

# Towards a population ecology of stressed environments: the effects of zinc on the springtail *Folsomia candida*

HELEN L. NOËL,\* STEVE P. HOPKIN,\* THOMAS H. HUTCHINSON,†  
TIM D. WILLIAMS† and RICHARD M. SIBLY\*

\*School of Animal and Microbial Sciences, University of Reading, PO Box 228, Whiteknights, Reading RG6 6AJ, UK; and †AstraZeneca Global Safety, Health and Environment, Brixham Environmental Laboratory, Freshwater Quarry, Brixham, Devon TQ5 8BA, UK

## Summary

1. To understand population dynamics in stressed environments it is necessary to join together two classical lines of research. Population responses to environmental stress have been studied at low density in life table response experiments. These show how the population's growth rate (*pgr*) at low density varies in relation to levels of stress. Population responses to density, on the other hand, are based on examination of the relationship between *pgr* and population density.

2. The joint effects of stress and density on *pgr* can be pictured as a contour map in which *pgr* varies with stress and density in the same way that the height of land above sea level varies with latitude and longitude. Here a microcosm experiment is reported that compared the joint effects of zinc and population density on the *pgr* of the springtail *Folsomia candida* (Collembola).

3. Our experiments allowed the plotting of a complete map of the effects of density and a stressor on *pgr*. Particularly important was the position of the *pgr* = 0 contour, which suggested that carrying capacity varied little with zinc concentration until toxic levels were reached.

4. This prediction accords well with observations of population abundance in the field. The method also allowed us to demonstrate, simultaneously, hormesis, toxicity, an Allee effect and density dependence.

5. The mechanisms responsible for these phenomena are discussed. As zinc is an essential trace element the initial increase in *pgr* is probably a consequence of dietary zinc deficiency. The Allee effect may be attributed to productivity of the environment increasing with density at low density. Density dependence is a result of food limitation.

6. *Synthesis and applications.* We illustrate a novel solution based on mapping a population's growth rate in relation to stress and population density. Our method allows us to demonstrate, simultaneously, hormesis, toxicity, an Allee effect and density dependence in an important ecological indicator species. We hope that the approach followed here will prove to have general applicability enabling predictions of field abundance to be made from estimates of the joint effects of the stressors and density on population growth rate.

*Key-words:* Allee effect, Collembola, hormesis, toxicity

*Journal of Applied Ecology* (2006) **43**, 325–332

doi: 10.1111/j.1365-2664.2006.01133.x

## Introduction

Several lines of evidence suggest that the effects of stressors on populations cannot be calculated accurately if density dependence is ignored. Thus Walker *et al.* (2006), interpreting peregrine falcon population fluctuations

whose breeding success had been reduced by egg-shell thinning, and Grant (1998), in a theoretical analysis, both showed that substantial reductions in some vital rates may have little overall effect on populations if they are compensated for by reductions in the intensity of density dependence. Theoretical work by Grant & Benton (2000) has shown that elasticity analyses of population growth rate may be a poor guide to elasticities of population size when density dependence operates through just one class of individuals, for instance juveniles competing for food, and Grant & Benton (2003) used a discrete time model of *Tribolium* populations to demonstrate that density-independent analyses of the effects of stress can be a poor guide to population responses. Reviewing the relevant experimental work, Forbes, Sibly & Calow (2001) found examples of all possible types of interaction between stressors and density dependence: less-than-additive, additive and more-than-additive. They concluded that because the number of factors influencing the outcome is large, no general a priori predictions are feasible. Subsequent studies have shown less-than-additive effects (Barata, Baird & Soares 2002; Liess 2002; Moe, Stenseth & Smith 2002; Forbes, Sibly & Linke-Gamenick 2003; Hooper *et al.* 2003; Noël *et al.*, in press). Moe, in press) provides a recent review. There have also been studies of the joint effects of environmental stress and food or nutrient level. In a wide-ranging review of the effects of multiple stressors on aquatic organisms, for instance, Heugens *et al.* (2001) conclude that organisms are usually more susceptible to toxins when food or nutrient levels are decreased.

Thus it appears that responses at a population level cannot be predicted accurately if density dependence is ignored, because the effects of density may interact with or compensate for those of stress. Progress therefore depends on measuring population responses to stress and density simultaneously (Sibly & Hone 2002). Until now most studies have been of responses to either one or the other. In introducing the relevant literature, we deal first with stress responses, then population dynamics, and then the few studies that have considered both together.

Population responses to environmental stress have generally been assessed in terms of effects on population growth rate (*pgr*). Life table response experiments (LTRE) are used to measure the response of the species' age-specific vital rates to a variety of concentrations of environmental stressors, such as metals and environmental chemicals (reviewed in Caswell 2001). *pgr* is calculated for each life table and risk assessment is based on an analysis of the way that *pgr* declines as the concentration of the chemical increases. The approach is a development of the classic ideas of Birch (1953), in which he plotted the *pgr* of grain beetles in relation to the levels of temperature and humidity in the grain stores in which they lived. These LTRE have generally been carried out in conditions of high food availability or low population density. They leave open the questions of how populations behave at higher densities, and how stressors affect population dynamics and carrying capacity.

Population responses to density have been studied to gain an understanding of population dynamics. One approach has been to consider the population consequences of particular forms of relationship between *pgr* and population density. The earliest treatments supposed the relationship was a straight line, giving rise to logistic population growth (Verhulst 1838; Pearl & Reed 1920), but a recent analysis of more than 1780 time series of population counts has concluded that the relationship is negative and concave, viewed from above, in mammals, birds, fish and insects (Sibly *et al.* 2005).

The carrying capacity of a study environment is defined here as the value of population density at which population growth is zero, and, in the absence of complicating factors (Begon, Townsend & Harper 2006), this is the population density at which the population is expected to exist. Carrying capacities may, however, be lowered by lack of food or other resources, or by the presence of adverse factors (Sibly, Williams & Jones 2000). Knowledge of how carrying capacity is affected by stress is therefore crucial to understanding how populations are affected by stress in the field. Without it we can have little understanding of the determinants of species' ranges and patterns of ecological zonation. Despite the importance of information about the effects of stress on carrying capacity, however, there have been remarkably few experimental studies in this area. There is some theoretical understanding of how population dynamics are determined in the neighbourhood of carrying capacity. In particular, May *et al.* (1974) have shown that, after environmental perturbation, the slope of the relationship between *pgr* and log density determines the rate of return of the population to carrying capacity.

To study population dynamics in stressed environments it is clearly necessary to put together the above lines of research that have studied *pgr* either in relation to levels of stress or in relation to population density. The way forward is to combine them and study the joint effects of stressors and density. This was proposed in general terms by Royama (1992), but at that time no real examples of the form of the relationship were known. The relationship can be pictured as a contour map in which *pgr* varies with stress and density in the same way that the height of land above sea level varies with latitude and longitude. Recently some attempts have been made to map out the joint effects of stressors and density on *pgr*, and some evidence about the form of the relationship has been obtained for a marine copepod *Tisbe battagliai* (Sibly, Williams & Jones 2000), a tropical cladoceran *Moinodaphnia macleayi* (Barata, Baird & Soares 2002), a polychaete *Capitella capitata* (Forbes, Sibly & Linke-Gamenick 2003) and a midge *Chironomus riparius* (Hooper *et al.* 2003). A companion paper reports the responses of the spring-tail *Folsomia candida* (Collembola) to an antihelminthic drug, Ivermectin (Noël *et al.*, in press). Here we report the responses of *Folsomia candida* Willem 1902 to environments contaminated with zinc.

We chose to study the population responses of a springtail to zinc because there have been several field studies of springtail abundance in relation to concentrations of this metal (Strojan 1978; Bengtsson & Rundgren 1988; Russell & Alberti 1998; Gillet & Ponge 2003; Lock, Janssens & Janssen 2003; Fountain & Hopkin 2004a, b). Zinc is an essential element for all organisms, but at high concentrations it becomes toxic. High concentrations occur in terrestrial ecosystems in particular as a result of smelting and mining activity. Springtails are vulnerable to zinc because they live in leaf litter and soil. Although they are among the most widely distributed and abundant terrestrial arthropods, and their population densities frequently reach  $10^5 \text{ m}^{-2}$ , their population ecology has been little studied (Hopkin 1997). We chose *F. candida* as our study organism because it is an important ecological indicator species and has been widely studied in terms of life-history parameters (Fountain & Hopkin 2005).

A microcosm experiment is reported that mapped the joint effects of zinc and population density on the *pgr* of the springtail *F. candida*. This allowed the plotting of a complete map of the effects of density and a stressor on *pgr*. The map can be used to predict the effects of zinc concentration on population abundance. We show that the predictions explain the patterns of population abundance along gradients of zinc concentration reported in field studies. Such maps can predict the effects of stress not only on population abundance but also on population stability.

### Materials and methods

We used the 'Reading strain' of the parthenogenetic springtail *F. candida* (Hopkin 1997; Fountain & Hopkin 2001). *Folsomia candida* is a eudaphic springtail that lives permanently in the soil. It is relatively easy to culture in the laboratory, where the generation time at 20 °C is 2–3 weeks (Wiles & Krogh 1998). Our experiment involved establishing four replicate populations in food-limited microcosms at five initial densities and five concentrations of zinc, i.e.  $4 \times 5 \times 5 = 100$  microcosms in total. Each microcosm consisted of a 60-mL plastic container (6 cm high, 3.7 cm in diameter) with a plastic screw-top lid [Sterilin (Bibby), Scientific Laboratory Supplies Ltd (Barlonaold Scientific Beacon Road, Stone, Staffordshire, UK), catalogue number 125AP]. A culturing substrate mixture was made up in small quantities (80 g plaster of Paris, 10 g graphite powder and 70 mL distilled water) and poured into the containers to provide a layer 0.5 cm deep. The plaster of Paris was allowed to set, then remoistened. A glass coverslip (13 mm in diameter) was placed on the surface of the substrate of each microcosm.

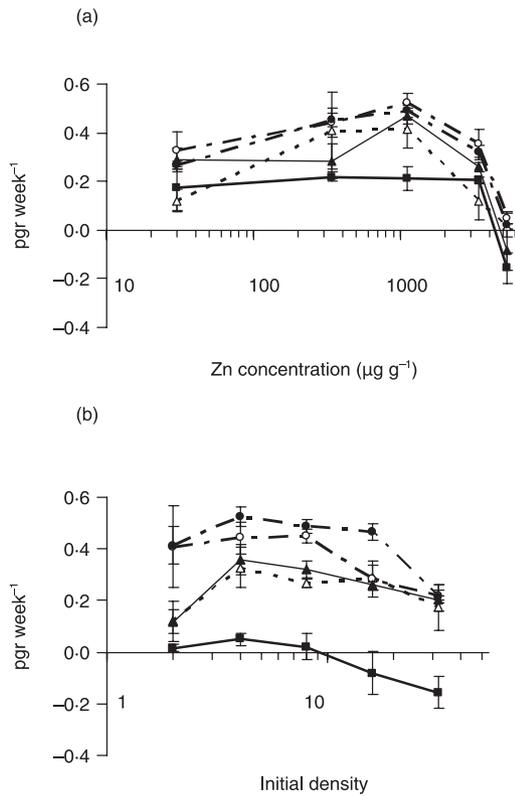
The food, placed on the coverslip, consisted of yeast prepared by making up stock solutions of 1 g of dried baker's yeast to 2 mL of double-distilled water (control) or 2 mL solution of the zinc nitrate (BDH (BDH Chemicals, Doole, Dorset, UK)) to give the five desired

concentration of zinc on a wet weight basis. Target concentrations of zinc ( $\mu\text{g Zn g}^{-1}$  wet weight) in the yeast suspension were control, 300, 1000, 3000 and 10 000. Actual concentrations determined by atomic absorption spectrometry were: 30 (control), 341 (300), 1109 (1000), 3407 (3000) and 5277 (10 000)  $\mu\text{g g}^{-1}$ .

To start the experiment, the required number (two, four, eight, 16 or 32 individuals) of juvenile *F. candida*,  $10 \pm 1$  days old, were taken from synchronized cultures (Wiles & Krogh 1998; International Organization for Standardization 1999) and added to each container. A food ration of  $5 \mu\text{L week}^{-1}$  was selected on the basis of a pilot experiment (Noel, 2004) that suggested that one springtail eats  $0.275 \mu\text{L}$  food every 7 days; thus populations of sizes two, four and eight were initially resource sufficient, 16 was at carrying capacity and 32 was resource limited. The food supply was replenished each week after any uneaten food had been discarded. The internal surfaces of the lids were sprayed with double-distilled water weekly to maintain high humidity in the test containers.

Populations were monitored for egg production by direct observation in week 1 using an Olympus MVZ 10×–40× microscope and a hand counter. Automated image analysis was employed in weeks 0 and 5–7 to estimate population size. Images were obtained using a colour video camera (JVC 3CCD (JVC Professional Europe Ltd., JVC House, JVC Business Park, London, UK), RGB (Red Green Blue); equipped with a 12.5–75 mm zoom lens and polarizing filter to reduce light reflections) connected to a frame grabber (Matrox Meteor, Matrox Video and Imaging Technology Europe Limited, Slough, Buckinghamshire, UK) with a cold fibre optic light source (Schott KL1500, Schott AG, Pia Bender, Otto-Schott-Str. 2, Mainz, Germany) to illuminate the specimens. The overall effect maximized the contrast between background substrate and animals. Images were processed and analysed using a customized programme developed by KS 300 Imaging System (Release 3.0; Carl Zeiss Vision GmbH, Haubergmoos, Germany). The software calculated the area of each individual within the outline of the live animal (not including antenna) seen from above. Only objects above a threshold of  $0.01 \text{ mm}^2$  were processed, to exclude small impurities and reflections from the background but still include small juveniles. Cover-slip and food was replenished and the lid sprayed with double-distilled water after this procedure.

The *pgr* for each population was measured per week as  $^{1/4} \log_e(A_t/A_1)$  for densities two–32, where  $A_t$  denotes the measured population area in week  $t$ . We expected that our experimental design would provide information about the form of density dependence in the neighbourhood of  $pgr = 0$ , on the basis of the pilot experiment described above. Unfortunately in the event no information was available for some zinc concentrations. However, in the later weeks of the experiment density increased, providing additional information, and this was used to estimate *pgr* for densities 64 and 128, in preparing



**Fig. 1.** The effects of stressor and density on *pgr* shown as line graphs in two forms. Bars indicate standard errors ( $n = 4$ ). (a) Mean *pgr* per week in *Folsomia candida* exposed to concentrations of zinc at different initial densities (symbols representing initial densities two ( $\Delta$ ), four ( $\circ$ ), eight ( $\bullet$ ), 16 ( $\blacktriangle$ ) and 32 ( $\blacksquare$ )). (b) Same data as in (a) but plotted against initial density, with symbols representing zinc concentrations 30  $\mu\text{g g}^{-1}$  ( $\Delta$ ), 341  $\mu\text{g g}^{-1}$  ( $\circ$ ), 1109  $\mu\text{g g}^{-1}$  ( $\bullet$ ), 3407  $\mu\text{g g}^{-1}$  ( $\blacktriangle$ ), 5277  $\mu\text{g g}^{-1}$  ( $\blacksquare$ )).

Fig. 2, by interpolation in plots of  $\log_e(A_{t+1}/A_t)$  against  $A_t$  for each zinc concentration.

Statistical analyses were performed using the general linear model (GLM) ANOVA routine in Minitab release 13.1, with Zn concentration and log initial density as factors (not covariates), followed where appropriate by Bonferroni simultaneous tests (BST). The contour plot in Fig. 2 was fitted by Minitab Contour command, which produces general purpose contour plots.

**Results**

The effects of stressor and density on *pgr* are shown as line graphs in two forms in Fig. 1. *pgr* was affected by log density and zinc concentration and there was no interaction ( $F_{4,75} = 9.50, P < 0.001, F_{4,75} = 42.08, P < 0.001, F_{16,75} = 1.10, \text{NS}$ , respectively). *pgr* increased with zinc concentration until concentration 1109  $\mu\text{g Zn g}^{-1}$  (Fig. 1a), after which there were substantial falls (BST comparing concentration 1109  $\mu\text{g Zn g}^{-1}$  with extremes,  $t = 4.91, P < 0.001, t = 11.94, P < 0.001$ , respectively). *pgr* increased with density between initial densities two and four, but then declined (Fig. 1b; BST comparing density four

with extremes,  $t = 3.29, P = 0.006, t = 5.54, P < 0.001$ , respectively).

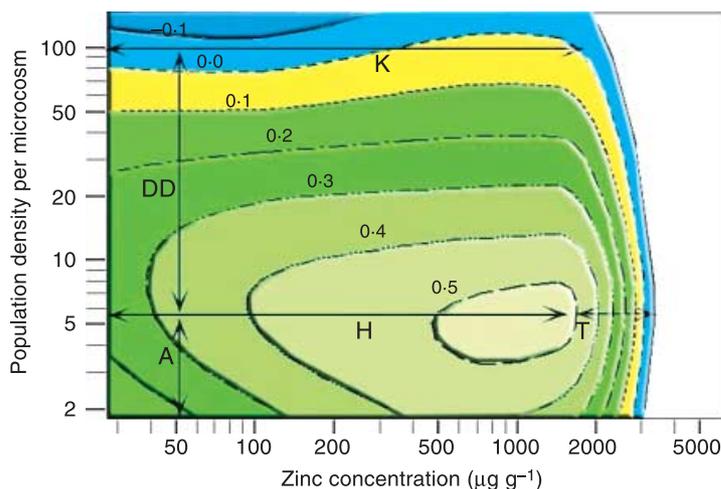
The joint effects of density and zinc on *F. candida* could be seen more clearly by plotting contours of *pgr*, as in Fig. 2, which shows all the key features of our results. A horizontal transect through Fig. 2 showed that *pgr* increased with zinc concentration at low zinc concentrations (H), but the reverse occurred at higher concentrations (T), and at 5277  $\mu\text{g Zn g}^{-1}$  the effects of zinc were toxic at all population densities. A vertical transect showed an Allee effect where *pgr* increased with density at low population density (A) but the reverse occurred at higher densities (DD). The *pgr* = 0 contour (K) was of particular significance because it indicated the stable equilibrium population size or carrying capacity, which varied little with zinc concentration until toxic levels were reached.

To help in the interpretation of these results some supporting information regarding fecundity and food supply is presented in Figs 3 and 4. Fecundity estimates were feasible in the first week, and these are presented in Fig. 3. Fecundity was affected by log density and zinc concentration and there was no interaction ( $F_{4,75} = 3.32, P = 0.02, F_{4,75} = 26.00, P < 0.001, F_{16,75} = 1.55, \text{NS}$ , respectively). Fecundity was markedly reduced at the two highest zinc concentrations (BST,  $t = 7.3, P < 0.001, t = 7.7, P < 0.001$ , respectively, using Zn concentration 1109  $\mu\text{g Zn g}^{-1}$  as reference). At the three lower zinc concentrations, fecundity was also affected by density and exhibited an Allee effect (an increase with density) at the lower densities and a decrease at higher densities (BST comparing densities two vs. eight and eight vs. 32,  $t = 3.09, P = 0.01, t = 2.88, P = 0.02$ , respectively).

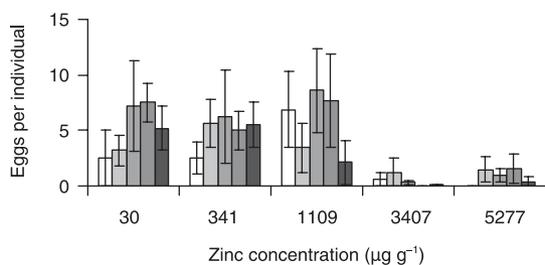
While it was not feasible to make precise measurements of food consumption, some assessment was possible by recording at the end of each week whether or not the previous week's food ration had been completely consumed. The relationships between food consumption, population density and zinc concentration are shown in Fig. 4. The weekly food ration was never completely consumed at the highest zinc concentration (5277  $\mu\text{g Zn g}^{-1}$ ). At lower concentrations of zinc, all the food was consumed in every week by the springtails with an initial density of 32 individuals but, as initial density declined, the number of weeks with food remaining increased (GLM using weeks food not completely consumed as the response variable, Zn concentration as a factor, and log density as a covariate,  $F_{1,72} = 410.8, P < 0.001$ ).

**Discussion**

Our main results are shown in Fig. 2. The position of the *pgr* = 0 contour (K in Fig. 2) is particularly important, and suggests that carrying capacity varies little with zinc concentration until toxic levels are reached. This prediction accords well with observations of abundance in the field. Effects of metal contamination on field abundance of Collembola have been examined at four



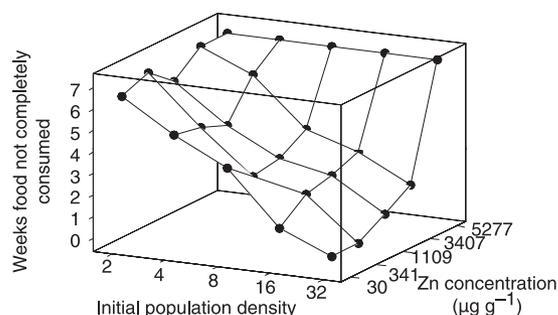
**Fig. 2.** Joint effects of initial population density and zinc concentration on  $pgr$  represented in a contour map in which height represents  $pgr$ . Numbers indicate the  $pgr$  of a given contour. Lightly shaded green areas show most rapid growth, blue areas represent population decline, and the yellow contour indicates carrying capacity, when  $pgr = 0$ . Arrow A refers to the Allee effect, DD to inverse density dependence, H to the hormesis effect, T to toxicity and K to responses at carrying capacity. The microcosm floor area was  $10.75 \text{ cm}^2$ . Contours were fitted using Minitab Release 13.1.



**Fig. 3.** Fecundity in *Folsomia candida* exposed to different concentrations of zinc at different initial densities. The intensity of shading of the bars indicates the initial densities in order from two (no shading) through four, eight, 16 to 32 (maximum shading). Intervals indicate standard errors ( $n = 4$ ).

European locations. In each case the metal contamination was derived from current or past industrial activity using zinc. The study sites were a former dumping area for metal-rich smelting waste at Wolverhampton, England,  $7907 \mu\text{g Zn g}^{-1}$  dry weight (wt) (Fountain & Hopkin 2004a; Fountain & Hopkin 2004b), a zinc smelter at Aubry, France,  $35\,000 \mu\text{g Zn g}^{-1}$  dry wt (Gillet & Ponge 2003), a zinc, cadmium and lead mining area near Heidelberg, Germany,  $3863 \mu\text{g Zn g}^{-1}$  dry wt (Russell & Alberti 1998), a lead-zinc mining area at Plombières, Belgium,  $5000 \mu\text{g Zn g}^{-1}$  dry wt (Lock, Janssens & Janssen 2003), and a brass mill at Gusum, Sweden,  $3000 \mu\text{g Zn g}^{-1}$  dry wt (Bengtsson & Rundgren 1988). In all cases it was concluded that there was no effect of zinc on springtail density over a substantial zinc gradient. Interestingly, in Pennsylvania, North America, at a site located in the vicinity of a zinc smelter works, Strojjan (1978) only found a significant decrease in the density of Collembola at the most contaminated site with a zinc concentration of  $26\,000 \mu\text{g Zn g}^{-1}$  dry wt in the topsoil.

The spacing of the  $pgr$  contours in the vicinity of the  $pgr = 0$  contour determines the form of population regula-



**Fig. 4.** Effects of zinc concentration and initial population density on food consumption for the 7 weeks of the experiment. Food consumption was assessed by recording each week whether or not the weekly food ration had been completely consumed, and the vertical axis shows the number of weeks some food was left over.

tion, specifying the way that  $pgr$  changes with density (for the theoretical background to this approach see May *et al.* 1974; Lande *et al.* 2002; Lande, Engen & Saether 2002). Narrow spacing in the density direction indicates that the population will bounce back quickly after perturbation; wide spacing implies to a slow response. The 'strength of density dependence' can be calculated as (May *et al.* 1974; Lande *et al.* 2002):

$$-\frac{\partial(pgr)}{\partial(\ln \text{density})} \Big|_{\text{carrying capacity}}$$

Interpolating from Fig. 2,  $pgr$  declines from 0.1 to -0.1 as density increases from about 60 to about 150. Thus  $\Delta pgr$  is -0.2, and  $\Delta \log_e$  density is about 0.92, so the strength of density dependence is about  $0.22 \text{ week}^{-1}$ . The reciprocal of the strength of density dependence indicates the time needed to recover equilibrium after a perturbation, here approximately 4.5 weeks. This is

longer than the generation time (about 3 weeks) and so the population 'undercompensates' for environmental perturbations (Begon, Townsend & Harper 2006). Additionally, it appears from Fig. 2 that there is little effect of zinc concentration on the spacing of the *pgr* contours until zinc concentrations become toxic. This suggests that the stability characteristics of populations will be similar along a gradient of zinc concentration. Such information is needed to evaluate the stability of populations in the field.

The vertical transect through Fig. 2 shows an Allee effect in *pgr* (A) followed by negative density dependence (DD). The effects of density on *pgr* are very similar to its effects on first-week fecundity, shown in Fig. 3. It is possible that the density effects on fecundity are entirely responsible for the A and DD effects on *pgr* shown in Fig. 2, but difficulties in ascertaining mortality and recruitment after the first week of the experiment make it difficult to prove this. Negative density dependence (DD) is likely to be a result of food limitation, as at higher densities populations exhausted their food supply earlier (Fig. 4), but it seems unlikely that the Allee effect is related to the food supply, as the food ration was never completely consumed at the lowest density (Fig. 4). However, there have been suggestions that the productivity of the environment may increase with density at low densities (Ferson & Burgman 1990; Stephens & Sutherland 1999). Food production could, for example, be improved by the presence of the faeces of conspecifics. In accordance with this proposal, Booth & Anderson (1979) demonstrate that increasing nitrogen availability increases rates of moulting and egg laying in *F. candida*. A frequently cited possible cause of Allee effects is difficulty in locating mates in low-density populations (Sinclair 1996; Courchamp, Clutton-Brock & Grenfell 1999), but this cannot apply to our populations of parthenogenetic *F. candida*. However, at low densities there could be benefits to delaying reproduction if reproductive success increases with density and if there is a reasonable probability of finding a denser population.

The horizontal transect (H → T in Fig. 2) shows an improvement in performance with chemical concentration at low concentrations, reversing at high concentrations. This is referred to as hormesis (Calabrese & Baldwin 2003). Because zinc is an essential trace element, the decrease in *pgr* as zinc concentration is reduced (H in Fig. 2) may simply be a result of dietary zinc deficiency. Reduced performance at the highest concentration was to be expected as food consumption was lower (Fig. 4), but at a zinc concentration of 3407 µg Zn g<sup>-1</sup> food consumption was not apparently reduced. The observed reduction in performance at this zinc concentration may be a result of interference by zinc with the processes of egg production and oviposition (Fig. 3). Hormesis effects have also been shown to occur in the springtails *Protaphorura armata* and *Orchesella cincta* during feeding experiments (Van Straalen, Schobben & de Goede 1989; Posthuma

& Van Straalen 1993). The toxic effects of zinc at high concentrations are seen in the field when, above a critical concentration, there is a dramatic decrease in springtail abundance (Strojan 1978). When assessing the environmental risks of essential metals such as zinc, both deficiency and toxicity should be evaluated (Lock, Desender & Janssen 2001).

The protection of populations is a legislative requirement of ecological risk assessment in both the USA and the European Union (EU), but is not implemented in practice for lack of suitable methodologies (European Commission 2000). Methods based on estimating risks to individuals are used instead, even though it is known that populations may not be reliably safeguarded by analysis of single individual endpoints (Forbes & Calow 1999; Kammenga, Van Gestel & Hornung 2001; Herbert *et al.* 2004). We hope that the approach followed here will provide a broad context for ecotoxicological work (Van Straalen 2003) and will prove to have general applicability enabling predictions of field abundance to be made from estimates of the joint effects of the stressors and density on population growth rate.

### Acknowledgements

We thank Monks Wood Centre for Ecology and Hydrology for analysis of the zinc samples, Steven Pountney for technical support, and Mark Pagel and Alan Berryman for comments on earlier versions of the manuscript. Helen Noël was supported by a BBSRC research studentship, with additional funding provided by AstraZeneca UK.

### References

- Barata, C., Baird, D.J. & Soares, A.M.V.M. (2002) Demographic responses of a tropical cladoceran to cadmium: effects of food supply and density. *Ecological Applications*, **12**, 552–564.
- Begon, M., Townsend, C.R. & Harper, J.L. (2006) *Ecology: From Individuals to Ecosystems*, 4th edn. Blackwell Publishing, Malden, MA.
- Bengtsson, G. & Rundgren, S. (1988) The Gusum case: a brass mill and the distribution of soil Collembola. *Canadian Journal of Zoology*, **66**, 1518–1526.
- Birch, L.C. (1953) Experimental background to the study of the distribution and abundance of insects. I. The influence of temperature, moisture and food on the innate capacity for increase of three grain beetles. *Ecology*, **34**, 698–711.
- Booth, R.G. & Anderson, J.M. (1979) The influence of fugal food quality on the growth and fecundity of *Folsomia candida* (Collembola: Isotomidae). *Oecologia*, **38**, 317–323.
- Calabrese, E.J. & Baldwin, L.A. (2003) Toxicology rethinks its central belief: hormesis demands a reappraisal of the way risks are assessed. *Nature*, **421**, 691–692.
- Caswell, H. (2001) *Matrix Population Models*, 2nd edn. Sinauer Associates, Sunderland, MA.
- Courchamp, F., Clutton-Brock, T. & Grenfell, B. (1999) Inverse density dependence and the Allee effect. *Trends in Ecology and Evolution*, **14**, 405–410.
- European Commission (2000) *Guidance Document on Terrestrial Ecotoxicology*. Directorate General for Agriculture. European Commission, Brussels, Belgium.
- Ferson, S. & Burgman, M.A. (1990) The dangers of being few: demographic risk analysis for rare species extinction.

- Proceedings of the 15th Natural Areas Conference. *New York State Museum Bulletin*, **471**, 129–132.
- Forbes, V.E. & Calow, P. (1999) Is the per capita rate of increase a good measure of population-level effects in ecotoxicology? *Environmental Toxicology and Chemistry*, **18**, 1544–1556.
- Forbes, V.E., Sibly, R.M. & Calow, P. (2001) Toxicant impacts on density-limited populations: a critical review of theory, practice and results. *Ecological Applications*, **11**, 1249–1257.
- Forbes, V.E., Sibly, R.M. & Linke-Gamenick, I. (2003) Joint effects of a toxicant and population density on population dynamics: an experimental study using *Capitella* sp. I (Polychaeta). *Ecological Applications*, **13**, 1094–1103.
- Fountain, M.T. & Hopkin, S.P. (2001) Continuous monitoring of *Folsomia candida* (Insecta: Collembola) in a metal exposure test. *Ecotoxicology and Environmental Safety*, **48**, 275–286.
- Fountain, M.T. & Hopkin, S.P. (2004a) Biodiversity of Collembola in urban soils and the use of *Folsomia candida* to assess soil 'quality'. *Ecotoxicology*, **13**, 555–572.
- Fountain, M.T. & Hopkin, S.P. (2004b) A comparative study of the effects of metal contamination on Collembola in the field and in the laboratory. *Ecotoxicology*, **13**, 573–587.
- Fountain, M.T. & Hopkin, S.P. (2005) *Folsomia candida* (Collembola): a 'standard' soil arthropod. *Annual Review of Entomology*, **50**, 201–222.
- Gillet, S. & Ponge, J.F. (2003) Changes in species assemblages and diets of Collembola along a gradient of metal pollution. *Applied Soil Ecology*, **22**, 127–138.
- Grant, A. (1998) Population consequences of chronic toxicity: incorporating density dependence into the analysis of life table response experiments. *Ecological Modelling*, **105**, 325–335.
- Grant, A. & Benton, T.G. (2000) Elasticity analysis for density-dependent populations in stochastic environments. *Ecology*, **81**, 680–693.
- Grant, A. & Benton, T.G. (2003) Density-dependent populations require density-dependent elasticity analysis: an illustration using the LPA model of *Tribolium*. *Journal of Animal Ecology*, **72**, 94–105.
- Herbert, I.N., Svendsen, C., Hankard, P.K. & Spurgeon, D.J. (2004) Comparison of instantaneous rate of population increase and critical-effect estimates in *Folsomia candida* exposed to four toxicants. *Ecotoxicology and Environmental Safety*, **57**, 175–183.
- Heugens, E.H.W., Hendriks, A.J., Dekker, T., Van Straalen, N.M. & Admiraal, W. (2001) A review of the effects of multiple stressors on aquatic organisms and analysis of uncertainty factors for use in risk assessment. *Critical Reviews in Toxicology*, **31**, 247–284.
- Hooper, H.L., Sibly, R.M., Maund, S.J. & Hutchinson, T.H. (2003) The joint effects of larval density and <sup>14</sup>C-cypermethrin on the life history and population growth rate of the midge *Chironomus riparius*. *Journal of Applied Ecology*, **40**, 1049–1059.
- Hopkin, S.P. (1997) *Biology of the Springtails (Insecta: Collembola)*. Oxford University Press, Oxford, UK.
- International Organisation for Standardisation (1999) *Reference number 11267: 1999 (E) Soil Quality—Inhibition of Reproduction of Collembola (Folsomia candida) by Soil Pollutants*. International Organisation for Standardisation, Geneva, Switzerland.
- Kammenga, J.E., Van Gestel, C.A.M. & Hornung, E. (2001) Switching life-history sensitivities to stress in soil invertebrates. *Ecological Applications*, **11**, 226–238.
- Lande, R., Engen, S. & Saether, B.E. (2002) Estimating density dependence in time-series of age-structured populations. *Philosophical Transactions of the Royal Society of London, Series B, Biological Sciences*, **357**, 1179–1184.
- Lande, R., Engen, S., Saether, B.E., Filli, F., Matthysen, E. & Weimerskirch, H. (2002) Estimating density dependence from population time series using demographic theory and life-history data. *American Naturalist*, **159**, 321–337.
- Liess, M. (2002) Population response to toxicants is altered by intraspecific interaction. *Environmental Toxicology and Chemistry*, **21**, 138–142.
- Lock, K., Desender, K. & Janssen, C.R. (2001) Effects of metal contamination on the activity and diversity of carabid beetles in an ancient Pb-Zn mining area at Plombières (Belgium). *Entomologia Experimentalis et Applicata*, **99**, 355–360.
- Lock, K., Janssens, F. & Janssen, C.R. (2003) Effects of metal contamination on the activity and diversity of springtails in an ancient Pb-Zn mining area at Plombières, Belgium. *European Journal of Soil Biology*, **39**, 25–29.
- May, R.M., Conway, G.R., Hassell, M.P. & Southwood, T.R.E. (1974) Time delays, density-dependence and single-species oscillations. *Journal of Animal Ecology*, **43**, 747–770.
- Moe, S.J. (in press) Density dependence in ecological risk assessment. *Population-Level Ecological Risk Assessment* (eds L.W. Barnhouse, W.R. Munns Jr & M.T. Sorensen). SETAC Press, Pensacola, FL.
- Moe, S.J., Stenseth, N.C. & Smith, R.H. (2002) Density-dependent compensation in blowfly populations gives indirectly positive effects of a toxicant. *Ecology*, **83**, 1597–1603.
- Noël, H.L. (2004) *Population growth rate and carrying capacity in the springtail Folsomia candida exposed to environmental chemicals*. Ph.D. thesis. Reading University, Reading.
- Noël, H.L., Hopkin, S.P., Hutchinson, T.H., Williams, T.D. & Sibly, R.M. (in press) Population growth rate and carrying capacity for the springtail *Folsomia candida* exposed to ivermectin. *Ecological Applications*, in press.
- Pearl, R. & Reed, L.J. (1920) On the rate of growth of the population of the United States since 1790 and its mathematical representation. *Proceedings of the National Academy of Sciences USA*, **6**, 275–228.
- Posthuma, L. & Van Straalen, N.M. (1993) Heavy-metal adaptation in terrestrial invertebrates: a review of occurrence, genetics, physiology and ecological consequences. *Comparative Biochemistry and Physiology*, **106C**, 11–38.
- Royama, T. (1992) *Analytical Population Dynamics*. Cambridge University Press, Cambridge, UK.
- Russell, D.J. & Alberti, G. (1998) Effects of long-term, geogenic heavy metal contamination on soil organic matter and microarthropod communities, in particular Collembola. *Applied Soil Ecology*, **9**, 483–488.
- Sibly, R.M. & Hone, J. (2002) Population growth rate and its determinants: an overview. *Philosophical Transactions: Biological Sciences*, **357**, 1149–1170.
- Sibly, R.M., Barker, D., Denham, M.C., Hone, J. & Pagel, M. (2005) On the regulation of populations of mammals, birds, fish and insects. *Science*, **309**, 607–610.
- Sibly, R.M., Williams, T.D. & Jones, M.B. (2000) How environmental stress affects density dependence and carrying capacity in a marine copepod. *Journal of Applied Ecology*, **37**, 388–397.
- Sinclair, A.R.E. (1996) Mammal populations: fluctuation, regulation, life history theory and their implications for conservation. *Frontiers of Population Ecology* (eds R.B. Floyd, A.W. Sheppard & P.J. Barro), pp. 127–154. CSIRO Publishing, Melbourne, Australia.
- Stephens, P.A. & Sutherland, W.J. (1999) Consequences of the Allee effect for behaviour, ecology and conservation. *Trends in Ecology and Evolution*, **14**, 401–405.
- Strojan, C.L. (1978) The impact of zinc smelter emissions on forest litter arthropods. *Oikos*, **31**, 41–46.
- Van Straalen, N.M. (2003) Ecotoxicology becomes stress ecology. *Environmental Science and Technology*, **37**, 324A–330A.
- Van Straalen, N.M., Schobben, J.H.M. & de Goede, R.G.M. (1989) Population consequences of cadmium toxicity in soil microarthropods. *Ecotoxicology and Environmental Safety*, **17**, 190–204.
- Verhulst, P.F. (1838) Notice sur la loi que la population suit dans son accroissement. *Correspondence Mathématique et Physique*, **10**, 113–121.

Walker, C.H., Hopkin, S.P., Sibly, R.M. & Peakall, D. (2006) *Principles of Ecotoxicology*, 3rd edn, in press. Taylor & Francis, London, UK.

Wiles, J.A. & Krogh, P.H. (1998) Tests with the collembolans *Isotoma viridis*, *Folsomia candida* and *Folsomia fimetaria*.

*Handbook of Soil Invertebrate Toxicity Tests* (eds H. Løkke & C.A.M. Van Gestel), pp. 131–156. John Wiley, Chichester, UK.

Received 7 June 2005; final copy received 4 November 2005

Editor: Rob Freckleton