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Interaction between temperature and cadmium toxicity in the isopod *Porcellio scaber*

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Summary

1. Temperature has an important effect on all physiological processes in animals that rely on external sources of heat (ectotherms). In an attempt to elucidate the interaction between temperature and the response of ectotherms to heavy metals, a study was made of growth (increase of body mass) of the isopod *Porcellio scaber* under four constant temperature regimes (12, 16, 20, 24 °C), and four different exposures to cadmium (0·016, 0·071, 0·14 and 0·31μmol g^{-1} in the diet), in a factorial experiment.
2. There were significant effects on growth rate for both cadmium and temperature, and the interaction between cadmium and temperature was also significant. The average growth rate per week increased with increasing temperature, but the results showed that when cadmium was present at concentrations higher than 0·071 μmol g^{-1}, it disturbed the temperature-induced growth enhancement.
3. There was a tendency for cadmium to be least toxic at intermediate temperature (16 °C), but the 50% and 10% effect concentrations in the diet, estimated by loglogistic curve fitting, did not significantly vary with temperature. The average values were EC_{50} = 0·330 μmol g^{-1} and EC_{10} = 0·041 μmol g^{-1}.
4. The Arrhenius model was used to describe the temperature–growth rate relationship, and activation energies were estimated for each cadmium exposure. At the highest cadmium concentration the Arrhenius model did not describe the data very well. The lowest activation energy was observed at 0·14 μmol g^{-1}.
5. Cadmium accumulation in isopods was linearly related to the cadmium concentration in food, for all temperature levels. The significant increase in cadmium concentration with temperature indicates that the effect of temperature on cadmium accumulation is stronger than its effect on body growth. As a whole the data illustrate the importance of taking temperature into account when conducting ecotoxicological studies with soil invertebrates.

Key-words: Arrhenius activation energy, growth

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Introduction

Temperature is one of the most important environmental factors determining life-cycle events in ectotherms, because of its direct influence on metabolism. Many studies have been carried out on the temperature responses of ectotherms (Taylor 1981; Atkinson 1994; Van Straalen 1994), usually focused on the effects of temperature on life-history processes such as moulting, body growth and reproduction. Effects of temperature on the toxicity of pollutants have largely been ignored. When ectotherms are exposed to toxic pollutants the rate of uptake and elimination may be changed by environmental conditions such as temperature and food supply (Rainbow 1988; Barron 1990; Janssen & Bergema 1991; Smit & Van Gestel 1998). Studies on the interaction between temperature and pollutant toxicity are therefore necessary (Axelsen 1997).

Temperature responses may be described in terms of a model based on biophysical mechanisms for reaction kinetics (Sharpe & DeMichele 1977). One of the main parameters in this model is the Arrhenius activation energy, which measures the energy threshold to be surmounted by a rate-limiting enzyme for the reaction to take place. This parameter may be estimated from observations on the rate of metabolism (or processes connected to it, such as moulting and growth) at a series of experimental temperatures. Widianarko, Donker & Van Straalen (1994) made an evaluation of cadmium effects on Arrhenius activation energy of three populations of isopods, *Porcellio scaber*. The results showed that the Arrhenius model

could be used in uncontaminated conditions, but in the presence of high concentrations of cadmium (0·333 μmol g^{-1}), the Arrhenius equation did not describe the relationship between growth and temperature very well.

In the present work a comparative growth study on isopods, *Porcellio scaber*, exposed to four different levels of temperature, was conducted using four cadmium concentrations in the sublethal range. The aim was to improve our understanding of the effects of temperature on cadmium toxicity and internal cadmium concentrations in ectothermic animals.

Materials and methods

ANIMALS

Individuals of a population of *Porcellio scaber* (Isopoda; Crustacea) were sampled in the middle of December 1995, from 'Spanderswoud', a mixed deciduous forest near Hilversum (the Netherlands). Isopods were identified using the key by Hopkin (1991). Animals of small size were selected (fresh body mass range 20–30 mg) and were sexed under a dissecting microscope. An equal number of males and females were used.

FOOD

Food was prepared from dried ground poplar leaves supplemented with 10% peptone. Cadmium was added to the food as a $Cd(NO_3)_2$ solution in different concentrations (0·065, 0·14, 0·30 μmol Cd per g dry litter). The mixtures were dried, stored as a powder and moistened again when needed, in the proportion 1 g of food to 3 ml of demineralized water.

The range of cadmium concentrations was based on previous experiments where the highest concentration was chosen so as still to allow isopods to grow (Donker & Bogert 1991). The actual concentrations in the food after metal analysis using acid digestion and atomic absorption graphite furnace spectrophotometry (Type 1100B, Perkin Elmer, Überlingen, Switzerland) were 0·071, 0·14 and 0·31 μmol Cd g^{-1} dry litter. The actual Cd concentration in control litter was 0·016 μmol Cd g^{-1}. Fresh food was offered once per week.

EXPERIMENTAL CONDITIONS

Four temperatures (12, 16, 20, 24 °C) and four types of food (uncontaminated, and three levels of contamination) were used, with 30 replicates. In total $4 \times 4 \times 30 = 480$ individuals were involved in this experiment.

Two weeks before the experiment, isopods were acclimatized in four climate chambers, according to the temperature levels mentioned above. For all climate chambers the light:dark regime was 12:12 h and the air humidity was 70%.

During the experiment, animals were kept individually in polystyrene boxes (diameter 5 cm), with a perforated lid. Each box was filled with plaster to ≈ 1-cm depth. Plaster was kept moist during the whole experiment. A moistened piece of earthenware was put in the box to provide a humid shelter for the isopods. Boxes were allocated to random positions on trays within each climate chamber.

MEASUREMENTS

Individual body mass was measured for a certain period, depending on the temperature (every week for 24 °C, every 2 weeks for 20 °C, every 3 weeks for 16 °C and every 4 weeks for 12 °C). The period of observation was different for each temperature: 5 weeks at 24 °C, 10 weeks at 20 °C, 15 weeks at 16 °C and 20 weeks at 12 °C. At the end of the observation period dry body mass for isopods was determined, then isopods were digested in 500 μl of a digestion mixture (HNO_3:$HClO_4$ = 7:1) in 2-ml Pyrex tubes in a block heater. All cadmium measurements were done by graphite furnace atomic absorption spectrophotometry (AAS), after appropriate dilutions of the digests. Quality control of the analysis was maintained by digesting samples of certified reference material (bovine liver, Reference material no. 185, Community Bureau of Reference, Brussels, Belgium). The average concentration measured in these samples was 6% lower than the certified value; no corrections were made.

DATA ANALYSIS

The growth rate (mg $week^{-1}$) was estimated for each individual isopod from the mass changes. Growth rate data were then analysed for temperature and cadmium effects by two-way ANOVA. All data were checked for homogeneity of variances with Bartlett's test (Sokal & Rohlf 1995). EC_{50} and EC_{10} values for cadmium toxicity towards body growth were estimated using the loglogistic model (Haanstra, Doelman & Oude Voshaar 1985).

Activation energy was estimated for each cadmium concentration using the Arrhenius equation, fitted to the data for growth rate as a function of temperature. The Arrhenius equation can be written as follows:

$$r(T) = r_{15}\exp\left\{\frac{H_A}{288\,R} - \frac{H_A}{R\,T}\right\}, \qquad \text{eqn 1}$$

where T is temperature (in K), $r(T)$ is the rate of the process at temperature T, r_{15} is the rate at 15 °C, H_A is the activation energy for the process (in J mol^{-1}) and R is the universal gas constant (= 8·31 J K^{-1} mol^{-1}). Parameter estimations for H_A and r_{15} were obtained by means of the least-squares fitting routine in the SYSTAT software package, run on an Apple microcomputer.

Results

Mortality of isopods was expressed on a weekly basis for each temperature treatment by fitting an exponential curve to the survival data. Overall mortality was low, but it was temperature and concentration dependent. A rate of 0·5% per week was observed at the lowest temperature and the lowest cadmium concentration (12 °C, 0·016 μmol g^{-1}), while the highest mortality (3·5% per week) was observed for isopods exposed to the highest temperature and the highest cadmium concentration (24 °C, 0·31 μmol g^{-1}). All animals dying during the experiment were excluded from data analysis prior to their death.

The changes in body mass of the isopods could be described well by a linear increase. Some indication was obtained for an S-shaped growth curve over the period of observation but the deviation from linearity was too small to allow the use of curvilinear growth curves (Fig. 1). The greatest increase was seen in the isopods cultured at 24 °C and fed uncontaminated food. At 12 °C isopods grew very slowly and a long period of observation (20 weeks) was necessary to obtain a reliable estimate of the growth rate. Figure 1 shows the mass increase determined five times over the exposure period for each temperature. Although the animals were selected for equal body mass at the start of the experiment, small differences in body mass between the temperatures were already apparent at the beginning of the exposure period, owing to the 2 weeks' acclimation time at each temperature (Fig. 1).

To determine the relationship between growth rate and temperature, growth rate (mg $week^{-1}$) was estimated from the data by linear regression for each individual. The individual growth rates were then transformed into logarithms to obtain homogeneity of variances and subjected to a two-way analysis of variance, see Table 1. The results showed a highly significant effect of temperature and cadmium concentration, while the interaction between these two factors was also significant (Table 1). The relationship between average growth rate and temperature for each cadmium concentration used is demonstrated in Fig. 2. The figure shows that the average growth rate per week increased with increasing temperature for the lowest cadmium concentrations (0·016 and 0·071 μmol g^{-1}). For the highest two (0·14 and 0·31 μmol g^{-1}) no marked differences between the growth at 20 °C and 24 °C were observed. At high Cd exposures, the isopods appear to be unable to achieve their normal body growth at high temperature.

The dose–response relationships of growth are described in Fig. 3. A marked effect for temperature on growth rate (mg $week^{-1}$) can be seen, as the growth rate increased with increasing temperature. It can be also seen from the figure that growth rate decreased

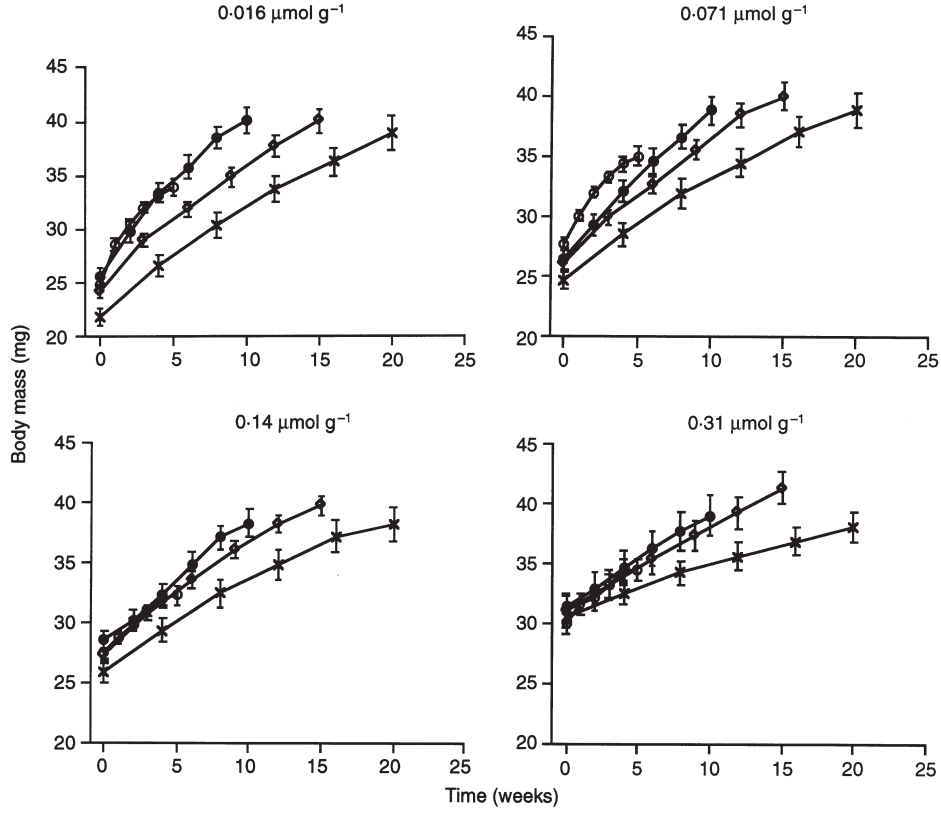

Fig. 1. Average body mass as a function of time (weeks) for *Porcellio scaber* exposed to different cadmium concentrations in the food, at different temperature levels: 24 °C (○), 20 °C (●), 16 °C (◇) and 12 °C (×). Standard errors are given for each data point.

with increasing cadmium concentration in the food in all temperature levels.

The loglogistic model was fitted to the data and parameter estimates were obtained for EC_{50} and EC_{10} for growth at each temperature (see Table 2). There was a tendency for both EC_{50} and EC_{10} to follow an optimum curve with the highest values at 16 °C, but the 95% confidence limits were wide, and both EC_{50} and EC_{10} were not statistically significant between the temperatures (Table 2).

Figure 4 shows the fit for the Arrhenius equation for body growth rate over the temperature range of 12–24 °C (285–297 K) for individuals exposed to control food and to three cadmium concentrations of contaminated food. The Arrhenius equation described the relationship between growth and temperature well, except for the highest cadmium concentration. The normal temperature response of *Porcellio scaber* seems to be disturbed by Cd toxicity.

Table 1. Analysis of variance for the effect of temperature and cadmium concentration on log-transformed growth rate (mg week^{-1}) of the isopod *Porcellio scaber*

Source of variation	Sum of squares	df	Mean square	*F*-ratio	*P*
Cd	4·560	3	1·520	101·388	< 0·001
Temperature	5·665	3	1·888	125·975	< 0·001
Temp. × Cd	0·297	9	0·033	2·202	0·021
Error	6·026	402	0·015		

The estimates for growth rate at 15 °C (r_{15}) and activation energy (H_A) are shown in Table 3. There were no significant differences among the activation energies (H_A) in the cadmium concentrations used, but the differences in r_{15} were significant. We can also see from Table 3 that there is no correlation between the estimates for r_{15} and H_A.

Cadmium concentrations in isopods were measured at the end of the observation period. The rate of accumulation (μg g^{-1} week^{-1}) was estimated for each individual simply by dividing the concentration by the length of the exposure period. The rate of cadmium accumulation in control animals was about the same for all levels of temperature used (Fig. 5). Cadmium accumulation increased more or less linearly with the cadmium concentration in food, for all temperature levels. At the high cadmium concentration, effects of temperature on cadmium accumulation became most obvious (Fig. 5). The significant increase in cadmium concentration with temperature indicates that the effect of temperature on cadmium accumulation is stronger than its effect on body growth.

Discussion

The data obtained in this and other experiments using isopods exposed to combinations of metals and

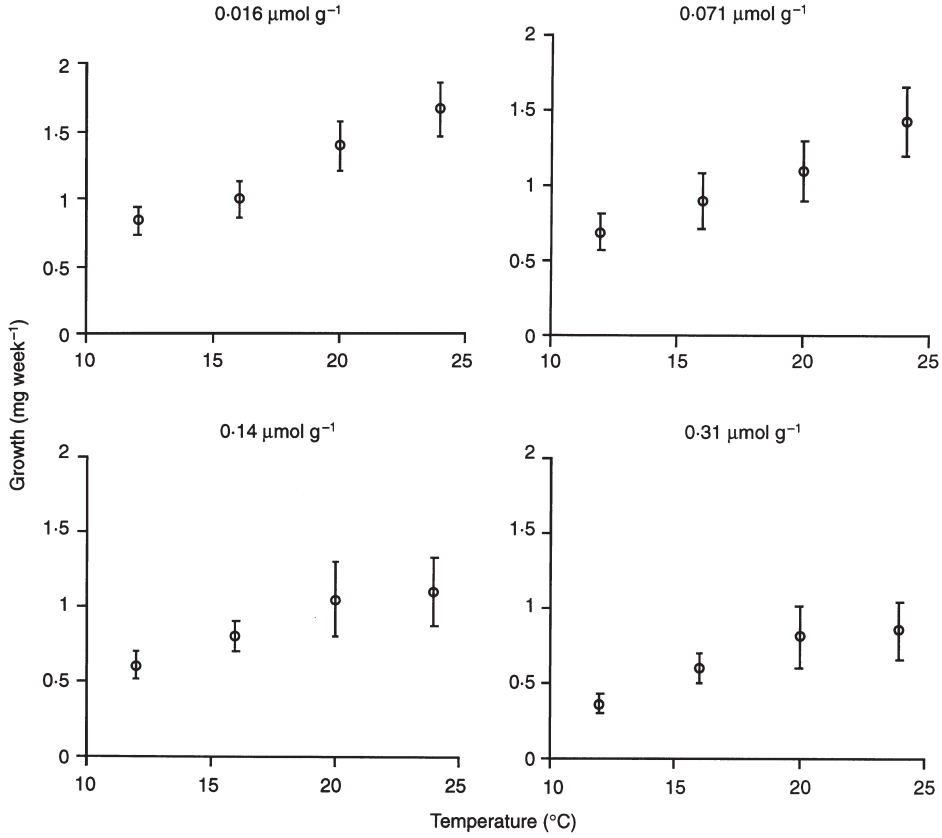

Fig. 2. Average growth per week for each level of temperature, for isopods exposed to four different cadmium concentrations in the food. Standard deviations are given for each data point.

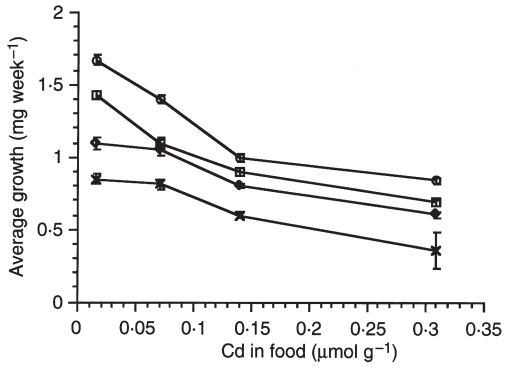

Fig. 3. Concentration–response relationships for isopods exposed to cadmium at four different temperature levels: 24 °C (○), 20 °C (□), 16 °C (◇) and 12 °C (×). Standard errors are given for all data points.

Table 2. EC_{50} and EC_{10} values for the effect of cadmium on growth of the isopod *Porcellio scaber* at four different temperatures. EC_{50} and EC_{10} were calculated for growth rate (mg $week^{-1}$) over the exposure period indicated. The 95% confidence interval is given below each estimate

Temperature (°C)	Exposure period (weeks)	EC_{50} (μmol g^{-1})	EC_{10} (μmol g^{-1})
24	5	0.270	0.0275
		0·198 0·370	0·0078 0·096
20	10	0·343	0·012
		0·128 0·920	0·0001 0·826
16	15	0·457	0·079
		0·311 0·671	0·029 0·211
12	20	0·248	0·045
		0·202 0·304	0·022 0·092

temperature (Widianarko *et al*. 1994; Donker *et al*. 1998) provide clear evidence of interaction between temperature and metal toxicity. In the present experiment, growth started to decrease significantly at a dietary cadmium concentration of 0·14 μmol g^{-1}, in agreement with Donker & Bogert (1991), who reported that the growth of reference isopods was reduced at 0·17 μmol g^{-1} of Cd in the food. In the study of Crommentuijn *et al*. (1995), *Porcellio scaber* was, however, considerably less susceptible to cadmium (EC_{10} for growth was estimated as 0·85 μmol g^{-1} in that study). These differences between studies demonstrate that before isopods can be considered as standard test animals for soil assessments (Drobne 1997), considerably more attention should be paid to an analysis of factors modifying toxicity, such as metal speciation in the food and exposure conditions.

Growth reduction is mostly probably due to a disturbance of the metabolism by cadmium intoxication, rather than to avoidance of contaminated food. Although isopods may avoid food contaminated with metals (Van Capelleveen *et al*. 1986), this response is unlikely to be of significance in the present case, as cadmium has a repellent effect at concentrations significantly above the ones used here. In the study of Khalil, Donker & Van Straalen (1995) even a Cd concentration of 5 μmol g^{-1} in the diet did not reduce consumption of *Porcellio scaber*, although growth was seriously affected. The linear increase of internal Cd with external exposure in our experiments (Fig. 5) also indicates a constant consumption within each temperature treatment.

Growth rate increased significantly with temperature between 12 and 24 °C. This growth stimulation is obviously due to an increase in the rate of all physiological processes in the isopods, as in other ectotherms (Cossins & Bowler 1987; Nugegoda & Rainbow 1987; Widianarko *et al*. 1994). At 0·14 and 0·31 μmol Cd g^{-1}, however, the stimulatory effect of temperature was smaller and hardly any increase of growth rate was observed between 20 and 24 °C. The high concentration of cadmium seems to disturb the temperature-induced growth enhancement for isopods. This result is in agreement with Widianarko *et al*. (1994), who reported that at a cadmium concentration of 0·333 μmol g^{-1} the normal temperature response of isopod growth was disturbed.

Although the analysis of variance provided clear evidence for a significant interaction between temperature and cadmium, this interaction is difficult to translate into toxicological criteria. Both EC_{50}s and EC_{10}s for isopod growth seemed to follow an optimum curve; however, the differences were not significant, because of wide confidence intervals and the fact that the experiment was not designed to estimate toxicological criteria precisely.

Comparing the cadmium concentrations in food and in the animal, a linear relationship was found for each temperature used. This result is in a good agreement with isopod studies by Donker & Bogert (1991), Van Hattum *et al*. (1993) and Crommentuijn *et al*. (1995). Similarly, Rainbow & White (1989) observed that cadmium accumulation in three crustacean

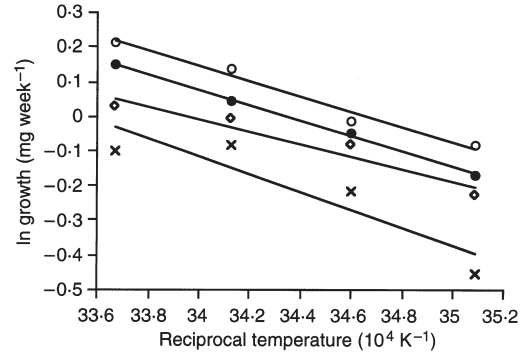

Fig. 4. Arrhenius plot showing the relationship between growth (body mass increase) and the inverse Kelvin temperature, for isopods exposed to different Cd concentrations. The lines represent linear regresssions for each of four Cd exposures in the food: 0·016 μmol Cd g^{-1} (○), 0·071 μmol Cd g^{-1} (●), 0·14 μmol Cd g^{-1} (◇) and 0·31 μmol Cd g^{-1} (×).

Table 3. Parameter estimates for the Arrhenius equation describing the response of isopod body growth to temperature (12–24 °C). The 95% confidence intervals are given below each estimate

Cd conc. (μmol g^{-1})	Activation energy (kJ $mole^{-1}$)	Growth rate at 15 °C (mg $week^{-1}$)
0·016	42	0·969
	35 49	0·916 1·022
0·071	42	0·828
	35 50	0·782 0·874
0·14	33	0·742
	24 43	0·689 0·794
0·31	47	0·496
	35 57	0·457 0·535

species was a function of concentration and exposure time. According to Hopkin & Martin (1985) and Hopkin (1990) *Porcellio scaber* is not able to excrete cadmium. This implies that the uptake rate of cadmium may be estimated directly from the internal concentration and the exposure time.

Axelsen (1997) suggested that toxicity experiments conducted at different temperatures can only be compared when exposure times are expressed in physiological time units. Donker *et al.* (1998) used the physiological time concept of Van Straalen (1983) to correct for the effect of temperature on growth rate of isopods and to compare the toxicity of zinc at different temperatures. Physiological time corrections were not applied to the present data, because these did not change any of the conclusions. This is explained by the relatively flat response to temperature in the present experiment (activation energies were low in comparison with Donker *et al.* 1998), which may be due to the animals being sampled from the field in winter. The extent to which metal toxicity interacts with temperature may depend on the acclimatization state of the animals.

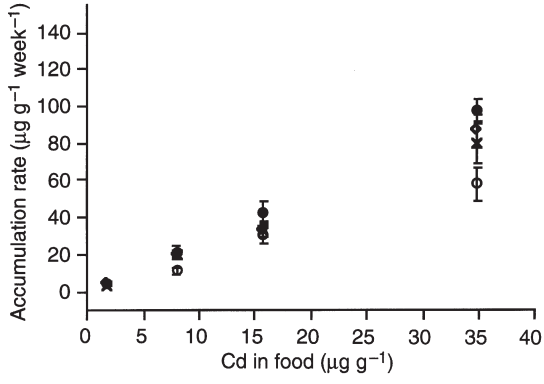

Fig. 5. Cd concentration in food *vs* rate of cadmium accumulation (μg g^{-1} $week^{-1}$) by *Porcellio scaber*, for all temperature levels: 24 °C (○), 20 °C (●), 16 °C (◇) and 12 °C (×). A standard error is given with all data points.

It is clear from this paper and the ecotoxicological literature that temperature may interact with metal toxicity. Given the limited data available, no general trend can yet be formulated on how the metal–temperature interaction is realized in the different species and for the different metals. In soil toxicity studies using the springtail *Folsomia candida* exposed to zinc, Smit & Van Gestel (1998) observed a positive correlation between EC_{50} (reproduction) and temperature over the range 13–24 °C, but a negative correlation between LC_{50} and temperature; Sandifer & Hopkin (1997) found no difference between EC_{50}s established at 15 and 20 °C using the same species exposed to Cd, Cu, Zn and Pb. The most common pattern seems to be that soil invertebrates are more susceptible to metal toxicity at both high and low temperatures, despite the fact that metal accumulation is stimulated only by high temperatures.

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