) Sibling species of the marine pollution indicator *Capitella* (Polychaeta). Science 192: 567-569
Harvey RW, Luoma SN (1985a) Separations of solute and particulate vectors of heavy metal uptake in controlled suspension-feeding experiments with *Macoma balthica*. Hydrobiologia 121:97-102
Harvey RW, Luoma SN (1985b) Effect of adherent bacteria and bacterial extracellular polymers upon assimilation by *Macoma balthica* of sediment-bound Cd, Zn and Ag. Mar Ecol Prog Ser 22:281-289
Kemp PF, Swartz RC (1988) Acute toxicity of interstitial and particle-bound cadmium to a marine infaunal amphipod. Mar Environ Res 26:135-153
Landrum P, Harkey GA, Kukkonen J (1996) Evaluation of organic contaminant exposure in aquatic organisms; the significance of bioconcentration and bioaccumulation. In: Newman MC, Jagoe CH (eds) Ecotoxicology. A hierarchical treatment. Lewis Publishers, Inc, Boca Raton, FL, p 85-132
Langston WJ, Spence SK (1995) Biological factors involved in metal concentrations observed in aquatic organisms. In: Tessier A, Turner DR (eds) Metal speciation and bioavailability in aquatic systems. John Wiley and Sons, New York, p 407-478
Luoma SN (1983) Bioavailability of trace metals to aquatic organisms—a review. Sci Total Environ 28:1-22
Mason AZ, Jenkins KD (1995) Metal detoxification in aquatic organisms. In: Tessier A, Turner DR (eds) Metal speciation and bioavailability in aquatic systems. John Wiley and Sons, New York, p 479-608
Pearson TH, Rosenberg R (1978) Macrobenthic succession in relation to organic enrichment and pollution of the marine environment. Oceanogr Mar Biol Annu Rev 16:229-311
Power EA, Chapmann PM (1992) Assessing sediment quality. In: Burton AG Jr (ed) Sediment toxicity assessment. Lewis Publishers, Inc, Boca Raton, FL, p 1-18
Rasmussen E (1973) Systematics and ecology of the Isefjord marine fauna (Denmark) with a survey of the eelgrass (*Zostera*) vegetation and its communities. Ophelia II:1-507
Ray S, McLeese D, Pezzack D (1980) Accumulation of cadmium by *Nereis virens*. Arch Environ Contam Toxicol 9: 1-8
Reynoldson TB (1987) Interactions between sediment contaminants and benthic organisms. Hydrobiologia 149:53-66
Rhoads DC (1974) Organism-sediment relations on the muddy sea floor. Oceanogr Mar Biol Annu Rev 12: 263-300
Self RFL, Jumars PA (1978) New resource axes for deposit feeders? J Mar Res 36:627-641
Simkiss K (1996) Ecotoxicants at the cell-membrane barrier. In: Newman MC, Jagoe CH (eds) Ecotoxicology: a hierarchical treatment. Lewis Publishers, Inc, Boca Raton, FL, p 59-84
Simkiss K, Taylor MG (1995) Transport of metals across membranes. In: Tessier A, Turner DR (eds) Metal speciation and bioavailability in aquatic systems. John Wiley and Sons, New York, p 1-44
Sørensen JA, Nielsen JB, Andersen O (1993) Identification of the gastrointestinal absorption site for cadmium chloride *in vivo*. Pharmacol Toxicol 73:169-173
Spacie A, Hamelink JL (1985) Bioaccumulation. In: Rand GM, Petrocelli SR (eds) Fundamentals of aquatic toxicology. Hemisphere, New York, p 495-525
Tenore KR, Chesney EJ Jr (1985) The effects of interaction of rate of food supply and population density on the bioenergetics of the opportunistic polychaete, *Capitella capitata* (Type 1). Limnol Oceanogr 30(6):1188-1195
Theede H (1980) Physiological responses of estuarine animals to cadmium pollution. Helgoländer Meeresunters 33: 26-35
Tsutsumi H (1987) Population dynamics of *Capitella capitata* (Polychaeta: Capitellidae) in an organically polluted cove. Mar Ecol Prog Ser 36:139-149
Tsutsumi H (1990) Population persistence of *Capitella* sp. (Polychaeta; Capitellidae) on a mud flat subject to environmental disturbance by organic enrichment. Mar Ecol Prog Ser 63:147-156
Tsutsumi H, Fukunaga S, Fujita N (1990) Relationship between growth of *Capitella* sp. and organic enrichment of the sediment. Mar Ecol Prog Ser 63:157-162
Tsutsumi H, Kikuchi T, Tanaka M, Higashi T, Imasaka K, Miyasaki M (1991) Benthic succession in a cove organically polluted by fish farming. Mar Pollut Bull 23:233-238
Ueda T, Nakamura R, Suzuki Y (1976) Comparison of ^{115}Cd accumulation from sediments and seawater by polychaete worms. Bull Jpn Soc Sci Fish 42(3):299-306

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