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Reduced survival and body size in the terrestrial isopod *Porcellio scaber* from a metal-polluted environment

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Abstract

Terrestrial isopods (woodlice) may show trade-offs in life history parameters when exposed to toxins. We have shown previously [Jones and Hopkin (1996) *Functional Ecology* 10, 741–750] that woodlice which survive to reproduce in sites heavily polluted with metals from an industrial smelting works do not alter their reproductive allocation. This study investigates whether there are differences in the survival and body size of *Porcellio scaber* from these same populations. Specimens were collected from eight sites at different distances from the Avonmouth smelter, UK. The sites represented a gradient of concentrations of Zn, Cd, Pb and Cu in the woodlice, from background levels to a grossly contaminated sites close to the smelter. In laboratory trials, the number of days survived by starved males showed a significant decline with increased concentrations of Zn in those animals. The maximum size of both sexes declined significantly from the least to the most polluted sites. The most polluted sites had significantly fewer large animals. The cost of detoxifying assimilated metals appears to be reduced energy reserves and smaller body size.

Keywords: Metal pollution; Starvation; Stress; Woodlice; Zinc

1. Introduction

Selective forces drive animals towards maximizing their fitness via life history strategies that are appropriate for local conditions (Southwood, 1988). Animals have evolved finely tuned regulatory systems that maintain the concentration of available metals in their tissues at levels that allow physiological processes to function at optimal efficiencies. However, exposure to metals from anthropogenic sources can disrupt this homeostasis and threaten the functional integrity of the animal. The physiological cost of detoxifying surplus metals to within tolerable limits may represent a stress factor that reduces an animal's fitness and causes changes in its resource allocation, thereby forcing trade-offs in life history parameters (Sibly and Calow, 1989).

Woodlice (terrestrial isopods) are important detritivores in many habitats (Hassall and Sutton, 1978; Schaefer, 1990; Ma et al., 1991a), and are suitable for assessing the ecotoxicological effects of metals (Drobne, 1997). The life histories of woodlice (see references in Sutton et al., 1984; Ma et al., 1991b; Dangerfield and Telford, 1995) can be affected by stress induced by natural environmental fluctuations. For example, in some species of woodlice it is not uncommon for harsh climatic conditions to cause periods of starvation which can result in reduced growth and increased mortality (Gere, 1962; Paris and Pitelka, 1962; Healey, 1963; Sutton, 1968). Woodlice experience additional stress when exposed to high levels of metals in the diet, which can reduce feeding rates (Drobne and Hopkin, 1995; Donker et al., 1996) and may combine with natural stresses to reduce fitness and lower 'performance', thereby increasing the probability of early mortality (Hopkin, 1990a). Woodlice with very high concentrations of metals can have significantly lower energy reserves (Donker, 1992), decreased moult frequency (Drobne and Strus, 1996), and can show reduced locomotion (Sørensen et al., 1997).

Does the cost of combatting stress in woodlice lead to trade-offs in the allocation of their reduced resources between growth, reproduction and prolonging survival?

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We have demonstrated that woodlice that survive to reproduce in sites grossly polluted with metals released from a large industrial smelting works at Avonmouth, UK, show no reduction in reproductive allocation compared with woodlice from a range of similar but less polluted sites in the area (Jones and Hopkin, 1996). However, is there any evidence of increased early mortality or reduced growth rates in woodlice from populations which persist in these polluted sites closest to the Avonmouth smelter? In this paper we ask if there are differences in: (1) survival of woodlice under starvation; and (2) the size of individual woodlice sampled from populations along this pollution gradient at Avonmouth.

2. Materials and methods

2.1. Study area

The world's largest combined primary zinc, lead and cadmium smelter is situated at Avonmouth, north west of Bristol, UK. The smelter emits large quantities of particulate Zn, Pb, Cd and Cu which has given rise to high levels of metal-pollution and caused severe ecological disruption in the Avonmouth area. For details of the effects of these emissions see Hopkin (1989), Martin and Bullock (1994), Jones and Hopkin (1996) and Spurgeon et al. (1994).

2.2. Field sampling

Eight roadside grassland/scrub sites around the Avonmouth area (Fig. 1) were visited on 13 June 1990. These sites exhibit a wide range of concentrations of Zn, Cd, Pb and Cu in surface soils, nettle leaves (*Urtica dioica*), snails and woodlice (Jones, 1991; Hopkin and Hames, 1994). The sites are numbered in ascending order of the mean concentration of metals in woodlice collected at each site (concentrations in woodlice are given in Jones and Hopkin, 1996, Table 1). The sites represent a 'metal-pollution gradient', with the concentrations at site 1 being close to background levels, while site 8 is the most polluted. The sites were located within 4 km of the Severn Estuary and all experience similar weather conditions.

Specimens of the woodlice *Porcellio scaber* Latreille were collected by two people (DTJ and SPH) hand-searching under rocks and dead wood for 30 min over an area of approximately 20 m^2. Crevices and holes in the substrate were examined and all observed woodlice were collected so as not to bias the size range of samples towards larger individuals. No attempt was made to estimate absolute population densities. On previous visits (Jones, 1991) no woodlice were found during intensive searching in the immediate vicinity of the smelter, (i.e. closer than sites 7 and 8). Specimens were identified and selected for use within 5 h of collection. Many of the gravid females were used to investigate reproductive allocation (Jones and Hopkin, 1996) while males, covering a wide range of body sizes, were selected for the survival trial.

2.3. Survival trial

Because of differences in the number of individuals collected, between 20 and 25 *Porcellio scaber* from each site were used. Woodlice were housed in transparent plastic trays, each tray consisting of 25 uniform chambers arranged in a 5×5 grid. Chambers were cubic with sides 2 cm in length. Large specimens were able to turn around within the chamber, and a lid prevented migration between chambers. One animal was placed in each chamber. The trays were then placed in a large plastic box lined with wet absorbent paper and closed with a tight-fitting lid to maintain a humid atmosphere. The box was stored at 16°C under a 16 h light/8 h dark regime. Trays were inspected daily and all faeces, and

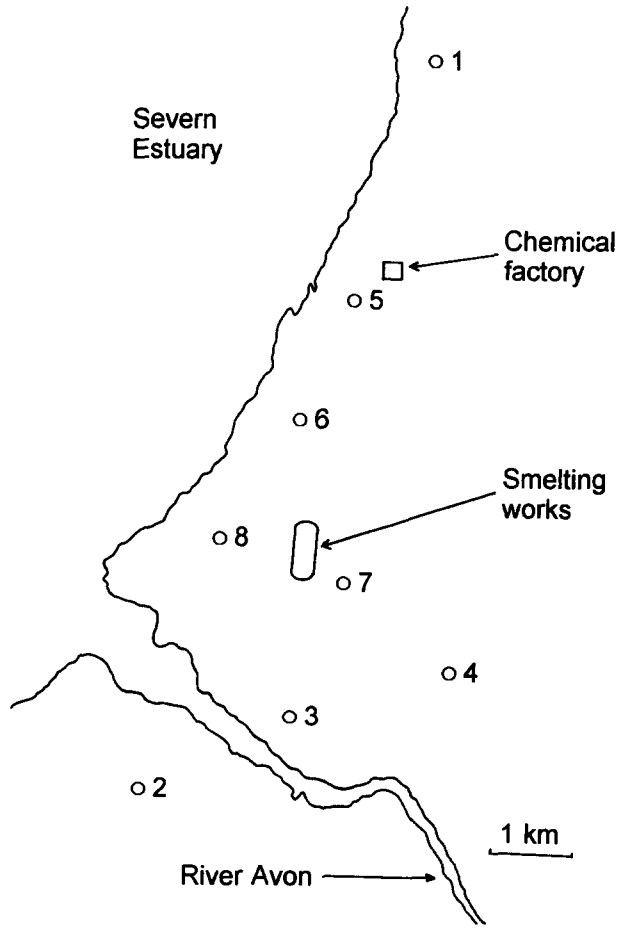

Fig. 1. Map of the Avonmouth area showing the location of the eight sampling sites (open circles), the industrial smelting works, and the chemical fertilizer factory.

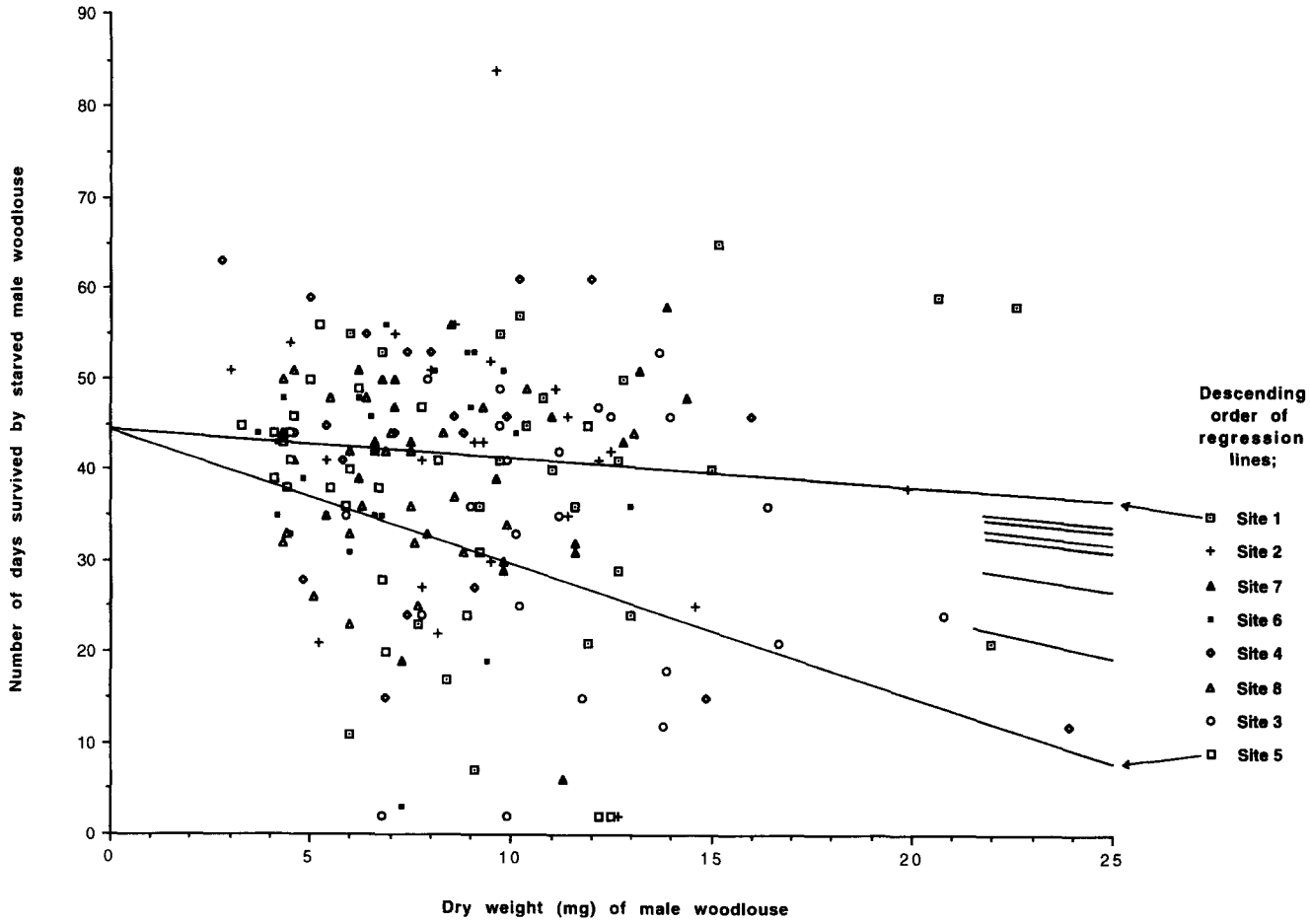

Fig. 2. Relationship between the number of days survived by starved male *Porcellio scaber* and their dry mass (mg) at death. Analyses using general linear models gave significant differences among sites in the gradients of the regression lines but no significant differences among the intercepts.

any exuvea from moulted animals were removed with a fine brush. Dead animals were removed and retained for chemical analysis.

2.4. Size of woodlice

In woodlice, an individual's body length can vary enormously depending on the degree of contraction of the tergites (Sutton, 1968). By contrast, the woodlouse head capsule is a single rigid structure that does not grow between moults. Donker et al. (1993a) found the width of the head to be less variable than fresh weight, and it is also thought to be a better indicator of age. Therefore, head-width was used as a surrogate for the size of individuals when comparing population structure. Head-width is defined as the greatest width of the head in the horizontal plane when in dorsal view, measured at the level of the eyes and including the eyes (Sunderland et al., 1976).

Specimens were assigned to one of three categories: (1) gravid females (developing embryos visible in the brood pouch); (2) non-gravid females; and (3) males (as indicated by the presence of male genitalia). It is very difficult to separate small, non-gravid females from immatures since only the male genitalia can be distinguished easily in small adults. Therefore, immatures were grouped with non-gravid females. Size histograms are drawn for those sites with more than one hundred individuals, as it was considered that a smaller number would not be representative of the population from which the sample was taken. Accordingly, histograms are not given for sites 4 and 6.

2.5. Chemical analyses

As each animal in the survival trial died it was dried at 70°C to constant mass and stored. At the end of the experiment the concentration of Zn, Cd, Pb and Cu in each specimen was determined using flame atomic absorption spectrometry (Spectra AA-30, Varian Inc.) and flameless AAS (Varian Graphite Tube Atomizer-96) using the methods described by Jones and Hopkin (1996). All weights are expressed on a dry mass basis.

2.6. Statistical analysis

Differences among sites in mean survival time, and head-width were sought using one-way ANOVAs. Subsequent analyses using t-tests, employing the pooled standard deviation, was used to identify which sites were significantly different from each other. Differences among slopes and intercepts were considered using general linear models; testing common line, varied intercept (i.e. common slope) and varied slope models (SAS Institute, 1988). Trends in survival time over the range of concentrations of Zn were considered by testing for a significant upper boundary to the scatter of data points, using the method developed by Blackburn et al., 1992. The data were divided into classes of equal concentrations of Zn (class size of 200 $\mu g\,g^{-1}$) and the relationship between the maximum survival time in each class and the concentration of Zn were sought using least-squares regression. Differences in the expected number of large animals at each site were considered using a chi-squared (χ^2) test. Rank correlation was used to test if the sequence of sites ranked in order of measured variables differed significantly from the order of sites in the pollution gradient. Differences were considered significant if $p < 0.05$.

3. Results

3.1. Survival under starvation

The range and mean number of days survived by starved males from each site is given in Table 1. There was no significant difference among sites in the survival time ($F = 1.12$, $df = 7$, 182, NS). In the field *Porcellio scaber* has a maximum life expectancy of 30 months (Sutton et al., 1984). We can expect survival to be influenced by age, with some larger animals being close to the end of their natural life and therefore having a shorter survival time when starved. Therefore, a comparison of mean survival time may fail to detect significant differences among sites.

To test for underlying differences, survival time was plotted against the weight of individual males. An analyses using general linear models (Fig. 2) gave no significant difference among the intercepts of the regression lines from the eight sites (varied intercept model; $F = 1.09$, $df = 7$, 174, NS) but there was a significant difference among sites in the gradients (varied gradient model; $F = 2.35$, $df = 7$, 174, $p < 0.05$). The descending order of regression lines shown in Fig. 2, however, does not correlate significantly with the ranking of sites in the pollution gradient ($n = 8$, $r = 0.405$, NS). Sites 5 and 3 show the greatest reduction in survival of larger animals, implying that factors other than levels of metals are affecting survival.

If high levels of metals are causing a reduction in the length of survival then it may be related directly to the concentration in the individual woodlice. The intraspecific range of concentrations of metals within populations of woodlice is known to be very wide and to overlap among sites in the Avonmouth area (Jones, 1991). Hence, differences caused by metal-pollution may not be observed in site-specific comparisons. To test this hypothesis, males from all sites were pooled and the relationship between the number of days survived and the concentration of Zn, Cd, Pb and Cu in the individuals was plotted. However, no significant correlation existed between survival and the concentration of any metal.

For populations exposed to prolonged stress the number of individuals still alive at the cessation of that stress is a more relevant ecological variable than the mean survival time for members of that population. Consequently, although no significant negative correlation was observed between survival and concentrations of metals, it is important to consider the maximum survival time at different concentrations of metals. Hopkin and Hames (1994) have shown that Zn is the metal most responsible for the early mortality of woodlice when in combination with other metals at Avonmouth. Therefore, to consider changes in survival over a range of concentrations of Zn, the upper boundary of the scatter of data points was sought (Fig. 3). The data have a

Table 1
The mean, standard error, minimum and maximum number of days until death from starvation of male *Porcellio scaber* collected from sites in the Avonmouth area, and the distance of each site from the smelting works

Site	Distance (km)	n	Mean ± SEM	Minimum	Maximum
1	6.3	25	38.9 ± 3.2	7	65
2	3.3	24	41.3 ± 3.2	2	84
3	1.6	24	32.5 ± 3.1	2	53
4	2.3	20	41.9 ± 3.6	12	63
5	3.3	24	37.0 ± 2.8	2	56
6	1.8	23	40.6 ± 2.5	3	56
7	0.8	25	40.3 ± 2.3	6	58
8	0.8	25	38.9 ± 1.6	23	51

Table 2
The mean, standard error, and maximum head-width (mm) of gravid females, all females (combining gravid and non-gravid females), and males of *Porcellio scaber* collected from six sites in the Avonmouth area

Site	Gravid females			All females			Males		
	n	Mean ± SEM	Maximum	*n*	Mean ± SEM	Maximum	*n*	Mean ± SEM	Maximum
1	342	2.184 ± 0.014	2.97	619	2.029 ± 0.014	2.97	189	1.797 ± 0.024	2.94
2	78	1.929 ± 0.025	2.59	117	1.850 ± 0.026	2.59	68	1.752 ± 0.042	2.72
3	121	2.143 ± 0.020	2.72	378	1.792 ± 0.021	2.81	142	1.708 ± 0.028	2.59
5	122	1.797 ± 0.021	2.47	212	1.685 ± 0.018	2.50	74	1.566 ± 0.036	2.31
7	95	1.860 ± 0.021	2.47	154	1.827 ± 0.021	2.47	91	1.719 ± 0.032	2.53
8	198	1.931 ± 0.014	2.50	358	1.801 ± 0.014	2.50	167	1.664 ± 0.022	2.50

See Fig. 1 for the position of the sites relative to the smelting works.

significant negative upper slope ($n = 10$, $r = -0.93$, $p < 0.001$) indicating that survival time declines as concentrations of Zn in the animals increases. Under natural conditions starvation may be just one of many stress factors that an animal experiences. Consequently, when all stress factors in the field are combined, mortality caused by starvation may occur more rapidly in the Avonmouth populations than indicated in Fig. 3.

3.2. Size of woodlice

The mean and maximum head-widths of *Porcellio scaber* from six of the Avonmouth sites are given in Table 2. There were significant differences among sites in the head-width of gravid females ($F = 85.5$, $df = 5,951$, $p < 0.01$), all females ($F = 52.3$, $df = 5,1839$, $p < 0.01$), and males ($F = 6.91$, $df = 5,728$, $p < 0.01$). The descending

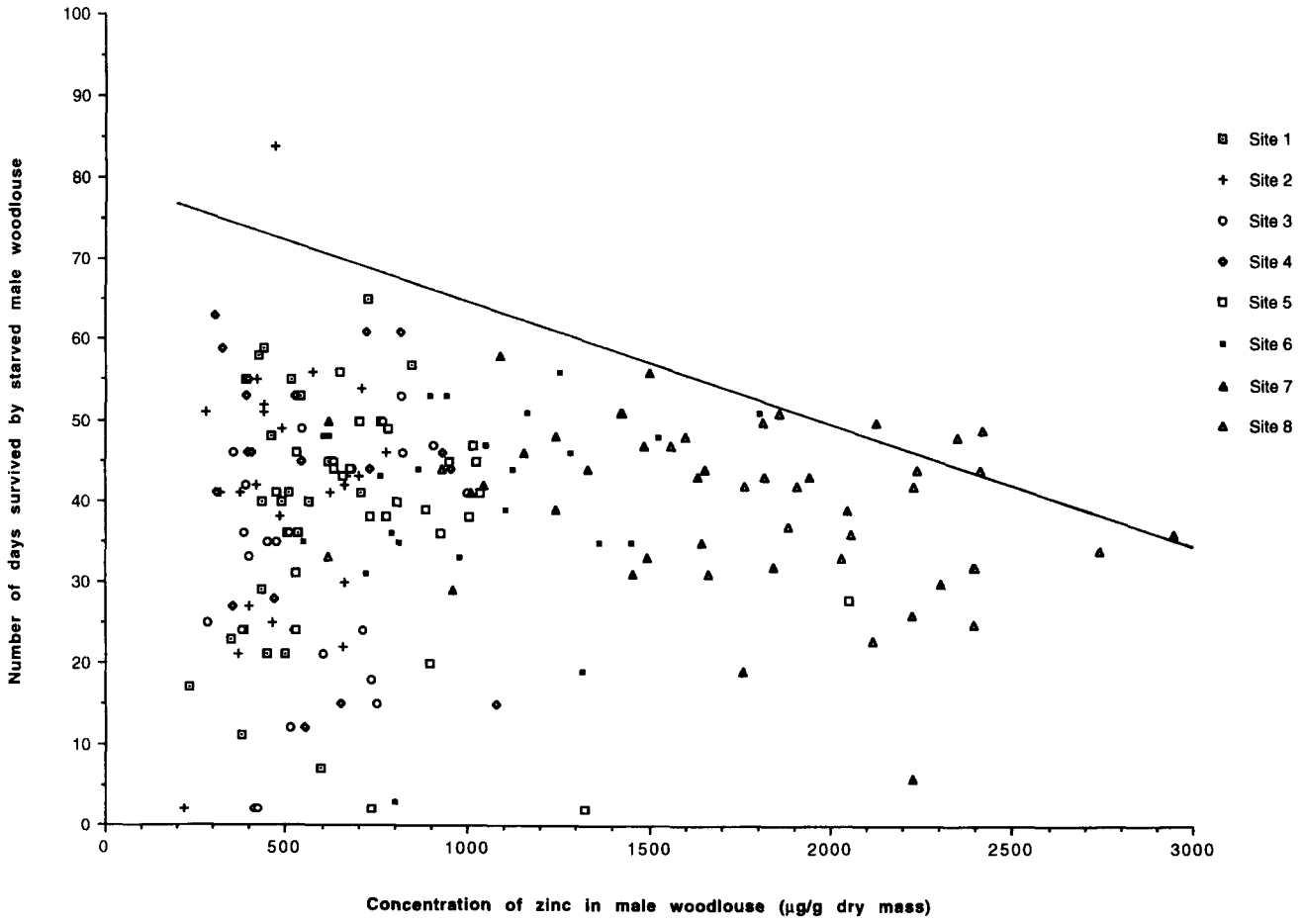

Fig. 3. Relationship between the number of days survived by starved male *Porcellio scaber* and their concentration of zinc ($\mu g\,g^{-1}$ dry mass) at death. A significant negative upper boundary slope exists; $y = 79.8 - 0.015x$.

Table 3
The descending order of mean head-width (mm) of *Porcellio scaber* from six sites in the Avonmouth area

Category	Ranked mean head-width
Gravid females	Site $1_a > 3_a > 8_b > 2_b > 7 > 5$
All females	Site $1 > 2_a > 7_a > 8_a > 3_a > 5$
Males	Site $1_a > 2_{ab} > 7_{ab} > 3_{ab} > 8_b > 5$

Sites with the same subscript are not significantly different from each other.

order of mean size in each category (see Table 3) does not correlate significantly with the ranking of sites in the pollution gradient. In each category, however, the mean size of woodlice at site 1 was always significantly larger than the mean size at sites 8 and 5 (Table 3).

The head-width frequency distributions of *Porcellio scaber* from the six sites are illustrated in Fig. 4. When the six sites were ranked in order of the maximum size of gravid females there was no significant correlation with the sequence of sites in the pollution gradient ($r = 0.754$, NS). However, the maximum size did show a significant rank correlation for the categories all females ($r = 0.841$, $p = 0.036$) and males ($r = 0.829$, $p = 0.042$). The largest females at site 1 were four size classes bigger than the largest females at sites 5, 7 and 8 (Fig. 4(a)). In the case of males, the largest males at site 1 were four size classes bigger than the largest males at sites 7 and 8, and five classes bigger than those at site 5 (Fig. 4(b)). This implies that maximum size of both sexes declined as concentrations of metals increased along the pollution gradient at Avonmouth.

To investigate the possibility of a significant reduction in the number of large animals, a head-width size of 2.05 mm was chosen, and the number of individuals in each category larger and smaller than this size was calculated. For the purposes of this analysis animals greater than 2.05 mm are described as 'large' individuals. Fig. 4 displays the percentage of large animals collected from each site. Significant differences among

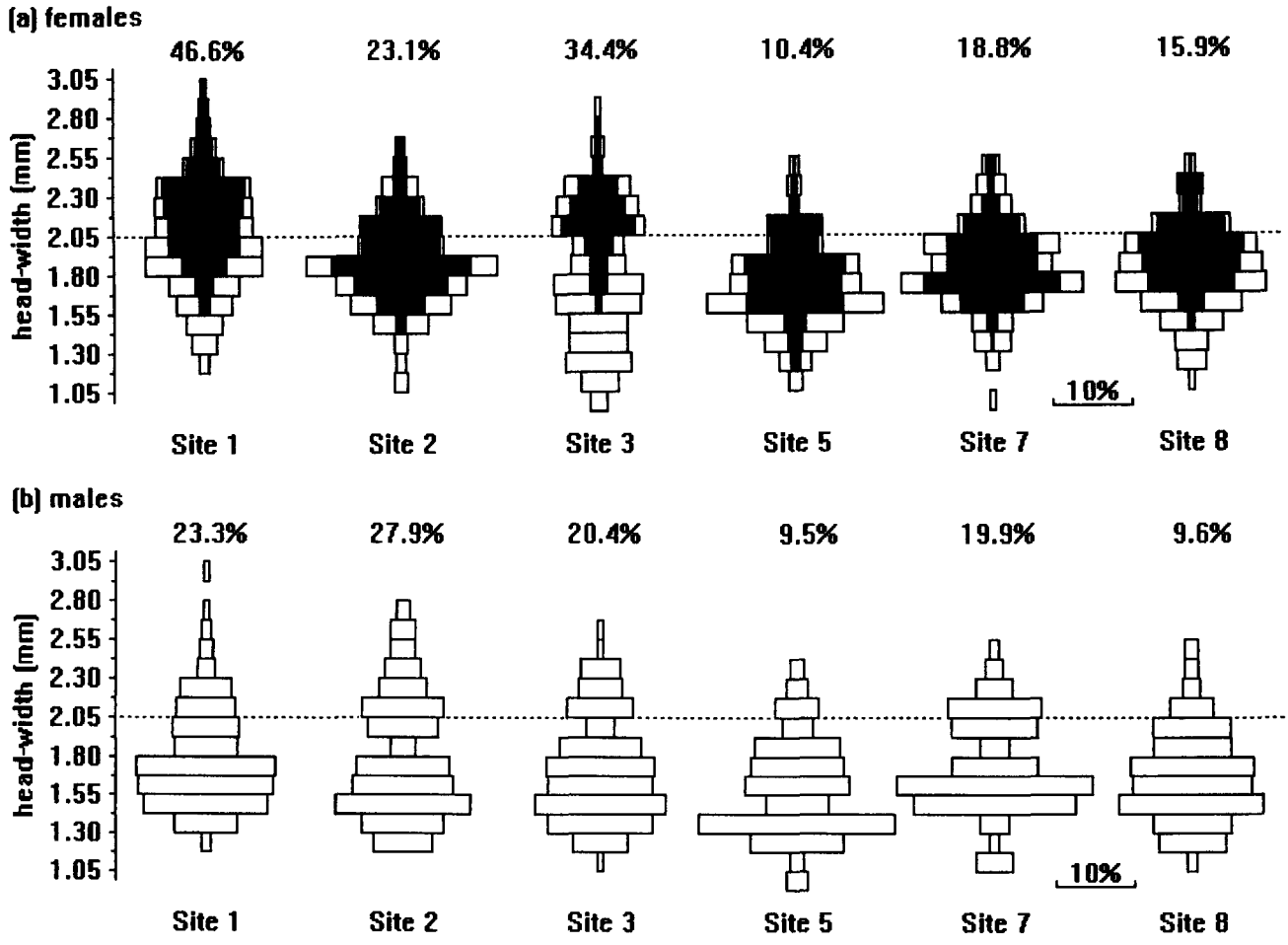

Fig. 4. Size histograms of *Porcellio scaber* females (a), and males (b), based on the head-width frequency distribution of woodlice collected from six sites in the Avonmouth area. The number of individuals in each class is shown as the percentage of the total number of females or males sampled at each site. Female histograms (a) show the percentage of gravid (solid bar) and non-gravid (open bar) individuals in each class. The percentage of animals with a head-width greater than 2.05 mm (dashed line) is indicated above each histogram.

Table 4
The descending order of standardized residuals (SR) at each site (given as subscript) from a χ^2 test of the number of *Porcellio scaber* with a head-width larger than 2.05 mm

Category	Ranked SR
Gravid females	Site $1_{+6.3} > 3_{+4.6} > 2_{-2.1} > 7_{-4.0} > 8_{-4.1} > 5_{-4.7}$
All females	Site $1_{+7.5} > 3_{+1.5} > 2_{-1.4} > 7_{-2.6} > 8_{-4.9} > 5_{-5.3}$
Males	Site $2_{+1.9} > 1_{+1.6} > 3_{+0.6} > 7_{-0.4} > 5_{-1.8} > 8_{-2.6}$

There were significant differences among sites in the three categories. Positive SR values indicate observed numbers greater than expected, negative values indicate observed numbers less than expected.

sites were found in the expected number of large animals (gravid females, $\chi^2 = 219$, $df = 5$, $p < 0.01$; all females, $\chi^2 = 170$, $df = 5$, $p < 0.01$; males, $\chi^2 = 20$, $df = 5$, $p < 0.01$). The standardized residuals (SR) (see Table 4), which correct for the different number of individuals collected from each site, indicate how the observed number of large individuals at each site vary from the expected number. Although only the ranking of the male SR correlates significantly with the sequence of sites in the pollution gradient (males; $n = 6$, $r = 0.886$, $p < 0.05$), the values of the SR (Table 4) clearly show that relative to sites 1, 2 and 3, there are significantly fewer large *Porcellio scaber* than expected at sites 5, 7 and 8.

4. Discussion

4.1. Survival under stress

The starvation experiment demonstrates that the survival potential of starved male woodlice declines significantly with increasing concentrations of Zn in those animals. This result concurs with Donker's (1992) finding that *Porcellio scaber* collected near a Zn smelter at Budel (The Netherlands) showed a significant negative correlation between survival time and concentration of Zn. Hopkin and Hames (1994) have shown that female *Porcellio scaber* die before reproductive age when fed litter containing concentrations of metals similar to those found in surface litter around the Avonmouth smelter. This fact, together with the absence of larger females of *P. scaber* from the heavily polluted sites (Fig. 4(a) and Table 2) suggest that females are also prone to mortality under prolonged stress. Donker et al. (1993a) concluded that life expectancy in both sexes of *P. scaber* was lower than normal in the Budel smelter population.

These results are indicative of a negative relationship between the energy reserves of individual woodlice and the concentration of metals in those individuals. Indeed, Donker (1992) found that *Porcellio scaber* from the Budel smelter had significantly smaller energy reserves when compared to animals with lower concentrations of metals from a population in an unpolluted site. Stress reduces fitness and causes a depletion of an animal's energy reserves (Sibly and Calow, 1989), just as metal detoxification in woodlice costs energy (Hopkin, 1990a). If all other stress factors are being applied equally, then total energy depletion in woodlice, caused by combatting all forms of stress, will be greatest in those individuals with the highest metal burden.

At Wytham Wood, southern England, drought drastically reduced the population density of the woodlouse *Trichoniscus pusillus*. However, when this stress was eventually alleviated by the resumption of normal rainfall patterns, the population density returned to pre-drought levels within 18 months (Sutton, 1968). The presence of high levels of metals in leaf litter close to the Avonmouth smelter does not fluctuate to any great extent relative to the length of the woodlouse life-cycle (Jones, unpublished data). Metal contamination represents permanent stress that will lower the fitness of woodlice and increase their chance of early mortality. Any additional stress in the Avonmouth area, such as extreme weather conditions causing prolonged starvation, would have the effect of eliminating those animals with the highest concentrations of metals.

4.2. Size of woodlice

Significant differences were observed in the mean and maximum size of *Porcellio scaber* among sites in the Avonmouth area. The largest mean and maximum size of both sexes occurs at the site least polluted with metals (site 1) whilst the populations with the smallest maximum size occur at the three most polluted sites (sites 5, 7 and 8) from the six considered. This is consistent with the findings of Donker (1992) and Donker et al. (1993a) that *P. scaber* of both sexes are smaller at the Budel smelter compared to an uncontaminated site.

If metals from the smelter were the only factor influencing woodlice size in the Avonmouth area then we would expect the smallest mean size to be recorded at site 8. One possible cause of the smallest mean size occurring at site 5 is the presence of other pollutants. Site 5 is only 0.5 km from a chemical plant manufacturing fertilizers (Fig. 1). Emission of pollutants from this factory could accentuate the deleterious effects of the metals. However, there are no published data on the release of toxins from this factory.

The reduction in the mean and maximum size across the six sites may be caused by two factors:

1. if the incidence of mortality increased with age above normal levels then an increasing proportion of animals would be lost from the larger size classes, thereby causing a reduction in the mean size of individuals. If the increase in mortality was severe enough all individuals in the top size classes would

eventually be eliminated thus lowering the maximum size of animals in the population;
2. a reduction in the rate of growth of individuals would lower the mean size of woodlice, and reduce their maximum size over a normal lifespan.

Why should the incidence of mortality increase with age in animals with high concentrations of metals? Woodlice avoid the toxic effects of metals by depositing assimilated metals as insoluble granules in the epithelium of the hepatopancreas. Most of the granules are not voided from the gut but are retained for the lifetime of the woodlouse, and if the hepatopancreas becomes saturated with metals the animal becomes moribund and dies (Hopkin, 1990a). As the animal grows at each moult the hepatopancreas increases in volume. In early life this increase is sufficient to accommodate assimilated metals but in later life the interval between moults lengthens (Sutton, 1980) causing the hepatopancreas to expand at a slower rate. Eventually, assimilated metals exceed the storage capacity of the hepatopancreas and surplus metals begin to interfere with biochemical processes in other tissues. The critical concentration of Zn in an individual of *Porcellio scaber* at which the detoxification capacity of the hepatopancreas is exceeded is about $2500\,\mu g\,g^{-1}$ (Hopkin, 1990b). Individuals at sites 7 and 8 have levels of Zn above this concentration and are therefore susceptible to early mortality (Hopkin and Hames, 1994). These animals may either die of Zn poisoning directly, or once moribund they are less able to protect themselves from predation or desiccation.

The starvation experiment indicates that woodlice with the highest concentrations of metals do suffer earlier mortality when stressed compared to animals from the less polluted sites. However, laboratory studies have shown that the growth rate of *P. scaber* can decline with increasing levels of Zn in the diet (Joosse et al., 1983; Van Capelleveen, 1985). Donker et al. (1993a) interpreted the smaller size of *P. scaber* at the Budel smelter as being caused by a reduction in growth rates. However, it is also known that early mortality in the Budel population causes the loss of larger *P. scaber* of both sexes (Donker, 1992; Donker et al., 1993a). We conclude that the observed reduction in both the mean and maximum size of woodlice at the sites closest to the Avonmouth smelter is caused by higher early mortality due to Zn poisoning but we speculate that this effect is compounded by a slowing down of the growth rate.

4.3. The cost of metal detoxification

The populations of *Porcellio scaber* found adjacent to the Avonmouth smelter (sites 7 and 8), and *P. scaber* at the Budel smelter, all show reductions in size and increased early mortality. This may be interpreted as being caused by reduced energy reserves resulting from the cost of detoxifying high levels of metals in the diet. Donker et al. (1993b) reported that the Budel population persists through increased reproductive effort, which is one possible strategy that may be adopted when trade-offs occur (Southwood, 1988; Sibly and Calow, 1989). However, woodlice from all sites in the Avonmouth pollution gradient show no significant differences in reproductive allocation (Jones and Hopkin, 1996).

Hopkin and Martin (1982) found that the size of the hepatopancreas (measured as the dry mass) of *Oniscus asellus* from different sites correlated most strongly with levels of Zn in the leaf litter. The authors suggested that animals from heavily polluted sites have a larger hepatopancreas, which in turn confers a greater detoxification capacity. Studies on *Porcellio scaber* from the Budel smelter indicate that these animals had a greater capacity for detoxifying Cd (Donker and Bogert, 1991) and Zn (Donker et al., 1996) relative to animals from other sites. This may help to explain why some Avonmouth woodlice can survive to produce broods at normal levels of reproductive allocation even though they have body burdens of Zn above the potentially lethal concentration (Jones and Hopkin, 1996).

Donker et al. (1993b) found that *Porcellio scaber* from the Budel smelter mature quicker but reproduce at a smaller size compared with woodlice from an unpolluted site. We have no data on the age at reproduction in the Avonmouth area but populations do show a significant decline in the mean size of females along the pollution gradient. In England, *Porcellio scaber* usually produce one brood in a lifetime (Sutton et al., 1984), although under favourable field conditions a female may reproduce again (S.L. Sutton, pers. comm.). Some of the largest gravid females at site 1 (see Fig. 4(a)) may be older individuals breeding for a second time. As a consequence of increased early mortality it is likely that all gravid woodlice at sites 5, 7 and 8 were first time breeders. The smaller size of woodlice at the most polluted sites, combined with the probable loss of a second brood caused by early mortality will give rise to smaller cohorts, compared with populations at less polluted sites. Woodlice attempting to colonize areas adjacent to the Avonmouth smelter will be exposed to levels of metals higher than those found at sites 7 and 8, which may cause death before breeding (Hopkin and Hames, 1994) and thus account for the absence of woodlice close to the smelter.

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