

Responses of the parthenogenetic isopod, *Trichoniscus pusillus* (Isopoda: Oniscidea), to changes in food quality

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Summary

Long-term observations of *Trichoniscus pusillus* revealed that chemical composition and microbial activity of the leaf litter serving as food influenced the reproductive success of females and the mortality rates of juveniles as well. Of the food sources investigated, only alder litter, exhibiting high microbial activity, allowed the maintenance of a stable population with frequently reproducing females. This study concludes that the food type is a significant factor for population parameters of this parthenogenetic isopod. Our results on *T. pusillus*, belonging to the taxon Synocheta, are compared with data on terrestrial isopod species of the taxon Crinocheta.

Key words: Woodlice, terrestrial isopods, reproduction, growth, population dynamics, food quality

Introduction

From a soil-ecological point of view, the most important terrestrial isopods (Isopoda: Oniscidea Latreille, 1829) belong to the Euoniscoidea Legrand 1943, which break down further into the Crinocheta Legrand 1943, and the Synocheta Legrand 1946. The taxon Synocheta includes small soil-dwelling species that strongly depend on sufficient humidity due to high cuticular evaporation rates and their size (cf. Heeley

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1941; Edney 1954; Sutton 1980). *Trichoniscus pusillus* (Brandt) 1833 (Synocheta: Trichoniscidae) is one of the most abundant isopod species in western Europe (e.g. Sutton 1980). The females of this triploid species reproduce parthenogenetically (Vandel 1960), and males are very rare (Frankel et al. 1981). During the reproductive season, ranging from May to September (Meinertz 1950; Tomescu 1973), 1–3 breeding waves have been observed (Heeley 1941; Standen 1973; Tomescu 1973). After a gravidity of about 4–5 weeks, between 4 and 18 mancae are released from the brood pouch (Heeley 1941; Standen 1973; Tomescu 1973). The low number of relatively large offspring can be expected due to the endogeic habitat (cf. Schmalfuss 1977; Sutton et al. 1984).

In contrast to our well-developed knowledge on the phenology in *T. pusillus*, we know little about nutritional factors that influence population dynamics in this species and other synochete isopods. In the “more terrestrial” group of crinochete isopods, nutritional conditions have been demonstrated to be significant with respect to population parameters (Merriam 1971; Rushton & Hassall 1983). Different food sources exhibit different effects on growth, mortality and reproduction in *Armadillidium vulgare* (Crinocheta: Armadillidiidae) (Rushton & Hassall 1983). In multivariate analyses, factors determining individual fitness could be split into physical and chemical characteristics of the leaf litter, the pH level of the leaf litter, and its microbial colonization (Zimmer & Topp 1997; Zimmer 1998). In these studies, population dynamics strongly depend on the chemical composition of the leaf litter in *Oniscus asellus* (Crinocheta: Oniscidae), but mainly on the density and activity of litter-colonizing microbiota in *Porcellio scaber* (Crinocheta: Porcellionidae). The present study revealed information on the influence of “food quality” on population dynamics in the synochete isopod, *Trichoniscus pusillus*, that can be compared to our corresponding knowledge on Crinocheta.

Materials and Methods

Females of *T. pusillus* were collected in October 1994 in a mixed deciduous forest near Cologne, Germany. In the laboratory, individuals were kept in small Petri dishes, the bottoms of which were covered with plaster of Paris to maintain sufficient humidity. Additionally, moistened filter papers were placed in the lids of the dishes (cf. Zimmer & Topp 1997). *T. pusillus* was never observed feeding on the plaster or the filter paper. Prior to our studies, the entire populations were fed a mixture of leaf litter originating from the forest where the isopods had been collected.

When the experiment started in spring 1995, the food source was changed to microbially inoculated leaf litter of exclusively either alder (*Alnus glutinosa*), birch (*Betula pendula*) or oak (*Quercus robur*) that had previously been soaked in sulphurous acid of pH 2 and pH 5, respectively, to simulate leaching as described by Zimmer & Topp (1997). Experimental pH manipulation is known to cause changes in physico-chemical characteristics of the leaf litter, that in turn result in food sources with different levels of microbial colonization and activity after microbial inoculation (Zimmer & Topp 1997; Zimmer 1998). Thus, we obtained two different pH varieties (“-20” and “-50”) of three different litter species (“al-”, “be-”, “qu-”), i.e. six different “food qualities” that are characterized through their respective pH value, microbiological activity, chemical characteristics, and physical parameters in Table 1. During our studies, food was replaced monthly with fresh leaf litter prepared in the manner described above. Faeces were not removed from the Petri dishes to allow for coprophagy (cf. Hassall & Rushton 1985).

Table 1. Microbiological and physico-chemical characteristics of different food sources. – Data are given as median \pm median absolute deviation of monthly measurements (1995–1997: n = 180)

		Alnus glutinosa		Betula pendula		Quercus robur	
		al 20	al 50	be 20	be 50	qu20	qu50
pH level		3.5 \pm 0.3	5.9 \pm 0.3	3.3 \pm 0.2	5.5 \pm 0.3	3.1 \pm 0.4	5.6 \pm 0.3
total microbial counts,	10 ¹⁰ cells g ⁻¹	4.7 \pm 0.3	3.5 \pm 0.2	1.9 \pm 0.5	2.3 \pm 0.1	1.9 \pm 0.2	4.4 \pm 0.9
cellulase activity,	μ g Glc (g h) ⁻¹	220 \pm 90	700 \pm 95	300 \pm 92	230 \pm 99	240 \pm 91	340 \pm 81
respiratory activity,	μ g CO ₂ (g h) ⁻¹	89 \pm 11	127 \pm 13	49 \pm 12	50 \pm 8	88 \pm 10	44 \pm 6
water content,	%	27 \pm 4	30 \pm 4	40 \pm 1	40 \pm 4	37 \pm 7	37 \pm 5
physical strength,	g mm ⁻²	13 \pm 2	12 \pm 2	19 \pm 4	22 \pm 3	58 \pm 5	41 \pm 9
phenolics,	mg g ⁻¹	27 \pm 1	16 \pm 1	30 \pm 1	11 \pm 1	36 \pm 1	15 \pm 1
hydrolyzable tannins,	mg g ⁻¹	48 \pm 5	34 \pm 3	8 \pm 2	2 \pm 1	29 \pm 2	14 \pm 1
condensed tannins,	mg g ⁻¹	13 \pm 1	10 \pm 1	16 \pm 1	13 \pm 1	10 \pm 2	8 \pm 1
C:N ratio		15 \pm 1	16 \pm 1	27 \pm 2	29 \pm 2	30 \pm 1	28 \pm 2
cellulose content,	mg g ⁻¹	444 \pm 17	421 \pm 7	468 \pm 5	468 \pm 8	507 \pm 13	507 \pm 9
lignin content,	mg g ⁻¹	178 \pm 11	189 \pm 7	151 \pm 13	156 \pm 9	284 \pm 11	298 \pm 12

Each food variety was fed to 32 individually-maintained females. Our study was performed at 15 °C and 16h L : 8h D. During winter (November-February), these values were reduced successively to 5 °C and 8h L : 16h D. Once a week we checked the populations for dead individuals and counted mancae. From these data, we calculated reproductive success (mancae per female) for each female as well as longevity of individuals (concerning the offspring of initially studied females, i.e. “juveniles”) and percent survival of juveniles at a given age (Kaplan-Meyer).

Since most of our data were not normally distributed, multiple comparison of samples was performed with Kruskal-Wallis H tests. Subsequently, significant differences were localized by using Mann-Whitney U tests. Prior to ANOVA, data were transformed to normality and approximate homoscedasticity (cf. Levy 1980). In case of ANCOVA, we made sure that the dependent variable and the control variable correlated significantly (cf. Bortz 1993). According to Overall and Woodward (1977), we did not test for independence of the test variable and the control variable.

Results

In the laboratory, the populations of *T. pusillus* developed in markedly different ways with respect to food quality. Both reproductive success (number of offspring per reproducing female: Fig. 1) and mortality of juveniles (percent survival: Fig. 2) varied between different “food qualities”.

Taking into account the entire data set, mean reproductive success (Fig. 1) varied largely between 4 and 6 mancae per female. However, reproductive success was significantly ($\alpha = 0.05$) higher in populations feeding on “al20” and on “be50” than when feeding on the other food sources that did not differ from each other ($p > 0.4$).

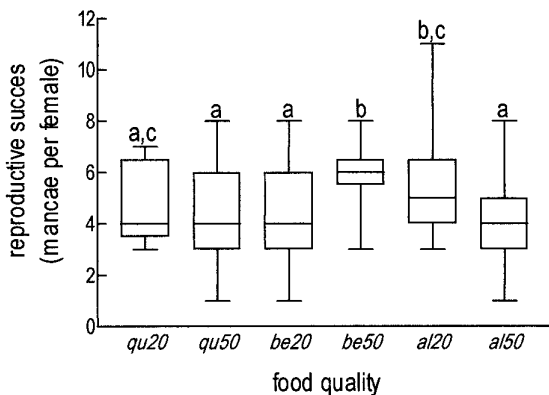


Fig. 1. Reproductive success of reproducing females of *T. pusillus* in 1995, when feeding on different food sources. – “qu-”: leaf litter of *Quercus robur*; “be-”: leaf litter of *Betula pendula*; “al-”: leaf litter of *Alnus glutinosa*; “-20”: leaf litter acidified at pH 2.0; “-50”: leaf litter acidified at pH 5.0. Data are given as range, quartiles and median of 8–32 females. Letters indicate significant differences in reproductive success (U test: $\alpha = 0.05$)

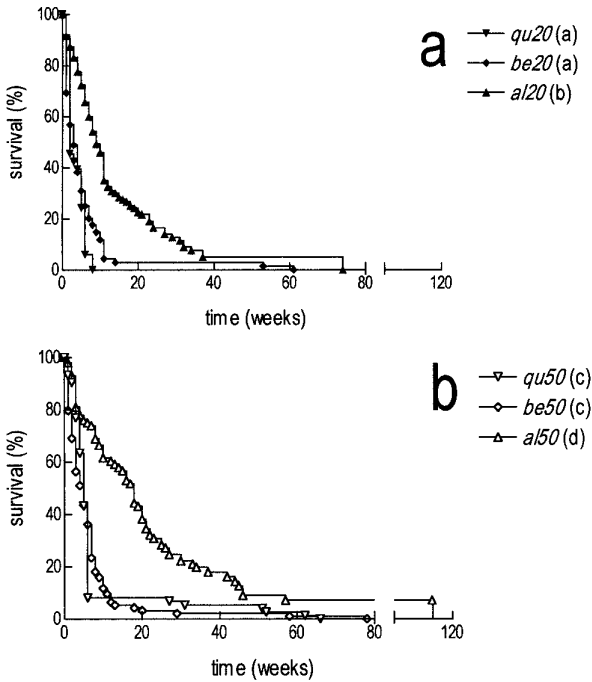


Fig. 2. Survival of juveniles of *T. pusillus* feeding on different food sources. – “qu-”: leaf litter of *Quercus robur*; “be-”: leaf litter of *Betula pendula*; “al-”: leaf litter of *Alnus glutinosa*; “-20”: leaf litter acidified at pH 2.0 (a); “-50”: leaf litter acidified at pH 5.0 (b). Letters in brackets indicate significant differences in survival (Kaplan-Meier: $\alpha = 0.05$).

The former food sources (“al20” and “be50” in Fig. 1) led to similar values of reproductive success ($p > 0.3$).

Females feeding on oak or birch litter reproduced, but only in the first year of our study (Tab. 4). Reproduction in successive years was only observed in animals feeding on alder litter. However, the percent of reproducing females was markedly lower in the second year than in the first year of our study, while the third year was characterized by an increase in the number of reproducing females that were descendants of initially studied females.

Comparing the survival of juveniles (Fig. 2) feeding on the same litter types with different pH values (Fig. 2a vs. 2b) as well as survival of juveniles feeding on different leaf litter types at similar pH levels (Fig. 2a, 2b), demonstrated a strong influence of the food source. Overall, the lowest survival rates were obtained with oak litter (“qu-”) as the food source, although its pH 5-manipulated variety (Fig. 2b) did not differ from that of birch litter (“be-”). Mortality of juveniles was higher on pH 2-manipulated leaf litter (“-20” in Fig. 2a), but this was not true for birch litter. Longevity of individuals ranged from 1–8 weeks (feeding on “qu20”) to up to 113 weeks (feeding on “al50”).

Table 2. Two-factorial ANOVA to estimate the effects of physico-chemical characteristics („leaf litter“) and microbial colonization (“microbiota”) of leaf litter (cf. Table 1) on longevity (a) and reproductive success (b) in *T. pusillus*. – ns: not significant; *: $p < 0.05$; **: $p < 0.01$; ***: $p < 0.001$

a	<i>df</i>	<i>F</i>	<i>p</i>
explained	5	14.27	***
“leaf litter”	2	31.67	***
“microbiota”	1	11.37	***
<i>interaction</i>	2	1.69	ns
b	<i>df</i>	<i>F</i>	<i>p</i>
explained	5	2.48	*
“leaf litter”	2	1.09	ns
“microbiota”	1	0.58	ns
<i>interaction</i>	2	4.48	*

Table 3. ANCOVA to estimate the effects of particular physico-chemical characteristics of leaf litter (cf. Table 1) on longevity in *T. pusillus*, when litter-colonizing microbiota served as covariates. – ns: not significant; *: $p < 0.05$; **: $p < 0.01$; ***: $p < 0.001$

	<i>df</i>	<i>F</i>	<i>p</i>
model	6	68.4	***
covariates	1	386.3	***
condensed tannins	3	4.9	**
hydrolyzable tannins	2	4.8	*
“toughness”	1	1.5	ns
“softness”	1	1.4	ns

Table 4. Percent of reproducing females of *T. pusillus* in successive years (1995–1997), when feeding on different food sources. – “*qu*–”: leaf litter of *Quercus robur*; “*be*–”: leaf litter of *Betula pendula*; “*al*–”: leaf litter of *Alnus glutinosa*; “–20”: leaf litter acidified at pH 2.0; “–50”: leaf litter acidified at pH 5.0

	1995	1996	1997
<i>qu 20</i>	33	–	–
<i>qu 50</i>	63	–	–
<i>be 20</i>	67	–	–
<i>be 50</i>	63	–	–
<i>al 20</i>	54	25	50
<i>a 50</i>	54	11	100

In order to compare the simultaneous effects of different leaf litter types (i.e. species-specific physico-chemical characteristics) and litter-colonizing microbiota (as influenced by pH manipulation) on maintenance and development of laboratory populations of *T. pusillus*, we calculated analyses of variance (Two-way ANOVA). In analyses on reproductive success, the differences between the tested varieties increased after including the reproductive success of further generations of reproducing females. Based on the “reproductive value” of a single female of given age (Fisher 1930), a modified “net rate of reproduction” (cf. Wilson & Bossert 1971) may represent a single female’s contribution to maintenance and growth of the entire population. However, we chose the conservative analysis of calculating reproductive success on an individual basis rather than including successive generations. Furthermore, we took into account only those values which were a result of the first year of our study. Years two and three did not result in successful reproduction in isopods feeding on birch and oak litter.

The population parameters reproductive success and individual longevity served as dependents of the species-specific characteristics (“litter”) and the microbial colonization (“microbiota”) of the litter. Both “litter” ($p < 0.001$) and “microbiota” ($p < 0.01$) significantly explained the variance of longevity (Table 2a). By contrast, neither “litter” nor “microbiota” influenced the reproductive success directly (Table 2b). However, a combination of these food characteristics affected the number of offspring, as indicated by a significant statistical interaction ($p < 0.05$). Hence, the influence of litter-colonizing microbiota was altered with changing leaf litter type, i.e. the species-specific physico-chemical characteristics.

In case of individual longevity as dependent on “leaf litter” (Table 2a), we performed an analysis of covariance (ANCOVA) to elucidate the effect of particular physical and chemical characteristics of the leaf litter. Due to correlative relations between physico-chemical parameters, we reduced these leaf litter characteristics (as given in Table 1) to a few main factors; 1) condensed tannins, 2) hydrolyzable tannins, 3) “toughness” (= physical strength + cellulose content + lignin content + phenol content), and 4) „softness“ (= water content – C:N ratio). When litter-colonizing microbiota served as covariates in ANCOVA (Table 3), our analysis demonstrated a significant influence of phenolic compounds (condensed and hydrolyzable tannins) of the leaf litter on longevity in *T. pusillus* ($p < 0.05$). By contrast, the linear combinations of “toughness” and “softness” did not influence longevity in this analysis. Comparing our results on longevity (Fig. 2) with the species-specific differences in phenolic compounds of the leaf litter (Table 1), it is obvious that condensed tannins negatively influenced longevity, while relatively high contents of hydrolyzable tannins positively influenced longevity.

Discussion

Factors controlling population dynamics are well-known for some isopod species. Climatic factors are most commonly attributed to control over isopod populations (McQueen & Carnio 1974; McQueen 1976a, b; Miller & Cameron 1987). In Crinocheta, the influence of the food source on population parameters has been emphasized (Merriam 1971; Rushton & Hassall 1983; Zimmer & Topp 1997; Zimmer 1998). The present study indicates the significance of the food source with respect to the popula-

tion parameters longevity and reproductive success in the synochete *T. pusillus*. Thus, we can consider the characteristics of the leaf litter described herein to determine the “food quality” for this isopod.

With respect to longevity, both species-specific physico-chemical characteristics of the leaf litter ($p < 0.001$) and microbial colonization of the leaf litter ($p < 0.01$) affected *T. pusillus* (ANOVA: Table 2a). Similar observations have been made concerning the mortality of juvenile *O. asellus* (Zimmer 1998). Juvenile growth rates depended on the chemical composition of the litter, i.e. the content of condensed tannins, in *O. asellus*, and were influenced by both species-specific physico-chemical characteristics (toughness and content of hydrolyzable and condensed tannins) and microbial colonization of the litter in *P. scaber* (Zimmer 1998).

These results indicate that, in contrast to adult isopods, juveniles of the studied species respond essentially similarly to differences in certain parameters of “food quality”. This interspecific coincidence may be due to similar nutritional requirements. Since food preferences correspond with morphological features of the mouth parts in terrestrial isopods (cf. Hassall 1977), the negative effect of tough leaf litter in *P. scaber* may be due to size and strength of the juveniles’ mouth parts (cf. Zimmer 1998). By contrast, *T. pusillus* did not depend statistically on the factors “toughness” or “softness” of the leaf litter in our studies (ANCOVA: Table 3). Probably, isopods of this small species mainly graze on litter-colonizing microbiota rather than feeding on leaf tissue (M. Zimmer, unpubl. SEM observations). These microbiota, in turn, may depend on the chemical compounds that cause tough or soft tissue. Microorganisms serve as an important food source in *P. scaber* (Zimmer & Topp 1998a) and in other species as well (Coughtrey et al. 1980; Gunnarsson & Tunlid 1980; Ullrich et al. 1991).

Several compounds of leaf litter, particularly condensed tannins that are found in high concentrations in birch litter (cf. Table 1), have been described as affecting nutrition (Savoie & Gourbière 1989), mortality (Zimmer & Topp 1997) and growth rates (M. Zimmer unpubl.) in terrestrial isopods. In the present study, condensed tannins negatively influenced *T. pusillus*, while hydrolyzable tannins increased longevity (ANCOVA: Table 3). The latter observation coincides with potential positive effects of tannin hydrolysis in *P. scaber* due to an enhancement of the number of endosymbiotic microorganisms (Zimmer 1999).

Since aspects of “food quality” influence growth rates in terrestrial isopods (Merriam 1971; Rushton & Hassall 1983; Zimmer 1998), and their reproductive success depends on the size of females (Standen 1973; Sutton et al. 1984), “food quality” can be expected to have an effect on reproductive success. In a phenological study on *T. pusillus*, Tomescu (1973) observed changes in reproductive success of females during their ontogeny. The author described a single brood consisting of 4–6 embryos in one-year-old and relatively small females. Females reproduced twice (6–7 embryos each) in their second year, and relatively large three-year-old females had up to three broods of 8 to 9 embryos.

All of the females reproducing in the third year of our studies (when feeding on alder litter: “al-” in Table 4) were descendants of the initially observed females. Due to their age (1–2 years) and their small size, these females released fewer mancae from their brood pouch than their mothers did before. Thus, the overall reproductive success in alder-fed populations was comparably low (cf. Fig. 1).

As indicated by ANOVA, species-specific physico-chemical characteristics of the

litter and litter-colonizing microbiota affected the reproductive success of *T. pusillus* in terms of a statistical interaction (Table 2b). Hence, the influence of litter-colonizing microbiota was altered with changing leaf litter type. In representatives of the Crinocheta, *Oniscus asellus* and *Porcellio scaber*, the experimental pH manipulation and microbial colonization of the litter, respectively, influenced the reproductive success, while species-specific physico-chemical characteristics of the leaf litter proved to be insignificant (Zimmer 1998).

Based on the present data, we conclude that *T. pusillus*, as well as other species of terrestrial isopods (*A. vulgare*: Merriam 1971; Rushton & Hassall 1983; *O. asellus*: Zimmer 1998; *P. scaber*: Zimmer & Topp 1997; Zimmer 1998), is affected by the quality of the available food source. Adults and juveniles of *T. pusillus* behave similarly to juveniles of *O. asellus* in their response to both microbial colonization and species-specific physico-chemical characteristics of the leaf litter (Zimmer 1998), while juveniles of *P. scaber* mainly depend on litter-colonizing microbiota (Zimmer & Topp 1997). The influence of litter-colonizing microbiota on *P. scaber* is probably due to microbiota being an important food source (Zimmer & Topp 1998a), while the insignificance of species-specific physico-chemical characteristics of the leaf litter may correspond to the existence of endogenously produced enzymes that degrade lignocellulose (Zimmer & Topp 1998a, b). Although microbiota are digested by *O. asellus* as well (Coughtrey et al. 1980; Gunnarsson & Tunlid 1986; Ullrich et al. 1991), and endogenous cellulases have been proposed in this species (Hartenstein 1964), nothing is known about these parameters in *T. pusillus*. Thus, no general differences between Crinocheta (represented by *P. scaber* and *O. asellus*: Zimmer & Topp 1997; Zimmer 1998) and Synocheta (represented by *T. pusillus*, this study) can be deduced from the present results.

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