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Influence of a selective feeding behaviour by the blue mussel *Mytilus trossulus* on the assimilation of ^{109}Cd from environmentally relevant seston matrices

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ABSTRACT: The objective of this study was to determine the influence of a selective feeding strategy on the assimilation efficiency of ^{109}Cd (^{109}Cd-AE) by the blue mussel *Mytilus trossulus*. Two complementary experiments which used 5 seston matrices of different seston quality (SQ) were implemented: (1) algae labeled with ^{109}Cd was mixed with unlabeled silt, and (2) labeled silt was mixed with unlabeled algae. ^{109}Cd-AE was determined by a dual-tracer ratio (^{109}Cd/^{241}Am) method (DTR) and based on the ingestion rate of ^{109}Cd by the mussel (IRM) (total amount of ^{109}Cd ingested over the 4 h feeding period). As a result of the non-conservative behavior of ^{241}Am, the DTR underestimated mussel ^{109}Cd-AEs as compared to the IRM. Therefore only IRM-determined ^{109}Cd-AE was considered further. When only algae was spiked, ^{109}Cd-AEs were proportional to diet quality (DQ), ($r = 0.98$; $p < 0.05$) with maximum ^{109}Cd-AE occurring at the mussel's filter-feeding 'optimum' and where maximum carbon assimilation rates have been observed. However, for the spiked-silt exposures, ^{109}Cd-AE was independent of DQ, with maximum values of ~85% occurring in all diets except for silt alone. ^{109}Cd-AE for the silt-only exposure was 36%, suggesting that digestive processes which occur in diets of both algae and silt were not operating as effectively in the silt-only exposures. ^{109}Cd-AE correlated with ^{109}Cd in mussel tissue ($r = 0.63$; $p < 0.05$), with the radiotracer assimilated from the silt-labeled matrices corresponding to the greatest amounts of ^{109}Cd activity within the mussel. These results suggest an active and passive assimilation of ^{109}Cd from the algae and silt components of seston respectively. Active ^{109}Cd-AE will be proportional to DQ with maximum assimilation possibly occurring at the mussel's filter-feeding optimum. Passive ^{109}Cd-AE will be dependent on amounts of metal associated with the inorganic component of seston, with digestive processes that are activated in the presence of algae concurrently desorbing inorganic cadmium. Although both components of the diet will be important for determining amounts of Cd that can be potentially assimilated from seston by filter-feeding organisms, the contribution from the inorganic component of seston will likely overwhelm that from the organic fraction. Therefore, predictive models of metal accumulation by seston-ingesting organisms need to consider the role of both seston components in contributing to amounts of metal ultimately assimilated by the organism.

KEY WORDS: *Mytilus trossulus* · ^{109}Cd-AE · Inorganic seston · Organic seston

INTRODUCTION

Filter-feeding bivalves are extremely important economically, primarily as a human food resource, but also ecologically, as they occupy an important link between primary producers and higher trophic levels. They also are efficient accumulators of trace metals and thus are highly sensitive to changes in environmental metal concentrations. As a result, they have been employed worldwide in biomonitoring programmes such as 'Mussel Watch' as indicators of changes in aquatic metal levels in response to human activities. Given this importance, much research has focused on assessing factors which influence metal accumulation by these

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invertebrates. One important endpoint of this research has been the development of predictive models of metal accumulation by filter-feeding invertebrates so that effective measures to reduce metal contamination in our environment can be taken (e.g. Luoma et al. 1992, Thomann et al. 1995).

To date, an adaption of the steady-state bioaccumulation model of Thomann (1981) has been a primary model employed to predict metal uptake and accumulation by invertebrates (e.g. Thomann et al. 1995). A major advance in the application of this model to environmental problems was the study of Luoma et al. (1992), who applied the use of laboratory derived assimilation efficiency (AE) to account for physiological processes that might influence the amounts of metal accumulated by the organism from a single food source such as algae. Given the now recognized importance of incorporating AE into predictive models of metal accumulation, over the last 5 yr a number of studies have reported AEs for several metals, most notably cadmium, silver, cobalt and chromium, by invertebrates, from a variety of substrates, including algae (Borchardt 1983, Harvey & Luoma 1985, Zang et al. 1990, Absil et al. 1994, Wang et al. 1995) organically coated silica beads (Decho & Luoma 1994), and natural sediment (Gagnon & Fisher 1997).

An obvious and important aspect of the incorporation of AE into predictive models of metal accumulation is obtaining values that are representative of the diet that is actually consumed by the seston-ingesting organism under natural conditions. Herein lies the difficulty in the application of laboratory-derived AEs from a single food source, such as algae, for use in predictive models of metal accumulation. In the environment, filter-feeding organisms are exposed to a highly dynamic, complex food source which constantly changes in terms of quality (amount of organic relative to inorganic matter) and quantity (mg l^{-1}) (e.g. Fengly et al. 1992). In response to this dynamic food environment, many filter-feeding organisms have developed a highly selective feeding strategy that, depending on seston quality and quantity, allows for the selection of organic over inorganic particles (under conditions of high quantity/quality seston) or both organic and inorganic particles (under conditions of low quality/quantity seston) for ingestion (Bayne et al. 1993, Arifin & Bendell-Young 1997, Ward et al. 1997). Depending on mussel feeding behavior, when seston is of high quality and abundant, metal contaminants associated with only the organic fraction of seston will be ingested and available for uptake. In contrast, when the mussels are exposed to low quantity/quality seston, metal contaminants associated with both inorganic and organic components of seston may be ingested and assimilated by the mussel. If this ability of the mussel to choose specific components of the seston in a quantity/quality dependent manner has not been taken into account, then predictive models of metal contaminant uptake based only on 1 component of the diet, such as organic content, may potentially underestimate the amount of metal the mussel is actually ingesting.

Therefore, the objective of this study was to determine the influence of a selective feeding strategy that either excludes (complete sorting) or includes (minimal sorting) the inorganic components of seston on the assimilation of ^{109}Cd by the blue mussel. To meet this objective we exposed mussels to environmentally relevant seston matrices (a mixture of silt and algae) that we had previously shown to either be completely ingested with no sorting occurring (low quantity/quality diets) or seston which had evoked a selective sorting process such that only organic matter was ingested (complete sorting) (Arifin & Bendell-Young 1997). Two sets of experiments with the various seston matrices were implemented: (1) algae labeled with ^{109}Cd was mixed with unlabeled silt, and (2) labeled silt was mixed with unlabeled algae. The resulting ^{109}Cd-AE from the various matrices were then related to diet quality. Ultimately, results from our study will help to identify the role of a selective feeding strategy which either excludes all inorganic matter from the diet or includes both organic and inorganic matter in the diet in the accumulation of metal by sediment-ingesting organisms. This information in turn will be used to help in the development of more accurate models for the prediction of metal accumulation by filter-feeding organisms.

MATERIALS AND METHODS

Field collection of mussels. Mussels *Mytilus trossulus* were collected from the intertidal area along the coast of Howe Sound, British Columbia, Canada. Mussels (44.9 ± 2.08 mm in shell length, 0.18 ± 0.01 g dry weight) were acclimatized to experimental conditions (temperature 13 ± 1°C, salinity = 28 ppt) for 2 wk prior to use in each experiment (Bayne et al. 1976). During the acclimation period, mussels were fed the diatom algae *Thalassiosira pseudonana* daily, and the seawater was changed on a regular basis. Prior to the feeding experiments, mussels were separated from their basal attachment to one another, brushed clean and kept for approximately 15 min under dry air. This procedure ensured that only live mussels were used in the experiment as those mussels that were not viable did not respond to being submerged in seawater following the 15 min exposure period.

Seston composition. Five seston (suspended particulate matter) matrices were selected based on our previ-

ous studies (Arifin & Bendell-Young 1997), which indicated that, depending on the quality and quantity of the seston, the mussel had the ability to select either just organic particles or both inorganic and organic particles for ingestion. Our previous studies showed that the sorting efficiency (i.e. the ability of the mussel to select organic over inorganic food particles from a diet comprised of both inorganic and organic food particles) of the blue mussel varied from −18 to 0% when exposed to the range between low seston quality (SQ) (~20%) and high SQ (60 to 70%), with a maximum sorting efficiency occurring at mid-SQ (40%). At this maximum sorting efficiency, mussels were capable of increasing a SQ of 40% to a diet quality (DQ) of 60 to 70%. Further, we noted that at maximum seston ingestion rates (where mussels cleared the greatest number of inorganic and organic particles from the water over a given period of time as compared to all other seston exposures), which occurred at a less than optimal SQ of 20%, the greatest amounts of carbon were assimilated by the mussel from the diet. This led us to speculate that if cadmium assimilation followed a diet/energy pathway, then the maximum ^{109}Cd-AE by the mussel would be observed at the mussels filter-feeding maximum or optimum. Based on these findings, 3 seston matrices were prepared: (1) algae with a SQ of 60%—this matrix represented the diet after maximum sorting of seston of only 40% organic matter (i.e. rejection of all inorganic particles and selection of only organic particles for ingestion); (2) 2.0 and 10% SQ—low quality/quantity, where no sorting occurs and both inorganic and organic components of the seston are included; and (3) 18 to 20% SQ—minimal sorting, where the filtering-maximum for this species was observed.

Pulse-chase feeding experiments. The experiment was conducted under flow-through conditions (Fig. 1). An 18 l source of filtered seawater was provided by sequentially filtering the seawater through 5.0 and 1.0 µm cartridge filters (Labcor Inc.). Seston matrices were prepared immediately before use in the exposure experiments by adding known volumes of radiolabeled algae or silt suspension into a polyethylene tank and the subsequent dilution of the 2 seston components to a volume of 18 l with the prepared filtered seawater. Two separate sets of experiments were conducted (Fig. 2). The first set of experiments included labeled algae alone and mixtures of labeled algae and unlabeled silt. The marine centric diatom *Thalassiosira pseudonana* was grown in 4.0 l Fernbach flasks containing

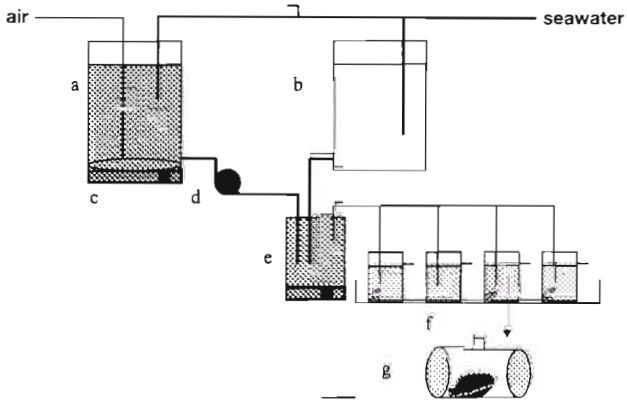

Fig. 1. Flow-through system for the study of the assimilation of ^{109}Cd by mussels *Mytilus trossulus*. (a) Mixed algae and silt, (b) filtered seawater, (c) stirrers, (d) peristaltic pump, (e) mixing tank, (f) experimental tanks, and (g) plexiglas chamber for a mussel exposed to radionuclides in seawater

3.0 l of filtered (1.0 µm) natural seawater using the nutrient-enrichment solution (ES) of Harrison et al. (1980). Two days after inoculations, the algae were spiked with 185 kBq l^{-1} ^{109}Cd (in 0.5 M HCl, Dupont) and 74 kBq l^{-1} ^{241}Am (in 1.0 M HCl, Isotope Product Lab.). Algae were exposed to the radiotracers for 4 d and kept on 14:10 h L/D cycle at 16°C. Cells were harvested after they had undergone log phase growth and were considered uniformly labeled. The labeled algae were counted by particle counter (Coulter counter, model TA-II), and diluted to obtain concentrations of 20 and 150 × 10^6 cells l^{-1}. Algae (20 × 10^6 cells l^{-1}) were then mixed with concentrations of 5, 20 and 50 mg l^{-1} of the unlabeled-silt component, to obtain SQs of 18.2,

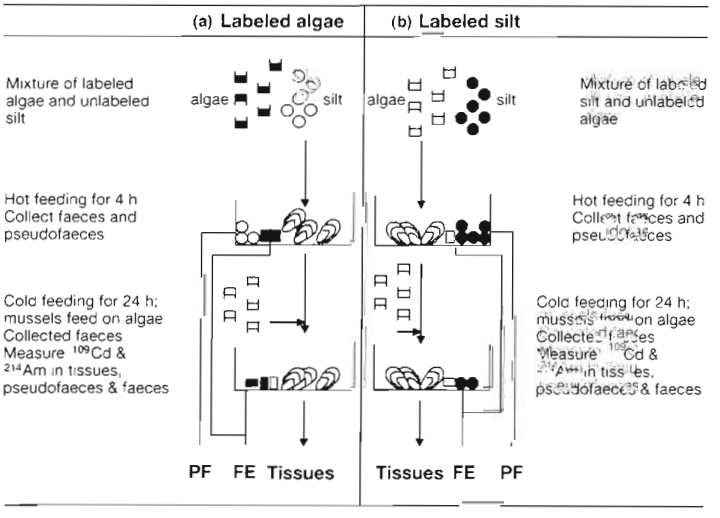

Fig. 2. Flow chart of the experimental protocol. (a) Labeled-algae experiment, and (b) labeled-silt experiment. PF: pseudofaeces; F: faeces

Table 1. Characteristics of suspended particulate matter (SPM) and feeding physiology of mussels (Arifin & Bendell-Young 1997). Algae : silt = ($\times 10^6$ cells l^{-1}):(mg l^{-1}); SQ = seston quality; DQ = diet quality, the actual food ingested by mussels after sorting process. IR_{POM}: the ingestion rate of particulate organic matter. IR_{PIM}: ingestion rate of particulate inorganic matter; C-AE: carbon assimilation efficiency. Values are given as mean ± SE

Seston		SPM	Quality (%)		IR_{POM}	IR_{PIM}	C-AE
Algae	Silt	(mg l^{-1})	SQ	DQ	(mg h^{-1} gdw^{-1})	(mg h^{-1} gdw^{-1})	(%)
0	50	30.4 ± 1.65	2.0	2.0	–	101.6 ± 10.81	–
20	50	43.4 ± 3.00	10.3	16.0	55.3 ± 3.42	290.4 ± 20.98	98.9 ± 0.40
20	20	25.1 ± 1.21	20.6	32.9	135.3 ± 14.14	275.8 ± 34.32	95.2 ± 1.82
20	5	9.7 ± 1.72	18.2	26.7	28.9 ± 2.77	79.1 ± 8.30	79.8 ± 4.89
150	0	15.7 ± 3.45	60.0	60.0	48.0 ± 5.41	–	63.1 ± 2.89

20.6 and 10.3% organic matter respectively (Table 1). The silt- and algae-only matrices were 2 and 60% organic matter respectively.

The mixtures of labeled algae and unlabeled-silt particles ('hot' feeding) were given to the acclimated mussels in the treatment tanks. Experiments were run in triplicate with n = 13 to 16 mussels per experimental treatment. Four to five mussels/treatment tanks were exposed to both seston and seawater, with 1 treatment tank used to expose mussels to seawater alone. A separate control tank was used to monitor the amount of seston delivered to the tanks. Seston from this tank was collected 3 to 4 times over the duration of the hot feeding period to obtain average ^{109}Cd activity for the 4 h exposure. After the hot feeding for 4 h, mussels were transferred into a 1.5 l chamber and fed with unlabeled algae ('cold' feeding). Complete faeces (FE) and pseudofaeces (PF) were collected at 15 min and 4, 8 and 24 h during the cold feeding period. After 24 h, the mussels were sacrificed to determine amounts of accumulated radiotracer. Radioactivity of ^{109}Cd and ^{241}Am in FE, PF and mussel tissues were measured using a Canberra Model 2030 gamma counter equipped with a Na-iodide crystal detector. Gamma emissions were detected at 22 keV for ^{109}Cd and 60 keV for ^{241}Am. The measurements were corrected for background, for the interference of ^{241}Am with ^{109}Cd by backscattering, and for the decay of isotopes.

The second set of experiments was identical to the labeled-algae experiments except mussels were exposed to mixtures of labeled silt with unlabeled algae. Kaolinitic mineral (average diameter of 4.8 µm) (Engelhard Corp., Pigments and Additives Division, Edison, NJ) was used for the silt component. Three different silt concentrations (5, 20 and 50 mg l^{-1}) were spiked with the same amount of radioisotope as the labeled-algae experiments in 25 ml plastic-beakers with 1.0 µm filtered seawater and sonicated to get uniform mixtures. After 24 h the labelled silt slurry was transferred to 4.0 l Ferbanch flasks and diluted to 3 l with filter seawater. The labelled silt was stirred vigorously then allowed to sit for 4 d (with occasional agitation) to allow for loosely bound ^{109}Cd to desorb from the silt surface. Previous studies by Stecko & Bendell-Young (1999) have demonstrated that the majority of radioisotope desorbs from sediment within the first 100 h of labeling (Fig. 3), hence the precaution of allowing silts to sit for 4 d prior to use in the feeding experiments. The silt solution was filtered, and the recovered radiolabelled silt was mixed with an unlabeled algae concentration of 20 $\times 10^6$ cells l^{-1} to obtain different SQs, as outlined for the labeled-algae experiments.

Mussels were exposed to the mixtures of labeled silt and unlabeled algae particles for a hot feeding period of 4 h, followed by a cold feeding periods for 24 h. After the hot and cold feeding period, FE, PF and mussel tissues were counted for radioactivity as outlined for the labeled-algae experimental procedure.

To ensure consistency of exposure and that the radiolabel did not desorb from the various seston matrices, both seston and water in the exposure chambers were sampled 3 to 4 times for each experiment throughout the 4 h feeding period. Radioactivity in water did not increase, indicating that no radiotracer desorbed from the prepared matrices over the course of the 4 h exposure (Fig. 4). The radioactivity of the seston matrix for all exposures also remained constant over the 4 h feeding period (Fig. 5), indicating that mussels were exposed to a constant amount of radioactivity via the prepared seston matrices throughout the course of the experiment.

Seston quality (SQ) versus diet quality (DQ). SQ is defined as

$$SQ = ([POM]_{seston}/[SPM]) \times 100\% \quad (1)$$

where POM is particulate organic matter and SPM is suspended particulate matter and both are in units of mg l^{-1}. DQ which corrects SQ for the selective feeding behavior of the mussel (i.e. rejection of inorganic seston components via PF production) is defined as

$$DQ = (IR_{POM}/(IR_{POM+PIM}) \times 100\% \quad (2)$$

where IR_{POM} is the amount of ingested POM, and $IR_{POM+PIM}$ is the amount of ingested organic and inorganic matter in units of mg h^{-1} gdw^{-1}, for a given SQ (Arifin & Bendell-Young 1997).

Estimates of assimilation efficiency. ^{109}Cd-AE is defined as the proportion of ingested ^{109}Cd retained after digestion of selected seston and gut evacuation. Wang et al. (1995) noted that less than 10% of ^{241}Am was retained in soft tissue after a 24 h depuration period, and most unassimilated ^{109}Cd was egested within the first 17 h, after which very little ^{109}Cd appeared in the FE or was lost from tissues. Based on this, ^{109}Cd-AE was determined after a 24 h depuration period.

^{109}Cd-AE was determined in 2 ways: (1) ^{109}Cd-AE were calculated based on the dual-tracer ratio method (DTR) described by Fisher & Reinfelder (1991) and Luoma et al. (1992) as follows:

$$^{109}\text{Cd-AE} = \{[(^{109}\text{Cd}/^{241}\text{Am})_{\text{seston}} - (^{109}\text{Cd}/^{241}\text{Am})_{\text{faeces}}]/(^{109}\text{Cd}/_{241}\text{Am})_{\text{seston}}\} \times 100\% \quad (3)$$

where $(^{109}\text{Cd}/^{241}\text{Am})_{\text{seston}}$ is the ratio of ^{109}Cd and ^{241}Am activity in seston and $(^{109}\text{Cd}/^{241}\text{Am})_{\text{faeces}}$ is the ratio of ^{109}Cd and ^{241}Am activities in FE. This method assumes that ^{109}Cd passes through the digestive tract at a similar rate as ^{241}Am and the loss rates of ^{109}Cd and ^{241}Am from FE into the media are comparable. (2) ^{109}Cd-AE (%) was computed based on the amount of ^{109}Cd ingested over the 4 h feeding period (IRM) as determined in Arifin & Bendell-Young (1997) (Table 1) as follows:

$$IR_{[Cd]algae} = [^{109}\text{Cd}]_{algae} \times IR_{POM\text{-}c} \quad (4)$$

where $IR_{[Cd]algae}$ is ingested ^{109}Cd from algae (dpm h^{-1} gdw^{-1}), $[Cd]_{algae}$ is ^{109}Cd radioactivity in labeled algae (dpm mg^{-1}) and $IR_{POM\text{-}c}$ is ingested organic particles after correction for sorting (mg^{-1} h^{-1} gdw^{-1}). Ingestion rates were determined as the product of the clearance rates (i.e. the number of particles filtered from solution by the mussel in a given period of time for a given seston concentration as determined by Arifin & Bendell-Young 1997) and the seston quantity minus PF production. When the labeled-silt component of seston was used for the exposures, Eq. (4) was modified as follows:

$$IR_{[Cd]silt} = [^{109}\text{Cd}]_{silt} \times IR_{PIM\text{-}c} \quad (5)$$

where $[Cd]_{silt}$ is ^{109}Cd radioactivity in labeled silt (dpm mg^{-1}) and $IR_{PIM\text{-}c}$ is ingested inorganic particles after correction for sorting (mg^{-1} h^{-1} gdw^{-1}).

The apparent ^{109}Cd-AEs (i.e. assimilation of cadmium from seston uncorrected for sorting) were calculated as follows:

$$\text{app.}^{109}\text{Cd-AE (\%)} = \{(IR_{[Cd]algae} - FE_{[Cd]})/(IR_{[Cd]algae} + PF_{[Cd]})\} \times 100\% \quad (6)$$

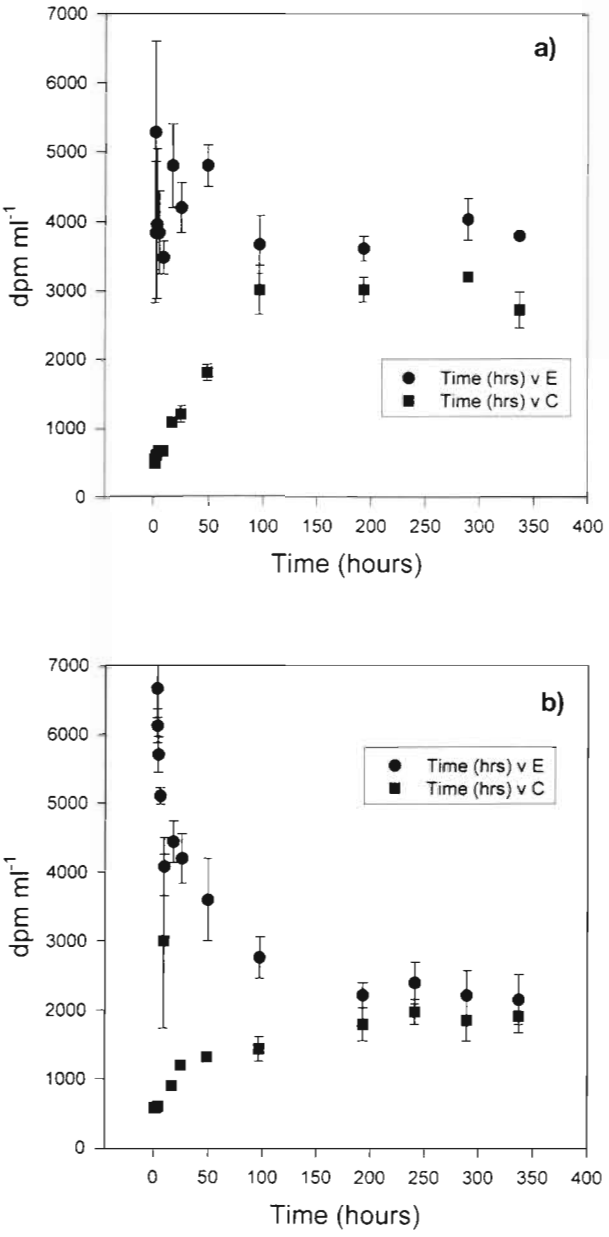

Fig. 3. Desorbtion of ^{109}Cd from 2 types of sediment, SPM (suspended particulate matter) and DS (deposited sediment) as a function of time. Values are means of 3 measurements ±1 SE. (a) Dissolved ^{109}Cd in exposure (E; with sediment) versus the control tank (C; no sediment added) for deposited sediment and (b) dissolved ^{109}Cd in E versus the C tank for suspended sediment. To determine the rate of ^{109}Cd desorbtion from the 2 types of sediment, sediment spiked with ^{109}Cd was added to one side of a tank (E) which had been divided in half with a with 0.45 µm membrane. No sediment was added to the other half, which served as a control. Filtered water samples were taken from both the E (sediment added) and C sides of the tank over a 340 h time period. Equilibrium (maximum desorbtion of ^{109}Cd from sediments) between the C and E tanks is reached at approximately 96 h for both types of sediments. Full details can be found in Stecko & Bendell-Young (1999)

and

$$\text{app.}^{109}\text{Cd-AE}\ (\%) = [(IR_{[Cd]silt} - FE_{[Cd]})/(IR_{[Cd]silt} + PF_{[Cd]})] \times 100\% \quad (7)$$

where $PF_{[Cd]}$ is the activity of rejected ^{109}Cd in pseudofaeces (dpm h^{-1} gdw^{-1})

The true ^{109}Cd-AEs from the algae and silt components of the diet, i.e. assimilation of cadmium from the diet that is actually ingested by the mussel after correcting for sorting, were determined as follows:

$$\text{true}^{109}\text{Cd-AE}\ (\%) = [(IR_{[Cd]algae} - FE_{[Cd]})/IR_{[Cd]algae}] \times 100\% \quad (8)$$

$$\text{true}^{109}\text{Cd-AE}\ (\%) = [(IR_{[Cd]silt} - FE_{[Cd]})/IR_{[Cd]silt}] \times 100\% \quad (9)$$

where $FE_{[Cd]}$ is the radioactivity of ^{109}Cd contained in the faeces (dpm h^{-1} gdw^{-1}).

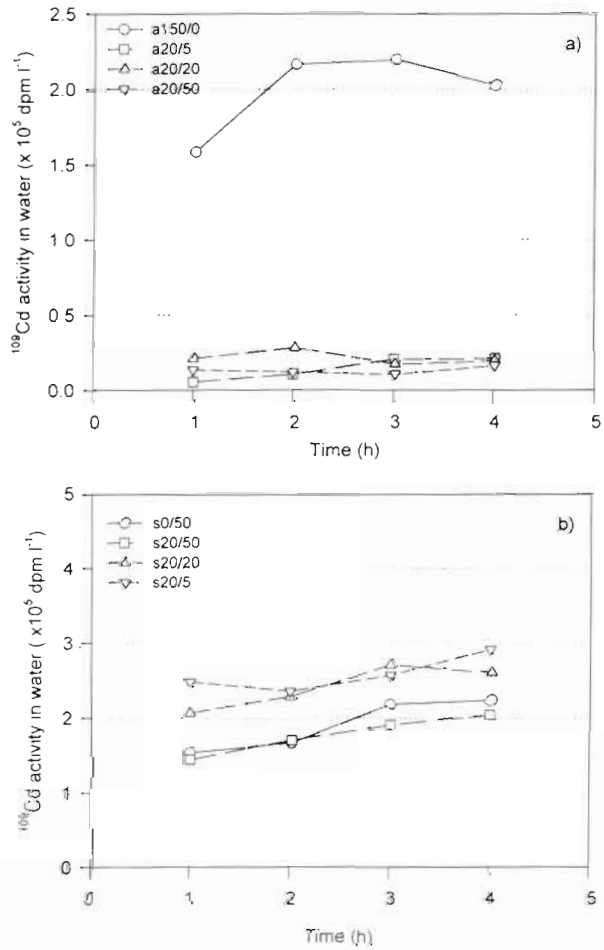

Fig. 4. ^{109}Cd activity in seawater throughout the 4 h experimental exposure. (a) Seawater from experiments in which only algae was labeled. (b) Seawater from experiments in which only silt was labeled. Ratios are amounts of algae to silt in each experiment

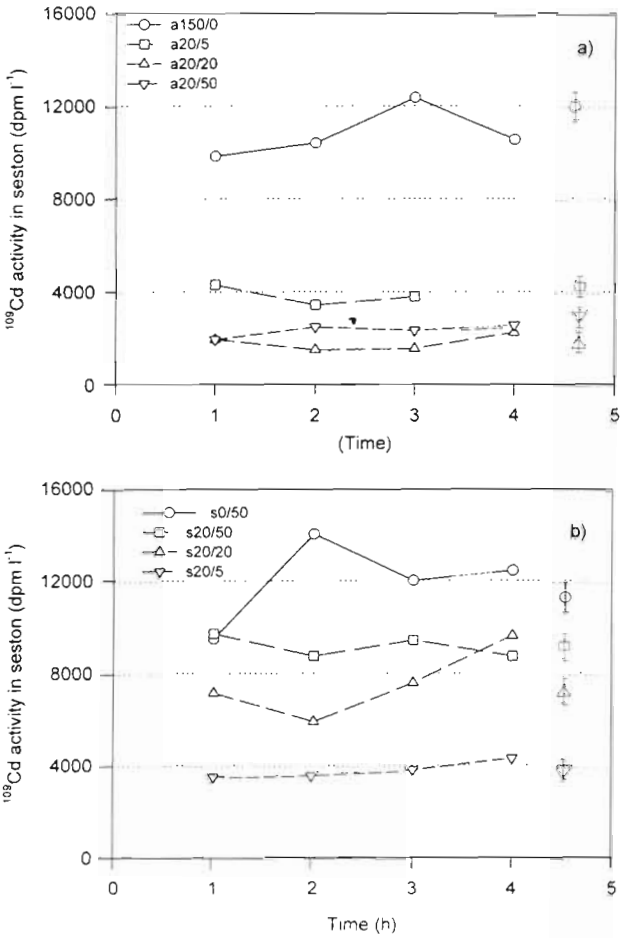

Fig. 5. ^{109}Cd activity in seston matrix throughout the 4 h experimental exposure. Final point at 4.5 h is the average ± 1 SD of all measurements taken throughout the exposure period. Ratios are amounts of algae to silt in each experiment

^{109}Cd activity in mussel tissue. To correct for the possible contribution of dissolved forms of the radiotracer to mussel tissue ^{109}Cd activity (i.e. uptake from solute plus diet rather than just that due to diet alone), ^{109}Cd activity determined for control mussels exposed only to seawater was subtracted from mussels exposed to both the labeled seston plus seawater. The corrected values, i.e. mussel tissue ^{109}Cd activity due to uptake from seston only, were used in determining the relationship between ^{109}Cd-AE and mussel tissue ^{109}Cd activity.

Statistical analysis. Statistical analysis for the partitioning of radiotracers (^{109}Cd, ^{241}Am) on faeces, pseudofaeces and ^{109}Cd-AE was implemented through the use of Systat 5.0 software. Differences in ^{109}Cd-AE determined by DTR versus IRM and differences between app. ^{109}Cd-AE and true ^{109}Cd-AE were determined through simple Student's *t*-tests. Simple correlation analysis was applied to determine relationships between ^{109}Cd-AE and (1) DQ, (2) corrected mussel tis-

Table 2. ^{109}Cd and ^{241}Am partitioning among SPM, pseudofaeces (PF) and faeces (FE); Algae : silt = (×10^6 cells l^{-1}):(mg l^{-1}). Values are given as mean ± SE

Seston Algae	Silt	SPM (× 10^{3}dpm mg^{-1}) ^{109}Cd	^{241}Am	PF (×10^3 dpm h^{-1} mussel^{-1}) ^{109}Cd	^{241}Am	FE (×10^3 dpm h^{-1} mussel^{-1}) ^{109}Cd	^{241}Am
Labeled algae							
20	50	0.1 ± 0.006	0.8 ± 0.02	2.7 ± 0.65	33.5 ± 4.66	1.2 ± 0.18	8.0 ± 0.72
20	20	0.5 ± 0.087	2.5 ± 0.30	1.6 ± 0.24	10.9 ± 1.88	1.8 ± 0.03	14.8 ± 1.03
20	5	1.0 ± 0.078	4.5 ± 0.43	1.3 ± 0.07	8.7 ± 0.21	3.1 ± 0.08	22.9 ± 0.78
150	0	2.4 ± 0.181	14.8 ± 1.17	2.7 ± 0.48	18.3 ± 3.62	5.5 ± 0.33	39.0 ± 2.75
Labeled silt							
0	50	2.1 ± 0.18	35.0 ± 0.50	22.8 ± 0.41	907.5 ± 79.46	15.1 ± 1.28	449.9 ± 59.00
20	50	3.5 ± 0.51	64.5 ± 11.74	34.3 ± 2.67	1628.8 ± 164.47	14.6 ± 1.06	377.0 ± 40.21
20	20	2.5 ± 0.18	54.2 ± 1.87	32.5 ± 1.90	1218.9 ± 61.16	17.8 ± 3.08	517.7 ± 98.82
20	5	12.5 ± 1.06	267.0 ± 13.58	16.3 ± 1.72	278.4 ± 115.28	15.9 ± 0.56	421.0 ± 18.85

sue ^{109}Cd activity and (3) carbon assimilation efficiency (C-AE) (from Table 1). All tests were accepted at a significance level of $p \leq 0.05$.

RESULTS

Radionuclide biodeposition rates

Amounts of ^{109}Cd and ^{241}Am rejected as PF and FE (egestion) represent the rate of radionuclide deposition (Table 2). Amounts of ^{109}Cd and ^{241}Am in PF and FE indicated that different biodeposition processes occurred for mussels exposed to the labeled algae versus those exposed to the labeled silt. For the labeled-algae experiments, the biodeposition rates of ^{109}Cd and ^{241}Am in PF were generally lower than those in the FE component, except at a SPM concentration of 43.4 mg l^{-1} (Fig. 6). The deposition rate of ^{109}Cd and ^{214}Am in FE decreased with a concurrent increase in the deposition rate of ^{109}Cd and ^{214}Am in PF with increasing SPM concentrations. In contrast, for the labeled silt experiments, ^{109}Cd activity in FE was relatively constant across treatment exposures (16 × 10^3 dpm h^{-1} mussel^{-1}), but the activity of ^{109}Cd in PF increased with increasing SPM concentration (16.3 × 10^3 to 34.3 × 10^3 dpm h^{-1} mussel^{-1}) (Fig. 7a). A similar pattern was also shown for ^{241}Am in PF with biodeposition rates increasing from 2.8 × 10^5 to 16.3 × 10^5 dpm h^{-1} mussel^{-1} with increasing SPM concentration (Fig. 7b). The active processes of rejecting the silt component of the seston by mussels resulted in an increase in ^{109}Cd and ^{241}Am deposition rate in PF; however, the deposition rate of the 2 radiotracers in FE remained constant.

This biodepositional pattern detected through the use of radiolabeled algae and silt suggests that the mussel is actively sorting the seston matrices (the selection of algae over silt resulting in an increased DQ), even though previously we have shown through gravimetric means that sorting of seston at a SQ of ~20% is minimal. The exception was at the highest SPM concentrations, where we have previously shown that the mussel reduces filtering activity (Arifin & Bendell-Young 1997).

^{109}Cd assimilation efficiency

Estimates of ^{109}Cd-AE from algae alone based on IRM were 6 times greater than those determined by DTR. In contrast, the 2 estimates of ^{109}Cd-AE from silt alone were not significantly different from each other

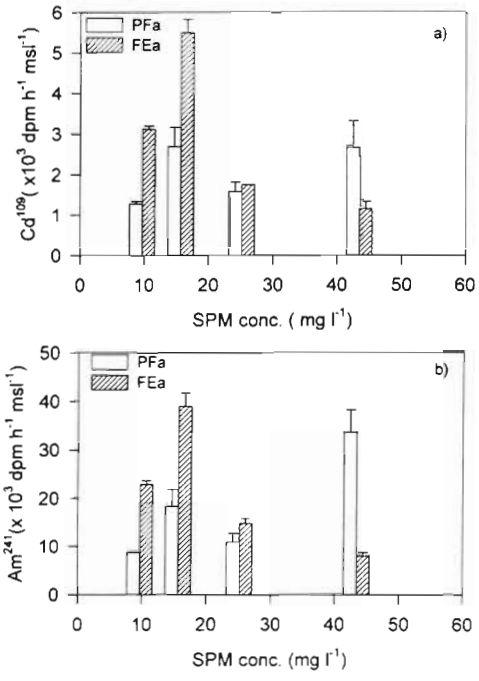

Fig. 6. *Mytilus trossulus*. Biodeposition rates of (a) ^{109}Cd, and (b) ^{241}Am in PF and FE of mussels exposed to the different seston matrices in the labeled-algae experiment. msl: mussel

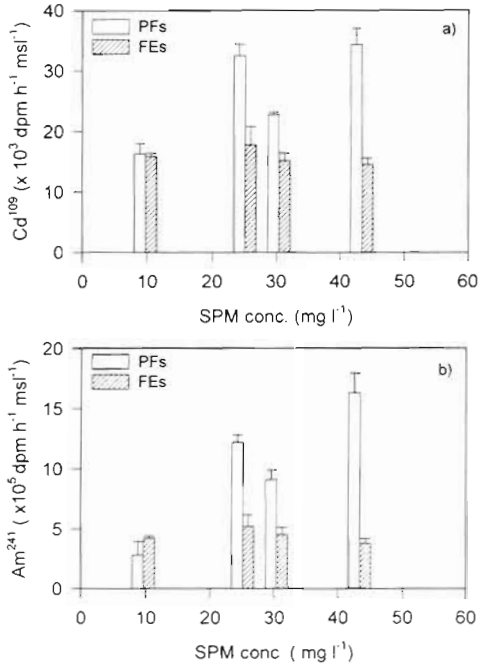

Fig. 7 *Mytilus trossulus*. Biodeposition rates of (a) ^{109}Cd, and (b) ^{241}Am in PF and FE of mussels exposed to the different seston matrices in the labeled-silt experiment. msl: mussel

(Fig. 8). For the labeled-algae and unlabeled-silt matrices (Fig 9a) and the unlabeled-algae and labeled-silt matrices (Fig. 9b), ^{109}Cd-AE based on DTR were generally less than those determined by the IRM.

Differences in ^{109}Cd-AE estimates based on DTR versus those based on IRM are the result of ^{241}Am behaving non-conservatively. When ^{241}Am functioned as an inert tracer, i.e. where the amount of ^{241}Am ingested was equal to the amount of ^{241}Am in FE, with the ratio of ^{241}Am in ingested food to ^{241}Am in FE being close to

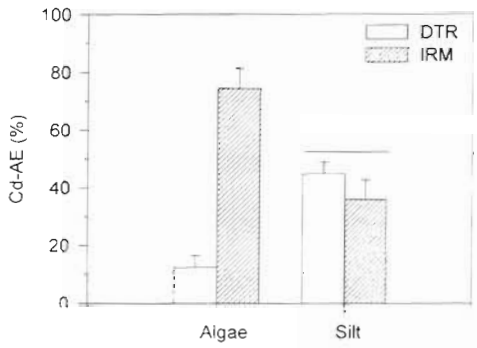

Fig. 8. *Mytilus trossulus*. ^{109}Cd-AEs from labeled-algae and labeled-silt using a dual tracer ratio method (DTR) versus those calcuated based on ^{109}Cd ingestion rate (IRM). Horizontal line: values not significantly different from each other Student's *t*-test; $p > 0.05$)

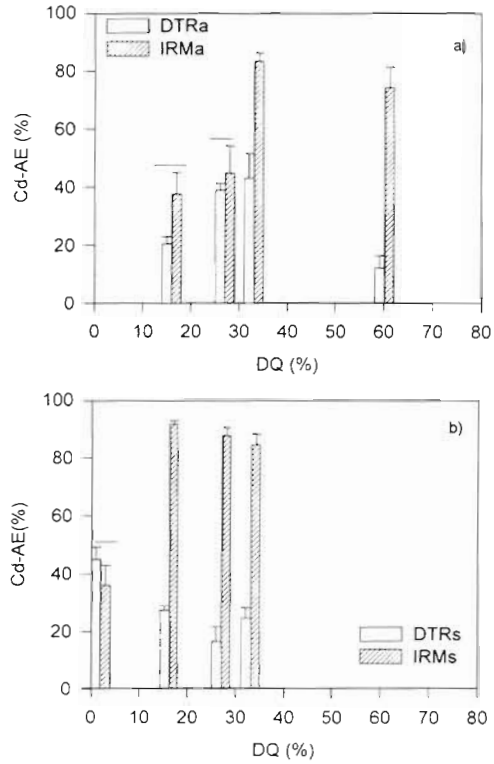

Fig. 9. *Mytilus trossulus*. ^{109}Cd-AEs calculated by DTR and IRM versus diet quality (DQ), (a) labeled-algae exposures, (b) labeled-silt exposures. Horizontal line: values that are not significantly different from each other (Students *t*-test; $p > 0.05$)

1 (at seston mixtures of labeled-algae and silt of 20:50, 20:5 and 0:50, Table 3), estimates of ^{109}Cd-AE based on the 2 methods were not different from each other However, when this ratio was greater than 1 (i.e. when ^{241}Am was taken up by the mussel and behaved non-conservatively), ^{109}Cd-AE based on DTR underestimated ^{109}Cd-AE in relation to IRM estimates. Further, for the labeled-algae exposures (with the exception of the seston mixtures outlined above), the ratio of ^{241}Am food/FE was approximately 4; for experiments where the silt was spiked this ratio was close to 8. These findings suggest that not only is ^{241}Am non-conservative, but also the amount that is taken up by the organism will be dependent on the type of substrate that is labeled. Because of this non-conservative behavior of ^{241}Am, ^{109}Cd-AEs based on DTR were not considered for further analysis.

Apparent and true ^{109}Cd-AEs calculated for both the labeled-algae and labeled-silt exposures were not significantly different from each other (Students's *t*-test, $p > 0.05$). Given that the quality of the seston matrices that we chose for these experiments was selected based on our previous findings that at a SQ of ~20% sorting should be minimal, both the apparent and true ^{109}Cd-AE should be comparable to each other. Our

Table 3. Determination of ^{09}Cd-AE based on the dual-tracer ratio method (DTR) and a measurement of ^{109}Cd ingestion rate by the mussel (IRM). (Cd/Am) = ratio of ^{109}Cd to ^{241}Am; (IR/FE) = ratio of ^{109}Cd in food ingested to ^{109}Cd in faeces. Values are given as mean ± SE

Seston Algae	Seston Silt	$(Cd/Am)_{food}$	$(Cd/Am)_{faeces}$	$(IR/FE)_{Cd}$	$(IR/FE)_{Am}$	Cd-AE (%) DTR	Cd-AE (%) FPM
Labeled algae							
20	50	0.22 ± 0.004	0.14 ± 0.003	1.7 ± 0.28	1.3 ± 0.08	20.5 ± 2.59	37.6 ± 7.44
20	20	0.21 ± 0.018	0.12 ± 0.008	6.4 ± 1.04	3.9 ± 0.49	43.1 ± 8.44	83.3 ± 2.92
20	5	0.18 ± 0.004	0.14 ± 0.009	1.9 ± 0.28	1.2 ± 0.17	39.0 ± 2.35	44.8 ± 9.37
150	0	0.16 ± 0.005	0.14 ± 0.002	4.5 ± 1.02	3.9 ± 0.99	12.4 ± 4.20	74.4 ± 7.01
Labeled silt							
0	50	0.06 ± 0.005	0.03 ± 0.002	1.6 ± 0.16	0.9 ± 0.15	45.0 ± 4.19	36.0 ± 6.93
20	50	0.06 ± 0.003	0.04 ± 0.002	12.6 ± 1.74	8.7 ± 1.52	27.4 ± 1.61	91.7 ± 1.18
20	20	0.05 ± 0.002	0.03 ± 0.001	7.1 ± 1.35	5.5 ± 1.06	24.7 ± 3.63	84.6 ± 3.57
20	5	0.05 ± 0.002	0.04 ± 0.001	9.0 ± 1.89	7.3 ± 1.18	16.6 ± 5.05	87.7 ± 2.86

present studies showed that, although there was no statistically significant differences between the 2 measurements of ^{109}Cd-AE, true ^{109}Cd-AE was always greater than apparent ^{109}Cd-AE (Fig. 10). As previously indicated by the ^{109}Cd and ^{241}Am biodepositional patterns, some sorting of the seston by the mussel is still occurring.

True ^{109}Cd-AE determined for the labeled-algae experiments correlated with DQ ($r = 0.98$; $p < 0.05$; Fig. 11), with maximum ^{109}Cd-AE occurring at a DQ of 33% (25 mg l^{-1} SPM). With the exception of the silt-only exposures, true ^{109}Cd-AE determined for the silt-labeled experiments were ~85% and were independent of diet quality. ^{109}Cd-AE for the silt only was 36%. ^{109}Cd in mussel tissues (after correcting for the possible contribution of uptake of the radiotracer from solution to mussel tissue activity) was positively correlated with ^{109}Cd-AE determined for all exposures ($r = 0.63$; $p < 0.05$; Fig. 12) with maximum mussel ^{109}Cd tissue concentrations corresponding to those matrices composed of labeled silt.

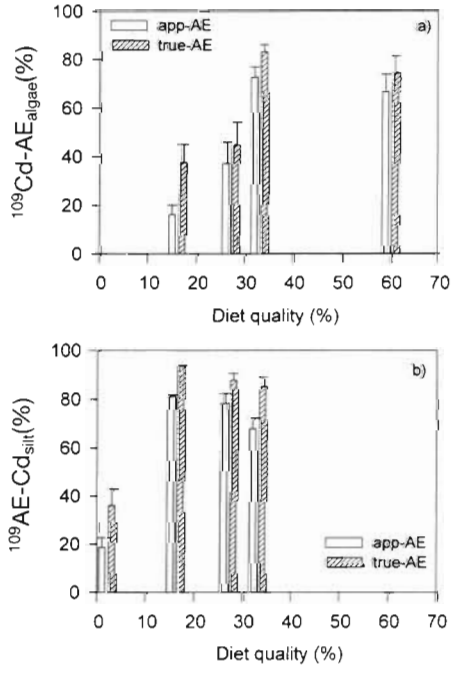

Fig. 10. *Mytilus trossulus*. Apparent (based on SQ) and true (based on DQ accounting for sorting by the mussel) ^{109}Cd-AEs in relation to DQ (mean ± SE) from (a) labeled-algae exposures and (b) labeled-silt exposures. Horizontal line: values that are not significantly different from each other (Student's *t*-test; $p > 0.05$)

DISCUSSION

Given the importance of incorporating how effectively a filter-feeding organism assimilates a metal of interest (in this case, cadmium) from its diet into predictive models of metal accumulation, over the past

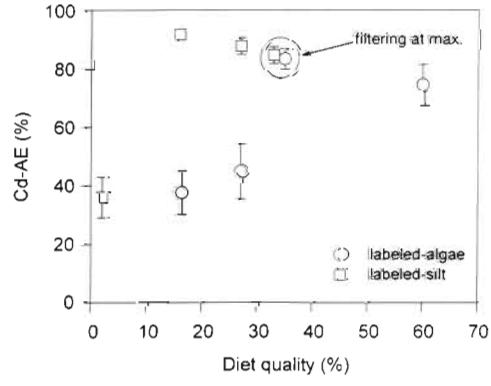

Fig. 11. *Mytilus trossulus*. ^{109}Cd-AEs (mean ± SE) for all exposures versus DQ (%) ($r = 0.98$, $p < 0.05$, for ^{109}Cd-AEs for the algae-spiked exposures vs DQ only)

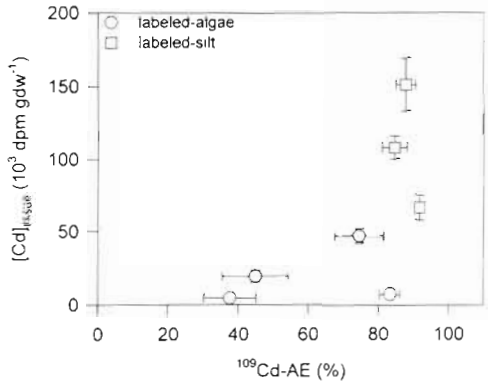

Fig. 12. *Mytilus trossulus*. ^{109}Cd-AEs for all exposures versus ^{109}Cd activity in mussel tissue ($r = 0.63$, $p < 0.05$). Values are given as mean ± SE

5 yr a number of studies have reported ^{109}Cd-AEs for several filter-feeding organisms from a number of single substrates (Table 4). Most notable are the studies of, Borchardt (1985) and Wang & Fisher (1996b), who have reported, based on studies where mussels were exposed to single diets of algae of different organic content, that cadmium assimilation is proportional to the assimilation of carbon by the mussel. These studies have indeed furthered our understanding on how mussels obtain, specifically, cadmium from a pure food source and potentially identified conditions which uptake from food may be maximized. However, an important aspect not included in the previous studies

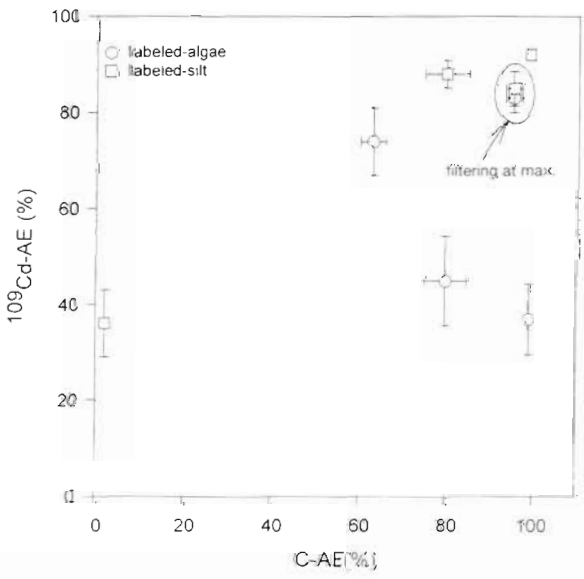

Fig. 13. *Mytilus trossulus*. ^{109}Cd-AEs for all exposures versus carbon assimilation efficiences (C-AE), determined by Arifin & Bendell-Young (1997) (see Table 1)

summarized in Table 4 is the response of the filter-feeding organism to its food environment.

The blue mussel is capable of highly selective feeding behavior, which, depending on the quality/quantity of its food environment, will result in the selection and ingestion of just organic matter (where the seston is sorted with the rejection of inorganic over organic particles) or the ingestion of both inorganic and organic seston components. Hence, rather than simply ingesting one food component such as algae, the mussel will ingest just organic matter or a combination of inorganic and organic matter depending on seston quality and quantity. Both components of seston have the potential therefore to contribute to amounts of cadmium ultimately assimilated by the organism.

^{109}Cd assimilation in relation to a selective feeding behavior

Results of the exposure experiments where the algae component of the matrix was labeled indicated ^{109}Cd-AEs were strongly correlated with DQ ($r = 0.98$). Maximum ^{109}Cd-AEs occurred at a DQ of 60% for just algae and at a DQ of 33% for 25 mg l^{-1} SPM, where maximum C-AEs for this species have been previously noted. This relationship supported the previous findings of Wang & Fisher (1996b), who noted a positive relationship between carbon assimilation and ^{109}Cd-AE for the filter-feeding blue mussel.

Given the findings of Wang & Fisher (1996b), we hypothesized further that ^{109}Cd-AEs would be proportional to C-AEs and that it would be at the mussels' filtering optimum (where maximum filtration rates were observed) that ^{109}Cd-AE by the mussel would be maximized. To test this hypothesis, we regressed ^{109}Cd-AEs against C-AEs previously determined by Arifin & Bendell-Young (1997) (Fig. 13, Table 1). However, a strong correlation between the 2 variables was not observed. Further, for exposures where silt was labeled, ^{109}Cd-AEs were independent of DQ (Fig. 11) and C-AEs (Fig. 13); maximum assimilation of 85% occurred for all DQs except for the silt-only exposure where the ^{109}Cd-AE was half of what was observed for matrices which contained organic matter

These 2 distinctly different patterns in ^{109}Cd assimilation from the labeled-algae versus the labeled-silt exposures suggests 2 processes. Firstly, an active assimilation of the metal from the algae. Reinfelder et al. (1997) have shown that ^{109}Cd-AE in a number of bivalves was directly related to the proportion of the element in the cytoplasmic fraction of ingested phytoplankton. In our experiments, cadmium would have been incorporated within the algae as well as associated with the algae surface); hence, increasing the

amount of algae would increase amounts of cadmium potentially available for uptake by the mussel. Thus, the more algae, the greater the active digestive processes to breakdown the algae and, hence, the greater the amounts of cadmium available for uptake. However, as suggested by our findings, amounts of cadmium assimilated by the mussel may not necessarily be proportional to amounts of assimilated carbon, i.e. there is no reason to assume that the 2 elements follow the same physiological pathways. Rather, for pure algae diets, DQ and carbon assimilation by the mussel are correlated with each other; therefore, ^{109}Cd-AEs determined for pure algae diets would be related to both variables. For diet mixtures, as noted in the pre-

Table 4. Cadmium assimilation efficiencies in mussels *Mytilus edulis*, *M. trossulus*, oysters *Crassostrea virginaca* and clams *Mercenaria mercenaria*, *Macoma balthica* and *Potamocorbula amurensis*. SL: standard length. –: not available

Species	Size (mm SL)	Experimental design (ST/ET/MT/S[a])	Food/particle type[b]	Particle quantity (mg l^{-1})	Cd-AE (%)	Source
Larvae						
C. virginaca	–	SS/300/–/26	*I. galbana*	0.80	61.3 ± 3.4	Reinfelder & Fisher (1994)[e]
M. mercenaria	–				23.9 ± 1.4	
Adult						
M. edulis	35	SS/30/15/28	*T. pseudonana*	0.11	42.0	Wang et al. (1995)[f]
				0.44	32.0	
				1.54	40.0	
M. edulis	30	SS/30/15/28	*T. pseudonana*	0.40	34.3 ± 4.7	Wang & Fisher (1996a)[f]
			P. tricornutum		15.3 ± 2.9	
			T. maculata		23.5 ± 3.0	
			Chrysophytes		12.4 ± 2.0	
			Dinoflagellates		26.2 ± 1.9	
M. edulis	30–35	SS/30/15/28	*T. pseudonana*	0.44	23.0 – 53.0	Wang & Fisher (1996b)[f]
M. edulis	30–35	SS/40-60/18/28	*T. pseudonana*	0.45	41.0 ± 2.7	Reinfelder et al. (1997)[g]
C. virginaca	40–50	SS/40–60/18/28	*I. galbana*	0.32	69.0 ± 8.6	Reinfelder et al. (1997)[g]
M. balthica	15				69.0 ± 2.3	
M. mercenaria	45–50				83.0 ± 17	
M. balthica	15	SS/40–60/18/28	*T. pseudonana*	0.45	88.0 ± 9.9	Reinfelder et al. (1997)[g]
M. mercenaria	45–50				66.0 ± 13	
M. balthica	10–17	SS/120/10/20	Fulvic acid–Si	High loading[c]	17.0 ± 3.0	Decho & Luoma (1994)[h]
			Humic acid–Si		38.0 ± 11.0	
			Uncoated–Si		35.0 ± 2.0	
P. amurensis	7.5–15	SS/15/10/20	Uncoated–Si	Low loading	56.0 ± 5.0	
			Humic acid–Si		12.0 ± 1.0	
			Fulvic acid–Si		9.0 ± 1.0	
M. edulis	–	SS/20/12/–	Natural sediment	6.00	15.0	Gagnon & Fisher (1997)[f]
			Fulvic acid–Si		23.0	
M. trossulus	45.0	FS/240/13/28	Silt	30.4 (2%)[d]	36.0	Present study[i]
			T. pseudonana	15.7 (60%)	74.4	
			T. pseudonana + silt	9.7 (18%)	44.8 [87.7][j]	
				25.1 (21%)	83.3 [84.6][j]	
				43.4 (10%)	37.6 [91.7][j]	

[a]ST = system, i.e. static system (SS) or flow-through system (FS); ET = exposure time with radiolabeled particles (min); MT = media temperature (°C); and S = salinity (‰)

[b]Diatom, i.e. *Isochrysis galbana*, *Thalassiosira pseudonana*, *Phaeodactylum tricornutum*; chrysophyte algae, i.e. *Chlorella autotrophica* and *Nanochloris atomus*; dinoflagelate algae, i.e. *Alexandrium tamarense* and *Prorocentrum micans*; Prasinophyceae, i.e. *Tetraselmis maculata*. Fulvic acid-Si: silicate coated with fulvic acid; humic acid-Si: silicate coated with humic acid

[c]High loading: feeding experiments with clam exposed to high Cd concentrations (considered exposed to high sediment pollution); low loading: clams exposed to low Cd concentrations

[d]Mussels exposed to 30.4 mg l^{-1} suspended particles with 2% organic content (% quality)

[e]AE calculated after 12 h gut clearance

[f]AE calculated as the percentage of the radioactivity of each isotope retained by the mussel at 70 h divided by the amount of radioactivity ingested

[g]AE calculated as intercepts of physiological turnover portions of radiotracer–retention curve

[h]AE calculated after 24 h gut evacuation for *P. amurensis*, 72 h for *M. balthica*. %AE = [dpm tissue at 24(72) h]/((dpmΣFE) + dpm tissue at 24(72) h] × 100

[i]PF separated from FE; AE calculated after 24 h gut evacuation. %AE = [(dpm ingested food)–(dpmΣFE)/(dpm ingested food)] × 100

[j]Values in square brackets are Cd-AEs from labeled-silt component

sent study, when mussels are challenged with algae mixed with silt, different digestive processes are possibly evoked (e.g. longer gut residence time) as compared to with a pure algae diet, uncoupling the relationship between DQ and carbon assimilation.

Secondly, concurrent with the active breakdown and release of cytoplasmic ^{109}Cd, as indicated by the results of the labeled-silt exposures, is the passive release of cadmium associated with the silt surface. Importantly, this desorption was independent of DQ, suggesting that even at a minimal organic content (i.e.10%) digestive processes that are occurring within the gut of the mussel are sufficient to remove the same amount of cadmium from the silt as compared to a diet that contains 3 times the amount of organic matter. Of further note, in the silt-only exposure (in the absence of organic matter) ^{109}Cd-AE was still 36% Owen (1966) has reported that the pH of the digestive track of mussels is close to 5.5. Hence, the acidic environment of the gut is such that the passive desorption of cadmium results from the surface of inorganic particles.

^{109}Cd in mussels in relation to ^{109}Cd-AE

Given that AEs are representative of the amount of radiotracer assimilated by the mussel from its diet, the calculated ^{109}Cd-AEs and the amount of radiotracer incorporated into the mussels tissue (corrected for uptake of the radiolabel from solution) should be highly correlated with each other. When ^{109}Cd-AEs for both the labeled-algae and labeled-silt experiments were regressed with ^{109}Cd in the mussel tissue, a weak but significant correlation was found ($r = 0.63$; $p < 0.05$), such that greater ^{109}Cd-AEs correlating with higher mussel tissue ^{109}Cd activity. Greatest tissue concentrations of ^{109}Cd corresponded to diet exposures where the silt rather than the algae was labeled. This is an important finding, in that it suggests that metal desorbed from the inorganic component of seston tends to be more readily incorporated into the animal tissue and therefore more biologically available, as compared to metal associated with the algal component of the diet.

Several studies (e.g. Rule & Alden 1996, Thomas & Bendell-Young 1998) have reported that cadmium concentrations in seston-ingesting organisms are highly correlated to cadmium concentrations associated with the easily reducible inorganic fraction of sediment (i.e. metals associated with the surfaces of manganese oxides). It is conceivable therefore, assuming that sorption of the ^{109}Cd onto silt represents similar sorption processes that occur on the surfaces of oxides of manganese, that, although seston-ingesting organisms may ultimately be selecting for the organic component of the diet, the passive uptake of cadmium from the inorganic component of seston may overwhelm the contribution of metal from the organic component of sediment alone. This explains the findings in nature, where concentrations of cadmium associated with the easily reducible component of a sediment are correlated to cadmium levels in the associated biota.

Of further note, and as yet unexplained, is that the lowest ^{109}Cd levels in mussel tissues were observed at the mussels 'filter-feeding optimum', where we thought that we would have observed maximum levels. If this value is omitted from the relationship between ^{109}Cd in mussel tissue and ^{109}Cd-AE from the labeled-algae exposures, the expected positive relationship between the 2 variables exists. Based on these 3 points, amounts of ^{109}Cd incorporated within the mussel tissue at the filtering maximum should have been ca 50 dpm gdw^{-1}. The unexpectedly low recovery of ^{109}Cd within mussel tissue noted at the filtering maximum implies a possibly unaccounted for excretory route at this maximum.

Summary and conclusions

Our study indicated 2 distinct patterns in the assimilation of ^{109}Cd, depending on whether the ^{109}Cd had been incorporated into the algae or adsorbed onto the silt component of the diet. When mussels were exposed to a diet where only algae had been spiked, ^{109}Cd-AE was proportional to diet quality, with a maximum ^{109}Cd-AE occurring at the 'filtering optimum' for this species. However, when the silt was spiked, ^{109}Cd-AE was independent of diet quality, and, with the exception of the silt-only exposures, was maintained at a maximum value of 85% It is possible that the addition of algae to the labeled-silt diet activates digestive processes that result in greater assimilation of silt-bound ^{109}Cd as compared to diets comprised of silt alone. Hence, uptake of cadmium from seston will be dependent on both active (i.e. digestion of organic matter) and passive (i.e. desorption from the surfaces of the inorganic silt particles) processes.

Within the natural environment, seston is composed of both inorganic and organic components; hence both will be important in providing a route of metal exposure to sediment-ingesting organisms. Importantly, the relative importance of the inorganic component of the seston will be greatest under conditions of low quantity and quality of seston, when mussels are ingesting both components of the seston. Under these conditions, maximum desorption of the metal from the inorganic component of the seston is expected to occur. In contrast, under conditions of high seston quality, where the mussel is capable of a highly selective feeding

strategy (i.e. excluding all inorganic components over organic components), only those metals associated with the organic component of the seston will be available for uptake. Our previous studies have indicated that this sorting maximum occurs at a seston quality of ~40%. Under these conditions, cadmium assimilation should be proportional to the amount of cadmium associated with the organic content of the diet, with maximum values being achieved at the organism's maximum filter-feeding capability.

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