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Postembryonic ontogenetic development in *Porcellio scaber* (Isopoda: Oniscidea): the significance of food

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Summary

Postembryonic ontogenetic development in *Porcellio scaber* was observed on an individual basis over 90 weeks. Under optimal nutritive conditions, the duration of development to maturity showed high inter-individual variability and ranged from 60 to 90 weeks. Both growth rates and mortality of juvenile woodlice depended on the available food source, the alder litter being of highest, the oak litter of lowest, and the birch litter of intermediate quality. The experimentally manipulated pH level of the litter that, in turn, affected some leaf litter traits and the density and activity of litter-colonizing microbiota was of minor significance. Previous results and the present study suggest that food sources of low nutritive value affect isopod populations by (1) increasing the mortality and (2) reducing the reproductive success of adult females, and by (3) increasing mortality and reducing growth rates of juveniles, and therefore by (4) delayed maturity.

Key words: Developmental stage, food quality, growth rate, isopods, longevity, maturation, microbial activity, microbial biomass, mortality

Introduction

In terrestrial isopods (Isopoda: Oniscidea), representing important members of the saprophagous soil fauna, studies on the post-embryonic ontogenetic development have mainly focused on the morphological characteristics of different juvenile stages (e.g., Heeley, 1941; Radu and Tomescu, 1971; Tomescu, 1972, 1973; Tomescu and Craciun, 1987). A few authors observed that growth rates depend on photoperiod (Beyer, 1965) or on individual tactics (Sutton, 1970; Sunderland et al., 1976; Willows, 1987a, 1987b; Grundy and Sutton, 1989; Zimmer and Kautz, 1997). Since terrestrial isopods (as well as other saprophagous soil animals) mainly feed on food sources that are considered to be low quality, it is obvious that growth rates further depend on the available food source (Kheirallah and Awadallah, 1981; Kheirallah and El-Sharkawy, 1981; Zimmer and Topp, 2000). In turn, growth rates determine both maturation and fecundity (Merriam, 1971; Standen, 1973; Sutton et al., 1984; Hassall and Dangerfield, 1990; Dangerfield and Hassall, 1992), and thus, both growth rates and mortality directly influence isopod population dynamics, being important from an ecological point of view with respect to decomposition processes. Studies on the significance of different food sources for isopod populations in the laboratory revealed an influence of nutritive conditions on juvenile mortality, but did not determine the responsible food parameters (Zimmer and Topp, 1997a).

Isopod populations are strongly affected by acidification of soil and leaf litter (Ullrich et al., 1991; Zimmer and Topp, 1997a), although individuals may buffer acidic pH levels of ingested food inside their gut lumen (Zimmer and Topp, 1997b). Reduction of microbial biomass or activity of leaf litter through acidification (e.g., Bewley and Stotzky, 1983) accounts only in part for the observed effects (Zimmer and Topp, 1997a, 2000). Thus, the reasons why isopods are negatively affected by acidified leaf litter remain open to debate. The present study focuses on the influence of different pH-manipulated food sources on mortality, development and growth rates of juvenile *Porcellio scaber* to elucidate (1) the effects of the nutritive value of the food as determined by the physico-chemical and microbial characteristics of the leaf litter on juvenile development and maturation, and (2) the developmental responses of juvenile isopods to acidification of leaf litter.

Materials and Methods

Isopods (*Porcellio scaber* Latr. 1804) were collected in the vicinity of Cologne, Germany, during early spring. In the laboratory they were maintained in translucent plastic boxes, the bottoms of which were covered with moistened plaster of Paris to provide high humidity. A mixture of different leaf litter species freshly collected in the field served as food and shelter. After 4 weeks of gradual acclimatization to experimental conditions (15°C, 16h L:8h D), individual gravid females were separated in small Petri dishes with bottoms of plaster. Since it is known that nutritional conditions during gravidity influence the females' fecundity (Zimmer and Topp, 1997a), they were kept under quantitatively and qualitatively optimal nutritive conditions [artificial diet: Zimmer (1999), modified after Carefoot (1984)].

Mancae, the first juvenile stages, were kept separately under different food regimes immediately after their release from the brood pouch. The mancae of one female were assorted randomly to different food sources, allowing for direct comparison of the influences of genetic vs. environmental conditions.

Climatic conditions in the incubator were chosen so as to mimic seasonal changes in daily mean temperature and day length. Day length was gradually changed from 8 h during December to 16 h in July and back to 8 h in December. Accordingly, temperature increased stepwise from 5°C in December to 15°C in July, and decreased to 5°C in December again.

Food sources that differed in terms of chemistry, pH level and microbial activity were obtained from leaf litter of different deciduous tree species, namely alder (*Alnus glutinosa*), birch (*Betula pendula*), and oak (*Quercus robur*), which had been collected immediately after litter fall. For storage in the laboratory, leaf litter was air-dried. Soaking the air-dried leaf litter in sulphurous acid of pH 2 and 5, respectively, for 7 days changed litter chemistry and pH (Zimmer and Topp, 1997a, 2000; Kautz et al., 2000). Both litter pH and chemistry (henceforth referred to as "litter manipulation") affected subsequent microbial colonization of different litter types in a pool of freshly collected litter (cf. Zimmer and Topp, 1997a), resulting in a total of six different experimental food sources (Table 1). A nutrient-rich cellulose-based artificial diet (Zimmer, 1999, modified after Carefoot, 1984) served as high-quality food, and the development of juvenile isopods that fed on this food source was considered optimal in the present study.

Numeric data of both leaf litter characteristics (Table 1) and juvenile development of isopods did not show normal distribution. Consequently, data are presented as median (M) ± median absolute deviation (MAD), and predominantly non-parametric statistics were used for treatment comparison. Multiple comparison was performed with Kruskal-Wallis H-tests. Subsequently, significant differences were localized by using Mann-Whitney U tests. The same approach was chosen to analyze the effects of experimental factors on the developmental stage of overwintering juveniles. In analyses of covariance (ANCOVA), genetic (affiliation to a "family"; gender) and environmental (litter type, pH-manipulation) conditions served as factors, and the hatching date (day of the year) served as covariate, both affecting the longevity of juveniles, the duration of particular developmental stages, and the age at maturity. Prior to these parametric statistics, data were transformed to normality and approximate homoscedasticity (cf. Levy, 1980). Mortality rates were analyzed in terms of survival fractions at any given time, according to the Kaplan-Meier method. Subsequent pair-wise comparison of treatments with respect to the individual's risk of mortality was performed according to the Mantel-Haenszel test.

Results

Litter manipulation

Litter characteristics that differed between litter types were mainly those that determine litter toughness, including the C:N ratio (cf. Zimmer and Topp, 1997a), but also microbial density and activity. Experimental

Table 1. Microbial, physical and chemical characteristics of pH-manipulated leaf litter that served as experimental food sources for *Porcellio scaber*. Different superscript letters indicate significant differences ($\alpha = 0.05$; N = 9)

	Alnus glutinosa		*Betula pendula*		*Quercus robur*	
pH level	3.5 ± 0.3^{a}	5.9 ± 0.3^{b}	3.3 ± 0.2^{a}	5.5 ± 0.3^{b}	3.1 ± 0.4^{a}	5.6 ± 0.3^{b}
Total microbial counts, 10^{10} cells g^{-1}	4.7 ± 0.3^{a}	3.5 ± 0.2^{b}	1.9 ± 0.5^{c}	1.2 ± 0.1^{c}	1.9 ± 0.2^{c}	$4.4 \pm 0.9^{a,b}$
Cellulase activity, µg GLc $(g\ h)^{-1}$	220 ± 90^{a}	700 ± 95^{b}	330 ± 92^{b}	$230 \pm 99^{a,b}$	$240 \pm 91^{a,b}$	340 ± 81^{b}
Respiratory activity, µg CO_2 $(g\ h)^{-1}$	89 ± 11^{a}	127 ± 13^{b}	49 ± 12^{c}	50 ± 8^{c}	88 ± 10^{a}	44 ± 6^{c}
Water content, %	27 ± 4^{a}	30 ± 4^{a}	40 ± 1^{b}	40 ± 4^{b}	37 ± 7^{b}	37 ± 5^{b}
Physical toughness, g mm^{-2}	13 ± 2^{a}	12 ± 2^{a}	$19 \pm 4^{a,b}$	22 ± 3^{b}	58 ± 5^{c}	41 ± 9^{d}
Phenolics, mg g^{-1}	27 ± 1^{a}	16 ± 1^{b}	30 ± 1^{a}	11 ± 1^{c}	36 ± 1^{d}	15 ± 1^{b}
Hydrolyzable tannins, mg g^{-1}	48 ± 5^{a}	34 ± 3^{b}	8 ± 2^{c}	2 ± 1^{d}	29 ± 2^{b}	14 ± 1^{e}
Condensed tannins, mg g^{-1}	13 ± 1^{a}	10 ± 1^{b}	16 ± 1^{c}	13 ± 1^{a}	10 ± 2^{b}	8 ± 2^{b}
C:N ratio	15 ± 1^{a}	16 ± 1^{a}	27 ± 2^{b}	$29 \pm 2^{b,c}$	30 ± 1^{c}	28 ± 2^{b}
Cellulose content, mg g^{-1}	$444 \pm 17^{a,b}$	421 ± 7^{b}	468 ± 5^{a}	8^{a}	507 ± 13^{c}	507 ± 9^{c}
Lignin content, mg g^{-1}	$178 \pm 11^{a,b}$	189 ± 7^{a}	151 ± 13^{c}	$9^{b,c}$	284 ± 11^{d}	298 ± 12^{d}

pH-manipulation clearly influenced the pH level of the litter types that served as food sources for juvenile isopods (Table 1). Furthermore, both microbial density and activity were affected by pH manipulation in alder and oak litter, but not so in birch litter. However, the contents of phenolic litter compounds were also significantly changed by the experimental pH. Thus, from effects of pH manipulation, the effects of particular litter characteristics cannot be deduced.

Ontogenetic development

During development, juveniles of *P. scaber* undergo two manca (sensu Holdich et al., 1984) stages (MI: 1 day; MII) and 12 juvenile stages (J1–J12). Mancae differ markedly from juveniles with respect to morphology in that the seventh segment of the pereion and the corresponding pereiopods are not yet (MI) or only weakly (MII) developed (cf. Tomescu and Craciun, 1987). The size (head width) of mancae [MI: (0.48 ± 0.01) mm; MII: (0.58 ± 0.02) mm] did not differ between treatments ($P > 0.7$; Kruskal-Wallis test). Later juvenile stages showed stage-wise growth with a mean increase of 0.09 ± 0.03 mm per stage, resulting in a head width of 1.56 ± 0.02 mm in J12.

Even under optimal nutritive conditions (high-quality artificial diet), juvenile mortality was high, only 7% of one year's offspring reaching maturity (Fig. 1). Under this food regime, development to maturity took 60–90 weeks (cf. Fig. 1). During winter, food uptake was low in every experimental treatment, as indicated by empty hindguts (that can easily be detected in juveniles). Similarly, little molting, and thus little growth, occurred during winter (cf. Fig. 1).

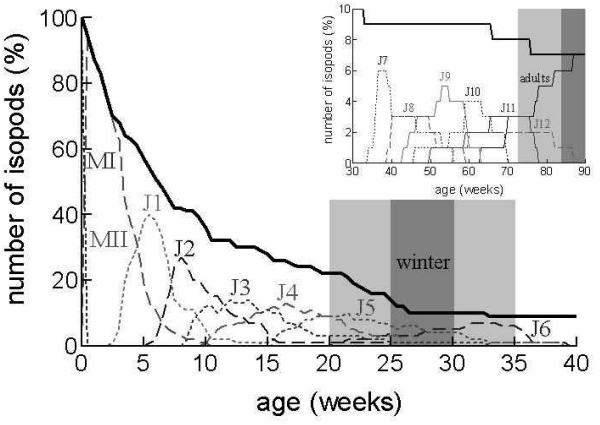

Fig. 1. Temporal pattern of developmental stages and decreasing number of juveniles during development of *P. scaber* in the laboratory, when provided optimal food conditions.

At stage J6 (head width: 1.01 ± 0.02 mm), males can be distinguished from females by the appearance of external sexual characters (gonopods) — few males can be recognized at stage J5. The later juvenile stages (J7–J12) are considered pre-adult, since despite showing male external sexual characters, these individuals are not yet mature (as estimated from field data on the size of gravid females). After maturity, up to 10 adult stages (A1–A10) can be distinguished by size, given a longevity of roughly 3 years (in the laboratory; cf. Sutton et al., 1984). Adult size (head width) increased by 0.1 ± 0.04 mm per stage, with 1.58 ± 0.05 mm in the smallest adults (A1) and a maximum of 2.44 ± 0.03 mm in A10.

Influence of nutritive conditions

Juvenile mortality (Fig. 2; Kaplan-Meier method) strongly depended on the leaf litter characteristics (Table 1). While there was a clear effect of litter type, the effects of experimental pH manipulation were not consistent between different litter types; pH 2 manipulated litter resulted in higher mortality for the oak (Fig. 2C) litter, but in lower mortality for the birch litter (Fig. 2B). When isopods fed on alder litter (Fig. 2A), mortality was lower in case of pH 5 manipulated litter during early development, but higher in pre-adult and adult stages. The development of juvenile isopods feeding on the pH 5 manipulated alder litter was similar to that when feeding an "optimal diet". Survival after 1 year was slightly lower on artificial diet (cf. Figs. 1 and 2A).

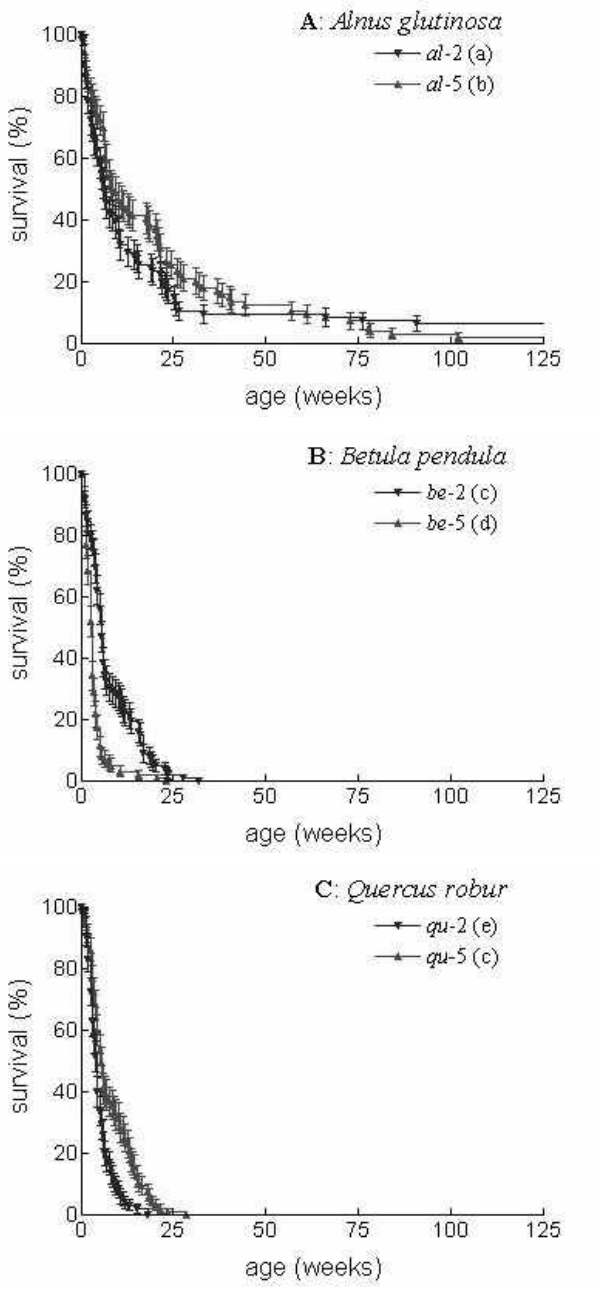

Fig. 2. Mortality (Kaplan-Meier method) of juvenile *P. scaber* feeding on different food sources (Table 1) during development. Different superscript letters indicate significant differences (α = 0.05). *al-*, *Alnus glutinosa*; *be-*, *Betula pendula*, *qu-*, *Quercus robur*; -2, pH 2 manipulated; -5, pH 5-manipulated.

ANCOVA (Table 2) did not reveal an influence of litter manipulation on longevity, but the litter type, genetic factors ("family") and the hatching date (covariate) influenced longevity. Comparison of cohorts from different years (1995, 1996 and 1998) revealed no annual differences in mortality or growth rates ($P > 0.5$). As judged from those individuals that reached pre-adult stages, no differences between males and females could be observed with respect to longevity ($P > 0.7$). For those isopods that survived the first winter, longevity significantly depended upon the stage at which they passed the winter ("overwintering stage") (ANOVA: $F = 17.3$; $P < 0.001$).

In contrast to longevity, the size of a particular developmental stage was independent of the available food source ($P < 0.6$; Kruskal-Wallis test). Thus, the age of individuals at a given stage, but not their size, was different between treatments. With respect to maturity, Merriam (1971) observed a minimum reproductive size that obviously can be reached at different ages, depending on individual growth rates. In this context, the stage at which the first winter is spent appears to be significant, since essentially no growth

Table 2. ANCOVA tables for individual longevity in juvenile *Porcellio scaber* feeding on different food sources (Table 1)

	df	Longevity		
		SS	*F*	*P*
Covariate (hatching date)		65,895	173.9	<0.001
Litter type	3	30,365	26.7	<0.001
Litter manipulation	1	30	0.1	0.778
Family	32	24,594	2.0	0.001
Type × manipulation	2	1,475	1.9	0.144
Type × family	43	19,449	1.2	0.194
Manipulation × family	26	8,142	0.8	0.713
Type×manipulation× family	33	17,652	1.4	0.068
Error	435	164,820		
Total	576	332,422		

Table 3. Mean (±SD) duration of developmental stages of juvenile *Porcellio scaber* feeding on different food sources (Table 1). – *al-*, *Alnus glutinosa*; *be-*, *Betula pendula*, *qu-*, *Quercus robur*; -2, pH 2-manipulated; -5, pH 5-manipulated

	al-2	al-5	be-2	be-5	qu-2	qu-5
MII	4 ± 1	3 ± 1	3 ± 1	4 ± 2	4 ± 1	3 ± 1
J1	6 ± 1	7 ± 2	6 ± 2	6 ± `	7 ± 2	7 ± 1
J2	3 ± 2	3 ± 2	6 ± 2	4 ± 2	5 ± 3	5 ± 2
J3	4 ± 2	4 ± 2	5 ± 2	6 ± 3	3	5 ± 2
J4	5 ± 2	6 ± 3	8	9	—	12
J5	8 ± 2	9 ± 3	—	—	—	—
J6	10 ± 3	5 ± 2	—	—	—	—
J7	8 ± 3	6 ± 2	—	—	—	—
J8	5 ± 2	7 ± 3	—	—	—	—
J9	6 ± 2	6 ± 1	—	—	—	—
J10	6 ± 3	5 ± 3	—	—	—	—
J11	4 ± 2	5 ± 1	—	—	—	—
J12	4 ± 2	5 ± 1	—	—	—	—
Age at maturity	66 ± 11	87 ± 23	—	—	—	—

occurs then (see above). Neither litter type nor pH manipulation affected the overwintering stage of juvenile isopods ($P > 0.2$; Kruskal-Wallis test), but the overwintering stage of juveniles differed between different hatching dates ($P < 0.001$; Kruskal-Wallis test).

The duration of developmental stages (Table 3) was markedly affected by the nutritive conditions of juveniles (ANCOVA: Table 4). Developmental stages differed with respect to the significance of litter type and manipulation, but the hatching date (covariate) was significant for the duration of every tested developmental stage up to J8. In contrast, neither gender nor family influenced stage duration.

Discussion

Under laboratory conditions with unlimited access to high-quality artificial diet, development to maturity in *P. scaber* takes at least 14 months (60 weeks), but may take up to 22 months (90 weeks). The observed differences in individual growth rates, resulting in differences in stage duration (Table 3), but not in individual differences in stage size, may also be due to being affiliated to the early or late brood (cf. Zimmer and Kautz, 1997; Table 4) — the hatching date partly determines the extent of development prior to the first winter (Table 4), and thus the age at maturity, since there is essentially no development during winter (cf. Fig. 1). Individual differences leading to conspicuous phenological variability in isopod populations (Sunderland et al., 1976: "cohort splitting") have been interpreted as different individual tactics to maximize reproductive success through spreading of risk under unpredictable climatic conditions (Zimmer and Kautz, 1997).

Longevity of juvenile isopods is significantly influenced by genetic factors ("family"), but other factors such as climatic (summarized in Warburg et al., 1984) and nutritive (Merriam, 1971; Sunderland et al., 1976; Table 2) conditions are significant, too. Furthermore, the hatching date, determining the time span between hatching and the first winter, proved significant in the present study, possibly due to longevity being influenced by the overwintering stage that, in turn, depends on the hatching date. It is likely that harsh climatic conditions during winter are easier to cope with for later developmental stages of species that do not undergo diapause. Thus, it may be advantageous for an isopod female to reproduce early in the season, but young females of *P. scaber* are not yet mature in early spring, and 2-year-old females appear to breed twice during the reproductive season (Zimmer and Kautz, 1997).

The available food source obviously affects post-embryonic ontogenetic development of *P. scaber*, as far as longevity/mortality and the duration of early developmental stages are considered. The design of the present study did not allow for the determination of particular food characteristics that may be held responsible for influencing individual development. Hassall and Rushton (1984) described a deterrent effects of phenolics in birch litter, and condensed tannins increased mortality in adult *P. scaber* (Zimmer and Topp, 1997a). As shown clearly in Table 1, different pH treatments clearly differed with respect to their contents of phenolic litter compounds. On the other hand, birch litter used in the present study did not

Table 4. ANCOVA tables of the duration of different developmental stages of juvenile *Porcellio scaber* and the age at maturity when feeding on different food sources. Since MI does not feed, this developmental stage was not considered. Due to unbalanced experimental design (food-dependant mortality rates), statistical interactions were not calculated

			MI				J1				J2	
	df	SS	F	P	df	SS	F	P	df	SS	F	P
covariate (hatching date)		3114	495.3	<0.001		2158	1362.8	<0.001		2216	348.1	<0.001
litter type	3	155	8.2	0.001	3	26	5.4	0.011	3	43	2.3	0.144
litter manipulation	1	83	13.2	0.001	1	0	0.0	0.893	1	29	4.5	0.060
gender	2	6	0.5	0.634	2	13	2.4	0.083	2	5	0.4	0.703
family	19	104	0.9	0.617	17	46	1.7	0.157	17	265	2.5	0.076
error	23	145			14	22			10	64		
total	66	3664			52	2329			47	2749		

			J3				J4				J5	
	df	SS	F	P	df	SS	F	P	df	SS	F	P
covariate (hatching date)		2810	278.6	<0.001		5745	292	<0.001		9917	117.8	<0.001
litter type	3	267	8.8	0.0064	3	166	3	0.117	1	36	0.4	0.539
litter manipulation	1	2	0.2	0.7015	1	118	6	0.044	1	144	1.7	0.248
gender	2	31	1.5	0.2729	2	71	2	0.231	2	61	0.4	0.714
family	16	17	1.7	0.1597	15	813	3	0.090	13	1175	1.1	0.508
error	8	81			7	138			5	421		
total	41	4452			35	7291			27	12191		

			J6				J7				J8	
	df	SS	F	P	df	SS	F	P	df	SS	F	P
covariate (hatching date)		4509	47.1	0.006		2827	61.1	0.016		2097	233.0	0.004
litter type	1	902	9.4	0.055	1	445	9.6	0.090	1	1	0.1	0.747
litter manipulation	1	487	5.1	0.109	1	19	0.4	0.588	1	28	3.1	0.218
gender	2	39	0.2	0.826	2	1	0.0	0.988	2	16	0.9	0.523
family	11	967	0.9	0.606	9	185	0.4	0.839	8	78	1.1	0.564
error	3	287			2	93			2	18		
total	21	7201			18	3598			16	2295		

			J9				J10				J11	
	df	SS	F	P	df	SS	F	P	df	SS	F	P
covariate (hatching date)		3361	4.0	0.184		1867	233.4	0.042		143	0.8	0.455
litter type	1	302	0.4	0.611	1	58	7.3	0.226	1	8	0.1	0.758
litter manipulation	1	239	0.3	0.648	1	12	1.5	0.435	1	16	0.1	0.786
gender	2	189	0.1	0.900	2	74	4.7	0.311	2	9	0.1	0.837
family	6	1054	0.2	0.943	5	403	10.1	0.235	2	331	5.9	0.241
error	2	1690			1	8			1	338		
total	14	6955			12	2472			9	1630		

			J12				maturity	
	df	SS	F	P	df	SS	F	P
covariate (hatching date)		671	21.0	0.137		185324	286.0	0.038
litter type	1	23	0.7	0.553	1	9944	15.3	0.159
litter manipulation	1	4	0.1	0.795	1	2218	3.4	0.315
gender	2	17	0.3	0.807	2	2861	2.2	0.430
family	2	23	0.4	0.765	2	1997	1.5	0.495
error	1	32			1	648		
total	9	775			9	204592		

contain more phenolics than the other litter types. Thus, high mortality on birch (and oak) litter must have other reasons. The litter type with highest growth rates and lowest mortality, alder litter, was characterized by a high content of hydrolyzable tannins. A representative of this class of phenolics has been demonstrated to result in increased digestibility of food through promoting bacterial endosymbionts (Zimmer, 1999). Another leaf litter trait that is likely to affect juvenile isopods is its physical toughness (cf. Zimmer and Topp, 2000). In the present study, litter toughness differed between litter types, but was hardly affected

by the experimental pH manipulation. Hence, effects of litter toughness are reflected by effects of the "litter type" (Tables 2 and 4). Further prominent differences between alder litter and birch or oak litter appear to be differences in microbial density and activity (Table 1). Microbial density and activity were also affected by the experimental pH manipulation; "litter manipulation", however, proved to be of little significance for longevity in the present study. Thus, microbial density and activity may be relatively insignificant with respect to juvenile mortality.

While the leaf litter type has strong effects on juvenile development, acidification of the litter and the resulting differences in microbial colonization ("litter manipulation"; cf. Zimmer and Topp, 1997a, 2000; Kautz et al., 2000) only influences the first feeding stage (MII). Given that ingested gut microbiota support pH homeostasis inside the gut lumen (Zimmer and Topp, 1997b), this observation may be due to low microbial densities in the guts of mancae feeding on acidified leaf litter. Later stages probably contain sufficient microbiota to cope with low leaf litter pH. In addition, bacterial endosymbionts in midgut glands may compensate for digestibility-reducing effects of low microbial density in acidified litter (cf. Zimmer and Topp, 1998a, 1998b; Zimmer, 1999). Since nothing is known of how and when juvenile isopods obtain these endosymbiotic bacteria (cf. Zimmer, in press), it might well be that this process takes place after manca stages. Further investigations should focus on the development of microbial populations in the guts of juvenile isopods, as influenced by acidification.

Taking into account previous results (Zimmer and Topp, 1997a, 2000) and the present study, I conclude that food quality in relation to adult *P. scaber* is determined by leaf litter chemistry (e.g., phenolics) and acidity (affecting leaf litter-colonizing microbiota) but in juveniles mainly by the C:N ratio, litter-colonizing microbiota and those characteristics influencing litter toughness that are not affected by litter acidification. Both juveniles and adults of this species differ markedly from other isopod species in this respect (cf. Zimmer and Topp, 2000). Food sources of low nutritive value affect isopod populations by (1) increasing the mortality and (2) reducing the reproductive success of adult females (Zimmer and Topp, 1997a, 2000; Kautz et al., 2000), and by (3) increasing mortality and reducing growth rates of juveniles (this study), i.e., by (4) delayed maturity (this study).

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