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Effects of temperature increases on the feeding activity of two species of isopods (*Porcellio scaber, Porcellionides pruinosus*) in laboratory tests

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Abstract

As a consequence of global warming, especially an increase in temperature, basic ecological services provided by Central European soil organisms such as organic matter decomposition might be impacted. Therefore, we investigated whether the feeding activity of isopods, namely a native temperate species, *Porcellio scaber*, and a Mediterranean species, *Porcellionides pruinosus,* would be affected by an increase in temperature. In detail, the consumption of litter by isopods at 20 °C and 28 °C was studied. During tests running for two weeks, the woodlice were fed with leaves not only from temperate (*Acer plantanoides*) but also Mediterranean (*Acer opalus*) maple trees. While the higher temperature clearly affected *Porcellio scaber* (higher mortality but also higher consumption), no such effect was found for the Mediterranean species. The results presented here indicate that *Porcellionides pruinosus* is able to take over the role of *Porcellio scaber* in Central Europe in litter decomposition in the case of, i.e., distribution changes due to global warming, as it is adapted to higher temperatures and demonstrates a constant feeding rate independent of the food source provided.

Keywords: Isopoda, temperate, Mediterranean, maple leaves, decomposition, global warming.

1. Introduction

The issue of global warming dominates the public attention world-wide. It is still debated whether it is part of a natural process, having regularly reoccurred over the last millennia, or an abnormal, more rapid and unstoppable climate change caused by human activity. However, independent of the causes of global warming, reliable studies predict an increase in temperature of 4 °C by 2100 (Thuiller 2007). In such a scenario, mobile species could migrate to areas maintaining the ecological conditions they are adapted to, leading to a change in their geographical ranges (Pearson 2006, David 2009).

Crucially linked with any change in the diversity and dispersal of species due to global warming are the ecological services these species provide in the respective ecosystems, such as the decomposition of organic matter (an important part of nutrient cycling in terrestrial ecosystems) (De Groot et al. 2002). This is particularly important when regarding soil not only as the basis of human agriculture but also as habitat for hundreds of species per local site. These species have adapted to the very complex properties of the soil, e.g. its organic material (as a nutrient basis), texture (i.e. its composition of sand, silt and clay) and structure (providing habitat space) (Lavelle & Spain 2004). Climate change and in particular an increase in temperature will have a direct impact on the moisture of the soil. Despite some first attempts to predict the reaction of soil organisms to global climate change (Blankinship et al. 2011), not much is generally known on the behavioural and functional reactions of individual species to global warming. Thus, practical tests are essential for understanding the ecological consequences. Such experiments should be performed with soil organisms which are ecologically relevant and easy to handle (Dunger & Fiedler 1997, Jänsch et al. 2005), such as woodlice which react to climatic factors in general and are dependent on suitable soil moisture levels (Hornung et al. 1998, Drobne 2007). An increase in temperature over longer periods may trigger the immigration of Mediterranean species into Central Europe in exchange for those presently living in these areas (cf. David & Handa 2010). The question remains whether these new species will be able to continue providing the ecological services necessary for the maintenance of terrestrial ecosystems.

A main goal of the present study was thus to ascertain how an increase in temperature affects the feeding behaviour (and thus the ecological function) of terrestrial primary decomposers such as isopods. Terrestrial isopods (i.e. woodlice) are important drivers of the decomposition of organic matter in forest ecosystems (Swift et al. 1979, Hassall et al. 1987). They prefer moist and partially degraded food resources such as litter. Moreover, they are not completely protected against water loss, as they do not have an outer wax layer on their cuticula (Sutton & Holdich 1984). Most of the terrestrial isopods still breathe using modified gills and their distribution therefore depends on sufficient moisture (Warburg 1987). Thus, they are well suited for this investigation. Furthermore, experiments with these animals are rather rare compared to ones using, for example, earthworms (i.e. Eggleton et al. 2009, Uvarov et al. 2011).

A further important goal was whether the reactions of species from temperate latitudes, such as *Porcellio scaber*, differ from those of closely related Mediterranean species, such as *Porcellionides pruinosus*. Species from the Mediterranean region are adapted to food from Mediterranean plants (with differences in nutrient status and structural characteristics), higher temperatures and lower soil moisture levels, indicating that their feeding rate could be lower if they obtain their food resources from temperate plants and if they live at lower temperatures. For temperate species, in contrast, the opposite could be true. In other words, non-adaptation could lead to lower feeding rates and thus lower rates of decomposition of organic matter. In order to test the validity of this hypothesis, all combinations of the two species, two temperatures and two food resources were studied.

2. Materials and Methods

2.1. Test organisms

Since it is essential that the two test species be relatively easy to obtain as well as meet international recommendations for selecting organisms for ecological experiments (Römbke et al. 2006), two common woodlice species were chosen: *Porcellio scaber* (a temperate species) and *Porcellionides pruinosus* (a Mediterranean isopod). *Porcellio scaber* (Latreille 1804) occurs in temperate regions. This species changes its behaviour under increasingly dry habitat conditions: living normally hidden in the litter layer or in the upper mineral soil, they leave these darker habitats and become photopositive, which enables them to move to more suitable areas and thus avoid desiccation (Brown 1980). Nowadays, this species often lives close to human buildings, is one of the most common native isopod species of Central and Northern Europe and thus can be easily collected in high numbers. *P. pruinosus* (Brandt 1833) is widely dispersed throughout Mediterranean and tropical regions and thus can easily adapt to higher temperatures and altered moisture levels (Garcia 2004). Moreover, this isopod is also often associated with humans, often found near human habitats such as gardens.

2.2. Materials

Ecotoxicological laboratory tests are usually performed at 20 °C (e.g. OECD 1984). The second temperature used in the present study (28 °C) represents non-temperate conditions, but is also high enough that effects on the feeding rate can be detected (Garcia 2004). In this study a standard natural soil, LUFA St. 2.2, was used to ensure comparability of results, since this loamy sand is used in many ecotoxicological and ecological experiments (Løkke & Van Gestel 1998) and is considered to be a typical Central European agricultural soil. LUFA St. 2.2 is characterised as follows (data provided by LUFA Speyer, 67346 Speyer, Germany): texture: 84.5% sand, 7.4% silt, 8.1% clay; pH-value ($CaCl_2$): 6.1; organic matter: 4.64%; water-holding capacity (WHC_{max}): 50%.

Leaves of two *Acer* species were chosen as food sources, since maple leaves are relatively soft and palatable and therefore well suited as food resources for isopods (Szlavecz & Maiorana 1998). *Acer platanoides* ('Norway Maple') is widely distributed in Northern and Central Europe, representing one of the most common trees in German cities and mixed forests (Rothmaler 1976). *Acer opalus* ('Italian maple') is typically found in southern European mountains, particularly near the Mediterranean Sea (Roloff & Bärtels 2008). Information on the nutrient status (mainly N) or the defence mechanisms (e.g. phenol content) of both leaf species was not available.

2.3. Experimental setup

The Mediterranean woodlouse, *Porcellionides pruinosus,* was provided by Prof. P. Sousa (University of Coimbra, Portugal). The temperate woodlouse, *Porcellio scaber*, was sampled in a garden near Frankfurt/Main. Maple leaves were sampled in the Botanical Garden of Frankfurt/Main (*Acer opalus*) and in a park near Hochheim (*Acer platanoides*). Leaves of both species were air dried, as woodlice prefer this form as food resources. The tests were performed using Bellaplast vessels (11 cm x 15.5 cm, height 6 cm) and transparent covers with holes allowing air exchange. Ten adults of *P. scaber* and six adult *P. pruinosus* with an average fresh weight of 47.8 mg and 25.7 mg per individual isopod (i.e. all isopods per species were of approximetely the same size) were used per replicate (all individuals were in an intermolt stage). They were acclimatised for three days to the respective temperature before beginning the experiments. All combinations with litter from the two tree species and different temperatures were tested per isopod species (Tab. 1). Each of these four experiments per species lasted 14 days and was replicated three times.

The experiments were set up in two climate rooms differing only in temperature (20 °C versus 28 °C), which was regularly controlled with temperature sensors. At the beginning of the experiments, the LUFA 2.2 soil was moistened with 20 ml of deionised water per 140 g. The plastic vessels were then filled with 140 g of the prepared soil, giving a layer of approximately 2 cm and producing an even surface. The leaf material was cut out using an apple borer and the amounts used per test vessel weighed (approximately 10–15 mg per leaf).

After acclimatisation, the woodlice were placed in groups of ten (*P. scaber*) or six (*P. pruinosus*) into each of the replicated vessels, which were then closed using the prepared covers. During the experiments, isopod behaviour was observed and recorded every two days. After one week (day 7), the leaves were removed from the vessels, air dried and independently weighed. New leaves were put in the vessels and the soil was re-moistened. At the end of the study (day 14), the weights of the remaining leaf material as well as the woodlice was again recorded.

Tab. 1 Combinations of isopod species, temperature and food-resource species in the various treatments within the experiments (n = 3 for each combination).

	Species	Temperature	Food
1.	*Porcellio scaber*	20 ± 2ºC	*Acer opalus*
2.	*Porcellio scaber*	20 ± 2ºC	*Acer platanoides*
3.	*Porcellio scaber*	28 ± 2ºC	*Acer opalus*
4.	*Porcellio scaber*	28 ± 2ºC	*Acer platanoides*
5.	*Porcellionides pruinosus*	20 ± 2ºC	*Acer opalus*
6.	*Porcellionides pruinosus*	20 ± 2ºC	*Acer platanoides*
7.	*Porcellionides pruinosus*	28 ± 2ºC	*Acer opalus*
8.	*Porcellionides pruinosus*	28 ± 2ºC	*Acer platanoides*

2.4. Data analysis

The weights of the groups of adult woodlice per test replicate were measured at the beginning, midpoint and end of the experiments. The leaf litter remaining after 7 and 14 days was removed, again air dried and weighed per replicate. Consumed leaf litter was ascertained as the difference in weight between day (D-) 0 and D-7, as well as between D-7 and D-14. Consumption was determined at the end of week 1 (D-7) and week 2 (D-14) as the amount of leaf litter consumed per gram isopod mass remaining in the vessels at D-7 and D-14, respectively.

To test for significant differences in the consumption patterns, the data (mg consumed leaf material/g isopods) was submitted to an analysis of variance with experimental week, *Acer* and isopod species, temperature and/or mortality as main factors. Due to the non-normal distribution of the data, differences in these parameters were tested for significance using a non-parametric ANOVA for multiple observations (= samples) per cell (= dependant variable) (modified Friedman test; Zar 1999, Schöps & Russell 2004). This ANOVA is based on ranked per sample data, on the χ_r^2 rather than the F distribution and can easily handle unbalanced sampling designs. It reduces to a Mann-Whitney U-test when only factor pairs are tested and was always used here instead of a U-test (when appropriate) to ensure consistency throughout the statistical analyses. A post-hoc Tukey-like multiple comparison procedure for this non-parametric ANOVA (Zar 1999) tested for significant differences between single factors.

3. Results

3.1. Experimental conditions and observations

Temperatures remained constant in the climate rooms, except for one night in each week, where the temperature decreased overnight from 28 °C to 24 °C in the test with *Porcellio scaber*. The soil surface became dry during the first week in all vessels at 28 °C, wherefore the soil was then moistened in all vessels with 10 ml deionised water. *P. scaber* was seen more often on the soil surface at the higher temperature, while *P. pruinosus* mostly remained on the soil surface independent of temperature. The latter species tended to hide when the soil surface became very dry. Both species were rarely seen feeding when the vessels were controlled, but leaf material was regularly observed to have been fed upon, especially in the vessels with *P. scaber* (Fig. 1).

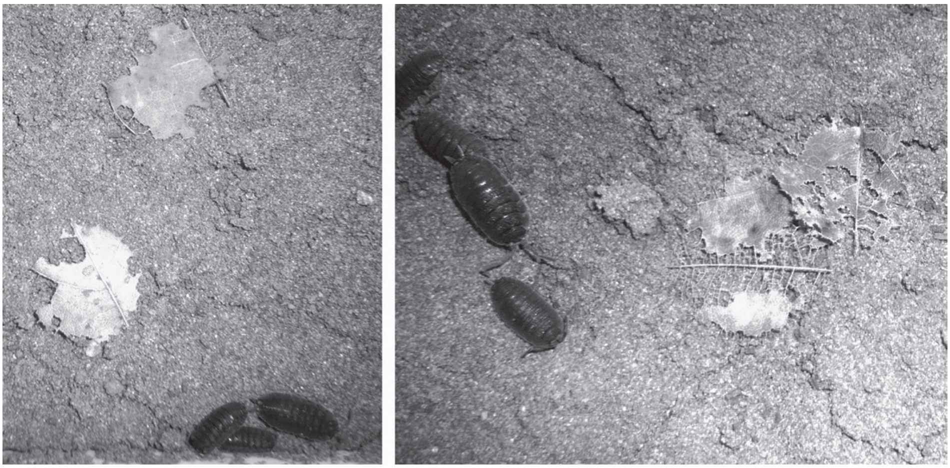

Fig. 1 Typical appearance of leaf material in the test with *Porcellio scaber* showing fed-upon litter of *Acer plantanoides* (left) or *Acer opalus* (right) after one week.

3.2. Mortality

Despite the relatively short duration of the experiments, mortality occurred in the test isopods, with 42 of the initial (at D_0) 192 individuals dying during the two weeks. Overall mortality during the experiments was higher in *P. scaber* (28.3%, average per treatment: 16.4% ± 21.4%) than in *P. pruinosus* (11.1%, average per treatment: 5.6% ± 11.7%; difference between species: $X_r^2 = 9.333$, P = 0.002; Tab. 2). No significant difference in mortality was observed between the two weeks of the experiment or between the leaves of the different tree species for either isopod species. Mortality of *P. scaber* was higher by a factor of 2.5 at 28 °C (23.4% ± 24.0%) than at 20 °C (9.4% ± 16.6%; $X_r^2 = 5.056$, P = 0.025), whereby no difference in mortality between the two temperatures was observed with *P. pruinosus*.

3.3. Consumption

Consumption of the leaf material was twice as high in the second week than in the first week of the experiment (average consumption $week_1$: 5.0 mg/g isopods, $week_2$: 10.0 mg/g isopods; $X_r^2 = 22.881$, $P < 0.001$; Fig. 2). This was true for both isopod species, but the increase was stronger in *P. pruinosus* (week$_1$: 5.3 mg/g isopods, week$_2$: 12.5 mg/g isopods; $X_r^2 = 13.762$, $P < 0.001$) than in *P. scaber* (week$_1$: 4.7 mg/g isopods, week$_2$: 7.5 mg/g isopods; $X_r^2 = 9.333$, $P = 0.002$). The increase in consumption in the second week of the experiment was similar with both leaf species (*A. opalus*: week$_1$: 6.0 mg/g isopods, week$_2$: 10.0 mg/g isopods; $X_r^2 = 13.762$, $P < 0.001$; *A. platanoides*: week$_1$: 4.0 mg/g isopods, week$_2$: 10.0 mg/g isopods; $X_r^2 = 9.330$, $P = 0.002$).

Tab. 2 Average mortality rates observed during the experiments for the two isopod species, the two temperatures and the two tested leaf species ± values represent standard deviations.

	Porcellio scaber			
	Acer opalus		*Acer platanoides*	
	20 °C	28 °C	20 °C	28 °C
Week 1	0 ± 0%	10.0 ± 15.3%	10.0 ± 10%	20.0 ± 9.9%
Week 2	0 ± 0%	27.8 ± 16.9%	27.8 ± 25.5%	28.6 ± 49.5%
	Porcellionides pruinosus			
	Acer opalus		*Acer platanoides*	
	20 °C	28 °C	20 °C	28 °C
Week 1	0 ± 0%	0 ± 0%	11.1 ± 9.6%	0 ± 0%
Week 2	16.7 ± 28.9%	5.6 ± 9.6%	0 ± 0%	11.1 ± 9.6%

Overall, consumption of the *A. opalus* leaf material (on average 8.0 mg/g isopods) was slightly higher than that of *A. platanoides* (on average 7.0 mg/g isopods), but this difference was only significant when all test variants were pooled ($X_r^2 = 5.357$, $P = 0.021$; Fig. 2). The differences in consumption of the two leaf species were not significant, however, when the individual isopod species were analyzed separately (*P. pruinosus*: $X_r^2 = 3.048$, $P = 0.081$; *P. scaber*: $X_r^2 = 2.333$, $P = 0.127$). Divergent consumption of the two *Acer* species could be determined in the experiments at 20 °C (on average: *A. opalus*: 7.1 mg/g isopods, *A. platanoides*: 5.5 mg/g isopods; $X_r^2 = 6.857$, $P = 0.009$), but not at 28 °C (*A. opalus*: 8.9 mg/g isopods, *A. platanoides*: 8.5 mg/g isopods; $X_r^2 = 0.429$, $P = 0.513$).

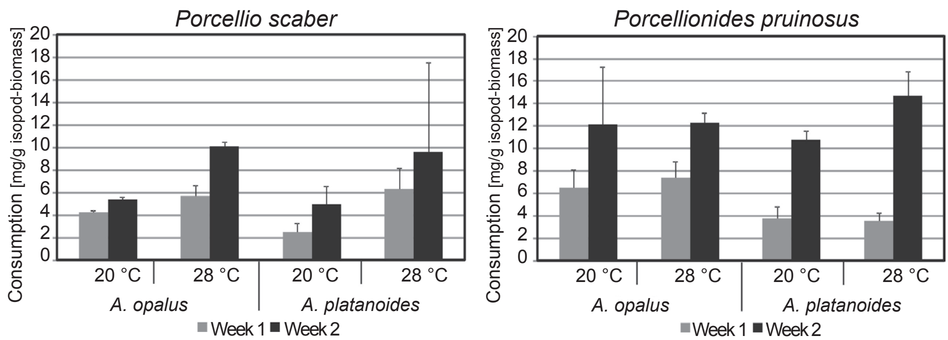

Fig. 2 Calculated feeding rates (consumption per 7 days) of the temperate isopod species, *Porcellio scaber* (left), and the Mediterranean species, *Porcellionides pruinosus* (right). N = 3 for each combination of factors. For statistical results, see text.

P. pruinosus generally consumed more leaf material (on average 8.9 mg/g isopods) than *P. scaber* (6.1 mg/g isopods; $X_r^2 = 10.500$, $P = 0.001$). However, these differences were only significant at 20 °C (*P. pruinosus*: 8.3 mg/g isopods, *P. scaber*: 4.3 mg/g isopods; $X_r^2 = 13.762$, $P < 0.001$). At 28 °C, *P. pruinosus* also consumed more leaf material (average of all experimental variants: 8.7 mg/g isopods) than *P. scaber* (5.9 mg/g isopods), but these differences were statistically not significant ($X_r^2 = 0.762$, $P = 0.383$).

Major differences in leaf consumption were found between the different temperatures. Throughout the entire experiment, more leaf material was consumed at 28 °C than at 20 °C (28 °C: 8.7 mg/g isopods, 20 °C: 6.3 mg/g isopods; $X_r^2 = 11.524$, $P < 0.001$; Fig. 2). These differences were equally significant for leaves of both tested tree species, but were in absolute values weaker in the Mediterranean species (*A. opalus*: 28 °C: 8.9 mg/g isopods, 20 °C: 7.1 mg/g isopods; $X_r^2 = 5.762$, $P = 0.016$; *A. platanoides*: 28 °C: 8.5 mg/g isopods, 20 °C: 5.5 mg/g isopods; $X_r^2 = 5.762$, $P = 0.016$). The consumption differences between temperatures were almost 100% for *P. scaber* (28 °C: 8.0 mg/g isopods, 20 °C: 4.3 mg/g isopods; $X_r^2 = 12.190$, $P < 0.001$). However, *P. pruinosus* fed only slightly more at 28 °C than at 20 °C and the differences were statistically not significant (28 °C: 9.5 mg/g isopods, 20 °C: 8.3 mg/g isopods; $X_r^2 = 1.714$, $P = 0.190$).

4. Discussion

4.1. Test methodology

In the tests, almost no methodological problems occurred. However, in some test vessels a few juveniles were observed, having hatched during the test. Since only very small juvenile individuals occurred, it is highly unlikely that they influenced either the adult body weights or the total feeding rate.

The level of moisture of the soil decreased expeditiously in the course of the experiment, especially at the higher temperature, although this could not be measured exactly in the present experimental setup. It is very likely that the high mortality rate of *P. scaber* was also an indirect result of the temperature increase. In parallel, the significantly lower mortality rate of *P. pruinosus* can be explained by its adaptation to Mediterranean conditions. Moisture- and temperature-related behavioural and life-history differences are suggested to play a pivotal role in survival of different isopod species in light of changing climate parameters (Hassell et al. 2010). It is thus recommended to investigate indirect effects of temperature increases further, e.g. by measuring soil moisture exactly throughout the study.

4.2. Climate factors and isopod feeding rates

The consumption of both isopod species increased significantly in the second week of the experiment, independent of the food source and the temperature. This result indicates that the isopods needed some time to adjust to the experimental conditions, despite the fact that these did not considerably differ from the conditions during acclimatisation. In general, leaves of the Mediterranean tree species were preferred compared to the temperate species, especially at 20 °C but not at 28 °C. The opposite result was found when testing the consumption of mixed Atlantic (= temperate) and Mediterranean litter types by a millipede (David & Gillon 2009). In this case, however, the two leaf-mixture types differed in their nutritional quality (i.e. different nitrogen contents). Since the present study is the first testing feeding behaviours of temperate isopod species, further literature comparisons are unfortunately not possible.

The results of this experiment show that the food consumption of the two species differs at the two temperatures. While *P. pruinosus* always fed more than *P. scaber*, the absolute amount of leaves consumed by this Mediterranean species was almost similar at both temperatures. In contrast, the temperate species *P. scaber* increased its consumption at 28 °C by almost 100%. This higher consumption could be attributed to the higher need of energy, i.e., caused by moisture stress. As mentioned above, at the same time the mortality of this species increased significantly at this temperature. Therefore, this species is not well adapted to Mediterranean conditions, characterized by higher temperatures and altered soil moisture levels. However, it is difficult to evaluate the functional consequences of this behaviour based on the results of this study alone, which raise important questions. For instance, will the decomposition of organic matter increase due to higher consumption by this species or will it decrease due to the higher mortality rate? Further long-term (preferably life-cycle, cf. David & Gillon 2009, Kight 2009, Hassell et al. 2010) studies are needed in order to answer this question as well as whether *P. scaber* will be able to adapt to higher temperatures and altered moisture levels in a 'reasonable' time period.

P. pruinosus reacted oppositely: the increase in consumption between the two temperatures was only slight, but due to its adaptation to Mediterranean conditions only few individuals died at the higher temperature (in fact no more than at the lower temperature). This behaviour can be attributed to the specific adaptations of this species, which has a very wide geographical (from the Mediterranean to the tropics) and habitat (including gardens) range. Thus, *P. pruinosus* apparently can live and thrive under temperate conditions (at least for the two weeks of the experiment). Despite the fact that both isopod species are classified as synanthropic, the range of environmental tolerance conditions regarding higher temperatures and altered soil moisture levels seems to be broader in the case of *P. pruinosus.* This is in direct contrast to results of Borchert et al. (2010), who suggested that temperate isopod species have broader tolerances and thus are more capable of withstanding expected temperature increases. Again, long-term studies with more than the two parameters tested have to be performed in order to decide whether these assumptions concerning the potential future role of *P. pruinosus* at Central European sites are correct or not. In this context, the plasticity of both species regarding their ecological requirements has to be taken into account, since both are widely distributed, meaning that regional populations probably differ in their adaptation to temperature and soil moisture levels.

While it is known that at least *P. scaber* does have food preferences and, thus, can distinguish between leaves from different tree species (e.g. Nair et al. 1994), the importance of the food source is not yet clear when assessing the results of this experiment. When assuming that the increase in temperature causes a change in plant distribution patterns, the diffusion of Mediterranean trees in Central Europe may not affect or even increase the feeding rate of isopods. Nevertheless, as we show this only with one example (maple), this conclusion is difficult to generalise and surely needs further studies (e.g. with structurally and biochemically different leaves from species such as *Quercus ilex*, which dominates wide areas in the Western Mediterranean).

The results presented here indicate that *P. pruinosus* is able to take over the role of *P. scaber* in Central Europe qualitatively in the case of global warming, as it is adapted to higher temperatures and demonstrates a constant feeding rate even at lower temperatures, independently from the food source provided. The experiments need to be repeated in order to address the factors limiting the generality of the results and therefore to clarify the conclusions (especially the influence of soil moisture and of different food types). In addition, the locomotory behaviour of the isopods under the different temperature and feeding regimes could be used as a further endpoint (e. g. Bayley & Baatrup 1996, Engenheiro et al. 2005, Hassell et al. 2010), since the behaviour (including the circadial rhythm) of the two species can be influenced by temperature. As an increase in temperature apparently has an impact on the feeding activity of native European isopods, this topic is worth being studied further in order to extent the knowledge about the possible ecological consequences of global warming in Central Europe.

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